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To my family, Anneli, Henri and Elisa

"*Mikä meitä oikeastaan ihastuttaa ja miellyttää tämän kylän kaltaisissa paikoissa? Voimme syyksi sanoa, että puuttuu se kaikki, mistä emme nykyajan yhteiskunnassa pidä: henkinen juurettomuus ja sisäinen tyhjyys, keinotekoiset tarpeet ja niiden keinotekoinen tyydyttäminen, hedelmätön itsekkyys ja mekaaninen yhdenmukaistuminen.*" – Göran Schildt –

ABSTRACT

The aim of this thesis was to assess the effects of soil spatial heterogeneity and microclimatic conditions on the decomposer community structure, biotic interactions within the community and soil processes mediated by the community. Several experiments were carried out in laboratory microcosms and in the field. The microcosms were constructed using coniferous forest soil materials. They were incubated at different moistures and temperatures and they contained different food webs of soil organisms, depending on the aims of the experiment. In two experiments, microcosms contained humus and four different litter materials, either separately in four patches or mixed with each other in one patch. In the field experiment, snow-covered forest soil was compared with roof-covered test plots in which snow did not protect the soil against frost. Microclimatic conditions, decomposer community structure and soil processes were connected by complex interactions. Enchytraeid biomass and N-mineralisation were closely correlated in coniferous forest soil, and a diverse community of microarthropods affected N-mineralisation only indirectly by regulating the enchytraeid populations at low and medium moistures. Hard frost disturbance on snowfree field plots and in microcosms decreased heavily the biomass of enchytraeids and the abundance and species richness of microarthropods. However, recovery of populations was fast and any effects on N-mineralisation remained temporary. Patchy soil structure maintained the species richness of microarthropods. Moreover, the effect of soil fauna on decomposition processes was more prominent in microcosms with one patch than in four patches. In the microcosms with plants, the increasing effect of soil fauna on carbon assimilation apparently compensated their stimulating effect on soil respiration, observed in the experiment without plants. Carbon dynamics, plant growth and faunal diversity were similar independently of the patch treatment at the end of the experiment, suggesting that the impacts of initial heterogeneity do not persist in the long run.

Key words: Decomposers; decomposition; enchytraeids; global climate change; hard frost; heterogeneity; mineralisation; patchiness; soil fauna.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals. I have personally performed most of the work. Experiment I was planned by other authors.

I   Sulkava, P., Huhta, V. & Laakso, J. 1996. Impact of soil faunal structure on decomposition and N-mineralisation in relation to temperature and moisture in forest soil. Pedobiologia 40: 505-513.

II   Huhta, V., Sulkava, P. & Viberg, K. 1998. Interactions between enchytraeid (Cognettia sphagnetorum), microarthropod and nematode populations in forest soil at different moistures. Applied Soil Ecology 9: 53-58.

III Sulkava, P. & Huhta, V. Effects of hard frost and freeze-thaw cycles on decomposer communities and N mineralisation in boreal forest soil. Manuscript (submitted).

IV   Sulkava, P. & Huhta, V. 1998. Habitat patchiness affects decomposition and faunal diversity: a microcosm experiment on forest floor. Oecologia 116: 390-396.

V   Sulkava, P., Huhta, V., Laakso, J. Gylen, E-R. 2001. Influence of soil fauna and habitat patchiness on plant (*Betula pendula*) growth and carbon dynamics in a microcosm experiment. Oecologia 129: 133-138.

1   INTRODUCTION

1.1 Decomposer communities and soil processes in relation to temperature and moisture

Soil microflora (fungi and bacteria) are responsible for most of primary decomposition and nutrient mineralisation in coniferous forest soil (Alexander 1977, Swift et al. 1979, Persson et al. 1980, Vogt et al. 1986). Soil animals (Tardigrades, Nematodes, Microarthropods and Oligochaeta) form a complex food web (see Laakso & Setälä 1998), containing millions of animals per one square metre (see e.g. Huhta et al. 1986). Excretions, faeces and carcasses of animals enrich the nutrient content of humus and promote decomposition and mineralisation. Soil fauna affect decomposition physically by modifying the soil structure and by stimulating microbial activity through grazing (Swift et al. 1979, Anderson et al. 1981, Anderson & Ineson 1983, Bengtsson & Rundgren 1983, Setälä et al. 1988, Verhoef & Brussaard 1990, Beare et al. 1992, Huhta et al. 1994, Huhta et al. 1998).

The most important physical factors controlling decomposition and mineralisation processes are temperature and moisture (Swift et al. 1979, Davidson et al. 1998). Soil respiration rate has been found to correlate with mean annual air temperature and precipitation, even though soil temperature is a better determinant of respiration rate than moisture (Anderson 1991, Raich & Schlesinger 1992). Jenny (1928a, 1928b) already showed a correlation between mean annual temperature and mineral nitrogen content of soil. Later, microbial biomass and N-mineralisation have been widely reported to increase with increasing temperature (Waksman & Gerretsen 1931, Clark & Gilmour 1983, Varnero et al. 1987, Insam et al. 1989, Andren et al. 1998), and the optimal temperature for decomposition is considered to be roughly +35°C (see Kätterer et al. 1998). Mineralisation practically ceases near the freezing point and, on the

other hand, when temperature approaches +45°C. However, if the availability of nutrients and carbon is markedly low due to high immobilisation, microflora may not be able to express the potential level of activity set by more favourable climatic conditions (Anderson 1992).

The dependence of soil processes on temperature is usually described by the Q_{10} function. This is reported to vary between 1.8 and 2.5 at the temperature range from 5°C to 35°C (Stanford et al. 1973, Raich & Schlesinger 1992, Kätterer et al. 1998). However, equations for the dependence of decomposition rate on temperature are not straightforward as the greatest relative sensitivity of decomposition processes to temperature occurs at low temperatures. According to Kirchbaum (1995), at near-zero temperatures decomposition increases with a Q_{10} of almost 8. Similarly, Lloyd and Taylor (1994) concluded that an exponential Q_{10} relationship between temperature and respiration can not be provided, because respiration rate is relatively more sensitive to temperature fluctuations at low soil temperatures. Finally, most studies for testing the Q_{10} theory have been carried out without plants, and Boone et al. (1998) showed that temperature stimulates soil respiration more effectively near rhizosphere than in the bulk soil.

Decreasing moisture generally reduces decomposition rate (Jenny et al. 1949, Kätterer et al. 1998, Akinremi et al. 1999). Clarholm et al. (1981) showed in a microcosm experiment that the amount of mineral nitrogen stayed constant at low moisture (20-40 % WHC) but increased strongly at high moisture (100% WHC). However, optimum moisture for decomposition seems to be no more than 50% WHC (Howard & Howard 1993). At low temperature (0°C to +2°C) the effect of moisture on respiration rate has also been found to be smaller than at higher temperature (+4°C to +8°C) (Fisher 1995).

Besides affecting microbial community structure and biomass, temperature and moisture also influence soil faunal communities. Low temperature and moisture generally decrease the numbers of soil animals (Abrahamsen 1971, Huish et al. 1985, Sohlenius 1985, Kennedy 1994, Harte et al. 1996). Clarholm et al. (1981) reported that the length of fungal hyphae was highest at high moisture, whereas bacterial biomass and the abundance of nematodes and microarthropods were highest at intermediate moisture. The abundance of microarthropods and the amount of mineral N increased at high temperature (+25°C), while fungal hyphal length, bacterial biomass and the abundance of nematodes reached maximum values between +15°C and +20°C. At +2°C, the abundance of faunal populations stayed constant and only bacterial biomass decreased slightly during the 28-week experiment (Clarholm et al. 1981).

Harte et al. (1995, 1996) heated field plots artificially and found that heating enhanced mesofaunal biomass and diversity in a cool and wet summer, but depressed diversity and biomass in a dry habitat and increased biomass in a moist habitat in a warm dry summer. These results were obviously affected by drying, because heating the soil by 1°C decreased its moisture approximately by 10%. In a field experiment, Kennedy (1994) found that elevation of soil temperature by +2°C in winter resulted in consistently greater microarthropod

populations. In this experiment soil temperature remained near the freezing point. On the other hand, Coulson et al. (1996) found that Oribatid mites did not respond to heating while the abundance of Collembola decreased under heating. These authors concluded that soil animals are adapted to harsh and unpredictable environments and can tolerate low temperature after a successful acclimatisation period.

Cold hardiness of different soil animals varies greatly. Alpine Collembola also show distinct seasonal changes in cold tolerance (supercooling point) (Shatz & Sømme 1981); during winter the supercooling point fluctuates between -9 and -15°C, and during summer between -6 and -9°C (van der Woude 1987). Sømme and Conradi-Larssen (1977) found that some collembolans can survive even at -40°C. However, earthworms and enchytraeids have been reported to be very sensitive to temperatures below 0°C (Dozsa-Farkas 1973, Holmstrup 1990, Bauer et al. 1998).

The role of soil fauna in decomposition and the interactions between soil faunal groups have been found to depend on abiotic conditions. Sohlenius (1985) showed that changes in temperature and moisture resulted in different dominance patterns in the nematode community, and Haukka (1987) revealed an interaction between enchytraeids and earthworms in relation to temperature and moisture. Effects of *Glomeris marginata* (Diplopoda) on N-release from decomposing oak leaves may also depend on temperature (Anderson et al. 1983) and the relative influence of a mixed microarthropod community on N mineralisation appears to depend on temperature and moisture (Persson 1989). Finally, Abrahamsen (1990) showed that although the presence of enchytraeid (*Cognettia sphagnetorum*) population enhanced N-release from coniferous forest humus in moist soil, the effect was negative in dry soil.

1.2 Global climate change

Global climate change is suggested to be a consequence of increasing amounts of greenhouse gases in the air. Atmospheric concentrations of the most important greenhouse gases CO_2, CH_4, NO_x, N_2O and CO have increased dramatically during the last 150 years (Houghton et al. 1990, Anderson 1992, Routti et al. 1994) and the amount of atmospheric CO_2 is still going to double during the next 30 years (Fajer & Bazzaz 1992, Tans & Bakvin 1995). Excess of greenhouse gases prevents radiation out of the atmosphere, resulting in warming of the air. Changes in air temperature in turn affect many climatic variables, such as humidity, and consequently ecological functions (Anderson et al. 1983, Persson 1989, Glantz 1992, Fischer et al. 1994, White et al. 1999). Global climate change is thus one of the most serious anthropogenic environmental hazards (see Parry et al. 1996), which may widely alter the structure and function of ecosystems (Shaver et al. 1992, Vitousek 1994, Zak et al. 2000). Raising air temperature may, for instance, reduce soil moisture in summer due to increased evaporation (Manabe et al. 1981, Anderson 1992), and

so decrease decomposition (Kätterer et al. 1998), and change the composition of dominating vegetation (Harte & Shaw 1995). Moreover, increased concentrations of greenhouse gases may impair the viability of plants (see e.g. Cotrufo & Ineson 1996, Lloyd & Farquhar 1996).

It is generally believed that the effects of global climate change on soil moisture and temperature mainly enhance N mineralisation and CO_2 emissions (Houghton et al. 1990, Andersson 1992, Lloyd & Taylor 1994, Harte et al. 1996, Heal et al. 1998, Leiras et al. 1999, Niklinska et al. 1999, White et al. 1999). Increase in annual heat sum of cold areas may change the direction of carbon and nutrient feedback loops and promote development of more productive ecosystems with smaller soil carbon pools (Anderson 1992). The mineralised nitrogen is assumed not to be retained in soil, nor lost from the ecosystem with increasing soil temperature, but rather to become available for plant growth due to higher potential for carbon mobilisation (Rastetter et al. 1992, Melillo et al. 1996, Houghton et al. 1998). However, Heal et al. (1998) also refer to scenarios that predict a decrease in decomposition rate. Moreover, increasing CO_2 concentration does not directly enhance soil microbial biomass or N mineralisation, and may even decrease root biomass (Kandeler et al. 1998, Zak et al. 2000).

As a consequence of climate change, boreal areas undergo the largest regional changes in temperature and soil moisture (Anderson 1992). At boreal latitudes, temperature and precipitation are expected to increase especially in late autumn and winter (Andersson 1991, Lloyd & Taylor 1994, Kirschbaum 1995, Harte et al. 1996). This may result in melting of snow during warm periods, and during occasional hard frosts the absence of protective snow cover may lead to low soil temperatures, thus increasing the risk of frost damages (Bleak 1970, Ping 1987, Andersson 1991, Callaghan et al 1998, Heal et al. 1998).

1.3   Soil heterogeneity, decomposers and decomposition

Soil is an extremely heterogeneous environment consisting of mineral particles, organic materials such as litter, patches of different compounds forming the humus, plant roots and a matrix of air and water. Habitat patchiness is known to influence many community, population and ecosystem level processes such as dispersal, predation, population dynamics, stability and regulation of populations, evolution of organisms, and food web organisation (Huffaker 1958, Menge & Sutherland 1976, Horne & Schneider 1995). It is also widely suggested that habitat patchiness increases biodiversity (Simberloff & Wilson 1969, Levin 1977, Levins 1979, Stenseth 1980). This was confirmed by Anderson (1978), who found a correlation between microhabitat diversity and species diversity of cryptostigmatid mites in forest soil. The diversity of decomposer communities may in turn have effects on ecosystem functioning, since soil community structure is known to influence processes such as decomposition and nutrient mineralisation (Verhoef & Brussaard 1990, Huhta et al. 1998).

One of the key factors controlling decomposition rate and microbial production is the ratio of available energy and nutrients, which is influenced both by soil fauna and habitat patchiness (Wardle et al. 1997). Consumption of detritus and modification of its physical structure by soil fauna increase decomposition and mineralisation rates by increasing the surface area of substrate for microbial attack (Verhoef & Brussaard 1990). Habitat patchiness may have a similar effect on decomposition rate. For instance, mixing of different litter types may bring nutrient rich and energy rich materials into contact with each other, thus creating material that has a more suitable energy/nutrient ratio for efficient decomposition (Seastedt 1984). However, experiments support this hypothesis only partially (Chapman et al. 1988, Blair et al. 1990, McTiernan 1997, Wardle et al. 1997).

Depending on the scale of patchiness, the impact of patchiness on decomposition processes may be modified by various soil organisms. For example, fungi can reduce the effect of habitat patchiness by transferring nutrients from nutrient rich sites to nutrient poor sites (Dowding 1976, Jennings 1976). On the other hand, soil fauna have a potential to control fungal growth by disrupting the hyphal connections by grazing (Hanlon & Anderson 1979, 1980, Moore et al. 1987, Sjögren 1994, Hedlund & Augustsson 1995). Soil fauna can also directly relocate nutrients by defecation, and transport microbial propagules into fresh substrates (Lussenhop & Wicklow 1984, Lussenhop 1992).

1.4 Aims of the thesis

Effects of soil moisture and temperature on decomposition and decomposer organisms have been the main interest in many experiments. However, most of them have been carried out at temperatures above +5°C, while lower temperatures prevail in boreal forest soil over a considerable part of the year. Moreover, there are only few studies in which the effects of temperature and moisture on decomposers are connected with decomposition and mineralisation rates. As a consequence of global climate change, temperature and precipitation are expected to increase especially in winter, which may result in melting of snow during warm periods, and during occasional hard frosts the absence of protective snow cover may lead to low soil temperatures. Although this phenomenon is apparent, effects of hard frost disturbance on soil system functioning have been disregarded in experiments assessing the effects of climate change on soils. In this thesis, I have aimed at linking soil microclimatic conditions and system functioning in four experiments (I, II, III a and b).

The question of habitat heterogeneity and its interplay with populations, communities and ecosystem processes is an important topic in modern ecology, with the main emphasis on the impact of habitat patchiness on species diversity and dynamics of populations (Hassell 1980, Addicot et al. 1987, Kotliar & Wiens 1990, Bell et al. 1993, Li & Reynolds 1995, Begon et al. 1996). Research and modelling of the effects of heterogeneity have concentrated on population and

community level processes, and have illustrated the problem from various points. However, connections between heterogeneity and ecosystem functioning are still very poorly understood, and more studies in this field are clearly needed (Dutilleul & Legendre 1993, Li & Reynolds 1995). Two experiments in this thesis (IV and V) were aimed at testing the effects of soil heterogeneity on decomposer communities, decomposition and carbon balance in miniecosystems.

2   METHODS

2.1   Decomposition and soil fauna in relation to temperature and moisture

2.1.1 Laboratory experiments (I-IIIa)

The effects of temperature and moisture on decomposer community and soil processes were studied in three microcosm experiments and in one field experiment. Experiments IIIa and b aimed to test the impacts of hard frost and freeze-thaw cycles. In the experiment I, microcosms were plastic (volume 2.3 l) and in the experiments II and IIIa glass jars (volume 0.4 l and 0.7 l, respectively). The substrate in the microcosms was defaunated coniferous forest humus. Experiment I contained also a litter layer of Norway spruce (*Picea abies*) needles and silver birch (*Betula pendula*) leaves. To ensure the presence of a diverse microbial community, bacteria, fungi and protozoa were re-inoculated into all microcosms using filtered water suspension of forest humus.

Experiment I had two faunal treatments, "simple" soil fauna (microbiota, nematodes, tardigrades and enchytraeids) and "complex" soil fauna (previous groups together with microarthropods). In experiment II, the faunal treatments were: (1) Enchytraeids (*Cognettia sphagnetorum* Vejd) alone, (2) enchytraeids with *Folsomia candida* (Willem) (Collembola), (3) enchytraeids with a mixed microarthropod community extracted from field samples, (4) *Folsomia* alone, (5) mixed microarthropods without enchytraeids, and (6) enchytraeids with predatory mites (Mesostigmata: Parasitinae). In experiment IIIa, the "simple" community included microbiota, nematodes and tardigrades, and the "complex" community these groups together with enchytraeids and microarthropods. The fauna in each experiment were extracted from coniferous forest soil, except *Folsomia candida* which was obtained from a laboratory culture (experiment II).

Microcosms were destructively sampled in each experiment; samples were used for extracting nematodes, enchytraeids (wet funnel methods) and microarthropods (high gradient extractor), and for measuring pH, NH_4-N (2 M KCl-extraction, SFS standard 3032), and microbial biomass (the SIR method, Anderson and Domsch 1978, Nordgren 1988). In experiment I, subsamples were taken three times before the final destructive sampling. The animals were counted, and microarthropods were identified to a taxonomic resolution that was possible using a dissecting microscope. Animal biomasses were estimated according to Abrahamsen (1973) for enchytraeids and Luxton (1975) for identified oribatids. Average individual weights counted from Huhta et al. (1986) were applied for other mites, Collembola and Nematoda.

In experiment I, evolution of CO_2 was measured eight times; aeration holes in microcosm lids were first sealed and air samples were taken with a syringe before and after ca. 2-h incubation. Air samples were analysed using an infrared CO_2 analyzer (Universal Carbon Analyzer EQ 92). In experiment IIIa, evolution of CO_2 was measured four times using the same method.

2.1.2 Field experiment (IIIb)

The field experiment was designed to test the impacts of hard frost on decomposer community and N-mineralisation. The study site was a silviculturally managed pine (*Pinus sylvestris*) stand. Ten test plots (2.2 x 3.1 m) were randomly chosen in a homogeneous area of 60 x 60 m. Five of the plots were equipped with plastic roofs aimed to prevent snow to cover the ground, resulting in low soil and litter temperature during frost periods. The study plots were sampled four times during one year, i.e. in the autumn before snowfall, in the winter after severe frosts, in the spring after snowmelt, and in the second autumn. Microbial biomass, populations of soil fauna, pH and mineral nitrogen were assayed (methods as before).

2.2 Patchiness (IV-V)

The impact of patchiness of the litter layer on decomposer communities and decomposition rate, and, on the other hand, the impact of soil fauna on decomposition processes in relation to patchiness, were studied in experiments IV and V. Experiment V also aimed to find out how the community structure affects the carbon balance of miniecosystems, and whether habitat patchiness modifies the influence of soil fauna on plant growth and carbon dynamics.

Experiments IV and V were carried out in 6.8-l acrylic cylinders with defaunated forest humus. Four types of litter, i.e. silver birch (*Betula pendula*) leaves, alder (*Alnus incana*) leaves, Norway spruce (*Picea abies*) needles and rotten conifer wood, were cut in pieces, defaunated and placed in the containers either in four separate patches or mixed with each other in one patch. In

experiment V, a birch (*Betula pendula*) seedling was planted in the centre of each microcosm.

The experiments contained two different community structures; the "simple" community included microbiota, nematodes and tardigrades, and the "complex" one included these groups together with enchytraeids and microarthropods. The containers were equipped with airtight lids and tubing for air circulation. Air was compressed at a constant rate through each microcosm, and the outflow tubes were connected to an automatic carbon analyzer (Universal Carbon Analyzer EQ 92) for recording the CO_2 concentration every 3 hours. The microcosms were destructively sampled after 15 (exp. IV) or 45 weeks (exp. V), the decomposer communities were analysed, and pH and mineral nitrogen contents were measured separately from each substrate.

2.3   Comments on methodology

The microcosm technique has several advantages but also drawbacks in studies of ecosystem-level processes such as decomposition rate and nutrient dynamics. Microcosms are compact and can be tightly sealed, enabling exact measurement of carbon and nutrient balances as well as soil animal populations. However, species diversity is often low in microcosms in comparison with diversity in the field and tends to further decrease during incubation, while in the field locally extinct populations recover due to colonisation from the surroundings (refuges are hardly available for species living in microcosms). Also, the spatial scale of the microcosms tends to be too small for dispersal of some large collembolas and mesostigmatid mites, while the dispersal rate of most soil fauna is quite slow (Berthét 1964, Sjögren 1994, Sjögren et al. 1995, Salminen & Sulkava 1996). Notwithstanding these, the major interspecific interactions such as resource competition and predation take place in microcosms, and feedback's between population dynamics, community structure and decomposition processes occur as they do in the field. Thus, it is justified to study these processes in "miniecosystems" (see Verhoef 1996).

As soil heterogeneity and patchiness is a central topic in my experiments, reference should be made to various definitions of patchiness (see Addicot et al. 1987, Kotliar & Wiens 1990). Another concern is the scale; natural soil environment is heterogeneous at all possible scales ranging from millimetres up to kilometres. Moreover, Levin (1974) noted that habitat patchiness is not only a matrix of physical patches, but colonisation patterns, species interactions and dispersion abilities create patches of populations, which may further create physiological patches. Thus, patchiness of soil is not a stable situation but rather a dynamic process. The size of laboratory facilities sets limits to the scale in which experiments can be conducted. Microcosms of 17 cm in diameter and litter patches of a few centimetres were chosen to represent patchiness of the forest floor and to fit in the climate chambers available for the experiments. This scale can be considered reasonable from the viewpoint of hyphal growth and

horizontal movements of edaphic animals (Sjögren 1994, Salminen & Sulkava 1996, 1997).

Global climate change increases air temperatures, and its effects on the soil system have usually been studied by artificially warming the soil (Kennedy 1994, Coulson et al. 1996, Harte et al. 1995, 1996, Kandeler et al. 1998). However, as temperature and precipitation are expected to increase especially in late autumn and winter, snow may first melt during warm periods, and during occasional hard frosts the absence of protective snow cover may then lead to low soil temperatures and disturb the soil system (Bleak 1970, Ping 1987, Andersson 1991, Callaghan et al 1998, Heal et al. 1998). In this study (IIIb), soil plots were equipped with plastic roofs that prevented snow from covering the ground, resulting in low soil and litter temperatures during frost periods. The test plots were irrigated to prevent drying of the soil. Similarly, the effects of hard frost and freeze-thaw cycles on soil fauna and soil processes were tested in microcosms (IIIa). Thus my experiments approached the global change problem from a less studied viewpoint (see Andersson 1991, Lloyd & Taylor 1994, Kirschbaum 1995, Harte et al. 1996). Moreover, as the effects of moisture and temperature on the soil processes in summer were assessed in experiments I and II, my thesis deals with the effects of global climate change covering the whole year.

3   RESULTS AND DISCUSSION

3.1   Effects of temperature and moisture on soil communities, decomposition and mineralisation

Decomposition and mineralisation processes are regulated by substrate quality, soil microclimate and decomposer community structure (Swift et al. 1979). Low temperature in winter and low moisture in summer retard the activity of soil organisms and decrease decomposition rate virtually for most of the year. It is commonly assumed that both microbes and soil fauna respond to the changes in temperature and moisture equally and in a predictable way. However, this thesis revealed complex interactions between physical conditions and faunal community structure in relation to decomposition and mineralisation (I, II). Enchytraeid populations increased with increasing temperature and moisture, confirming the results of Abrahamsen (1971), whereas microarthropods were affected by temperature only, and microbial biomass decreased with rising temperature. The abundance of nematodes was highest at intermediate moisture and on average increased with increasing temperature. It appears that the effects of microclimate on microbes and soil fauna do not follow consistent lines, and as a result, the effects on decomposition are less predictable than assumed by simple models.

The presence of microarthropods reduced the populations of nematodes and enchytraeids at low and intermediate moisture, as well as net N mineralisation at each temperature (+2, +6, +15°C) in experiment I. Large gamasids feed on enchytraeids (Karg, 1971) at least occasionally, but the regulative effect was probably not explained by predation, since gamasids had no effect on *Cognettia* population (II). On the other hand, enchytraeids did not affect microarthropods at any moisture level (40, 53, 62 % WHC). Thus, competitive interactions probably explain the control of enchytraeids by microarthropods. Microarthropods are rather indifferent to changes in soil moisture level (Vannier 1970), and they can control enchytraeids during dry

periods when the latter are stressed by water deficit (Abrahamsen 1971). Thus, the interaction between microarthropods and enchytraeids appears to be complex, but still seems to be capable of influencing ecosystem-level processes.

Effects of soil microclimatic conditions on soil fauna were reflected in nitrogen mineralisation (I). The amount of mineral N correlated strongly with enchytraeid biomass and was indifferent to microarthropod biomass. Thus, enchytraeids seem to be more effective in promoting mineralisation than microarthropods (see also Setälä et al. 1991). Supporting this, microarthropods have been found to reduce N mineralisation in some experiments (see Faber & Verhoef 1991). However, the diverse community of microarthropods seemed to be able to affect N mineralisation indirectly by regulating enchytraeid populations in dry and intermediately moist soil, even though at high moisture content this control was not observed.

3.2 Global climate change and decomposition

The influence of soil microclimate on mineralisation has often been described to be stable and predictable. The concept of increasing soil respiration and N mineralisation with increasing moisture and temperature is widely accepted (Billings et al. 1982, Billings et al. 1983, Schlentner & Van Cleve 1985, Peterjohn et al. 1993, Goncalves & Carlyle 1994, Kirschbaum 1995). However, this thesis indicates that the impacts of soil temperature and moisture on C and N mineralisation are in complex interaction with the decomposer community structure (I, II). Changed abiotic conditions may interfere with the effect of decomposers on mineralisation. According to Lloyd and Taylor (1994), Kirschbaum (1995) and Harte et al. (1996), the effects of increasing temperature on CO_2 evolution and N mineralisation are stronger in areas of low than in high mean annual temperature. Thus, the effects of global climate change on soil microclimate may significantly affect the interactions between soil faunal groups especially at boreal latitudes.

At the boreal latitudes, global climate chance is expected to increase temperatures especially during winter, and will therefore probably decrease the thickness of snow cover in winter. Thaw periods may result in melting of snow and during occasional hard frosts the temperature in the surface soil may strongly decrease. In the field experiment (IIIb), hard frost (-27°C) caused severe disturbances in snowfree test plots: enchytraeid biomass and the abundance and species richness of microarthropods decreased strongly. Similarly, virtually all enchytraeids died in the microcosms, and microarthropod abundance and species richness decreased in the hard frost treatment. During freeze-thaw cycles the numbers of microarthropods increased. As the soil fauna may affect the decomposition and mineralisation rates and decrease in enchytraeid populations may have remarkable effects on decomposition and N-mineralisation (I, II), exceptional temperature conditions may evidently disturb the decomposer community and soil processes (see also Bleak 1970, Andersson 1991). However, the recovery of enchytraeid and many Oribatid mite

populations appeared to be fast, and the effects on populations and possibly on N-mineralisation remained temporary.

Global climate change may cause unpredictable changes in the decomposer community also in the summer. Soil moisture may increase or decrease during summer and expected warming has been reported to enhance or reduce soil animal populations and microbial biomass during summer (Kennedy 1994, Coulson et al. 1996, Harte et al. 1996, Kandeler et al. 1998). Moreover, as the experiments I and II revealed, interactions between soil moisture, temperature, decomposer organisms and soil processes are not straightforward. In earlier studies, soil respiration and N mineralisation have been reported to increase with increasing moisture and temperature (Billings et al. 1982, Schlentner & Van Cleve 1985, Goncalves & Carlyle 1994, Kirschbaum 1995, Leiros et al. 1999, Niklinska et al. 1999, Panikov 1999), and the models forecasting the effects of climate change on soil processes ignore the possible disturbances on the decomposer community. This study revealed that exceptional weather conditions in winter exert a stronger disturbance on soil animal populations, biomass and community structure than normal winter conditions with constant temperatures. Thus, the effects of global climate change on soil temperature during winter may disturb decomposers and further reduce mineralisation.

3.3 Habitat patchiness, soil fauna and decomposition

Habitat patchiness is generally assumed to enhance biodiversity (Simberloff & Wilson 1969, Levin 1977, Levins 1979, Schulze & Mooney 1994, Naeem et al. 1995, Lavelle 1996, Kerr & Packer 1997, Ekschmitt & Griffiths 1998). The reasoning behind this assumption is that more species should find suitable resources and abiotic conditions in a heterogeneous than in a homogeneous environment (Simberloff 1976). Supporting this, Anderson (1978) found a correlation between microhabitat diversity and species diversity of cryptostigmatid mites in forest soil. The present study also showed that a higher number of microarthropod taxa survived in a patchy litter layer than in a single patch with mixed litter (IV). However, the higher species richness in patchy litter was not reflected in the humus, and in the microcosms with birch seedlings no differences were found in species richness between mixed and patchy litters (V). As a whole, species diversity was maintained better in microcosms with plants (V) than in microcosms without them (IV). Similarly, mixed litter harboured more enchytraeids than the patchy one, while no difference was found in humus (IV). At the end of the experiment V, enchytraeid numbers differed little between mixed and separate litters. The explanation may either be the homogenising effect of roots and mosses, or then the ageing of litter materials had diminished the differences between the litter patches.

In experiment IV, CO_2-production was higher in microcosms with patchy litter than in microcosms with mixed litter in the absence of soil fauna, but

lower when fauna was present. The amount of NH_4^+-N was also higher in mixed litter than in patchy litter in the presence of fauna (IV, V). These observations do not support the hypothesis of Seasted (1984) that mixing of nutrient rich and energy rich materials should decrease the probability of local shortage of either energy or nutrients that could suppress decomposing processes (see Chapman et al. 1988, Blair et al. 1990 and Wardle et al. 1997). Supposedly, in a patchy litter layer soil fungi can create hyphal connections between different materials located some centimetres apart, thus enhancing the decomposition, while in mixed litter the scale of millimetres is more appropriate for the movement of soil fauna between patches.

The effect of soil fauna on decomposition was clearly greater in the mixed litter systems than in the patchy systems. The explanation may be the different roles of fungi and fungivorous invertebrates in decomposition and mineralisation, at the scale of the experimental design. Fungivorous soil fauna may disrupt hyphal connections between patches by grazing, thus reducing the decomposition rate (see Lussenhop 1992).

In the microcosms with plants and soil fauna, carbon balance approached the initial level by the end of the experiment (V), apparently due to the positive effects of soil fauna on plant growth and carbon assimilation (Setälä et al. 1990, Setälä & Huhta 1991, Haimi et al. 1992, Laakso & Setälä 1999), which compensated for the stimulating effect of fauna on the release of CO_2 from the soil (IV) (see Setälä & Huhta 1990). During the first growing period the effects of soil fauna and patch treatments on carbon dynamics were similar in the experiments with and without plants. Later on, the effect of patchiness on CO_2 dynamics disappeared in experiment V, whereas the enhancing effect of soil fauna persisted. The weak impact of patchiness in comparison to the faunal effect may be due to homogenising role of plant roots and progressing decay of the substrates. Thus it seems that in the long term, patchiness did not modify the effect of fauna on plant growth or carbon balance. That no faunal effect on the concentration of mineral N was observed is probably because the plants had assimilated most of available nutrients, particularly from the humus (see Setälä & Huhta 1991, Laakso & Setälä 1999).

4   CONCLUSIONS

This study shows that the enchytraeid *Cognettia sphagnetorum* is one of the most important decomposer species in coniferous forest soil, but also one of the most sensitive to competition and changes in microclimatic conditions. Enchytraeid biomass and N-mineralisation seem to be closely linked in coniferous forest soil, and a diverse community of microarthropods have capability of indirectly affecting N mineralisation by regulating enchytraeid populations in dry and intermediately moist soil. Global climate change evidently affects soil moisture and temperature throughout the year. During summer, increasing temperature and evaporation tend to dry up the soil environment, and thus the regulation of enchytraeid populations by microarthropods may deepen the summer minimum of decomposition. On the other hand, higher soil moisture and prolongation of the freeze-thaw season in autumn and spring may enhance decomposition. The results of the present experiments also show that exceptional temperatures during winter severely disturb enchytraeid and microarthropod populations. As other soil fauna seems to be able to regulate enchytraeid populations, which have notable effects on decomposition and N-mineralisation (I, II), exceptional temperature conditions evidently can disturb the decomposer communities and retard the soil processes. Based on these results, I suggest that the effects of global climate change on decomposition and even on soil carbon pools should not be predicted using simple models, but more effort should be focused on assessing the effects of climatic conditions on decomposer communities and soil processes.

This study also shows that patchy litter layer maintains the species diversity of microarthropods better than a more homogeneous environment. It also seems that soil heterogeneity exerts great but complex effects on soil processes. For instance, the effect of soil fauna on decomposition was clearly greater in the mixed litter systems than in the patchy systems. Similarly, CO_2-production differed between microcosms with patchy and mixed litter, although the presence of soil fauna clearly modified the effect of litter mixing on CO_2-production. Even if the presence of plants seems to reduce the effects of patchiness on decomposer community and decomposition, soil heterogeneity should not be ignored when studying the interactions between decomposer

community structure and soil processes.

Soil heterogeneity and different microclimatic conditions evidently result in changes in decomposer food webs and soil processes. However, many of the impacts may be temporary and it seems that the structure of forest soil is continuously changing, very much like the soil system functioning. Thus, generalisations of microcosm experiments should be applied to the field conditions with special care. It also seems that the continuum of soil heterogeneity together with changing microclimatic conditions provide challenging tasks for scientists assessing the functioning of ecosystems.

YHTEENVETO

Maaperän eliöyhteisön ja hajotusprosessien väliset vuorovaikutukset suhteessa mikroilmastoon ja laikuttaisuuteen

Väitöskirjatyössäni pyrin selvittämään lämpötilan ja kosteuden sekä maaperän heterogeenisuuden vaikutusta hajottajaeliöstöön, hajottajien välisiin vuorovaikutuksiin sekä hiilen ja typen mineralisaatioon. Lisäksi selvitettävänä oli miten poikkeukselliset talvilämpötilat (kova pakkanen ja jäätymis-sulamissyklit) vaikuttavat maaperäeläimiin ja mahdollisesti edelleen mineralisaatioon. Tutkimus käsittää viisi koetta laboratoriossa ja yhden kokeen maastossa. Laboratorion koeastioissa oli kangasmetsän humusta ja kariketta, joista maaperäeläimet oli eliminoitu. Näihin mikrokosmoksiin koottiin kokeen tarkoituksesta riippuen erilaisia hajottajayhteisöjä mikrobeista ja maaperäeläimistä, jotka oli eroteltu elävinä maanäytteistä (yhdessä kokeessa käytettiin myös laboratoriokasvatuksesta saatuja hyppyhäntäisiä). Heterogeenisuuden vaikutusten tutkimiseksi mikrokosmoksiin laitettiin neljää erilaista kariketta joko erillisinä laikkuina tai sama määrä sekoitettuna yhteen suureen laikkuun. Yhdessä kokeessa miniekosysteemiin istutettiin myös rauduskoivun taimia. Mikrokosmoksia pidettiin erilaisissa kosteuksissa ja lämpötiloissa koeasetelman mukaisesti. Maastokokeessa koeruutujen ylle tehtiin katokset estämään lunta peittämästä maata ja siten suojaamasta sitä talven pakkasilta. Koeruutujen humuksen hajottajaeliöyhteisöä ja mineralisaatiota verrattiin luonnolliseen lumen peittämään humukseen.

Kosteuden ja lämpötilan vaikutukset maaperäeliöihin, eri eläinryhmien välisiin vuorovaikutuksiin sekä edelleen hajotukseen ja mineralisaatioon olivat monimutkaiset. Mikroniveljalkaiset (punkit ja hyppyhäntäiset) kontrolloivat kangasmetsän maaperän tärkeimmän yksittäisen hajottajaeläinlajin änkyrimadon (*Cognettia sphagnetorum*) populaatiota riittävän kuivassa maassa hidastaen siten typen mineralisaatiota. Märässä maassa änkyrimato pysyi runsaana ja lisäsi typen mineralisaatiota. Poikkeuksellisen alhaiset talvilämpötilat ilman lumen suojaa olevissa koeruuduissa sekä laboratoriokokeissa romahduttivat änkyrimatopopulaation ja vähensivät mikroniveljalkaisten laji- ja yksilömääriä. Jäätymis-sulamissyklin aikana sensijaan mikroniveljalkaisten määrä kasvoi. Hajottajayhteisössä tapahtuneiden muutosten vaikutus typen mineralisaatioon oli kuitenkin lyhytaikainen.

Laikuttaisessa karikkeessa säilyi monilajisempi mikroniveljalkaisyhteisö kuin homogeenisessa. Maaperäeläinten vaikutus hajotukseen oli laikuttaisessa systeemissä heikompi kuin sekoitetussa, mutta kokonaisuutena laikuttaisuuden, hajottajaeliöstön rakenteen ja hajotuksen välinen suhde oli hyvin monimutkainen. Osaksi tämä johtunee ennakoimattomista vuorovaikutuksista maaperäeläinten ja sienten välillä. Monet maaperäeläimet syövät sienirihmastoa, ja niiden katkaistessa sienten yhteydet ravinne- ja energiarikkaiden laikkujen välillä eläimet saattavat hidastaa hajotusta. Kasvillisissa mikrokosmoksissa hiilitase palautui lopulta alkutasoon, kun mukana oli monimuotoinen eläinyhteisö. Maaperäeläinten positiiviset vaikutukset kasvin kasvuun voivat siten

kompensoida yleensä havaitun maaperäeläinten aikaansaaman hajotusaktiivi-suuden lisääntymisen ekosysteemitasolla. Kasvien juuristo sekoittaa laikuttai-suutta, ja siten laikuttaisuuden vaikutukset hajottajiin ja mineralisaatioon voivat hävitä ajan myötä, ts. laikuttaisuuden vaikutus tietyllä paikalla on lyhytaikaista.

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I

Impact of soil faunal structure on decomposition and N-mineralisation in relation to temperature and moisture in forest soil.

by

Pekka Sulkava, Veikko Huhta and Jouni Laakso 1996

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II

Interactions between enchytraeid (Cognettia sphagnetorum), microarthropod and nematode populations in forest soil at different moistures

by

Veikko Huhta, Pekka Sulkava and Katja Viberg 1998

Applied Soil Ecology 9: 53-58

III

Effects of hard frost and freeze-thaw cycles on decomposer communities and N mineralisation in boreal forest soil

by

Pekka Sulkava and Veikko Huhta

Manuscript (submitted)

IV

Habitat patchiness affects decomposition and faunal diversity: a
microcosm experiment on forest floor

by

Pekka Sulkava and Veikko Huhta 1998

Oecologia 116: 390-396

V

Influence of soil fauna and habitat patchiness on plant (*Betula pendula*) growth and carbon dynamics in a microcosm experiment

by

Pekka Sulkava, Veikko Huhta, Jouni Laakso and Eeva-Riitta Gylén
2001

Oecologia 129: 133-138