Effects of Wildfire and Prescribed Burning on Soil Fauna in Boreal Coniferous Forests

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Abstract

Fire is considered as the most important disturbance agent in many ecosystems. In northern Europe, fire suppression is today highly effective. This has led to a reduction of species that are dependent on fire for their long-term survival. Above ground positive responses of animal diversity to fire are common, whereas the knowledge of the responses of soil fauna to fire is fairly poor. The main aim of this thesis was to determine effects of wildfire and prescribed burning on survival and recovery of soil mesofauna. Other aims were to determine the effects of fire severity and, of distance to unburnt plots on recovery rates, and to estimate the lethal temperatures of common species.

Two wildfires and two prescribed burns were studied for three to five years. In the wildfires, soil fauna was studied in transects from the unburnt forest to the fire centre. The two prescribed burns had different experimental design, one block experiment (burnt clear-cut, unburnt clear-cut and forest) and one experiment in which fire severity was manipulated by addition of different amounts of felling residues.

All soil fauna species responded with decreased abundances one week after burning. This decline can partly be explained by high temperatures, because most microarthropod species cannot survive temperatures above 36-40 °C, which can be reached several centimetres below the charred soil surface. Long-term recovery rates differed between soil fauna groups and between different fire severities. In fires with light severity, total abundance of Collembola and, in one case, Mesostigmata, recovered within one year. In fires with moderate to strong severity, almost all animal groups needed more than five years to recover as regards abundance and species number. Surface-living species were more affected by fire than species living deeper in the soil. Only a few species had significantly higher abundances 3-5 years after moderate/strong burning, whereas most species studied had recovered 5 years after light burning. Consequently, fire severity (burn depth) seems to be a decisive factor explaining survival and recovery rate of soil mesofauna, and this factor should be considered when fire effects on soil organisms are evaluated in forthcoming studies.

Keywords: Collembola, Protura, Oribatida, Mesostigmata, Enchytraeidae, disturbance, fire, fire severity, recovery, soil fauna diversity.

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Till Patrik, Axel och Lillsprattel!

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Appendix

Papers I-IV

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

I. Malmström, A., Persson, T., Ahlström, K., Gongalsky, K. & Bengtsson, J. Dynamics of soil meso-and macrofauna during a 5-year period after clear-cutting and clear-cut burning in a boreal forest. (Manuscript).

II. Malmström, A. Soil fauna recovery after wildfire – effects of fire severity and distance to unburnt forests. (Manuscript).

III. Malmström, A., Persson, T. & Ahlström, K. Effects of fire intensity on survival and recovery of soil mesofauna after a clear-cut burning. (Manuscript).

IV. Malmström, A. Temperature tolerance in soil microarthropods. Simulation of forest-fire heating in the laboratory. (Manuscript).

Introduction

Background

Disturbance

Begon, Harper and Townsend (1990) define disturbance as "any relatively discrete event in time that removes organisms and open up space which can be colonised by individuals of the same or different species". Traditionally, undisturbed ecosystems were supposed to develop towards stable "climax" systems (Clements, 1936; Odum, 1969). Today, natural disturbances are viewed as integral parts of ecosystems and essential for their dynamics. A recent view of disturbances as parts of ecosystems is "the ecosystem renewal cycle" (Holling *et al.,* 1995; Peterson, Allen & Holling,1998; Bengtsson *et al*., 2000). According to this theory, ecosystems pass through four phases. The first two are equivalent with the classical succession theory, namely the exploitation (1) and conservation (2) phases. The two "new" phases are called the release or disturbance phase (3), in which the climax is broken down, and the reorganisation phase (4) during which the community reorganises. Biodiversity is very important during the succession and reorganisation phases, because a high number of species means that there are many species that can recolonise the disturbed area and make sure that the cycle continues (Bengtsson 2002).

Natural disturbances create a heterogeneous landscape and consequently they also create new niches. As they are a natural part of the ecosystem dynamics, most species are adapted to either survive disturbances, or to recolonise the disturbed area (Bengtsson 2002). Some disturbances are synchronized, or phased, over big areas. A forest fire may, e.g., destroy a wide area of a climax community. The whole area then proceeds through a more or less synchronized succession, with diversity increasing through the early colonization phase and falling again through competitive exclusion as the climax is approached. Other disturbances are much smaller and lead to a patchwork of habitats. If those disturbances are unphased, the result will be a mosaic of patches at different stages of succession. A climax mosaic like this is much more diverse in species than a big area undisturbed for a long time and occupied by just a few dominant climax species (Begon, Harper & Townsend, 1990). The intermediate disturbance hypothesis suggests that diversity is highest when disturbances have an intermediate frequency (Begon, Harper & Townsend, 1990). Natural disturbances tend to occur as pulses followed by a regeneration phase. Disturbances can be characterised by their frequency, duration, size or spatial extent, and their intensity or severity. Usually they have characteristic temporal and spatial scales (Holling *et al*., 1995).

Fires are considered the most important disturbance agent in many ecosystems including forest (Jonson, 1992, Granström, 2001), Australian woodlands (Hobbs & Atkins, 1990), grasslands (Hartnett, 1991; Pyne, Andrews & Laven, 1996), savannas (Swaine, 1992), and Mediterranean systems (Liacos, 1977; Ferreira de Almeida & Vilaca y Moura, 1992). In Swedish boreal forests, fires used to occur in intervals of 50-200 years before fire suppression started in the 19th century (Zackrisson, 1977; Engelmark, 1984).

Today, fire suppression in Fennoscandia is so effective that the amount of burnt substrate has decreased tremendously (Granström, 2001). This has lead to a decrease of species that are dependent on fire for their long-term survival, either directly (so called pyrophilous species) or indirectly by being favoured by the disturbance. Many of the fire-dependent species are considered threatened and are included in the national Red List (Gärdenfors, 2005). In order to maintain these species, prescribed burning for conservational reasons are becoming more common (Hörnsten, Nohlgren & Aldentun, 1995; Granström, 2001). To be able to manage biodiversity with prescribed burns, knowledge about the wildfires these try to mimic is needed. It is therefore important that we understand community responses to natural fires, as well as if these responses are similar to prescribed burns.

Prescribed burning

Pyne, Andrews and Laven (1996) defined wildfires as fires ignited by lightning and other natural causes or unintentionally by human actions. A prescribed fire is a fire burning with certain prescriptions resulting from planned ignition (DeBano, Neary & Ffolliott, 1998).

In some places, mainly in the USA and in the Mediterranean region, prescribed burning is used to control the accumulation of woody debris (Meffe & Carroll, 1994). In Scandinavia, prescribed burning of clear-cuts is an old forest regeneration method (Hörnsten, Nohlgren & Aldentun, 1995). This method is especially used in places with thick raw humus layer in order to improve the quality of the soil and to uncover it for the seedlings. Today, prescribed burning is not very common, and when it occurs small areas are normally burnt. Forest companies in northern and central Sweden are scheduled for about 4000 hectares of prescribed burning per year (5% of the cut area on dry and mesic forest land, averaged over a five-year period) (Granström, 2001). This type of burning aims at restoring habitats for animals and plants, provide good grazing for animals, and to keep an open landscape (Hörnsten, Nohlgren & Aldentun, 1995).

Naturally occurring wildfires differ in many ways from prescribed burning. Lightning ignitions are rare in the boreal region (0.05-0.25 per 10,000 ha per year), they peak in late June and early July and they tend to occur after prolonged drought (Granström, 2001). As a consequence, they tend to burn deeply into organic soil layers and not differentiate between forest types (Granström, 2001). Anthropogenic fires have, on average, occurred earlier in the season and during less severe drought than natural fires. A prescribed fire is normally designed to burn less hard than a wildfire. Severities of prescribed fires are usually low to moderate. Low severity fires normally burn the ground cover and spread to the herbaceous plants, while leaves, stems and tops of the trees are left largely unburnt (DeBano, Neary & Ffolliott, 1998). Wildfires can be much harder and more intense. The result is often more heterogeneous because some areas burn twice and some not at all. In this mosaic, a lot of dead or dying wood will appear.

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Fire effects on organisms

Burning normally reduces the number of organisms on a short-term basis, and fire severity measured as depth of burn seems to be an important factor affecting soil living organisms. Burning has been shown to reduce mycorrhiza (Dahlberg *et al.,* 2001), and species richness was reduced with increasing fire severity. Fire intensity directly controls the survival of all above-ground vegetation (Schimmel, 1993), while depth of burn is more important to the survival of the understorey vegetation (Schimmel & Granström, 1996). Generally, the mortality of ground-living arthropods seems directly related to the combustion of the litter and organic soil during the fire (Bellido, 1987). The number of invertebrates generally decreases after fire (Lyon *et al.,* 1978; Muona & Rutanen, 1994; Wikars, 1995; Saint-Germain *et al.*, 2005; Buddle *et al.,* 2006). Either the animals or their eggs are directly killed by the flames or by heat of the fire, or their food and shelter may be destroyed (Lyon *et al.,* 1978).

The majority of the pyrophilus species in the boreal forest is insects and fungi (Esseen *et al.*, 1997). Certain fungal species have been referred to as post-fire fungi, and are producing sporocarps almost exclusively in post-fire environments (Wikars, 2001). Ascomycetes are favoured over Basidomycetes. Pyrophilous insects can be dependent on substrates created by fire such as burnt wood (Wikars, 2001). Species could also have become behaviorally tied to fires as a means of mate finding (Wikars, 1992). They can also be adapted to burnt forest due to warmer microclimate and reduced competition (Wikars, 2001). Pyrophilous organisms in the boreal forest must have been under extreme selection for dispersal in time or space, since large distances between burns was typical in the past (Granström, 2001). Fire-dependent plant species, which rely on seed- or spore-banks, would need to have long-lived propagules that can survive between fires (Granström, 2001).

Fire effects on soil organisms

Most of the studies made on how biodiversity is affected by forest fires concern plants (Zackrisson, 1977; Schimmel, 1993; Schimmel & Granström, 1996; Linder, Jonsson & Niklasson, 1998) and beetles (Lyon *et al.,* 1978; Muona & Rutanen, 1994; Wikars, 1995; Saint-Germain *et al.,* 2005). A huge part of the organisms in the boreal forest is, however, living below ground. The soil is considered to contain one of the most diverse assemblages of living organisms (Giller, 1996).

Earlier studies have shown that fire usually reduces the total abundances of soil animals (Heyward & Tissot , 1936; Pearse, 1943; Karppinen, 1957; Huhta *et al*., 1967; Huhta, Nurminen & Valpas, 1969; Metz & Farrier, 1973; Metz & Dindal, 1975; Lucarotti, 1981; Tamm, 1986; Koponen, 1989; Koponen , 1995; Broza & Izhaki, 1997; McCullogh, Werner & Neumann, 1998; Wikars & Schimmel, 2001).

The duration of the fire effect and the recovery rate of the soil fauna community after a fire is, however, poorly understood. Huhta *et al.* (1967, 1969) found that collembolans recovered already during the second year after burning in a coniferous forest soil in Finland. Enchytraeids and oribatid mites did not recover in abundance in six years, while other Acarina than oribatid mites reached

numbers higher than in the control, the third year after fire. Broza and Izhaki (1997) found that the microarthropod community in forest soils in Israel did not recover during five years. Koponen (1995) could not see any dramatic effect on microarthropod numbers after fire in a subarctic birch forest in Finnish Lapland, although the numbers on the burnt sites were always lower than in the control. Lucarotti (1981) investigated a chronosequence of lichen woodland soils of different ages after burning. He found higher numbers of Collembola at the site that had burnt 4 years ago than at the control site that had not burnt in 137 years. The mites also started to increase at the 4-year-old site.

None of the previously mentioned studies tried to determine recovery at the species level. Total abundances have been shown to be an insufficient measure of recovery (Lindberg & Bengtsson, 2006). Karppinen (1957) is an exception in studying the recovery of individual oribatid species in a fire field in Finland. Haimi, Fritze and Moilanen (2000) found a clear difference in the community structure of collembolans because of ash addition and fire, but not in total abundances. This clearly shows the importance of a high resolution to detect changes in communities after a disturbance.

Generally, the mortality of ground-living arthropods seems to be directly related to the combustion of the litter and organic soil during the fire (Bellido, 1987). In spite of this, only a few studies take fire severity into account (Bellido, 1987; Hening-Sever, Poliakov & Brozoa, 2001; Wikars & Schimmel, 2001). No study has determined the effects of fire severity at the species level or how fire severity affects recovery rates. Other factors that could affect recovery rates are dispersal from unburnt areas but, to my knowledge, no studies have been made on this subject. Most studies are made some time after the fire, often several months. This makes it hard to distinguish between direct effects of fire, like heat or hazardous gases, from indirect effects like post-fire drought or starvation.

Defining fire effects

The lack of clear definitions of variables in fire ecology has been a problem. For example, the terms fire intensity and fire severity are commonly mixed up in the literature. I have based on more recent literature used the following definitions: Fire *frequency* is the number of fires in a specified time and area (DeBano, Neary & Ffolliott, 1998). Fire *interval* is the time between two successive fires in a designated area (DeBano, Neary & Ffolliott, 1998). Fire *intensity* refers to the rate at which a fire is producing thermal energy and can be measured in terms of temperature and heat release (DeBano, Neary & Ffolliott, 1998). Fire *severity* is usually measured as depth of burn and is a term that describes ecosystem response to fire (DeBano, Neary & Ffolliott, 1998). I have chosen to measure fire severity as depth of burn and destruction of the organic soil layer. To classify the fires, I have used the classification categories suggested by Ryan (2002). This classification is easy to use even when actual measures of the humus thickness before and after the fire are not possible, like at wildfire sites.
In this thesis, I have studied recovery rates of soil fauna communities after fire disturbances. In this case, I have chosen to use the term *recovery* when there are no significant differences from the control. That means that when no significant

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differences was found between the fire treatment and the control in some faunal variable measured, I have defined it as recovered.

Aims

The general aim of this thesis was to investigate the effects of fire, both wildfires and prescribed burns, on soil fauna, both on taxonomic groups and individual species. The specific aims were to:

1. Determine soil fauna recovery over time, both as total abundances, abundance of individual species, species numbers, diversity (papers I, II and III) and foodweb structure (paper I).

2. Determine soil fauna recovery over time as affected by distance to unburnt areas (paper II).

3. Determine the effect of fire severity (burn depth) on soil fauna survival (paper III) and recovery (papers II and III).

4. Determine heat sensitivity and lethal temperatures for humus-dwelling soil microarthropods (paper IV).

Material and methods

Sites and treatments

The studies included in this thesis concern two wildfires and three clear-cuts with prescribed burns. The sites used are shown in Fig. 1.

Bjuråker 256

Bjuråker 256 (paper I) is a fire experiment with burnt clear-cut, unburnt clear-cut and uncut forest in two replicated blocks. Bjuråker 256 is located in central Sweden and was a 120-year-old forest consisting mainly of (2/3) of Scots pine *Pinus sylvestris* (L) and (1/3) Norway spruce, *Picea abies* (L) Karst., before clear-felling. The clear-cutting took place in March 1999, and half of the clear-cut was burnt in June the same year. The burning combusted practically all vegetation, harvest residue and litter. On average, 34 (SD=30) mm of the top litter and humus layer was burnt off (Eva Ring, pers. comm.). The 40 mm humus layer was reduced by, on average, 12 (SD=10) mm. The fire was classified as a moderate fire according to Ryan (2002).
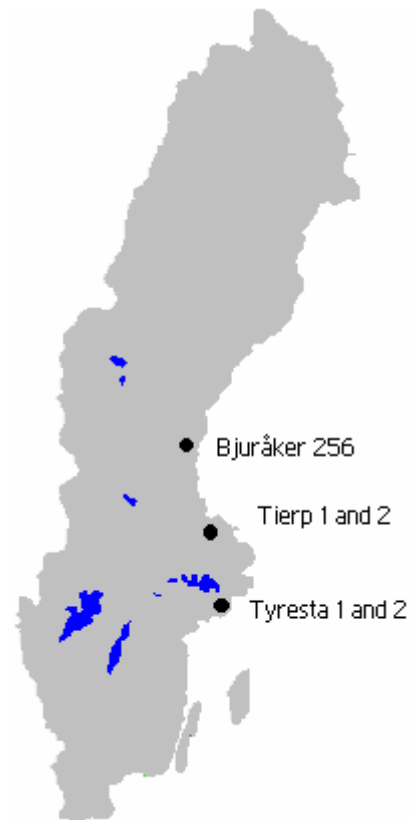
Fig. 1. Map of Sweden with the locations of the field experiments used in this thesis.

Tyresta

Two wildfires, one big and one small, took place in, or close to, Tyresta Natural Park and Nature Reserve situated 20 km south of Stockholm in central Sweden (paper II). The area is heterogeneous because of numerous fissure valleys. A sparse forest of Scots pine and common silver birch (*Betula pendula* Roth) is growing on the rocky outcrops, whereas the wetter mire elements are to a large extent covered by Scots pine and hairy birch (*Betula pubescens* Ehrh.). The pine forest affected by fire was dominated by 150-300 year-old trees and had never been affected by large-scale forestry.

The big wildfire started on 1 August 1999 and continued until August 10. During this time, 450 hectares of pine forest burned. The shallow organic soils on the bedrock were to a large extent burnt away, whereas the peat soils in the moist depressions were reduced, but seldom completely burnt. The fire was classified as a moderate to deep fire according to Ryan (2002). A line transect that represented a gradual increase in distance from forest edge was established, 30 m, 150 m, 300 m (L. Wikars unpublished data). At the end of this transect, two plots with contrasting fire severity were chosen. The light-burnt plot, had lesser burning

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depth than the other plots. The other plot (hard-burnt) was placed in an intensively burnt area affected by crown fires.

The small wildfire (22 hectares) occurred close to the 1999 big fire in 2001. The fire area is situated on a hill just outside the nature reserve. The small fire was not as intense as the big fire. This fire provided an opportunity to take soil samples to study effects of fire on soil microarthropods the first years after a wildfire and also an opportunity to somehow replicate the study of the first fire. The fire was classified as a light fire according to Ryan (2002). Two replicated line transects were placed at a distance of about 200 m from each other. Both transects consisted of three plots, of which one was located in the unburnt forest, one was located in the fire area about 30 m from the forest edge and the third was located in the central part of the area, about 100 m from the forest edge.

Tierp

Two clear-cuts situated outside Tierp in eastcentral Sweden were burnt for conservational reasons by the forest company Stora Enso. The first site (Tierp 1) was used to study the effects of fire severity on survival and recovery of soil fauna (paper III). The second site (Tierp 2) was used to sample individuals used for a laboratory experiment on temperature tolerance of soil microarthropods (paper IV). No unburnt clear-cut was left, but the nearby, unburnt forest was used as a control.

The original tree stand in Tierp 1 consisted of 100-120 year-old Scots pine and Norway spruce. It was clear-cut in early 2001 and was burnt in May 2002. The area was interrupted by shallow depressions with wet soil grown with *Carex* spp. and *Spagnum* mosses. The field vegetation on the clear-cut was dominated by bilberry, *Vaccinium myrtillus* L. and the bottom vegetation consisted mainly of the forest moss *Hylocomium splendens* (Hedw.) B.S.G. To study the effect of fire severity, hard-burnt plots and light-burnt plots were established. To manipulate fire severity, harvest residues were added as fuel or were entirely removed from 7 pairwise experimental plots. The fire was classified as a light fire according to Ryan (2002).

The original tree stand at Tierp 2 consisted of 107-year-old Scots pine, *Pinus sylvestris* (L), and Norway spruce *Picea abies* (L) Karst., and was clear-cut in 2002. The field vegetation on the clear-cut was dominated by bilberry, *Vaccinium myrtillus* L. and the bottom vegetation consisted mainly of the forest moss *Hylocomium splendens* (Hedw.) B.S.G.

Sampling and identification

In this thesis mainly microarthropods, but also enchytraeids (paper I) and macroarthropods (paper I) were studied. Among the microarthropods Collembola, Protura and Mestostigmata were enumerated in all areas studied. Oribatida was studied in paper I and paper III and Prostigmata and Astigmata were only investigated in paper I.

Microarthropods samples were taken with a steel frame down to the first cm of the mineral soil. The animals were extracted using Tullgren funnels (papers I-IV). Enchytraeid samples (paper I) were extracted in modified Baermann wet-funnels (O'Connor 1962). Macroarthropods and earthworms (paper I) were extracted using Tullgren funnels.

In Bjuråker 256 and Tyresta, animals were usually collected during the autumn (September to November), and in Tierp 1 and 2 samples were mainly taken during springtime. In all experiments except Tierp 2, samples were taken during successive years (Fig. 2).
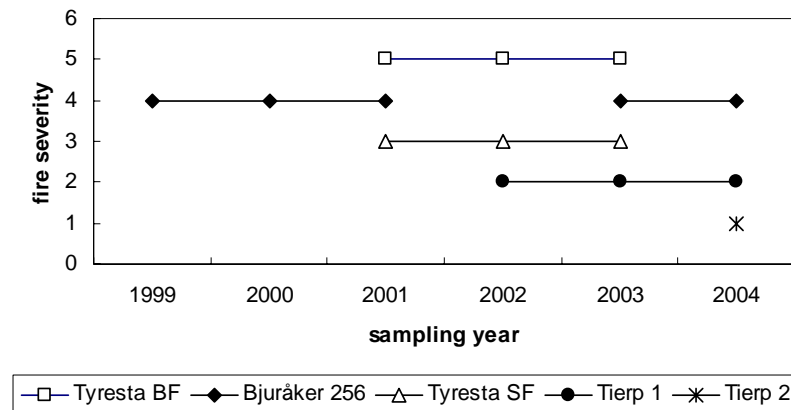

Fig. 2. Sampling years for the different experimental sites. The most severe fire is ranked as 5, the second most severe as a 4 and so forth. BF=big fire, SF=small fire.

For Enchytraeidae, Collembola and adult Oribatida, identification to species was done in most cases. Mesostigmatid mites were identified to species when possible, in other cases to genus or family. Prostigmatid mites were identified to family. The large macroarthropods were counted and identified to group level (family or order).

Measures of community diversity and composition

Community parameters such as total abundances (microarthropods, enchytraeids and macroarthropods), abundance of individual species (Collembola, Oribatida, Mesostigmata, Enchytraeidae), species numbers (Collembola, Oribatida, Mesostigmata) and diversity indices (Collembola, Oribatida) were measured. I used Simpson's index of diversity (1/D) and Simpson's measure of evenness ($E_{1/D}$ = (1/D)/S, where S is the number of species in the sample) (Magurran, 2004). In addition the mean number of species per plot was calculated, and to adjust for differences in sample size (no. of individuals) a rarefaction analysis was made (papers I, II and III). Furthermore, variation in community composition of microarthropods between treatments was analysed by ordination, using Principal Component Analysis (PCA) (papers II and III).

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Statistical analyses

The two wildfire areas in Tyresta (BF and SF) can be considered as natural experiments (Diamond, 1986), and were analysed as if "treatments" had been planned in advance, despite the fact that I had no control over the treatments. A drawback of natural experiments using, e.g., natural wildfires, is the low degree of control over fire intensity and replication (see Parr & Chown, 2003). This is in some sense also true for prescribed burns, since even if the experiments are planned, the fire intensity is hard to control. When it comes to fires, the fire in itself is also very heterogeneous and two fires will never behave the same way.

A common problem with large-scale natural experiments undertaken in natural landscapes is that they are almost impossible to replicate, usually owing to lack of funding, logistic constrains and/or the heterogeneity of ecosystems (Carpenter, 1990; Parr & Chown, 2003). In my case, I had no opportunity to make my own burnings. Prescribed burns are very expensive and labor intense, and as a consequence I have used clear-cuts that was burnt by others. In Bjuråker 256, I used a fire experiment set up by Skog Forsk. In Tierp 1, I used a clear-cut that was burnt by the forest company Stora Enso, as part of their certification program. This meant that no unburnt clear-cut was saved in the latter experiment, and as a consequence, no real control was obtained.

The faunal variables were analysed with repeated measure ANOVA with an autoregressive covariance structure of order one, AR(1) (papers I, II and III). The direct effects of fire severity (paper III) was analysed with a two-way ANOVA. All analyses were done with ln $(X+0.1)$ transformed data. To examine if surface-living species and groups were more affected by fire than those living deeper down in the soil, the percentage survival after burning was related to the proportion of individuals in the group or species that was living in the litter and fragmented litter layer of the soil in the samples from the unburnt clear-cut (paper III). This was done using the Spearman rank correlation method. To determine lethal temperatures for soil microarthropods (paper IV) dose-response curves were generated for Collembola and Oribatida. Differences in survival between different temperatures were also analysed using one-way ANOVA (Collembola, Oribatida, Mesostigmata). For proturans and individual species there were too few individuals to do an ANOVA and instead a Kruskal Wallis test was used.

The experiments in Bjuråker 256 and Tyresta SF, has two blocks and three treatments (n=2). In Tierp 1 seven blocks burnt with pair-wise plots burnt with different severity was used (n=7). In Tyresta BF, no replication was possible (n=1), and instead I used the individual samples from each plot as replicates. It must be noted that this is not a true replication of treatment effects, and can only indicate possible fire effects which may be confounded by other differences between the plots (Hurlbert, 1984). This means that the interpretation and generality of the present results can be questioned until confirmed (or rejected) in, for example, a meta-analysis of a number of wildfire studies (hitherto not undertaken), as discussed by Parr and Chown (2003). Nonetheless, I strongly argue that the present study contributes important data points for such an analysis in the future.

Results and discussion

Direct effects (Paper III)

All animal groups studied reacted with a decrease in total abundance one week after fire. Oribatid mites showed the strongest decrease in total abundances, followed by collembolans, proturans and mesostigmatid mites (Tab. 1). A significantly negative Spearman rank correlation between percentage occurrence in the litter and fragmented litter fraction of the sample and survival after burning was found for all microarthropod groups, except Mesostigmata (Tab. 1). Since no species were determined for proturans, this correlation was not possible to do for this group.

No difference in Simpson's diversity index could be found between the different fire treatments (H vs. L), but the diversity index was reduced compared to the pre-fire situation for both Collembola and Oribatida. Simpson's evenness decreased at hard-burnt plots for Collembola and increased at both light- and hard-burnt plots compared to the clear-cut before burning for Oribatida. This result can be interpreted as an increased dominance of dominant species for Collembola and a decreased number of rare species for Oribatida. For both groups, the number of species was reduced at the burnt sites, and the difference was still seen after a rarefaction analysis.

The effect of fire was strongest on species and groups living near the surface. Species living in the vegetation and in the upper soil layer will suffer from fire regardless of severity. The risk of being consumed by fire is great, and the heat at the surface is often several hundred degrees centigrade (DeBano, Neary & Ffolliott, 1998). Fire severity is increasing in importance for animals living deeper in the soil and that are able to migrate downwards during the fire. A more intense fire will release more heat into the soil (Steward, Peter & Richon, 1990) and, thus, kill more animals.

Table 1. *Survival of soil fauna groups one week after the clear-cut burning at Tierp expressed as % of the abundances one week before burn in relation to burning severity (light burn and hard burn) and microhabitat (% in the litter/fragmentation layer in relation to the whole organic layer). L=light burn, H=hard burnt*

|	% survival L	% survival H	% in LF layer	Spearman's rho and p-values L	Spearman's rho and p-values H	N=no. spp/taxa
Oribatida	13	3	73	r_s=-0.331, p=0.015	r_s=-0.345, p=0.011	54
Collembola	23	7	60	r_s=-0.496, p=0.006	r_s=-0.552, p=0.006	23
Protura	57	48	57	-	-	-
Mesostigmata	55	53	55	r_s=-0.028, p=0.909	r_s=-0.401, p=0.085	19

Fire severity (papers II and III)

In the big fire in Tyresta, all animal groups studied had lower abundances in the burnt plots than in the unburnt forest (Fig. 3). All animal groups also occurred in lower numbers in the hard-burnt plot than in the light-burnt plot. The samples were taken 2-4 years after the fire. Thus, there might have been initial effects of fire on total abundances that cannot be seen in this study.

Hard-burnt plots had lower diversity and a lower evenness value for Collembola than light-burnt plots and unburnt forest. The species number was lower at burnt plots than in the unburnt forest, but no difference was found between the different plots within the fire area.

In Tierp 1, there were clear direct effects of fire intensity on Collembola and Oribatida. After the initial effect, no difference could be detected between the two fire treatments. This is probably due to the fact that there was no difference in humus combustion between the two fire treatments in Tierp 1 (paper III). At the hard-burnt plots extra fuel was added, which resulted in a more intense fire that produced more heat. After the initial difference in fire intensity with more heat being transported down into the soil in the hard-burnt treatment, the animals on the hard-burnt plots were able to recover to the same extent as in the light-burnt plots. However, the extra heat did not seem to combust extra humus, probably because of high moisture in the humus layer.

To conclude, there were clear direct effects of fire severity on the organisms studied, but these effects only remained to a smaller extent 2-4 years after fire.
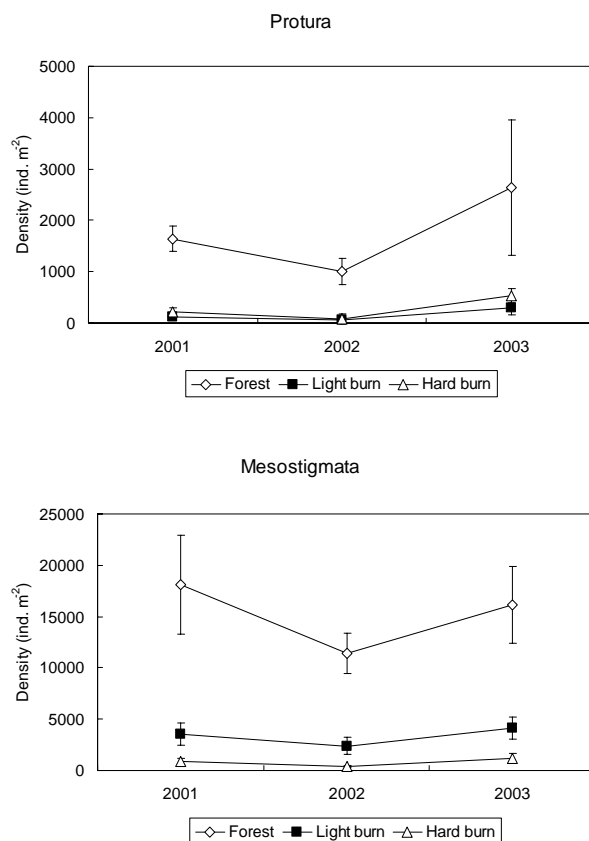
Collembola

Protura
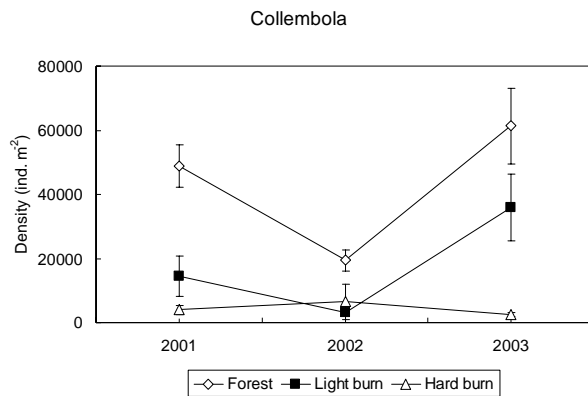
Mesostigmata

Fig. 3. Mean abundances (±S.E.) of Collembola, Protura and Mesostigmata in different treatments in the big-fire area in Tyresta in 2001-2003. Control = unburnt forest, Light burn =less severe fire, and Hard burn = more severe fire.

Recovery over time (papers I, II and III)

Total abundances

Different microarthropod groups showed different patterns in recovery of total abundances (Figs 4-7). For Collembola, no sign of recovery 5 years after the fire could be detected in Bjuråker 256 and Tyresta big fire (BF) (Fig. 4). In the Tyresta small fire (SF), on the other hand, no differences could be seen between the unburnt forest and the burnt treatments three months after fire. In Tierp 1, no unburnt clear-cut was left after the fire. The total abundances in the nearby forest did not differ significantly from those in the burnt clear-cut five months after burning after a marked increase in numbers of Collembola in the burnt area. The results from Tierp 1 show that a fast recovery of total abundances is possible after a light fire.

Mesostigmatid mites responded in a similar way as Collembola (Fig. 5), with a recovery of total abundances in Tierp 1. No recovery of total abundances could be found in Bjuråker 256, Tyresta BF or Tyresta SF. Proturans (Fig. 6) and oribatid

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mites (Fig. 7) responded with more dramatic decreases to fire disturbances than collembolans and mesostigmatid mites. Oribatida were not studied at Tyresta.

In Bjuråker 256 and Tierp 1, the effect of clear-cut burning was studied. In Bjuråker 256, the burning effect could be separated from the clear-cut effect because of the experimental set-up with an unburnt clear-cut. This was not the case in Tierp 1, where the whole clear-cut was burnt by the forest company, StoraEnso, as part of their certification program. In Bjuråker 256, no difference in total abundances between the unburnt forest and the unburnt clear-cut could be found for Collembola, Protura or Mesostigmata. Similar results were reported in Finland, where clear-cutting and gap felling did not seem to affect total collembolan numbers (Siira-Pietikäinen *et al.,* 2001). In earlier studies in Finland, done at the same latitude, collembolan numbers increased three years after clear-cutting, followed by a return to control numbers. Modest changes (Huhta, 1976) and decreases of mesostigmatid mites (Bengtsson, Persson & Lundkvist, 1997; Bird & Chatarpaul, 1986; Blair & Crossley, 1988) have been reported in earlier studies.

Oribatid mites reacted with a decrease in total abundances after clear-cutting in Bjuråker 256. This is in agreement with other studies, which all indicate a shorter or longer decline for this group after clear-cutting (Huhta *et al.* 1967; Huhta, Nurminen & Valpas, 1969; Vlug & Borden, 1973; Huhta, 1976; Abbott, Seastedt & Crossley, 1980; Bird & Chatarpaul, 1986; Blair & Crossley, 1988; Marshall, 2000; Lindo & Visser, 2004). Still five years after the clear-cutting at Bjuråker 256, no sign of recovery could be seen in oribatid mites. This indicates that a recovery would not be expected at the burnt sites in comparison with the unburnt forest in Tierp 1 several years after clear-cutting. The dramatic reduction in oribatid mites in the burnt clear-cut is probably a combination of clear-cut and burning effects. Total numbers of oribatid mites recovered, at least partly, at the burnt clear-cut in Bjuråker 256 in comparison with the unburnt clear-cut in 2004. This was entirely due to an increase in one species, *Oribatula tibialis*, and is not a general recovery.

Enchytraeidae increased in the unburnt clear-cut, but decreased in the burnt clear-cut in Bjuråker 256 (paper I). The total abundances at burnt and unburnt clear-cut approached each other three years after burning, but some more years of study is needed to evaluate whether this sign of recovery is to be confirmed or not. Burning seemed to increase the number of earthworms on the burnt area. The soil macroarthropods had lower densities in the burnt clear-cut than in the unburnt clear-cut and the mature forest. The most dominant aboveground invertebrates were leafhoppers, Cicadellidae, which became very abundant in the burnt plots in 2001 and 2003. With the exception of Cicadellidae, no macroarthropod group responded with increases in abundance after clear-cut burning at Bjuråker 256.

Oribatid mites are known to be more sensitive to disturbances than collembolans and mesostigmatid mites (Lindberg & Bengtsson, 2006). Proturans also responded more dramatically than collembolans and mesostigmatid mites in my study, but data on proturan sensitivity to any kind of disturbance are scarce in the literature.
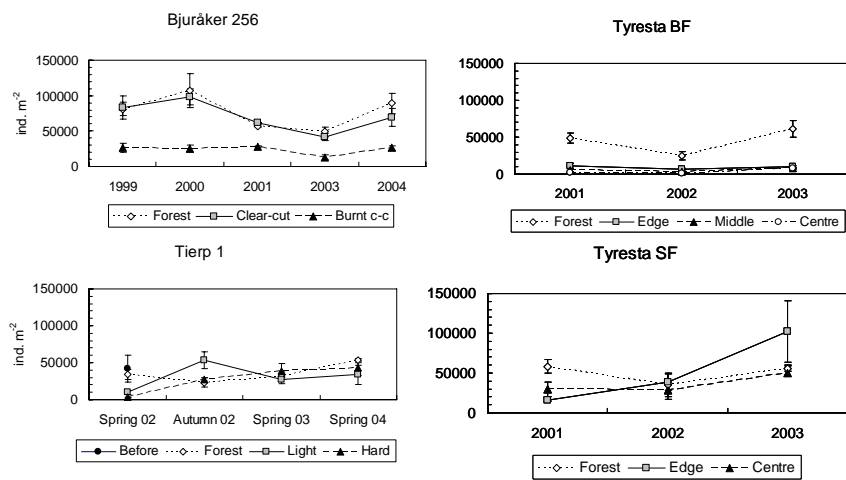
Fig. 4. Collembola responses to fires at different severities at the experimental sites used in this thesis. Bjuråker 256=moderate prescribed burn, Tyresta BF=moderate to deep wildfire, Tierp 1=light prescribed burn, Tyresta SF=light wildfire.

Fig. 5. Mesostigmata responses to fires at different severities at the experimental sites used in this thesis. Bjuråker 256=moderate prescribed burn, Tyresta BF=moderate to deep wildfire, Tierp 1=light prescribed burn, Tyresta SF=light wildfire.
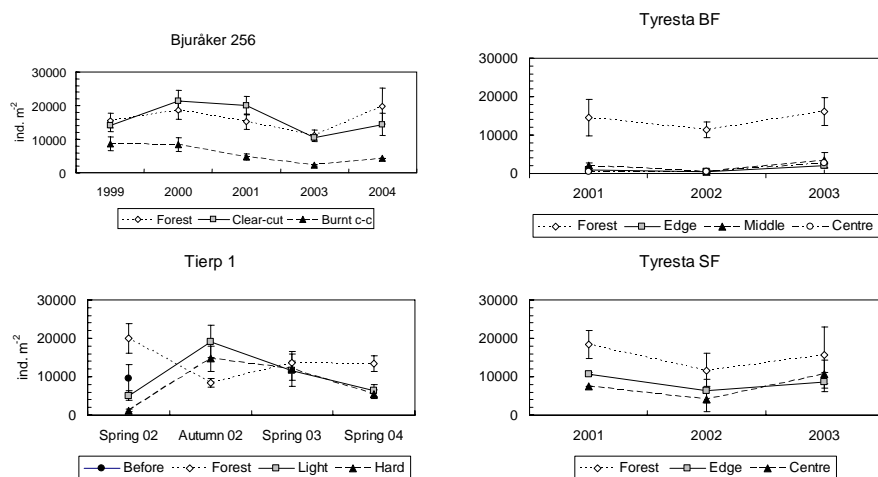
Fig. 6. Protura responses to fires at different severities at the experimental sites used in this thesis. Bjuråker 256=moderate prescribed burn, Tyresta BF=moderate to deep wildfire, Tierp 1=light prescribed burn, Tyresta SF=light wildfire.
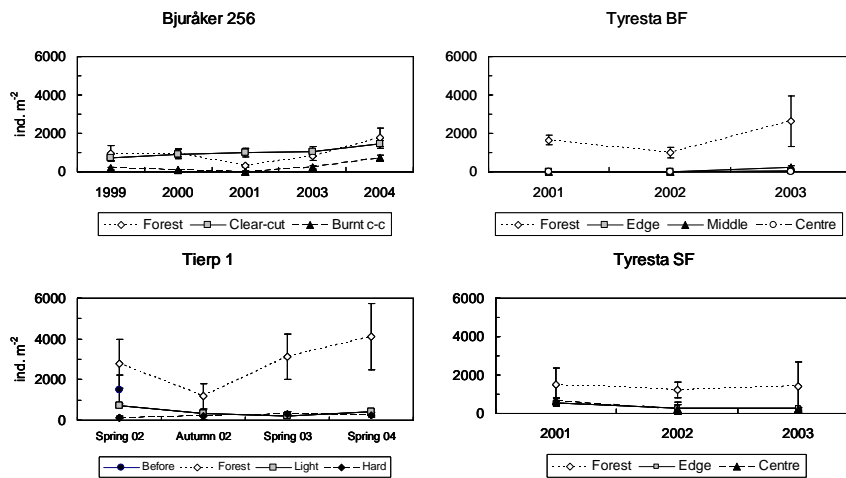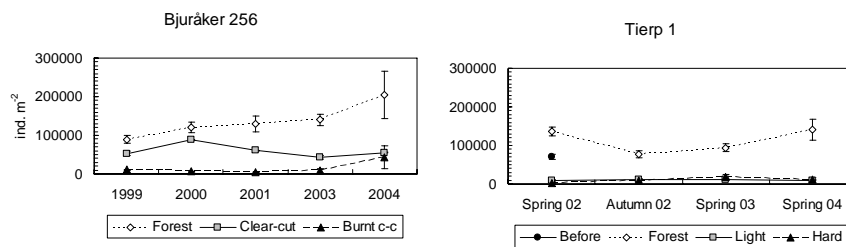

Fig. 7. Oribatida responses to fires at different severities at the experimental sites used in this thesis. Bjuråker 256=moderate prescribed burn, Tierp 1=light prescribed burn.

Species composition

In Tyresta SF no difference was found in total abundances for Collembola, but when a PCA was made, fire-related differences between the treatments were found (Fig. 8). The first axis (PC 1) explained 26 % of the variance, and was close to significant for fire treatment (p=0.066). Furthermore, the centre plot differed significantly from the forest along the first axis. The second axis (PC 2) accounted for 18 % of the variation and could be explained as a fire effect (p = 0.032).

Karppinen (1957) found that oribatid mites had almost recovered in number of individuals 3-4 years after a fire, but the species composition still differed after 27 years. Haimi, Fritze and Moilanen (2000) could also see a clear difference in community structure of collembolans due to fire, but not in total abundances. Lindberg and Bengtsson (2006) found evidence for total abundances not being a good measure of recovery, since the total abundances of an animal group returned to control values much faster than species richness and diversity indices. This

shows the importance of species determination and a high resolution when studying effects of disturbances. However, at Bjuråker 256 both Collembola and Mesostigmata showed no recovery in total abundance, but had partly recovered in terms of species richness. In contrast, oribatid mites showed an almost complete recovery in total abundance, but no recovery in species richness. The recovery in total abundance could be explained by an explosive increase in one single species. This further emphasizes the importance of studying total abundances and population responses of individual species in combination.
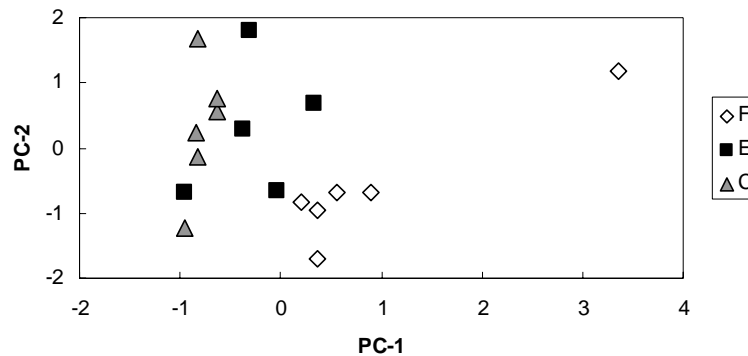

Fig. 8. PCA plot of the community composition of Collembola in Tyresta SF. The different treatments are F = unburnt forest, E = edge of transect, close to unburnt forest, and C = centre of the fire field. Samples were taken in 2001-2003.

In Tierp 1, total abundances of Collembola and Mesostigmata recovered at the burnt plots as indicated by the comparison with the unburnt forest. When a PCA was made, differences between the burnt sites and the unburnt forest were seen (not shown) although this can partly be attributed to a general clear-cut effect. Even if there was a recovery in total abundances there were still differences in species composition. This means that none of the areas studied in this thesis had soil animal communities that had completely recovered after fire for the first three to five years.

Diversity

The mean number of Collembola species was lower at the burnt plots than in the unburnt forest in Tyresta BF all years. In Bjuråker 256 there were fewer species at the burnt clear-cut than at both the unburnt clear-cut and the forest. The number of species was lower only during the first two years according to the rarefaction method. In Tierp 1, the mean number of species was lower during spring and autumn in 2002, the burn year also according to rarefaction. No difference in expected number of species based on rarefaction was found in Tyresta SF, even during the fist year. Species number, both mean numbers and expected numbers based on rarefaction, of oribatid mites were lower in both Bjuråker 256 and Tierp 1.

Hence, there was a general decrease in the number of Collembola species shortly after a fire. This is probably due to the fact that many of the surface-living species die in the fire and that the habitat is highly altered during the first years after burning. Collembolans are good dispersers with short generation times (Hopkin 1997). This is most likely why they can come back shortly after a severe disturbance.

The effects on species number of oribatid mites were more long lasting. Oribatid mites are often considered to have a higher degree of ecological specialisation than collembolans (Norton, 1985; Norton, 1994) and they are in many cases reported to be slow dispersers (Hutson, 1980a; Hutson, 1980b; Huhta, 1979). A longer recovery time is therefore expected for Oribatid mites with regard to species richness.

Simpson's diversity index was lower for Collembola at the burnt clear-cut in Bjuråker 256 than in both forest and unburnt clear-cut. The diversity was lower at the burnt plots in Tyresta BF, but increased closer to the forest with time. Collembola diversity was lower at burnt plots also in Tyresta SF and Tierp 1. Simpson's evenness measure for Collembola was lower in Tierp 1, whereas it was higher the first two years in Bjuråker but later it dropped dramatically. No difference in Simpson's evenness index could be found in Tyresta BF and SF. The Simpson diversity index for Oribatida was lower both at Bjuråker and Tierp 1, while the evenness measure was higher.

The fact that diversity is lower at burnt sites can be explained by either a reduction of species richness or a shift in dominance structure between species. The Simpson diversity index (1/D) is regarded to be sensitive to increasing dominance of certain species (Magurran, 2004) in addition to having a richness component. For Collembola, diversity at burnt plots was lower than at unburnt plots, but the number of species was not always lower. This indicates that some dominance shifts occurred. The most dominant Collembola species in the forest made up between 17 and 36% of the total abundance, while the most dominant species could make up as much as 81% of the total abundance at the burnt plots. The lower evenness measure for Collembola indicated the same thing, namely that the species were less evenly distributed. For Oribatida, no such big shift in dominance occurred. The increased evenness values for Oribatida indicated that rare species disappeared, making the remaining species more evenly distributed.

Fire severity

Burn depth can be expected to have a big impact on soil fauna. Fire severity affects the numbers of various arthropods (Vlug & Borden, 1973; Wikars & Schimmel, 2001; Hening-Sever, Poliakov & Broza, 2001), and in my study hard-burnt plots contained fewer individuals than light-burnt plots. Generally, the mortality of ground-living arthropods seems directly related to the combustion of the litter and organic soil during the fire (Bellido, 1987). Fire destroys the preferred part of the soil habitat for most soil organisms, i.e. the litter and uppermost humus layer, or if the fire is very severe, the entire humus layer. This

habitat destruction is likely to be the most important factor affecting survival in the soil both during and after a fire.

The recovery rates found for Collembola and Mesostigmata at the four experimental sites in my study indicate that fire severity can explain most of the differences found. The total abundances in the two severe fires (Tyresta BF and Bjuråker 256) showed no recovery after five years, while the abundances in the light fires (Tyresta SF and Tierp 1) recovered within some months after the fire or showed no reaction to fire at all. In Bjuråker 256, which was an experiment with two blocks, one of the burnt plots had a higher degree of humus combustion than the other. Enchytraeidae, Collembola and Mesostigmata all occurred in lower numbers in the more severely burnt plot than in the less severely burnt plot in 1999.

Distance to unburnt areas

No effect of distance to unburnt areas could be seen on microarthropod recovery in Tyresta BF, other than an increase in diversity with time closer to the forest (Tab. 2). This could be due to dispersal of species from the forest and into the transect. The mean number of species found in the burnt area was indeed lower than in the forest, especially in the centre. The decreasing species number along the transect could also be explained by a decreasing number of individuals found along the transect. There was also a very big shift in dominance structure in the burnt areas compared with the forest. The most dominant species in the forest in 2001 (*Mesaphorura yosii*) was making up 24 % of the total population. This is to be compared with 26 % (*Protaphorura armata*) in the edge treatment, 38 % (*Sminthurides schoetti*) in the middle and 81 % (*S. schoetti*) in the centre of the transect. The decrease in Simpson's diversity index towards the fire centre could indicate changes in dominance resulting from species having lower dispersal along the transect. However, no clear changes in Simpson's evenness measure could be detected.

Table 2. *Mean values of Simpson's diversity index in the transect in Tyresta in BF 2001-2003 for Collembolans. F = unburnt forest, E = edge (burnt area close to the forest), M = middle of transect, C = centre of the fire field. Values with different letters are significantly different (p<0.05)*

Area	Index	Treatment	2001	2002	2003
Tyresta BF	Simpson's D	F	7,4[a]	6,0[a]	6,5[a]
		E	6,5[b]	4,7[ab]	6,8[ab]
		M	4,3[b]	4,5[b]	4,4[ab]
		C	1,5[b]	3,3[b]	3,9[b]

No effect of distance to unburnt forest was seen on total abundances in Tyresta SF, but a PCA showed that the first axis showed significant differences between the unburnt forest and the centre plots in the transect (Fig. 8), whereas the edge plots were intermediate in species composition.

The lack of clear and consistent effects of distance on recovery rates may be explained by the very heterogeneous nature of fire fields. Some areas have burn

with low intensity (Esseen *et al.*, 1997; McCullogh, Werner & Neumann, 1998) and can serve as refugia for organisms, whereas others burn harder. It is possible that those areas play a more important role in the recolonisation process than distance to unburnt forest.

Another possible explanation is that distances of 100 to 600 m in a transect are not an appropriate scale to detect dispersal in microarthropods. If the distance from source area is too long, poor dispersers have not arrived yet. Active dispersal in microarthropods can be very slow (Ojala & Huhta, 2001), but most microarthropods are still reported to have rather good dispersal abilities (Dunger & Wanner, 2001). Surface-active species of microarthropods can be passively distributed by wind or run-off water, or they may disperse actively (Freeman, 1952; Hertzberg, 1997; Zhao & Amarine, 1997). Recolonisation of disturbed areas by gamasid mites often occurs by wind or phoresy on insects (Binns, 1982). There is also the possibility that microarthropods can be transported by other animals than arthropods, such as birds (Krivolutsky, Lebedeva & Gavrilo, 2004). Since many microarthropods seem to be good dispersers, there is also the possibility that the transect was too short to detect differences in dispersal. But in that case, dispersal limitation would not be a problem in recolonisation of fire areas.

Many authors seem to think that recolonisation after a fire is mainly by recruitment from surviving individuals remaining in the soil (Tamm, 1986; Winter, Schauermann & Schafer, 1980; Koponen, 1989; Bellido, 1987). In Tyresta BF, lower number of species was found at the burnt sites than in the unburnt forest, but the sample size (number of individuals) was much smaller at the burnt sites. In Tyresta SF, rarefaction showed that the differences in number of species were mainly due to differences in the number of individuals sampled. That indicates that most species probably survive in the soil. Parthenogenesis has been shown to be an advantageous trait for colonising species (Baur & Bengtsson, 1987), and many soil microarthropods are parthenogenetic (Lindberg & Bengtsson, 2005). Since species seem to survive in the field, this means that they can come back without depending on dispersal from areas outside the fire area, which in turn means that a delay in recovery indicates a lack of resources or habitat for species or individuals.

Buddle *et al.* (2006) compared arthropod assemblages in burnt and harvested forest. Fewer arthropods were caught in the burnt stands almost three decades after disturbance. This was partly explained by the reduction of the organic horizon that normally follows most wildfires. The re-establishment of this horizon may take many years. The post-fire restoration process of forest litter thickness in Scots pine in the Kola Peninsula and western Siberia has been shown to take 90-100 years in forest of thelichen type and 120-140 years in the green moss type (Gorshkov, Bakkal & Stavrova, 1996). So, a complete recovery of the soil-dwelling microarthropod community is not to be expected in many years. Fire normally occurs in the Swedish boreal forest with intervals of 50 to 200 years (Zackrisson, 1977; Engelmark, 1984). This means that our study only covers a very short period of the fire cycle, 0-2 years after the fire in the small fire area and 3-5 years in the big fire area.

Species specific responses to fire

Several species reacted to fire in the different fire experiments. The vast majority decreased in numbers because of fire. Two species of Collembola (*Willemia anophthalma* and *Friesea mirabilis*) and one species of Mesostigmata (*Veigaia nemorensis*) decreased in all places investigated. *F. mirabilis* was able to recover after some time in the less severe burns Tyresta SF and Tierp 1. Two Collembola species occurred in higher numbers in burnt plots than in unburnt plots. *Sminthurides schoetti* occurred in high numbers in the burnt plots in Tyresta BF. This species is mainly living in *Sphagnum* cushions and was sampled in high numbers in the burnt plots. *Bourletiella hortensis* was found in the burnt clear-cut in Tierp 1 in 2003 and 2004, and occurred in higher numbers at the hard-burnt plots. This species was found at burnt sites in an earlier fire study (Tamm, 1986) and is known to occur in open areas (Fjellberg, 1980). One Collembola species was found in one of the burnt sampling plots in Tierp 1 in 2004 only. The species *Sminthurinus trinotatus* is normally found only in greenhouses in Nordic countries and is probably a new species for Sweden (A. Fjellberg, *pers. comm.*).

The oribatid species *Oribatula tibialis* and a plant-sucking Cicadellidae species responded with large population increases some years after burning in Bjuråker 256. *Oribatula tibialis* also increased at the unburnt clear-cut. The prostigmatid mite *Nanorchestes* sp. responded to burning in a complex way. After an initial decrease by burning, no differences could be seen between the burnt and the unburnt clear-cut the second year. The third year after burning the numbers of *Nanorchestes* sp. in the burnt clear-cut exceeded the numbers in the unburnt clear-cut. In 2003 the numbers decreased again with lower numbers at the burnt clear-cut.

These species are examples of species that are favoured by fire in some way, but they are probably not fire-dependent species. No fire-dependent species of soil mesofauna were found in my study.

Lethal temperatures (paper IV)

The direct decreases of the abundances after of fire in Tierp 1 showed that animals are killed directly by the fire itself. The most possible cause of death is heat that is transported into the soil during the fire. In a laboratory study of lethal temperatures on humus-living microarthropods (paper IV), I found that at temperatures above 36 ℃ all animal groups studied started to decrease in number after an one-hour exposure. After a 4-hour exposure Collembola (Fig. 9), Protura (Fig. 10) and Mesostigmata (Fig. 11) started to decrease at 32 ℃ and at 30 ℃ after a 12-hour exposure. Oribatid mites (Fig. 12), both juveniles and adults, decreased in numbers when the temperature became 34 ℃ or higher after both 4 and 12 hours of exposure.

Terminal death point (TDP, i.e. the highest possible temperature for life (Madge, 1965) has been reported to vary between 33 and 48 ℃ for Collembola (Thibaud, 1977a; Thibaud, 1977b; Hodkinson *et al.*, 1996; Choudhuri, 1963), and between

28 and 45 ℃ for Oribatida (Madge, 1965, Hodkinson *et al*., 1996). Species living on the soil surface and in the vegetation can withstand higher temperatures than hypogeic animals (Thibaud, 1977). In my study, only humus-living animals were tested, and this probably shifted the TDP-values downward at group level, since surface-living species are more tolerate to high temperatures.

It is not easy to predict heat penetration in the soil during a fire. Soil texture and moisture are key variables regulating the downward and lateral transport of heat in the soil (Busse *et al*., 2005). In boreal forest systems, there is often an accumulation of a distinct organic soil layer that may insulate against heat penetration during fire (Schimmel & Granström, 1996). Schimmel & Granström (1996) measured temperature distribution in the soil during fires in northern Sweden. In the top mor layer, the time with temperatures above 60 ℃ varied from less than 1 minute to 75 minutes. In the mor humus, the depth at which 60 ℃ was reached was in the range of 20-30 mm below the char. However, my studies indicate that lethal temperatures for soil fauna are much lower, in the order of 30-40 ℃. These temperatures are likely to be found deeper in the soil and persist for longer duration.
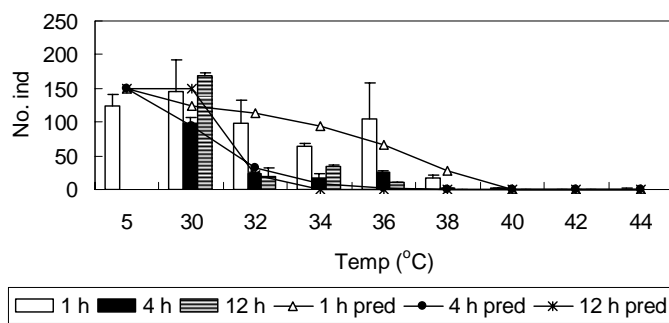

Fig. 9. Mean abundances (S.E.) of Collembola at different temperatures (5, 30, 32, 34, 36, 38, 40, 42, and 44 ℃) and exposure times (1 h, 4 h and 12 h). The predicted curves from the regression analysis are also shown in the figure.

Fig. 10. Mean abundances (S.E.) of Protura at different temperatures (5, 30, 32, 34, 36, 38, 40, 42, and 44 ℃) and exposure times (1 h, 4 h and 12 h).

Fig. 11. Mean abundances (S.E.) of Mesostigmata at different temperatures (5, 30, 32, 34, 36, 38, 40, 42, and 44 ºC) and exposure times (1 h, 4 h and 12 h).

Fig. 12. Mean abundances (S.E.) of Oribatida at different temperatures (5, 30, 32, 34, 36, 38, 40, 42, and 44 ºC) and exposure times (1 h, 4 h and 12 h). The predicted curves from the regression analysis are also shown in the figure.
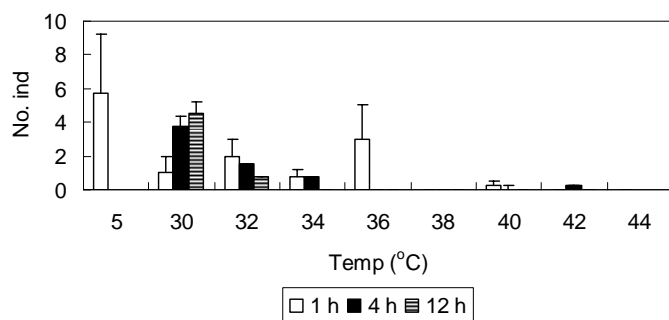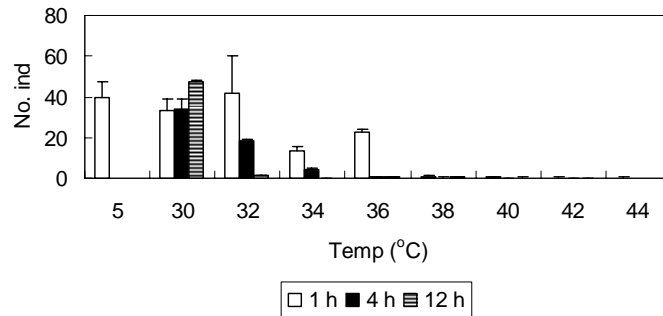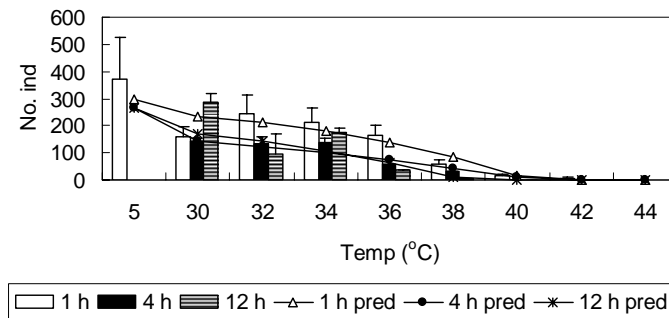
Conclusions

All soil fauna species responded with decreased abundances one week after burning. This decline can partly be explained by too high temperature, because most collembolan and oribatid species cannot survive temperatures above 36-40 ºC, and this temperature can be reached several centimetres below the charred soil surface. Long-term recovery rates differed between soil fauna groups and between different fire severities. In fires with light severity (one wildfire and one prescribed burn), total abundances of Collembola and, in one case, Mesostigmata, recovered within one year. In fires with moderate to strong severity (another wildfire and another prescribed burn), almost all animal groups needed more than five years to recover as regards abundance and species number. Individual species had different response patterns. Surface-living species were more subjected to fire

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than species living deeper in the soil, and although surface-living species have generally better dispersal ability, their recovery was probably delayed by the destruction of the topsoil resources and habitats. Only a few species had significantly higher abundances 3-5 years after moderate/strong burning, whereas most species studied recovered after a light burning. Consequently, fire severity (burn depth) seems to be a decisive factor explaining survival and recovery rate of soil mesofauna, and this factor should always be considered when fire effects on soil organisms would be evaluated in forthcoming studies.

Wildfires normally burn more intensively than prescribed burns and are more heterogeneous. My studies suggest that the most important factor affecting soil living organisms is most likely burn depth. In this thesis I have studied two severe fires, one wildfire and one prescribed burn, as well as two light fires, one wildfire and one prescribed burn. The largest differences seem to be between the different fire severities, and not between wildfires vs. prescribed burns, indicating that for soil fauna, prescribed burns can be quite good in mimicking wildfires. Most soil animals suffer from burning, at least on a short-term basis. There are, however, a few species that are favoured by burning or by the disturbance. Fire is a natural disturbance in the Swedish forest, and all species inhabiting the forest soil have probably encountered fire in their evolutionary past. This means that they should be able to survive and recover from a fire disturbance. I find it unlikely that soil fauna would be threatened by the present fire frequencies and severities for their long-term survival.

Studying fires, especially wildfires, is complicated and the experiments can be almost impossible to replicate. This means that the interpretation and generality of the present results can be questioned. However, fire is an important disturbance agent in many ecosystems worldwide, and despite these problems it is still important to study the effects of wildfires. If more studies on the effects of wildfires on soil fauna are undertaken in the future, a meta-analysis can be used to confirm (or reject) my results. If we do not study wildfires because of the lack of replication, such analyses will not be possible, and important information will be lost.

 To sum up, in this thesis I have shown that:

Fire severity is probably the most important factor determining how forest soil fauna is affected by fire.

In more severe fires, loss of habitat and resources results in a slow recovery of most soil faunal groups. In light fires, surface-living species are most affected and recovery rates may differ between species and higher taxa depending on e.g. distance to source areas. Oribatida were more affected than Collembola and Mesostigmata.

Lethal temperatures for soil fauna is in the order of 30-40 ℃, which implies that soil animals may be more severely affected than previously believed based on the distribution of temperatures above 50-60 ℃.

Prescribed burns as a biodiversity conservation method is unlikely to be good for forest soil fauna, and has additional effect to clear-cuttings. However, few if any soil animal species are likely to be threatened by present fire regimes. Since there are small differences between the effects of prescribed burns and wildfires on forest soil fauna, the present results do not question the use of this method for conservation of other components of forest ecosystems.

References

Abbott, D.T., Seastedt, T.R., & Crossley, D.A. 1980. The abundance, distribution and effects of clear-   cutting on Cryptostigmata in the southern Appalachians. *Environmental Entomology* 9, 618-623.

Baur, B. & Bengtsson, J. 1987. Colonizing ability in land snails on Baltic uplift archipelagos. *Journal of Biogeography* 14, 329-341.

Begon, M., Harper, J.L., & Townsend, C.R. 1990. Ecology. Individuals, populations and communities. 2nd edition. Blackwell Science, Oxford. 909 pp.

Bellido, A. 1987. Field experiment about direct effect of a heathland prescribed fire on microarthropod community. *Revue d'Écologie et de Biologie du sol* 24, 603:622. (In French, English abstract.)

Bengtsson, J. 2002. Disturbance and resilience in soil animal communities. *European Journal of Soil Biology* 38, 119-125.

Bengtsson, J., Nilsson, G.S., Franc, A. & Menozzi, P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management*. 132, 39-50.

Bengtsson, J., Persson, T. & Lundkvist, H. 1997. Long-term effects of logging residue addition and removal on macroarthropods and enchytraeids. *Journal of Applied Ecology* 34, 1014-1022.

Binns, E.S. 1982. Phoresy as migration – some functional aspects of phoresy in mites. *Biological Reviews of the Cambridge Philosophical Society* 57, 571-620.

Bird, G.A. & Chatarpaul, L. 1986. Effect of whole-tree and conventional forest harvest on soil microarthropods. *Canadian Journal of Zool*ogy 64, 1986-1993.

Blair, J.M. & Crossley, D.A. Jr. 1988. Litter decomposition, nitrogen dynamics and litter microarthropods in a southern Appalachian hardwood forest 8 years following clearcutting. *Journal of Applied Ecology* 25, 683-698.

Broza, M. & Izhaki, I. 1997. Post-fire arthropod assemblages in Mediterranean forest soils in Israel. *International Journal of Wildland Fire* 7, 317-325.

Buddle, C.M., Langor, D.W., Pohl, G.R. & Spence, J.R. 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbances in forest management. *Biological Conservation* 128, 346-357.

Busse, M.D., Hubbert, K.R., Fiddler, G.O., Shestak, C.J. & Powers, R.F. 2005. Lethal soil temperatures   during burning of masticated forest residues. *International Journal of Wildland Fire* 14, 267-276.

Carpenter, S.R. 1990. Large-scale perturbations: Opportunities for innovation. *Ecology* 71, 2038-2043.

Clements, F.E. 1936. Nature and structure of the climax. *Journal of Ecology* 24, 252-284.

Choudhuri, D.K. 1963. Temperature and its effect on the three species of the genus *Onychiurus* Collembola. *Proceedings of the Zoological Society* (Calcutta) 16, 97-117.

Dahlberg, A., Schimmel, J., Taylor, A.F.S. & Johannesson, H. 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. *Biological Conservation* 100, 151-161.

DeBano, L.F., Neary, D.G. & Ffolliott, P.F. 1998. Fire's effects on ecosystems. John Wiley & Sons, Inc. New York. USA, pp. 333.

Diamond, J. 1986. Overview: Laboratory experiments, field experiments, and natural experiments. In J. Diamond and T.J. Case (eds) Community Ecology, pp. 3-22. Harper & Row, NY.

Dunger, W. & Wanner, M. 2001. Development of soil fauna at mine sites during 46 years after afforestation. *Pedobiologia* 45, 243-271.

Engelmark, O. 1984. Forest fires in the Muddus National Park (northern Sweden) during the past 600 years. *Canadian Journal ofBotany* 62, 893-898.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. *Ecological Bulletins* 46, 16-47.

Ferreira de Almeida, A.M. & Vilaca y Moura, P.V.S. 1992. The relationship of forest fires to agro-forestry and socio-economic parameters in Portugal. *International Journal of Wildland Fire* 2, 37-40.

Fjellberg, A. 1980. Identification keys to Norwegian Collembola. The Norwegian entomological society, Ås, Norway.

Freeman, J.A. 1952. Occurrence of Collembola in the air. *Proceedings of the Royal Entomological Society of London* 27, 1-3.

Gärdenfors, U. (ed.) 2005. The 2005 Red List of Swedish Species. Artdatabanken, SLU. Almqvist & Wiksell, Uppsala, Sweden.

Giller, P.S. 1996. The diversity of soil communities, the "poor man's tropical rainforest". *Biodiversity and Conservation* 5, 135-168.

Gorshkov, V.V., Bakkal, I.J. & Stavrova, N.I. 1996. Postfire recovery of forest litter in Scots pine forest in two different regions of boreal zone. *Silva-Fennica* 30, 209-219.

Granström, A. 2001. Fire management for biodiversity in the European boreal forest. *Scandinavian Journal of Forest Research* 3, 62-69.

Haimi, J., Fritze, H. & Moilanen, P. 2000. Responses of soil decomposer animals to wood-ash fertilisation and burning in a coniferous forest stand. *Forest Ecology and Management* 129, 53-61.

Hartnett, D.C. 1991. Effects of fire in tallgrass prairie on growth and reproduction of prairie coneflower (*Rabitibda columnifera: Asteraceae). American Journal of Botany* 78, 429-435.

Henig-Sever, N., Poliakov, D. & Broza, M. 2001. A novel method for estimation of wildfire intensity based on ash pH and soil microarthropod community. *Pedobiologia* 45, 98-106.

Hertzberg, K. 1997. Migration of Collembola in a patchy environment. *Pedobiologia* 41, 494-505.

Heyward, F. & Tissot, A.N. 1936. Some changes in the soil fauna associated with forest fires in the longleaf pine region. *Ecology* 17, 659-666.

Hobbs, R.J. & Atkins, I. 1990. Fire-related dynamics of a *Banksia* woodland in South-western Australia. *Australian Journal of Botany* 38, 97-110.

Hodkinson, I.D., Coulson, S.J., Webb, N.R. & Block, W., 1996. Can high arctic soil microarthropods survive elevated summer temperatures? *Functional Ecology* 10, 314-321.

Holling, C.S., Schindler, D.W., Walker, B.W. & Roughgarden, J. 1995. Biodiversity in the functioning of ecosystems: an ecological synthesis. In: Perring C.A., Mäler K-G., Folke C., Holling C.S. & Jansson B-O, eds. Biodiversity loss. Economic and ecological issuses, Cambridge University Press, Cambridge, UK. pp 44-83.

Hopkin, S.P. 1997. Biology of the springtails. Insecta: Collembola. Oxford University Press. Oxford. 330pp.

Hörnsten, L., Nohlgren, E. & Aldentun, Y. 1995. Brand och bränning – en litteraturstudie. *SkogForsk. Redogörelse* nr 9.

Huhta, V. 1976. Effects of clear-cutting on numbers, biomass and community resoiration of soil invertebrates. *Annales Zoologici Fennici* 13, 63-80.

Huhta, V. 1979. Evaluation of different similarity indices as measures of succession in arthropod communities of the forest floor after a clear-cutting. *Oecologia* 41, 111-123.

Hutha, V., Karppinen, E., Nurminen, M. & Valpas, A. 1967. Effect of silvicultural practices upon arthropod, annelid and nematode populations in coniferous forest soil. *Annales Zoologici Fennici* 2, 87-145.

Huhta, V., Nurminen, M. & Valpas, A. 1969. Further notes on the effect of silvicultural practices upon the fauna of coniferous forest soil. *Annales Zoologici Fennici* 6, 327-334.

Hurlbert, S.J. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187-211.

Hutson, B.R. 1980a. Colonization of industrial reclamation sites by Acari, Collembola and other invertebrates. *Journal of Applied Ecology* 17, 255-275.

Hutson, B.R. 1980b. The influence on soil development of the invertebrate fauna colonizing industrial reclamation sites. *Journal of Applied Ecology* 17, 277-286.

Jonson, E.A. 1992. Fire and vegetation dynamics: Studies from the North American boreal forest. Cambridge University Press, Cambridge.

Karppinen, E. 1957. Die Oribatiden-Fauna einiger Schlag- und Brandflächen. *Annales Entomologica Fennica* 23, 181-203.

Koponen, S. 1989. Effect of fire on ground layer invertebrate fauna in birch forest in the Kevo district nature reserve, Finnish Lappland. *Folia Forestalia* 736, 75-80. (In finnish with English summary.)

Koponen, S. 1995. Postfire succession of soil arthropod groups in a subarctic birch forest. *Acta Zoologici Fennici* 196, 243-245.

Krebs, C.J. (1989). Ecological Methodology, 2nd ed., Addison-Welsey Educational Publishers, Inc., Menlo Park, CA. 620 pp.

Krivolutsky, D.A., Lebedeva, N.V. & Gavrilo, M.V. 2004. Soil microarthropods in the feathers of Antarctic birds. *Doklady Biological Sciences* 397, 342-345.

Liacos, L.G. 1977. Fire and fuel management in pine forest and evergreen brushland ecosystems in Greece. In: Mooney,H.A. and Conrad, C.E., technical coordinators. Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Forest service, General technical Report WO-3, pp. 289-298.

Lindberg, N. & Bengtsson, J. 2005. Population responses of oribatid mites and collembolans after drought. *Applied Soil Ecology* 28, 163-174.

Lindberg, N. & Bengtsson, J. 2006. Recovery of forest soil fauna diversity and composition after repeated summer droughts. *Oikos* 114, 1-13.

Linder, P., Jonsson, P. & Niklasson, M. 1998. Tree mortality after prescribed burning in an old-growth Scots pine forest in northern Sweden. *Silvica Fennica* 32, 339-349.

Lindo, Z. & Visser, S. 2004. Forest floor microarthropod abundance and oribatid mite (Acari: Oribatida) composition following partial and clear-cut harvesting in the mixedwood boreal forest. *Canadian Journal of Forest research* 34, 998-1006.

Lucarotti, C.J. 1981. The effect of fire and forest regeneration on mesofauna populations and microfungal species in lichen woodland soils. *McGill Subarctic Research Paper* 32, 7-26.

Lyon, L.J., Crawford, H.S., Czuhai, E., Fredriksen, R.L., Harlow, R.F., Metz, L.J. & Pearson, H.A. 1978. Effects of fire on fauna: A state of knowledge review. US department of agriculture, Forest service. General technical report WO-6, 13 pp.

Madge, D.S. 1965. The effects of lethal temperatures on oribatid mites. *Acarologia* 7, 121-130.

Magurran, A.E. 2004. Measuring biological diversity. Blackwell Science Ltd, Blackwell publishing, Oxford, UK. 256 pp.

Marshall, V.G. 2000. Impacts of forest harvesting on biological processes in northern forest soils. *Forest Ecology and Management* 133, 43-60.

McCullough, D.G., Werner, R.A. & Neumann, D. 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology*. 43,107-127.

Meffe, G.K. & Caroll, C.R. 1994. Principles of conservation biology. Sinauer Associates, Inc. 600pp.

Metz, L.J. & Dindal, D.L. 1975. Collembola populations and prescribed burning. *Environmental Entomology* 4, 583-587.

Metz, L.J. & Farrier, M.H. 1973. Prescribed burning and populations of soil mesofauna. *Environmental Ecology* 2, 433-440.

Muona, J., & Rutanen, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. *Annales Zoologici Fennici* 31, 109-121.

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Norton, R.A. 1985. Aspects of the biology and systematics of soil arachnids, particularly saprophagus and mycophagus mites. *Quaestiones Entomologicae* 21, 523-541.

Norton, R.A. 1994. Evolutionary aspects of oribatid mite life histories and consequences for the origin og the Astigmata. In: M. Houck, Editors, Mites. Ecological and Evolutionary analyses of Life-History Patterns. Chapman & Hall, New York pp. 99-135.

O´Connor, F.B. 1962. The extraction of Enchytraeidae from soil. In: Murphy PW (ed.) Progress in Soil Zoology, pp. 279-285. Butterworths, London.

Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164, 262-270.

Ojala, R. & Huhta, V. 2001. Dispersal of microarthropods in forest soil. *Pedobiologia* 45, 443-450.

Parr, C.L. & Chown, S.L. 2003. Burning issues for conservation: A critique of faunal fire research in Southern Africa. Austral Ecology 28, 384-395.

Pearse, A.S. 1943. Effects of Burning-over and Raking-off Litter on Certain Soil Animals in the Duke Forest. American Midland Naturalist 29, 406-429.

Peterson, G., Allen, C.R. & Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1, 6-18.

Pyne, S.J., Andrews, P.L., & Laven, R.D. 1996. Introduction to wildland fire. John Wiley & Sons, New York.

Ryan, K.C. 2002. Dynamic interactions between forest structure and fire behaviour in boreal ecosystems. *Silva Fennica* 36, 13-39.

Saint-Germain, M., Larrivée, M., Drapeau, P., Fahrig, L., & Buddle, C.M., 2005. Short.term response of ground beetles (Coleoptera: Carabidae) to fire and logging in a spruce-dominated boreal landscape. *Forest Ecology and Management* 212, 118-126.

Schimmel, J. 1993. On fire. Fire behaviour, fuel succession and vegetation response to fire in the Swedish boreal forest. Dissertation in Forest Vegetation Ecology 5. Swedish University of Agricultural Sience, Department of Forest Vegetation Ecology.

Schimmel, J. & Granström, A. 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 7, 1436-1450.

Siira-Pietikäinen, A., Pietikäinen, J., Fritze, H. & Haimi, J (2001). Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. *Canadian Journal of Forest Research* 31, 88-99.

Bengtsson, G., Hedlund, K. & Rundgren, S. 1994. Food- and density-dependent dispersal: evidence from a soil collembolan. *Journal of Animal Ecology* 63, 513-520.

Steward, F.R., Peter, S. & Richon, J.B., 1990. A method for predicting the depth of lethal heat penetration into mineral soils exposed to fires of various intensities. *Canadian Journal of Forest Research* 20, 919-926.

Swaine, M.D. 1992. Characteristics of dry forests in West Africa and the influence of fire. *Journal of Vegetation Science* 3, 365-374.

Tamm, J.C. 1986. Fünfjährige Collembolensukzession auf einem verbrannten Kiefernwaldboden in Niedersachsen (BRD). *Pedobiologia* 29, 113-127.

Thibaud, J-M. 1977a. Intermue et températures léthales chez les insects collemboles arthropléones I. –Hypogastruridae et Onychiuridae. Revue d'Écologie et de Biologie du sol 14, 45-61.

Thibaud, J-M., 1977b. Intermue et températures léthales chez les insects collemboles arthropléones II. –*Isotomidae, Entomobrydae* et *Tomoceridae*. Revue d'Écologie et de Biologie du sol 14, 267-278.

Wikars, L-O. 1992. Forest fires and insects. *Entomologisk Tidskrift* 113, 1-12. (In Swedish, English abstract.)

Wikars, L-O. 1995. Clear-cutting before burning prevents establishment of fire-adapted *Agonum quadripunctatum* (Coleoptera: Carabidae). *Annales Zoologici Fennici* 32, 375-384.

Wikars, L-O. 2001. Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. *Journal of Insect Conservation* 00, 1-12.

Wikars, L-O. & Schimmel, J. 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. *Forest Ecology and Management* 141, 189-200.

Winter, K., Schauermann, J. & Schaffer, M. 1980. Sukzession von Arthropoden in verbrannten Kiefernforsten. *Forstwissenschaftliches Centralblatt* 5-6, 324-340.

Vlug, H. & Borden, J.H. 1973. Soil Acari and Collembola populations affected by logging and slash burning in a coastal British Columbia coniferous forest. *Environmental Entomology* 2, 1016-1023.

Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29, 22-32.

Zhao, S. & Amarine, J.W. Jr. 1997. Investigation of snowborne mites (Acari) and relevancy to dispersal. *International Journal of Acarology* 23, 209-213.

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