Soil Fauna and Global Change

Responses to Experimental Drought, Irrigation, Fertilisation and Soil Warming

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Abstract

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To examine possible effects of global change on soil fauna abundance and diversity, two long-term field experiments in Norway spruce stands in Sweden were studied. Soil fauna (Oribatida, Mesostigmata, Collembola, predatory macroarthropods and Enchytraeidae) were sampled in plots experimentally simulating altered precipitation patterns and increased soil temperature. Six years of summer drought caused large decreases in abundance in all faunal groups and a reduction in species diversity of Oribatida and Collembola. Summer drought and irrigation caused shifts in the community composition of Oribatida and Collembola, but drought affected soil fauna more than irrigation. Increased soil temperature during 5 years resulted in positive responses in several Oribatida species and negative in some Collembola species.

Three years after the summer drought treatment had ceased, the soil arthropod communities had still not returned to control conditions. Total abundances recovered quickly, but species richness, diversity indices and community composition recovered slower. Mobile arthropod groups seemed to recover faster than groups with more limited dispersal ability, and Oribatida had the slowest recovery rate. Microarthropod species with wide habitat niche width recovered faster than those with narrow niche width, and parthenogenetic Oribatida recovered faster than sexually reproducing ones. Overall, Collembola were less affected by drought, and recovered faster than Oribatida.

Soil fauna decreased in plots receiving repeated additions of solid nitrogen fertiliser for 13 years, whereas slight increases were found in plots receiving liquid fertiliser. The fertilisation treatments caused shifts in the community composition of Oribatida and Collembola but did not cause changes in species richness.

In conclusion, climate change resulting in frequent summer droughts will probably decrease abundance and diversity of forest soil fauna. Moister conditions may primarily result in shifts in community structure. Intensive forest fertilisation for biofuel production will probably affect the composition of soil fauna communities. Oribatida communities seem to be particularly vulnerable to disturbances. Post-disturbance recovery of soil fauna seems to be slow and disturbances on a large spatial scale may affect the resilience of soil ecosystems, as disturbances may cause permanent changes in community composition.

Keywords: Collembola, disturbance, drought, Enchytraeidae, global change, irrigation, Mesostigmata, nutrient fertilisation, Oribatida, *Picea abies*, resilience, soil fauna diversity.

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Till Mamma och Pappa

Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Lindberg, N., Bengtsson, J. & Persson, T. 2002. Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *Journal of Applied Ecology* 39, 924-936.

II. Lindberg, N. & Persson, T. Effects of nutrient fertilisation, irrigation and soil warming on the microarthropod community in a boreal Norway spruce stand (Manuscript).

III. Lindberg, N. & Bengtsson, J. Recovery of forest soil fauna diversity and composition after repeated summer droughts (Manuscript).

IV. Lindberg, N. & Bengtsson, J. Population responses of oribatid mites and collembolans after a drought disturbance (Manuscript).

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Introduction

Background

Global climatic change is today seen as one of the major threats to the Earth's biodiversity (e.g., Hoffman & Parsons 1997; Wardle *et al.* 1998). Changes such as increased temperature, altered precipitation patterns and an increased frequency of extreme events (e.g., Mearns *et al.* 1984; Piervitali *et al.* 1997; Arnell 1999; IPCC 2000) are likely to affect many organisms. Apart from the loss of individual species, a loss of diversity may result in effects on ecosystem functions or a reduced resilience to environmental disturbances (Grime 1997; Naeem 1998; Hector *et al.* 1999; Walker *et al.* 1999; Schwartz *et al.* 2000; Loreau *et al.* 2001). A better understanding of these processes is needed to make predictions about how communities and ecosystems will respond to global change, and it will probably also have large implications for ecosystem management in the future.

The functional role of soil fauna

Among soil fauna, fungi-/detritivores such as Collembola, oribatid mites (Acari: Oribatida) and enchytraeids (Oligochaeta: Enchytraeidae) take part in important ecosystem functions such as decomposition, nutrient mobilisation, soil mixing and aggregate formation (e.g., Standen 1978; Persson 1983; Anderson 1988; Setälä & Huhta 1991; Laakso & Setälä 1999). Moreover, predatory soil fauna – mesostigmatid mites (Acari: Mesostigmata) and larger arthropods such as beetles, spiders and ants – may through predation regulate the populations of other faunal groups (Hyvönen & Persson 1996; Huhta *et al.* 1998) and thereby possibly influence decomposition processes.

In spite of their role in decomposition and the fact that soil organisms make up a substantial part of the global biodiversity (Giller 1996; Adams & Wall 2000), many of these species remain poorly known. Even the functional specificity of many common soil organism species is unclear. It is likely that, for example, many of the fungi- and detritivorous animals have similar functions, but the enchytraeid *Cognettia sphagnetorum* (Laakso & Setälä 1999) and some oribatid mites and collembolans (Hågvar 1998; Mebes & Filser 1998) may be functionally specific under certain conditions. Avoiding severe declines in the diversity of soil communities can therefore be seen as an insurance against possible disturbances of ecosystem functions. However, on a community level we know that soil fauna respond to many different environmental variables, and because they can indicate environmental stress through changes in species or community structure (Hågvar 1994; Van Straalen 1998), they can also be used as important indicators.

Effects of moisture and temperature on soil fauna

Effects of global change on soil fauna communities may include both moisture and temperature responses. Many soft-bodied animals such as enchytraeids and collembolans are sensitive to desiccation during dry conditions (Verhoef &

Witteveen 1980; Didden 1993). To avoid drought, soil animals undertake vertical movements deeper into the soil or redistribute to moist patches (Verhoef & Van Selm 1983; Didden 1993). They can also enter inactive stages, or survive as dormant eggs, which are reactivated by moisture (Hopkin 1997). Moreover, the moisture content of the litter may affect the ability of juveniles to penetrate their substrates successfully (Norton 1994). Moisture changes may also affect the fungal community and, thereby, have indirect effects on the fungivorous fauna and the oviposition of oribatid mites (Hågvar 1998). Heavy rains or floodings may lead to waterlogged conditions that cause mortality among adult collembolans and require water-resistant eggs for the populations to persist (Mertens *et al.* 1983; Tamm 1984).

Temperature also affects many aspects in the life of soil fauna. Seasonal temperature variations commonly induce vertical movements of soil animals in the soil profile (e.g., Luxton 1981; Didden 1993). The developmental rate of collembolans, mesostigmatid and oribatid mites is often temperature-dependent (e.g., Hopkin 1997; Walter & Proctor 1999; Bhattacharya *et al.* 1978). In some collembolans, fecundity and sex ratio in the populations may also be affected (Choudhuri 1961; Snider 1973). Altogether this indicates that a changing climate with altered moisture and temperature regimes probably will have effects on soil fauna. However, as the effects not only will depend upon the abiotic factors acting on the component species, but also upon the interactions between different species, studies on the community level are needed.

Global change and soil fauna

It has been argued that the effects of global warming on soil biota will be strongest in the polar regions (Hodkinson *et al.* 1998, but see also Kennedy 1994). Consequently, many of the studies concerning effects of climatic change on soil fauna have been performed in polar ecosystems, most of which have focused on temperature responses (e.g., Kennedy 1994; Webb *et al.* 1998; Hodkinson *et al.* 1998; Coulson *et al.* 2000). Studies in temperate and boreal regions are fewer. Briones *et al.* (1997) studied effects of temperature changes on soil fauna, whereas other studies have concerned effects of altered moisture regimes (Frampton *et al.* 2000a,b; Pflug & Wolters 2001; Paper I). Coniferous forests cover vast areas of these regions, for example about 20 million hectares of the land surface in Sweden (SNA 1996), and from this perspective deserve much more attention than so far. Scandinavian climate scenarios indicate that effects on both precipitation and temperature are to be expected during the next 100 years (SMHI 2000). In south-eastern Sweden, the risk of summer droughts will increase while other areas will receive more precipitation. At the same time, annual mean temperature is expected to increase by 3-4 ^{o}C (SMHI 2000). How such changes in precipitation and temperature will affect soil fauna is unclear.

Forest fertilisation and soil fauna

Global change will probably also induce responses in the form of shifts in land-use that will have effects on the biodiversity. To counteract the increase of CO_2 in the atmosphere and thereby reduce the greenhouse effect, the production and use of biofuels need to be increased to replace fossil fuels. Intensive forest fertilisation in Sweden has been mentioned as one possible method to increase forest growth and the incorporation of carbon into tree biomass (Bergh *et al.* 1999). Nutrient fertilisation of forests has often been used in modern forestry, and commonly causes changes in communities of plants and fungi (e.g., Kellner 1993; Kårén & Nylund 1996; Fransson *et al.* 2000). The fertiliser types have varied and the added amounts have often been moderate, in line with common forestry practices. Nevertheless, studies on soil fauna have often shown that abundances decrease shortly after additions of solid fertilisers (e.g., Lohm *et al.* 1977; Behan *et al.* 1978; Sohlenius & Wasilewska 1984; Koskenniemi & Huhta 1986). Negative impacts of ammonium nitrate applications on faunal abundances has been explained by a toxic effect (Huhta *et al.* 1983), or salt effects that can cause desiccation (Lohm *et al.* 1977).

The impact on soil fauna of high additions of fertilisers applied for a prolonged time is still poorly known. It is possible that many negative effects persist, but a community stabilisation over time could also occur through e.g., colonisation of resistant species or responses in the soil biota (plants or fungi), which may reduce the impact on the communities.

Soil fauna and disturbances

Although many studies on effects of disturbance on soil fauna have been published, certain disturbance types are over-represented. Commonly, studies on community effects of disturbances have concentrated on single "pulse disturbances" and have focussed on immediate and short-term effects. Many researchers have found strong effects of, e.g., pollution, pesticides and fire on soil fauna (Barrett 1968; Metz & Farrier 1973; Merrett 1976; Strojan 1978; Tamm 1986; Bengtsson & Rundgren 1988; Hoy 1990; Haimi *et al.* 2000; Haimi & Mätäsniemi 2002). Studies on effects of climate-related disturbances on soil fauna are fewer, but include effects of drought and icing (Coulson *et al.* 2000; Frampton *et al.* 2000a,b; Pflug & Wolters 2001; Paper I).

As the impact on a community is also dependent on e.g., the duration and the spatial scale of the disturbance, it is important to include more studies with different temporal and spatial disturbance regimes. For example, more knowledge is needed about effects of repeated and large-scale disturbances on communities and ecosystems (Paine *at al.* 1998; Romme *et al.* 1998). There is evidence that disturbance is the main structuring force of Oribatida communities (Maraun & Scheu 2000), and soil microarthropods may be strongly affected by everything from small-scale disturbances, such as earthworm activity (Maraun *et al.* 1999), to disturbances that often occur on a large spatial scale, such as drought.

Succession and dispersal of soil fauna

What specific traits are most important for succession sequences in soil fauna? In colonisation theory, body size and life-history traits such as life span, number of offspring and reproductive mode have often been used to explain successional patterns of plants and animals (Baker 1955; MacArthur & Wilson 1967; Grubb 1987; Baur & Bengtsson 1987). Parthenogenesis may for example facilitate a quick population establishment after a disturbance (Norton 1994), although the relation between such life-history traits and colonisation succession is not always clear-cut (Baur & Bengtsson 1987; Ås *et al.* 1992). The recovery process of soil fauna following climatic disturbances has seldom been studied, but there are many studies on colonisation of man-made habitats (e.g., Hutson 1980; Davis 1986; Judd & Mason 1995; Verschoor & Krebs 1995; Wanner & Dunger 2002). Post-fire recovery of communities has also received much interest (e.g., Huhta 1971; Merrett 1976; Tamm 1986; Webb 1994).

Comparison of post-disturbance responses of species with different traits may give valuable indications about the mechanisms involved. Very few studies of disturbance effects on soil microarthropods have so far used life-history traits to explain the patterns found (but see Siepel 1996; Maraun & Scheu 2000). Soil fauna is very diverse, and we can never expect to gain a complete knowledge of the ecology of all species. Nevertheless, it may still be possible to link taxonomical or functional groups of soil fauna to traits that govern their ability to survive, or re-establish after, certain disturbance types. Oribatid mites in general have traits similar to so-called "*K*-selected species" (i.e., late-succession species), while another soil microarthropod group, Collembola, have a wider array of life-history traits (Norton 1994). Post-disturbance effects on community composition of microarthropods may remain long after abundance effects have disappeared. Oribatida populations often have a longer recovery time after disturbances than Collembola, and Oribatida also seem to be slower re-colonisers of disturbed areas than Collembola (Strojan 1978; Hutson 1980; Lucarotti 1981; Wanner & Dunger 2002). It is still unclear whether these differences depend on differences in life-history traits, or other characteristics such as dispersal ability and habitat specialisation.

Good dispersal ability may enable a species to quickly re-colonise an area after a disturbance (Grubb 1987; Bengtsson & Baur 1993). It may also be crucial for populations to persist in fragmented patches (Gonzalez & Chaneton 2002) and enable adjustment of species distributions in response to climatic changes (Perry *et al.* 1990). However, we know very little about the dispersal abilities of many species of soil fauna. Poor dispersal rates probably characterise many microarthropod species (Norton 1994; Petersen 1995; Sjögren 1997; Ojala & Huhta 2001), but there are also examples of species such as the oribatid *Oppiella nova* and some collembolans of the genus *Mesaphorura* which quickly colonise newly created habitats (Hutson 1980; Koehler 1998; Wanner & Dunger 2002). This may be explained by the fact that some collembolans and oribatids are known to be wind-dispersed (Hopkin 1997; Wanner & Dunger 2002). Among the predatory mites, Mesostigmata are often phoretic on other animals (Karg 1993). Large soil arthropods, such as beetles and spiders, are mobile and use locomotion or dispersal by air (Merrett 1976; Dindal 1990). Other species may survive in low densities at a site and are able to respond quickly to better conditions. Special microhabitat preferences or an ability to withstand environmental stress are adaptations for this “survivor” strategy.

Aims of the thesis

The specific aims of my thesis were to examine:

1) effects on soil fauna of global change (increases in drought/precipitation and temperature).
2) the ability of soil fauna to recover after the cessation of a climatic disturbance, i.e., a simulated long-term drought.
3) effects on soil fauna of forest fertilisation as a means of replacing fossil fuels with bio-energy.

The impact of experimental manipulations of moisture and temperature on soil fauna abundance and diversity was studied in field experiments (Paper I, III-IV). The climatic scenarios were a) frequently occurring summer droughts, b) permanently moist summers, and c) increased soil temperature.

The recovery process of the soil fauna communities was followed after the drought disturbance had ended, and ecological characteristics and life-history traits that could explain the response patterns were evaluated (Paper III-IV).

The effects on soil fauna of an intensive forest fertilisation program were examined after long-term applications of high doses of nitrogen fertilisers (Paper II). The impact of fertilisation, in solid and liquid form, was studied and the effects on abundance, species richness and community composition of soil arthropods were evaluated.

Already existing experiments made it possible to study long-term responses of soil fauna in coniferous forest, an opportunity seldom given otherwise.

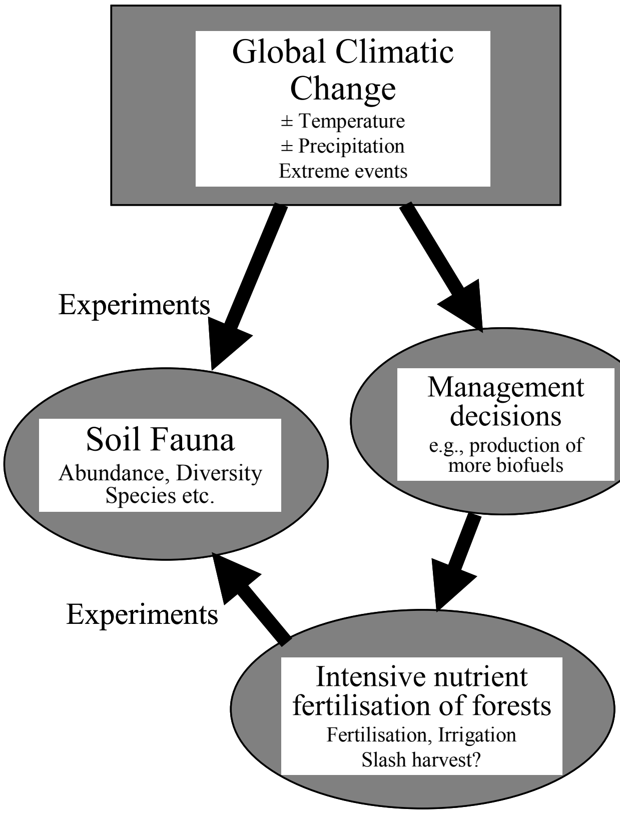

Fig. 1. The subject of this thesis: direct and indirect effects of global change on soil fauna characteristics.

Materials and methods

Sites

In this thesis, I used experimental field plots in forest stands with equipment that simulated altered climatic conditions. Two sites, one in SW Sweden (Skogaby, 56°33'N, 13°13'E) and one in N Sweden (Flakaliden, 64°07'N, 19°27'E), both with homogenous Norway spruce *Picea abies* (L.) Karst., were used for the studies (Fig. 2). At Skogaby (Paper I, III, IV), the stand was planted in 1966 and is growing on former *Calluna* heathland in a maritime climate in the temperate zone, 95-115 m above sea level. The stand was dense and the ground vegetation was very sparse. At Flakaliden (Paper II), the studies were performed in a stand planted in 1963 and situated in the boreal zone, 310-320 m above sea level. The ground layer at this site mainly consisted of mosses and *Vaccinium* shrubs. Both stands were established after clearcutting and although the local climate differed, they were representative for many forests in each region.

Fig. 2. Map of Sweden with the locations of the field experiments at Skogaby and Flakaliden.

Treatments

Experimentally simulated drought was induced by plastic roofs placed 0.5-1.5 m above ground in forested plots (Paper I, III, IV). They had openings for tree trunks and for maintenance purposes, and prevented 70% of the throughfall on the plots from reaching the ground during April to September (Alavi 1999). During winter the roofs were removed and all throughfall could reach the ground, resulting in a summer drought treatment (see Paper I for more details). The summer drought treatment had been running for 6 years at the time of my first sampling.

Wet summers were simulated by the use of a sprinkler system that regularly irrigated the forested plots during the summer months (Paper I & II), thereby providing permanently moist soil conditions between April and August (Paper II) or September (Paper I). The irrigation treatments had been running for 10 years at my sampling at Skogaby, and 13 years at Flakaliden.

The recovery of soil fauna after a drought disturbance was studied by using parts of the drought plots in Skogaby where the roofs had been permanently removed after 6 years of summer droughts. The recovery process was thereafter followed during three years (1997-1999).

Increased soil temperatures were simulated by the use of heating cables placed into the organic soil layer at regular intervals. Plots receiving irrigation were used to avoid soil drying (Paper II). Sensors connected to a datalogger monitored the soil temperature, and kept the temperature constantly 5 ^{o}C above the temperature at adjacent control plots between April and October, thereby prolonging the period with unfrozen soil by two months. The soil warming treatment had been running for 3 and 5 years, respectively, at the samplings in 1997 and 1999.

Effects of long-term forest fertilisation on soil fauna were studied in a nutrient optimisation experiment (Paper II). The nutrient treatments consisted of fertiliser additions including macro- and micronutrients, with nitrogen added as ammonium nitrate. Additions were made once a year in solid form or every second day as a nutrient solution together with irrigation. The amounts of N added varied between 75-100 kg ha^{-1} year^{-1}. For comparison, plots receiving only irrigation, as well as control plots without treatment were included. The fertilisation treatments had been running for 13 years at the time of sampling.

Sampling and identification

The faunal groups chosen for the studies were numerically important fungi-/detritivores such as Oribatida and Collembola, together with enchytraeids in Paper I. They all are abundant in forest soils and provide important ecosystem functions through their feeding on fungal hyphae and their fragmentation of litter. We also included the most common predatory arthropods at the sites in our studies, mesostigmatid mites and predatory macroarthropods (e.g., Araneae, Staphylinidae and larvae of Cantharidae).

In all studies, soil animals were sampled in autumn (September to November) by taking 2-4 soil samples from the organic layers in each plot, down to the mineral soil, using a metal corer or frame. Thereafter, the animals were extracted by the use of different funnel extraction techniques, and stored in 70% ethanol.

Conclusions drawn from single samplings in autumn should of course be carefully evaluated. Within-year and between-year population fluctuations are commonly seen in soil fauna communities, and between-year effects have shown to be strong in e.g., studies on responses of arctic soil fauna to increased temperatures (Hodkinson *et al.* 1998). However, our approach to use plots where the treatments had been applied intensively for many years should have reduced this risk considerably. Additionally, there are indications that the stability of soil fauna communities between years is relatively high (Bengtsson 1994; Wolters 1998).

For Enchytraeidae, Collembola and adult Oribatida, determination to species level was in most cases done. Mesostigmatid mites were determined to species level when possible, in other cases to genus or family. The large arthropod predators were only counted and determined to group level (family or order).

Diversity measurements

For oribatids and collembolans, community parameters were estimated such as abundance, species number and diversity indices. Rank-abundance curves and rank-shifts in species dominance (Paper I only), as well as species-specific treatment effects were measured. Furthermore, similarities in community composition of arthropods between treatments were analysed by ordination, using Principle Component Analysis (PCA). Bray-Curtis' index of similarity (Paper III) was also used to analyse community similarity between treatments.

Species-wise characteristics

To examine correlations between the effects of drought on Collembola and Oribatida, and the life-history and ecological characteristics of the species (Paper IV), we mainly used data from the literature. Data on the following traits were collected: 1) depth preference (surface-living, intermediate or deep-living), 2) body length, 3) reproductive mode (sexual or parthenogenetic), 4) habitat specialisation and 5) feeding category (Oribatida only; "fungivorous grazers" or "fungivorous browsers"). Habitat specialisation was given values between 1-7, being the number of the following habitats that each species occurred regularly in: 1) coniferous forest, 2) deciduous forest, 3) shrub heathland, 4) grassland, 5) ruderal areas, 6) cultivated fields and 7) tree trunks, stones and walls. The feeding categories of Oribatida were based on the classification by Siepel & DeRuiter-Dijkman (1993), depending on their ability to digest fungal cell walls or not, respectively.

Results and discussion

Effects of drought and irrigation (Papers I-II)

The study at Skogaby (Paper I) showed that long-term summer drought caused major effects on soil fauna communities: declines in overall abundances of soil fauna (Oribatida, Mesostigmata, Collembola, macroarthropod predators, Enchytraeidae) as well as the diversity of Oribatida (Tables 1 & 2). Additionally, there were indications from the literature that Collembola and Oribatida species that were favoured in the drought plots were species that had a higher resistance to desiccation (Verhoef & Witteveen 1980; Steiner 1995). Different microarthropod communities developed in the different treatments in Skogaby (Fig. 3), but summer drought affected community composition more than irrigation did.

Table 1. *Mean densities per m^2 (S.E.) of sampled soil fauna groups in the long-term moisture treatments at Skogaby and Flakaliden (n = 4). At Skogaby, Macfadyen high-gradient extraction was used for the microarthropods, Tullgren funnels for the predatory macroarthropods and Baermann funnels for Enchytraeidae. At Flakaliden, Tullgren extraction was used for all groups and only adult oribatid mites were counted. Enchytraeids were not sampled at Flakaliden*

	Skogaby (1997)			Flakaliden (1999)	
	Drought	Control	Irrigation	Control	Irrigation
Oribatida	70200 (33800)	220000 (32600)	317000 (46600)	93300 (38200)	59800 (4500)
Mesostigmata	2100 (430)	7400 (690)	13100 (4100)	13600 (2300)	11600 (2000)
Collembola	12800 (7800)	38000 (6300)	66000 (6800)	39000 (4100)	41200 (8300)
Predatory	190 (70)	860 (100)	890 (85)	800 (200)	620 (100)

macroarth.					
Enchytraeidae	3300 (1900)	36600 (8700)	97400 (10000)	–	–

At Skogaby, soil fauna abundances increased with irrigation (Table 1), and the community composition of Oribatida and Collembola was also affected. The results from Flakaliden (Paper II) did not support the pattern found at Skogaby, as irrigation had no positive effect on the abundances of groups such as Collembola, Mesostigmata and predatory macroarthropods (Table 1; enchytraeids were not included in this study). Additionally, at Flakaliden no large changes in community composition in response to the irrigation treatment were found in Oribatida or Collembola, apart from responses in a few single species (Fig. 5).

The differences in the community response might result from differing treatment intensities in relation to the natural moisture conditions at the sites or differences in nutrient availability. A limited availability of nutrients at Flakaliden may have prevented population increases of many soil organisms in spite of more suitable moisture conditions.

Experimental manipulations of soil moisture have been shown to affect most groups of soil fauna such as collembolans, oribatid mites, enchytraeids and nematodes (Whitford *et al.* 1981; Sohlenius & Wasilewska 1984; Briones *et al.* 1997; Frampton *et al.* 2000a,b; Pflug & Wolters 2001). The dramatic drought-induced decline in enchytraeids, mainly *C. sphagnetorum*, that we found may well have functional implications as studies have demonstrated its importance for ecosystem functions such as nitrogen cycling (Laakso & Setälä 1999).

Table 2. *Mean values of diversity variables (S.E.) in Oribatida and Collembola in the moisture treatments at Skogaby and Flakaliden (n = 4). Numbers are based on sample areas of 400 cm^2 in Skogaby and 200 cm^2 in Flakaliden*

	Skogaby (1997)			Flakaliden (1999)	
	Drought	Control	Irrigation	Control	Irrigation
Oribatida					
Mean species number	20 (1.7)	26 (0.6)	31 (0.9)	25 (1.2)	26 (2.1)
Shannon-Wiener	1.33 (0.10)	1.99 (0.07)	2.35 (0.08)	2.12 (0.39)	2.20 (0.12)
Rarefaction S_{500}	19	21	23	24.5	25
Collembola					
Mean species number	12 (0.6)	15 (0.8)	14 (0.6)	17 (1.1)	15 (1.0)
Shannon-Wiener	1.22 (0.36)	1.85 (0.04)	1.83 (0.03)	2.20 (0.04)	2.04 (0.06)
Rarefaction S_{500}	12	15	14	16	14

The mechanisms that directly influenced the community responses are at present unclear. Differences in physiological resistance to drought between species (Verhoef & Witteveen 1980; Siepel 1996) are likely to have been important, but also indirect responses through treatment effects on microhabitat heterogeneity (Anderson 1978), changes in biomass and diversity of fungi (Bissett & Parkinson 1979) or predation pressure (Paine 1966) may have occurred. I made no attempt to quantify these factors. According to the literature they may all have influenced the changes in abundance and diversity that were seen.

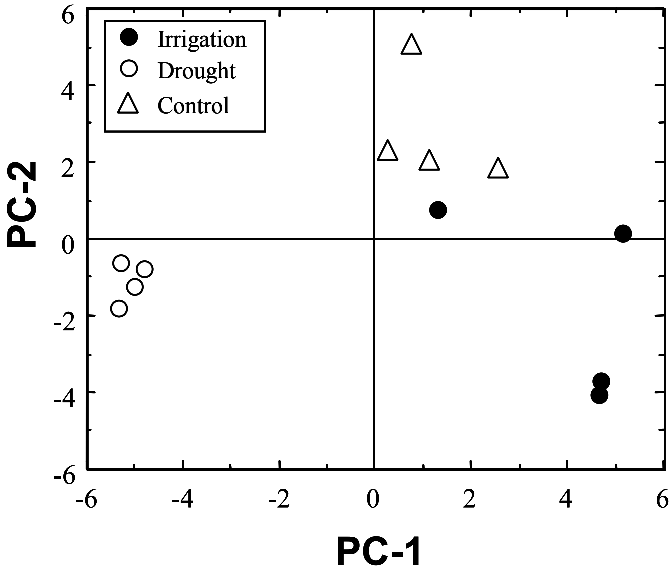

Fig. 3. PCA plot of the experimental plots at Skogaby based on the Collembola and Oribatida community composition in Tullgren samples. The effects of the moisture treatments on community composition are seen along the first and second PCA axis. Nineteen Collembola and 27 Oribatida species were included in the analysis.

Paper I supported the hypothesis that long-term drought will affect soil fauna abundance and diversity negatively. The results also indicated that community changes under such conditions will include a shift towards a dominance of drought-resistant species, while drought-sensitive species are more or less disappearing. Furthermore, the studies showed that many species of soil fauna reacted strongly on changes in soil moisture regimes, which confirm views in the literature about their usefulness as environmental indicators. However, no support was found for the view that a shift from log-normal dominance structure in soil fauna communities is a useful way to detect environmental stress (Hågvar 1994). Even in plots with long-term summer drought, we found no significant shifts from the log-normal shape.

Effects of increased soil temperature (Paper II)

The total abundances of Collembola showed a decrease in plots with soil warming, while an abundance increase could be seen for Oribatida. The abundances of other faunal groups (Mesostigmata and macroarthropod predators) were not significantly affected. At the species level, a number of different Oribatida and Collembola showed significant treatment effects, negative responses to soil warming dominating in Collembola and positive in Oribatida. These responses indicated that some changes in community structure were occurring, although this is not seen in Fig. 5. To better understand the effects of the increased temperature, a more intensive sampling scheme would have been needed. Responses of soil arthropods to temperature alterations may include shifts in fecundity, reproductive pattern or competitive ability (Hopkin 1997; Walter & Proctor 1999).

Long-term effects of nutrient fertilisation (Paper II)

Large changes in the soil fauna community were seen in the intensive fertilisation study at Flakaliden. Although many Oribatida and Collembola species showed decreases in plots receiving annual doses of solid fertilisers, some species seemed to be resistant and instead became characteristic for such plots. Species richness and diversity of Oribatida and Collembola was thereby not significantly affected by the fertilisation treatments (Fig. 4). Additionally, a number of species showed interaction effects between fertilisation and irrigation, as the addition of liquid fertiliser had a positive effect or no effect at all, in contrast to a negative effect of fertiliser only.

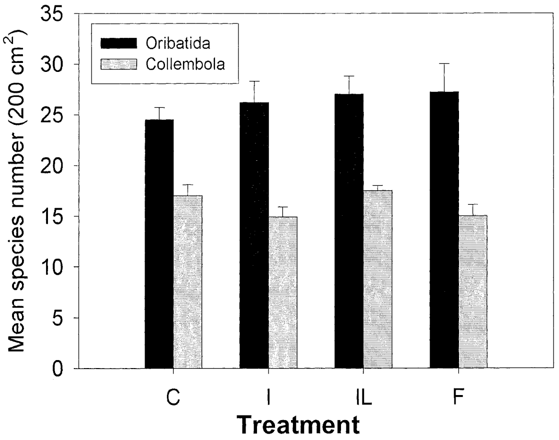

Fig. 4. Mean species richness (S.E.) of Oribatida (adults) and Collembola in the fertilisation experiment at Flakaliden (n = 4). C = control, I = irrigation, IL = liquid fertilisation, F = solid fertilisation. Numbers are based on a sampled area of 200 cm^2.

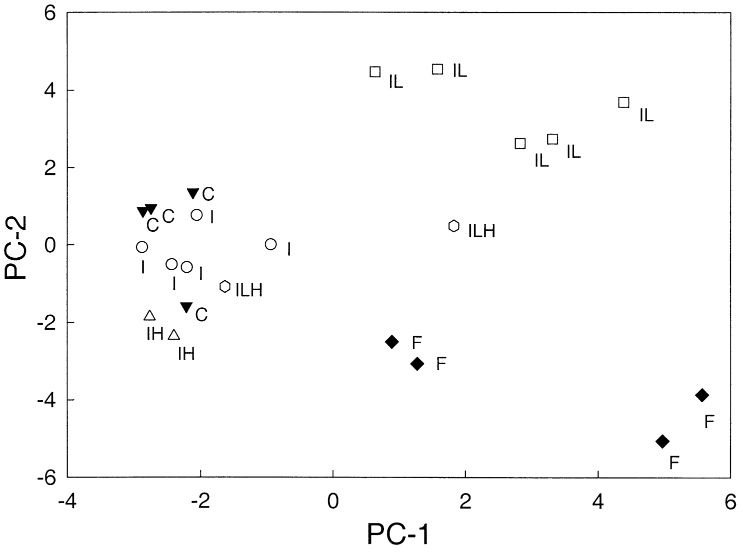

Fig. 5. PCA plot of the experimental plots and subplots at Flakaliden in 1999 based on the Collembola and Oribatida community composition in Tullgren samples. C = control, I = irrigation, IL = liquid fertilisation, F = solid fertilisation, IH = irrigation + warming, ILH = liquid fertilisation + warming. The effects of the fertilisation, irrigation and soil warming treatments on community composition are seen along the first and second PCA axis. Twenty-one Collembola and 38 Oribatida species were included in the analysis.

Similarly, the total abundances of soil fauna were negatively affected by the addition of solid fertiliser whereas fertilisation in combination with irrigation had a slightly positive effect. This interaction effect between fertilisation and irrigation was also seen in community composition (Fig. 4), and could at least partly be explained by the possibility that irrigation in combination with the fertiliser counteracted harmful toxic effects and high salt concentrations induced by fertiliser in solid form.

Similar to the drought and irrigation experiment in Paper I, a number of other abiotic and biotic factors were probably affected by the treatments and could have indirectly influenced the fauna. Ground vegetation can have effects on soil fauna (Petersen 1995; Bengtsson *et al.* 1998) and was indeed different between the treatments at Flakaliden (J. Skoglund, *pers. comm.*). The link to microbial diversity is also interesting, as fertilisation had caused changes in the fungal community (Fransson *et al.* 2000) which possibly also affected the fungivorous soil fauna. In general, high inputs of nutrients have been suggested to decrease the species diversity at local scales, for example in plant communities or in lakes (DiTommaso & Aarsen 1989; Schindler 1990). This has often been attributed to a decrease in resource heterogeneity (Tilman 1987; Rosenzweig & Abramsky 1993, but see also e.g., Hall *et al.* 2000). In our case it is not possible to say whether the lack of a fertilisation effect on species richness was because microhabitat heterogeneity was not affected, or because of other factors.

Post-disturbance recovery of soil fauna communities (Paper III)

Different variables have been used to describe community or ecosystem recovery after disturbances (Pimm 1984; Tilman & Downing 1994; Van der Heijden *et al.* 1998). To compare the recovery of different community parameters of forest soil fauna after a 6-year climatic disturbance, we used the already established experiment in Skogaby that simulated long-term summer droughts and had already resulted in large changes in soil fauna communities (Paper I). Both predators (macroarthropods, mesostigmatid mites) and fungi-/detritivores (oribatid mites, collembolans) were included in the study as differences in recovery ability due to feeding habits, dispersal ability and reproductive strategies are likely to exist.

Table 3. *Mean values (S.E.) of Shannon-Wiener's and Simpson's diversity indices for the Oribatida and Collembola communities at Skogaby 1997-1999 (n = 4). C = control, R = recovery, D = drought. Errors for mean values also include block effects and are not connected with the statistical model used. Within each diversity index and year, values with different letters are significantly different (P < 0.05; pairwise t-test)*

Group	Div. index	Treatment	1997	1998	1999
Oribatida	Shannon-Wiener	C	1.96(0.07)^{a}	1.88(0.06)^{a}	1.94(0.06)^{a}
		R	1.41(0.17)^{b}	1.52(0.17)^{a}	1.51(0.17)^{ab}
		D	1.31(0.10)^{b}	1.09(0.15)^{b}	1.25(0.22)^{b}
	Simpson	C	4.61(0.56)^{a}	4.39(0.30)^{a}	4.68(0.38)^{a}
		R	2.96(0.59)^{b}	3.39(0.66)^{ab}	3.35(0.49)^{ab}
		D	2.45(0.30)^{b}	2.32(0.40)^{b}	2.42(0.42)^{b}
Collembola	Shannon-Wiener	C	1.85(0.05)^{a}	1.81(0.07)^{a}	1.76(0.05)^{a}
		R	1.48(0.16)^{ab}	1.27(0.19)^{a}	1.49(0.13)^{a}
		D	1.22(0.36)^{b}	1.86(0.08)^{a}	1.45(0.11)^{a}
	Simpson	C	4.98(0.15)^{a}	4.43(0.44)^{a}	3.82(0.20)^{a}
		R	3.30(0.54)^{b}	2.77(0.52)^{b}	3.05(0.40)^{a}
		D	2.95(0.78)^{b}	5.32(0.45)^{a}	3.25(0.41)^{a}

We found that after six successive summers with droughts, the community of soil fungi-/detritivores and predators did not return to control levels within three years after the drought treatment ended. Total abundances had returned to control values after three years in all four faunal groups studied, although this recovery was slower for the Oribatida. However, species richness and diversity indices of Oribatida and Collembola in the recovery plots were still intermediate between drought plots and control plots after three years (Table 3). For Collembola, predatory mites and macroarthropods, recovery plots were approaching control plots, although some differences seemed to remain in species composition (Fig. 6b-d), and community similarity. This finding is in line with Bengtsson (2002), who argued that post-disturbance recovery of soil animal communities may take a long time. Hence, our results indicate that total abundance measurements are not sufficient to describe the recovery process of soil fauna accurately.

The interpretation of the results was complicated by large changes in abundances between years and the fact that drought and control plots became more similar in diversity and species composition over time. Nonetheless, our results suggest that the studied organism groups differ in the speed of recovery. Not only the recovery rates of the diversity measurements differed, but also the abundance recovery. No clear differences in recovery pattern between large soil predators and microarthropods could be seen, but there was a tendency for more mobile groups to recover faster. The oribatids showed the most consistent changes in diversity patterns and had a longer recovery time of both abundance and diversity than the other groups. The Oribatida community in the recovery treatment did not get more similar to the controls over time, and a PCA (Fig 6a) showed that the recovery plots still were different from control plots after three years. Together with similar data from the literature (e.g., Karppinen 1957; Strojan 1978; Hutson 1980; Lucarotti 1981; Hoy 1990), this indicates that Oribatida communities have a particularly long recovery time after disturbances. It also suggests that increased frequencies of disturbance could lead to major restructuring of soil fauna communities and, consequently, changes in ecosystem functioning.

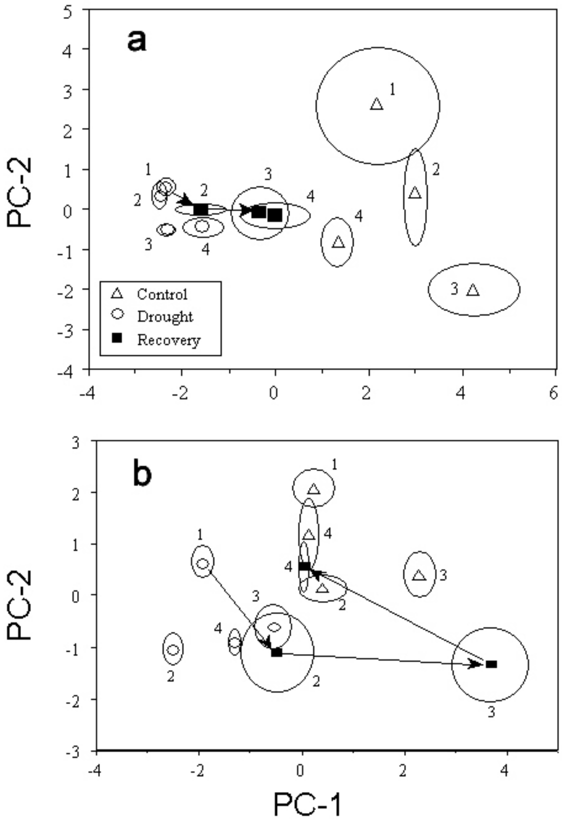

Fig. 6a-d. PCA plots of the community composition of Oribatida (a), Mesostigmata (b), Collembola (c), and predatory macroarthropods (d) in different treatments at Skogaby 1996-1999. Means are given, the ellipses indicate 1 S.E. (n = 4). Numbers denote consecutive years. Arrows have been drawn between the mean positions of the recovery plots. The effects of the drought and recovery treatments are seen along the first and second PCA axes. For Oribatida and Collembola, only large species were included in the PCA.

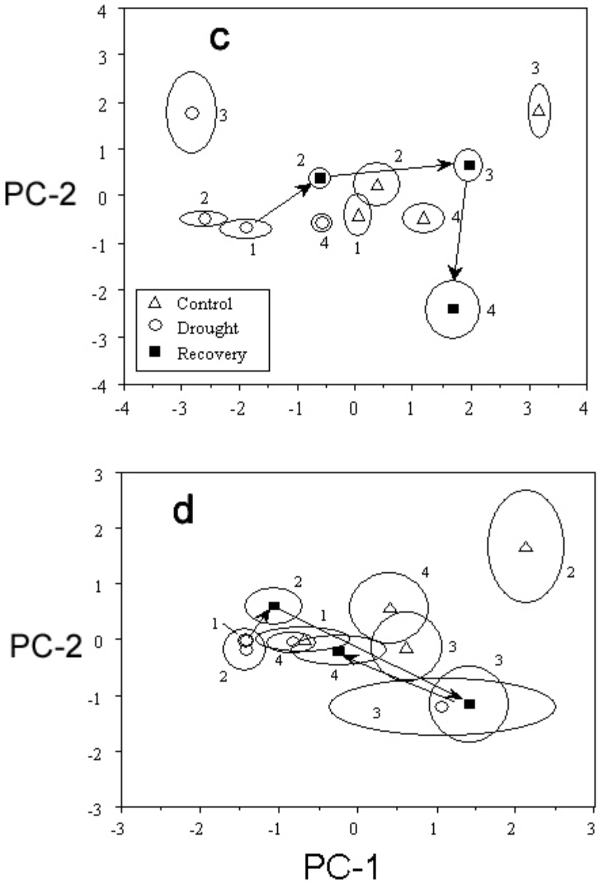

Fig. 6a-d. continued.

Population responses and ecological characteristics (Paper IV)

Oribatida and Collembola share many habits in common as they are mainly fungivorous, have about the same size, and are both very numerous groups in organic soil layers. However, their general life-history traits are often different (Norton 1994), and Oribatida and Collembola communities often differ in recovery time and colonisation rates after disturbances. Therefore, we decided to compare species-wise responses among Oribatida and Collembola after the drought disturbance.

We found that there were differences, although often weak, in ecological and life-history traits between groups of species with different drought responses. Among the Collembola, surface-living species with sexual reproduction were less negatively affected by the drought (Fig. 7). These species (often Entomobryidae) had narrower habitat preferences than the drought-affected species, and they prefer drier sites such as moss cushions and lichens on tree trunks, stones and walls.

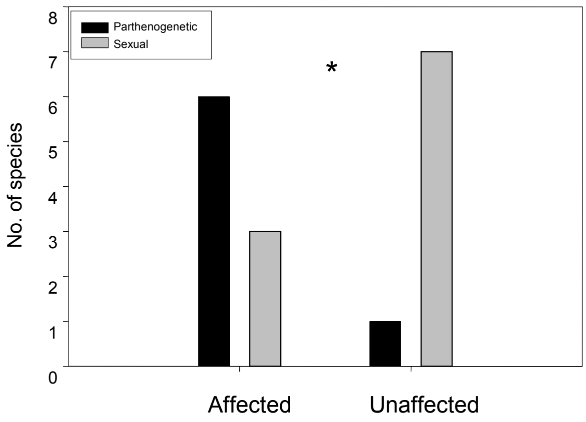

Fig. 7. Reproductive mode among the drought-affected and unaffected Collembola species at Skogaby. Difference between the groups according to a G-test.

After cessation of the drought treatment, drought-affected Collembola populations recovered more quickly than Orbatida (Table 4). Similarly, Oribatida were over-represented among the species that had not recovered after 3 years (Table 4).

Table 4. *Population recovery of the Oribatida and Collembola species showing a negative abundance effect of drought at Skogaby 1996-1999. Significant treatment differences (P < 0.05) between drought and control plots are indicated. C = control, D = drought. X = population recovery, ? = evaluation not possible*

Species	Difference C – D (1996) *P*	"Early recovery" after 1 year (1997)	"Late recovery" after 3 years (1999)	Pop. recovery 1997-99
Oribatida				
Liochthonius sp.	0.001		?	?
Phthiracarus cf. *borealis*	0.008			No
Atropacarus striculus	< 0.001			No
Nothrus silvestris	0.026			No
Camisia biurus	0.010		X	Yes
Camisia spinifer	0.040		?	?
Nanhermannia coronata	< 0.001		X	Yes
Cepheus cepheiformis	0.014		X	Yes
Adoristes ovatus	< 0.001			No
Tectocepheus velatus	< 0.001			No
Suctobelbella spp.	< 0.001		X	Yes
Oppiella nova	0.025		X	Yes
Chamobates borealis	0.005			No
Minunthozetes semirufus	0.025		?	?
Eupelops torulosus	0.003		X	Yes
Parachipteria punctata	< 0.001			No
Collembola				
Friesea mirabilis	0.011			No
Neanura muscorum	< 0.001	X		Yes
Willemia anophthalma	< 0.001	X		Yes

Protaphorura pseudovanderdrifti	0.014	X	X	Yes
Micraphorura absoloni	< 0.001	X	X	Yes
Mesaphorura macrochaeta	< 0.001	X	X	Yes
Isotomiella minor	< 0.001	X	X	Yes
Isotoma viridis	< 0.001	X	X	Yes
Isotoma notabilis	0.009	X	X	Yes
	Diff. C – D *P*	“Early recovery” (1997)	“Late recovery” (1999)	Recovery 1997-99

Reproductive mode seemed to be correlated with the recovery rate as the Oribatida species that did not show a population recovery more often were sexually reproducing than those that did (Fig. 8a). Also, six of the eight Collembola species that showed a fast population recovery were parthenogenetic. In both groups there was also a tendency for habitat generalists among the drought-affected species to recover before more specialised species (Fig 8b). Although the material was small and phylogenetic correlations with several traits were seen, the results indicate that both traits along the traditional “*r*-*K* continuum” in colonisation theory, dispersal ability and niche specialisation are important for recovery after disturbances. We were, however, unable to find general differences in characteristics between Collembola and Oribatida that could explain their different community responses. It is possible that there were general differences in other characteristics that were more important, such as dispersal ability or reproductive effort. They were not evaluated because of a shortage of reliable data in the literature.

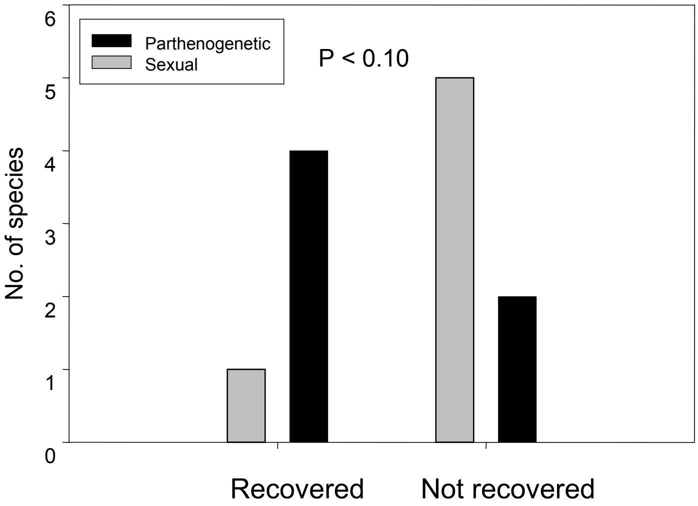

Fig. 8a. Reproductive mode among the drought-affected species of Oribatida at Skogaby showing population recovery, or no recovery, within three years after the drought treatment ceased. There was a difference in relative frequency of the reproductive modes ($P < 0.10$) according to a G-test.

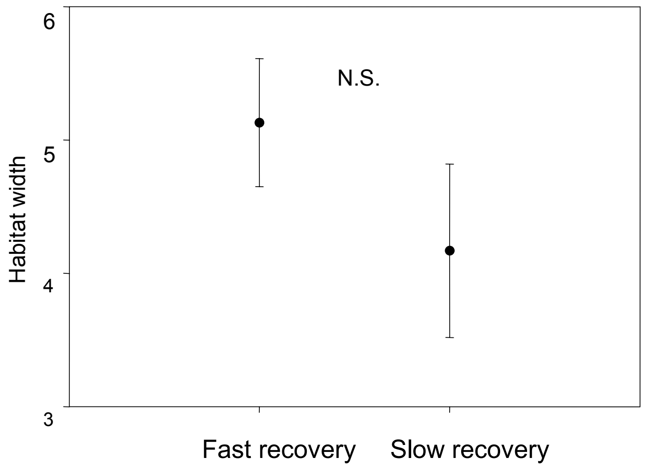

Fig. 8b. Mean habitat width (S.E.) among the drought-affected species of Oribatida and Collembola showing a fast population recovery and a slow recovery, respectively (see text). There was no significant difference between the groups (P > 0.10) according to a G-test.

The composition of the species pool will probably be of importance for the effects of future disturbances on soil fauna communities. At Skogaby, the microarthropod species that were least affected by, or benefited from, the drought disturbance were the habitat specialists of moss cushions, tree trunks and stones. They were the only species at the site that were able to withstand or thrive during the 6-year sequence of dry summers.

Concluding remarks

I have shown that altered climatic conditions resulting in major changes in soil moisture and temperature conditions are likely to affect soil fauna communities in Scandinavian coniferous forests. Frequent summers with drought are likely to affect many groups of soil fauna negatively, whereas moister conditions probably will at least affect the community structure and relative abundances. Soil fauna responses to an increased soil temperature may include species shifts in for example Oribatida and Collembola. Conflicting views exist of whether the soil fauna of temperate and boreal ecosystems is more or less vulnerable to global warming than that of the more studied polar ecosystems (Kennedy 1994; Hodkinson *et al.* 1998). In any case, ecosystems at lower latitudes are more likely to be affected by shifts in management practices in response to climate warming, such as forest fertilisation, than those at higher latitudes. Intensive fertilisation of coniferous forests, applied in solid form or with irrigation, will probably cause large changes in the microarthropod community.

The results indicate that recovery rates of microarthropod communities after disturbances are quite slow and that extreme events on a large spatial scale, such as repeated droughts, may result in permanent changes in the community composition of soil fauna. Different responses to the disturbances were seen when comparing the different faunal groups, both in direct impact and recovery patterns.

Long-lasting effects of drought seem to be more common in Oribatida than in the other groups studied. Thus, the threat to Oribatida by large-scale climatic changes may be larger than for other soil arthropods, as shown by the slow population recovery of many species. After the drought, different taxa (functional groups) varied in their rate of return to control values of diversity and species composition, and this suggests that soil food web structure and trophic interactions will be altered by increased disturbance frequencies. If this will have further effects on the resilience of the ecosystem (Maraun *et al.* 1998) remains unclear.

The relatively short treatment time and small spatial scale of the experiments may indicate that effects of large-scale climatic change on soil fauna will be even more pronounced than shown by our studies. Colonisation from the surroundings may have been important for the maintenance of some populations in the treatment plots. In spite of the small size of the drought plots at Skogaby, three years was not enough for the soil fauna communities to recover after the drought treatment had ceased. The consequences for soil biodiversity of intensive forest fertilisation will probably be dependent on the spatial extent of the areas used for this purpose. If only small areas are used, it will probably not impose any serious threat to soil fauna diversity. If, however, large-scale forest fertilisation programmes will be launched, the risk of losing species of soil fauna will increase substantially.

Mites and collembolans have so far not been included in any “red lists” for Sweden, mainly because of a lack of data on the ecology and distribution of many of our species. Nevertheless, it may still be desirable to include also species of these groups in nature conservation programmes in the future. For such purposes, it may be possible as a start to use general knowledge about the dispersal ability and the sensitivity to disturbances of a whole order or family. Oribatid mites may be such a microarthropod group at particularly high risk. Present information about the habitat and distribution range of a certain species could thereafter be combined with data on e.g., fecundity and reproductive mode (taken from related species if necessary) to evaluate possible threats to each species.

We still have a lot to learn about the soil biota and its diversity. This is reflected by the fact that five oribatid species new for Sweden, as well as two species probably undescribed by science, were recorded during these studies, in spite of a comparatively small sampling effort in a habitat that by no means is special in any sense of the word. Who knows how many new soil fauna species there is still left to discover out there in the Swedish forests?

Appendix A. *Mean densities m^{-2} (S.E.) of the Oribatida, Collembola, Mesostigmata and predatory macroarthropod taxa in the treatments at Skogaby 1996-1999 (n = 4). D = drought, R = recovery, C = control. x = present, but density not quantified. One specimen sampled per treatment corresponds to a mean density of 8 ind. m^{-2} for samples from 1996 and 1999 and 6 ind. m^{-2} for samples from 1997-98. Densities in italics were possibly biased by species confusion*

	1996		1997		
Species	D	C	D	R	C
Oribatida					
Paleacarus hystricinus	130 (42)	120 (68)	180 (94)	690 (300)	280 (190)
Eniochthonius minutissimus		x			100 (100)
Liochthonius sp.		700 (230)	250 (170)	600 (82)	2100 (880)
Brachychthoniidae sp.	8000 (2900)	19000 (9800)	22000 (11000)	24000 (5600)	18000 (5700)
Phthiracarus cf. *laevigatus*		50 (22)		19 (12)	19 (6)
Phthiracarus cf. *borealis*	25 (8)	340 (150)	19 (6)	38 (7)	630 (240)
Phthiracarus cf. *piger*		8 (8)			
Atropacarus striculus		2100 (790)	19 (12)	410 (390)	1400 (770)
Rhysotritia duplicata	360 (85)	2400 (1400)	110 (45)	380 (86)	1800 (650)
Euphthiracarus cribrarius					
Microtritia minima		33 (33)			
Nothrus silvestris	160 (76)	1200 (450)	390 (170)	2900 (2100)	8600 (2600)
Camisia biurus		140 (72)			69 (45)
Camisia spinifer		25 (8)			31 (19)
Camisia segnis				6 (6)	
Platynothrus peltifer		8 (8)			
Malaconothrus sp.	x	x			
Nanhermannia coronata	50 (22)	5800 (2100)	50 (34)	130 (83)	3700 (1300)
Damaeus gracilipes					
Damaeidae sp.				6 (6)	
Porobelba spinosa	700 (100)	180 (91)	1200 (340)	910 (440)	470 (170)
Cepheus cepheiformis		140 (91)	13 (13)	6 (6)	56 (21)
Adoristes ovatus	300 (110)	3600 (330)	390 (90)	1700 (990)	3700 (380)
Liacarus coracinus		8 (8)			13 (13)
Carabodes femoralis	58 (48)	280 (150)	25 (10)	31 (12)	94 (27)
Carabodes labyrinthicus	8 (8)	17 (10)	25 (18)	25 (18)	31 (16)
Carabodes areolatus		33 (33)			13 (13)
Tectocepheus velatus	600 (280)	21000 (5400)	980 (720)	8200 (7500)	20000 (2700)
Licneremaeus licnophorus	x				
Suctobelbella spp.	230 (120)	11000 (3900)	290 (170)	2100 (790)	6600 (1000)
Quadroppia quadricarinata			25 (25)		
Oppia falcata	x				
Oppiella nova	7400 (2500)	52000 (24000)	8000 (3600)	25000 (9100)	52000 (9700)
Medioppia subpectinata					
Microppia minus	x	x	25 (25)	6 (6)	200 (200)
Dissorhina ornata			81 (66)	130 (80)	50 (50)
Zygoribatula exilis	2900 (2400)	42 (32)	2100 (730)	180 (180)	50 (50)
Oribatula tibialis	110 (88)	230 (140)	50 (50)	100 (76)	360 (210)
Scheloribates pallidulus	520 (450)	530 (310)	63 (47)	63 (41)	25 (25)
Hemileius initialis	560 (280)	1600 (470)	180 (150)	360 (130)	2100 (710)
Chamobates borealis	700 (350)	3200 (480)	490 (190)	1800 (880)	8200 (3100)
Ceratozetella thienemanni		540 (530)	6 (6)		850 (850)
Minunthozetes semirufus		1100 (700)			160 (93)
Eupelops acromios		42 (32)	13 (7)	6 (6)	31 (16)
Eupelops torulosus	17 (10)	260 (140)	25 (18)	63 (38)	430 (63)
Oribatella calcarata	33 (19)	42 (32)	31 (16)	56 (28)	100 (100)
Parachipteria punctata		430 (230)		13 (7)	130 (63)
Collembola					
Friesea mirabilis		330 (150)		75 (75)	1900 (1300)
Neanura muscorum		140 (71)		140 (34)	170 (31)
Xenylla brevicauda	820 (470)	270 (180)	22000 (20000)	200 (180)	13 (7)
Micranurida pygmaea	x	x	63 (47)	1400 (470)	430 (240)
Willemia anophthalma		1200 (510)		1100 (230)	1600 (290)
Protaphorura pseudovanderdrifti	240 (110)	1700 (530)	210 (160)	3100 (1100)	2900 (610)
Micraphorura absoloni	200 (110)	4000 (1600)	170 (51)	2500 (1200)	3200 (1200)
Mesaphorura macrochaeta	1400 (490)	12000 (3700)	600 (170)	11000 (2800)	9400 (1700)
Paratullbergia callipygos		33 (33)		13 (13)	100 (60)
Anurophorus septentrionalis	800 (90)	1100 (720)		6 (6)	2100 (2100)
Anurophorus laricis	92 (42)		19 (19)	540 (140)	260 (140)

	1996		1997		
	D	C	D	R	C
Pseudanurophorus binoculatus		230 (160)			
Folsomia quadrioculata	130 (130)	5000 (3500)		1800 (1800)	3700 (1900)
Isotomiella minor	410 (130)	4300 (540)	820 (180)	15000 (6600)	7800 (1800)
Isotoma viridis		1500 (540)		240 (67)	320 (98)
Isotoma notabilis	8 (8)	440 (120)		290 (270)	110 (65)
Lepidocyrtus cyaneus	180 (50)	170 (130)	150 (80)	240 (130)	120 (46)
Lepidocyrtus lignorum	8 (8)	8 (8)			19 (12)
Orchesella flavescens		8 (8)	31 (6)	25 (10)	6 (6)
Orchesella bifasciata	420 (420)		160 (160)	31 (31)	
Entomobrya nivalis	50 (22)	33 (33)	44 (19)	19 (19)	
Entomobrya albocincta	8 (8)		50 (50)		
Entomobrya corticalis	170 (90)		110 (65)		
Entomobrya marginata	130 (87)		25 (18)		6 (6)
Tomocerus vulgaris					
Allacma fusca	8 (8)		13 (13)		
Megalothorax minimus		8 (8)		25 (25)	
Mesostigmata					
Pergamasus brevicornis	50 (40)	330 (86)	19 (12)	190 (53)	290 (56)
Lysigamasus lapponicus	130 (21)	2000 (960)	140 (48)	1000 (280)	880 (360)
Leptogamasus suecicus	67 (33)	810 (190)	6 (6)	1100 (270)	2600 (750)
Vegaia nemorensis	440 (92)	2300 (220)	310 (170)	3300 (790)	2100 (310)
Vegaia cerva	8 (8)	75 (34)		140 (28)	44 (36)
Vegaia kochi		25 (8)			6 (6)
Pachylaelaps sp.	120 (96)	58 (37)			13 (7)
Parasitus sp.		67 (38)			6 (6)
Hypoaspis sp.	320 (140)	180 (92)	310 (110)	440 (110)	440 (200)
Rhodacaridae sp.	120 (29)	310 (69)	110 (65)	31 (12)	56 (21)
Amblyseius sp.			31 (31)	25 (25)	
Gamasina sp.			160 (73)	110 (98)	
Zerconidae sp.	83 (35)	800 (330)	38 (16)	310 (66)	390 (230)
Trachytes sp.		170 (130)		88 (72)	250 (150)
Uropodina sp.	67 (24)	100 (29)	6 (6)	38 (24)	
Predatory macroarthropods					
Formica cf. *rufa*				6 (6)	
Carabidae sp. ad.				6 (6)	
Staphylinidae sp. ad.	58 (8)	120 (40)	56 (33)	69 (12)	140 (21)
Staphylinidae sp. larvae	8 (8)	8 (8)		38 (7)	31 (12)
Cantharidae sp. larvae	100 (30)	160 (58)	69 (31)	110 (33)	230 (58)
Athous sp. larvae	50 (22)	75 (37)	50 (42)	75 (48)	290 (73)
Dolopius sp. larvae	8 (8)			19 (6)	56 (33)
Elateridae sp. larvae					
Empididae sp. larvae		33 (33)			6 (6)
Linyphiidae sp.	25 (16)	125 (110)	19 (12)	19 (12)	81 (19)
Pseudoscorpiones sp.					25 (10)

Appendix A. *continued*

Species	1998			1999		
Oribatida	D	R	C	D	R	C
Paleacarus hystricinus	1800 (650)	660 (210)	250 (120)	480 (250)	42 (32)	130 (93)
Eniochthonius minutissimus		31 (31)	81 (45)		200 (200)	150 (110)
Liochthonius sp.	280 (140)		350 (230)	930 (630)	580 (340)	870 (310)
Brachychthoniidae sp.	68000 (17000)	52000 (16000)	38000 (5100)	50000 (16000)	43000 (19000)	28000 (8200)
Phthiracarus cf. *laevigatus*	6 (6)	63 (47)	88 (31)	75 (75)	42 (32)	42 (16)
Phthiracarus cf. *borealis*	25 (10)	450 (70)	1700 (460)	150 (120)	180 (52)	1800 (680)
Phthiracarus cf. *piger*		6 (6)			8 (8)	
Atropacarus striculus	110 (66)	430 (160)	1700 (590)	92 (70)	1200 (1100)	2200 (670)
Rhysotritia duplicata	250 (130)	690 (370)	1400 (460)	340 (150)	710 (340)	1600 (620)
Euphthiracarus cribrarius			6 (6)			
Microtritia minima			580 (580)			
Nothrus silvestris	1300 (710)	2200 (980)	12000 (2100)	1100 (220)	2900 (2300)	8700 (2800)
Camisia biurus	6 (6)	69 (21)	31 (6)	17 (17)	75 (21)	42 (25)
Camisia spinifer		6 (6)	44 (19)	8 (8)	8 (8)	8 (8)
Camisia segnis						
Platynothrus peltifer		13 (13)				
Malaconothrus sp.						8 (8)
Nanhermannia coronata	180 (170)	430 (380)	4200 (2000)	25 (25)	950 (880)	1500 (120)
Damaeus gracilipes					8 (8)	
Damaeidae sp.	6 (6)	6 (6)	6 (6)			
Porobelba spinosa	940 (280)	1000 (290)	780 (290)	830 (240)	75 (64)	290 (230)
Cepheus cepheiformis		38 (16)	120 (86)	17 (17)	50 (32)	25 (16)
Adoristes ovatus	1100 (120)	4100 (520)	6600 (660)	1200 (190)	1300 (300)	2200 (490)
Liacarus coracinus	6 (6)			8 (8)	8 (8)	
Carabodes femoralis		81 (81)	50 (42)	25 (8)	25 (25)	75 (44)
Carabodes labyrinthicus	25 (25)	31 (6)	38 (16)	100 (60)	33 (0)	50 (10)
Carabodes areolatus		19 (19)	19 (12)		17 (17)	8 (8)
Tectocepheus velatus	680 (410)	8000 (3500)	20000 (2400)	2500 (1900)	5800 (1600)	15000 (4300)
Licneremaeus licnophorus						
Suctobelbella spp.	1000 (130)	8700 (2700)	8400 (2300)	5300 (2300)	14000 (3300)	8500 (2000)
Quadroppia quadricarinata	25 (25)			33 (33)	67 (67)	33 (33)
Oppia falcata						
Oppiella nova	49000 (17000)	45000 (11000)	72000 (8700)	67000 (45000)	60000 (13000)	39000 (9900)
Medioppia subpectinata		6 (6)	50 (50)	8 (8)	67 (67)	100 (100)
Microppia minus	4400 (4400)	25 (25)	750 (750)	3600 (3600)		130 (130)
Dissorhina ornata		75 (75)				100 (100)
Zygoribatula exilis	460 (200)	31 (31)	13 (7)	290 (260)	8 (8)	
Oribatula tibialis	150 (130)	44 (44)	450 (350)	67 (47)	33 (33)	200 (97)
Scheloribates pallidulus	31 (16)	75 (60)		230 (230)	42 (25)	8 (8)
Hemileius initialis	530 (250)	830 (290)	2700 (980)	840 (220)	1100 (420)	2600 (960)
Chamobates borealis	1600 (510)	2200 (880)	6700 (1700)	2500 (1000)	2900 (1200)	6500 (3400)
Ceratozetella thienemanni		6 (6)	210 (210)	92 (92)		600 (600)
Minunthozetes semirufus		25 (25)	6 (6)		100 (79)	220 (120)
Eupelops acromios	6 (6)		12 (13)			8 (8)
Eupelops torulosus	6 (6)	170 (86)	280 (23)	58 (25)	210 (21)	210 (57)
Oribatella calcarata	88 (54)	44 (26)	31 (19)	42 (25)	17 (17)	
Parachipteria punctata			25 (10)		8 (8)	310 (220)
Collembola						
Friesea mirabilis	6 (6)	38 (24)	2600 (1000)		340 (330)	2700 (1100)
Neanura muscorum	160 (88)	350 (81)	1100 (180)	42 (16)	58 (8)	250 (100)
Xenylla brevicauda	7900 (4100)	180 (150)	150 (94)	42 (16)	33 (14)	210 (85)
Micranurida pygmaea	13000 (5600)	1700 (300)	6200 (1500)	830 (570)	300 (260)	320 (180)
Willemia anophthalma	6700 (1400)	6700 (1700)	8100 (3700)	5100 (2900)	650 (240)	1900 (530)
Protaphorura pseudovanderdrifti	2200 (1000)	2700 (1100)	2300 (620)	1600 (650)	2300 (740)	3400 (1300)
Micraphorura absoloni	6300 (2600)	14000 (3900)	9700 (2100)	2000 (660)	7500 (680)	2500 (690)
Mesaphorura macrochaeta	13000 (4100)	86000 (38000)	46000 (12000)	11000 (4100)	34000 (8900)	23000 (2600)
Paratullbergia callipygos	13 (7)	110 (98)		25 (25)	400 (240)	67 (67)
Anurophorus septentrionalis	*81 (28)*	*69 (16)*	*2400 (2100)*	*130 (56*	*590 (380)*	*3000 (2300)*
Anurophorus laricis				*(8) (8)*		
Pseudanurophorus binoculatus			980 (810)			210 (200)
Folsomia quadrioculata	180 (70)	1100 (1100)	11000 (6500)	610 (520)		3100 (2100)

Isotomiella minor	14000 (6600)	41000 (15000)	23000 (2200)	9300 (2700)	8400 (970)	7000 (1200)
Isotoma viridis	6 (6)	730 (240)	1700 (300)	120 (120)	2400 (750)	1100 (150)
Isotoma notabilis	140 (83)	4300 (580)	1900 (370)	42 (42)	2100 (680)	1500 (750)
Lepidocyrtus cyaneus	610 (290)	25 (14)	25 (18)	130 (28)		42 (21)
Lepidocyrtus lignorum	56 (21)				8 (8)	
Orchesella flavescens	69 (45)	6 (6)		33 (19)	8 (8)	8 (8)
Orchesella bifasciata	440 (340)			8 (8)	33 (33)	
Entomobrya nivalis	75 (37)	6 (6)		8 (8)		
Entomobrya albocincta	13 (13)					
Entomobrya corticalis	88 (39)					
Entomobrya marginata						
Tomocerus vulgaris					8 (8)	
Allacma fusca	19 (12)				17 (0)	
Megalothorax minimus	19 (12)	120 (55)	50 (20)	180 (160)	1200 (400)	290 (120)
Mesostigmata						
Pergamasus brevicornis	38 (13)	440 (130)	240 (43)	25 (16)	130 (46)	150 (44)
Lysigamasus lapponicus	150 (87)	3000 (550)	3800 (830)	620 (340)	3700 (950)	3800 (630)
Leptogamasus suecicus	2300 (600)	5200 (880)	7300 (1500)	150 (110)	1200 (150)	940 (210)
Vegaia nemorensis	4300 (1300)	8600 (890)	4900 (1200)	3500 (200)	4800 (840)	3200 (880)
Vegaia cerva	75 (32)	550 (190)	140 (51)	33 (14)	25 (16)	33 (14)
Vegaia kochi			13 (13)		8 (8)	17 (17)
Pachylaelaps sp.			6 (6)		33 (33)	8 (8)
Parasitus sp.		19 (12)	6 (6)			
Hypoaspis sp.	360 (100)	430 (100)	390 (130)	1100 (300)	810 (210)	700 (200)
Rhodacaridae sp.	150 (87)	150 (150)	180 (63)	50 (29)	100 (100)	240 (110)
Amblyseius sp.						
Gamasina sp.				25 (16)		
Zerconidae sp.	110 (66)	280 (140)	1100 (590)	130 (83)	220 (83)	1300 (550)
Trachytes sp.	25 (25)	140 (68)	75 (27)		200 (130)	200 (86)
Uropodina sp.		31 (19)	6 (6)		140 (61)	58 (34)
Predatory macroarthropods						
Formica cf. *rufa*						
Carabidae sp. ad.						
Staphylinidae sp. ad.	210 (54)	240 (77)	160 (54)	75 (21)	50 (32)	140 (50)
Staphylinidae sp. larvae	210 (160)	130 (40)	69 (43)	25 (8)	100 (14)	100 (24)
Cantharidae sp. larvae	160 (46)	100 (31)	130 (44)	130 (53)	67 (30)	250 (100)
Athous sp. larvae	50 (35)	110 (49)	180 (55)	58 (25)	180 (55)	180 (55)
Dolopius sp. larvae	6 (6)	31 (12)	19 (12)		25 (8)	17 (9)
Elateridae sp. larvae	31 (31)					
Empididae sp. larvae	25 (14)	130 (16)	75 (20)	8 (8)	120 (67)	33 (14)
Linyphiidae sp.	56 (19)	31 (6)	31 (6)	120 (32)	67 (45)	150 (95)
Pseudoscorpiones sp.	19 (6)	6 (6)		8 (8)		
		1998			1999	
	D	R	C	D	R	C

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