JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

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# Complexity of Soil Faunal Communities in Relation to Ecosystem Functioning in Coniferous Forest Soil – A Disturbance Oriented Study

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa (YAA303)
joulukuun 8. päivänä 2001 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Natural Sciences of the University of Jyväskylä,
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UNIVERSITY OF JYVÄSKYLÄ

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Publishing Unit, University Library of Jyväskylä

URN:ISBN:978-951-39-8857-9
ISBN 978-951-39-8857-9 (PDF)
ISSN 1456-9701

ISBN 951-39-1075-X
ISSN 1456-9701

Jyväskylä University Printing House,
Jyväskylä and ER-Paino, Lievestuore 2001

# ABSTRACT

Liiri, Mira
Complexity of soil faunal communities in relation to ecosystem functioning in coniferous forest soil – a disturbance oriented study
Jyväskylä: University of Jyväskylä, 2001, 36 p.
(Jyväskylä Studies in Biological and Environmental Science,
ISSN 1456-9701; 104)
ISBN 951-39-1075-X
Yhteenveto: Maaperän hajottajaeliöstön monimuotoisuuden merkitys metsäekosysteemin toiminnassa ja häiriönsiedossa
Diss.

Soil fauna are known to exert a significant influence on soil processes. However, little is known about the importance of the complexity of soil decomposer communities for ecosystem functioning, and the ability of these systems to withstand disturbances. The objective of the thesis was to relate complexity of soil faunal communities - using (i) functional complexity, (ii) species richness, and (iii) species identity as criteria - to the rate of ecosystem processes (i.e. primary production and nutrient leaching) and the system's susceptibility to disturbances. In addition, the impact of disturbances on soil biota was assessed. Abrupt increase in soil pH (due to wood ash application), and drought were used as disturbances. The experiments were conducted in the field, in field lysimeters, and in laboratory microcosms. The experiments showed that primary production and nutrient leaching and the ability of soils to resist and recover from disturbances were virtually unaffected by the functional complexity and the species richness of soil fauna. Apparently, the functional redundancy among soil fauna is high, and hence, only a small number of species is necessary for soil systems to maintain their functions. However, the enchytraeid, *Cognettia sphagnetorum*, had a significant effect on nutrient mineralisation and plant growth, but whether the effect was stimulative or retarding was largely dependent on environmental factors (i.e. ash-free/ash-treated soil; plant species growing in the microcosms). Soil fauna, in general, were rather resistant to disturbances. However, *C. sphagnetorum* clearly suffered from both wood ash application and drought, but the impact of drought on enchytraeid populations appeared to be temporary. It seems that due to the high resiliency of soil biota, short-term disturbances, such as drought, do not have major consequences on the functions of soil fauna. However, long-lasting perturbations, such as wood ash application, can cause significant changes in the functioning of soils, but the direction of such changes is likely to be context dependent.

Key words: *Cognettia sphagnetorum*; disturbance; functional complexity; nutrient cycling; primary production; soil fauna; species richness.

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# 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 written the first draft of all papers, which were completed with co-authors. In all, except in paper IV, I performed a large part of the work.

I Soil processes as influenced by the functional complexity of soil decomposer food webs under disturbance. Manuscript (submitted)

II Relationship between soil microarthropod species diversity and plant growth does not change when the system is disturbed. Oikos (in press)

III Influence of *Cognettia sphagnetorum* (Enchytraeidae) on birch growth and microbial activity, composition and biomass in soil with or without wood ash. Biology and Fertility of Soils 34: 185-195.

IV The significance of *Cognettia sphagnetorum* (Enchytraeidae) on ecosystem processes in wood ash-treated soil. Manuscript (submitted)

V Community composition of soil microarthropods of acid forest soils as affected by wood ash application. Manuscript (submitted)

# 1 INTRODUCTION

## 1.1 Influence of soil fauna on processes in coniferous forest soil

A large part of the energy fixed by photosynthetic plants eventually goes through the soil food web (Richards 1987). Organic matter returned to soil for example as dead plant residues or root exudates, is decomposed by the soil biota, and nutrients bound to this matter are consequently mobilised for uptake by plants or immobilised to microbial biomass. The major contributors to decomposition processes in soils are soil microbes, but the role of soil fauna in stimulating decomposition processes is well acknowledged. In various habitats, soil macrofauna are the functionally influential faunal group (Anderson et al. 1983, Couture & Fortin 1983, Haimi et al. 1992, Smith & Steenkamp 1992), but in boreal coniferous soils their abundance is low. In these soils micro- and mesofauna are often the most important faunal groups (Persson et al. 1980, Petersen & Luxton 1982). In these habitats, both microfauna, mainly consisting of protozoans and nematodes, and mesofauna, mainly consisting of enchytraeids and microarthropods (i.e. Collembola and Acari), can significantly increase the rate of decomposition of dead organic matter (Setälä et al. 1988, 1991) and nitrogen mineralisation (Huhta et al. 1988, Williams & Griffiths 1989, Abrahamsen 1990, Mikola & Setälä 1998a). Not surprisingly, the uptake of nutrients by plants (Ek et al. 1994) and, ultimatelly, primary production, are influenced by the activity of soil fauna (Setälä & Huhta 1991, Setälä 1995).

The mechanisms by which soil micro- and mesofauna affect soil processes are both direct and indirect. By producing nutrient-rich faeces and by fragmenting organic matter, fauna can directly contribute to soil processes. Fauna indirectly affect soil processes through their interactions with primary decomposers, i.e. soil bacteria and fungi (see reviews by Visser 1985, Moore et al. 1988, Lussenhop 1992, Didden 1993, Couteaux & Bottner 1994, Scheu & Setälä 2001). However, even though the stimulating role of soil fauna in soil processes and the mechanisms by which these organisms affect functioning of soil systems are acknowledged, little is known of how decomposer food web structure, community/functional group composition, or species richness/identity of decomposer fauna are associated with these crucial below-ground processes. This is particularly the case for temperate coniferous forest soils that harbour structurally complex detrital food webs and in which soil macrofauna with well known influence on e.g. soil structure and processes are lacking.

## 1.2 Ecosystem performance and functional complexity of biota

Due to the substantial complexity of natural communities, the formation of simple, causal relationships between individual species and ecosystem functioning can be beyond the bounds of possibility. Hence, it is often practical to reduce this complexity to a manageable level by dividing species into separate functional groups. Since functional groups, by definition, are functionally divergent entities, introduction or removal of such groups from an ecosystem can have significant effects not only on community composition but also on ecosystem function.

When ecosystem functioning is concerned, functional groups are usually defined as groups of species sharing similar biogeochemical features (Vitousek & Hooper 1994, Naeem 1998). This division of species into functional groups is, however, highly arbitrary. For example, functional categorisation of plants can be based on e.g. structural and life strategy characteristics, spatial arrangement, or temporal appearance of plant species (Körner 1994). Soil fauna can be grouped according to their body size (micro-, meso- and macrofauna), habitat selection (depth distribution), trophic position (Verhoef & Brussaard 1990) or life-history strategies of species (Siepel 1994). Due to this diversity, there are no universally valid functional groups, and the position of certain species within functional groups can change when changing the criteria defining these groups (see e.g. Schultze & Mooney 1994, Bengtsson 1998).

Despite the vagueness in the concept of functional groups (see Sullivan & Zedler 1998), the significance of functional group richness and community complexity to ecosystem functioning has been intensively studied, especially in above-ground habitats (Tilman et al. 1997a, Hooper 1998, Hooper & Vitousek 1997, 1998, Hector et al. 1999, Naeem et al. 1999, Sphen et al. 2000, Wardle et al. 2000, Symstad & Tilman 2001). These studies have shown that increasing the number of plant functional groups can lead to improved ecosystem functioning, measured as either plant biomass production (Tilman et al. 1997a, Hector et al. 1999, Naeem et al. 1999, Sphen et al. 2000, Wardle et al. 2000) or the ability of the plant community to withstand parasite infections (Joshi et al. 2000). Studies exploring the relationship between the community complexity of soil fauna and the intensity of ecosystem functioning have found conflicting results: increasing complexity of soil fauna has had both stimulative (e.g. Laakso & Setälä 1999), neutral (e.g. Irmler 2000) and retarding (Tian et al. 1998) effects on soil processes. However, an increasing amount of evidence suggests that, rather than community complexity (or functional group richness) *per se*, it is the identity or characteristics of those species lost from (or added to) an ecosystem that matters (Laakso & Setälä 1999, Wardle et al. 1999).

### 1.2.1 Energy channels in soils

One way to control the complexity of soil communities is to split soil food webs into different compartments (Berg et al. 2001). Soil food webs can be divided into separate energy/nutrient channels based on the ultimate derivation of energy, from either bacteria, fungi, plant roots or dead organic matter (Moore & Hunt 1988, Ingham et al. 1989, Wardle & Yeates 1993). Groups of species within these channels can be considered as functional entities, since interaction between species in separate energy channels is limited and the criteria for structure and stability of a particular energy channel is determined within a separate channel (Moore & Hunt 1988). The structure and the relative importance of energy channels can be manipulated by changing the soil environment. One way of doing this is to change soil pH by applying wood ash to the soil, since wood ash, besides being a fertiliser (Silfverberg 1996), increases soil pH. This process can increase the importance of the bacterial energy channel, since soil bacteria seem to gain relatively more from wood ash application than e.g. soil fungi (Bååth et al. 1995). The changes wood ash creates at the base of the decomposer food web can propagate to the higher levels of decomposer food web. Therefore, wood ash application has the potential to alter the composition and functional complexity of faunal communities by favouring bacterial feeding microfauna (Sohlenius 1979), i.e. nematodes and protozoa, over fungal feeding mesofauna (e.g. Heal & Dighton 1985).

Besides changing the relative importance of energy channels, application of wood ash can also reduce the ability of soil ecosystems to withstand other disturbances, such as drought. Soil bacteria, compared to soil fungi (Schnürer et al. 1986, Moore & Hunt 1988, Whitford 1989), and, similarly, bacterial feeding microfauna, compared to fungal feeding mesofauna (Moore & de Ruiter 1997), are more sensitive to desiccation. Therefore, the functioning of soil systems that derive most of their energy and nutrients from the bacterial-based energy channel is likely to be more prone to drought than those systems that depend on a fungal-based channel.

## 1.3 Species richness and ecosystem function

Increasing anthropogenic interference in natural ecosystems has caused an accelerating depletion of earth's species richness, raising the question of whether the functions of ecosystems and species within ecosystems (e.g. maintenance of atmospheric gaseous composition and cycling of nutrients) are endangered (Ehrlich & Ehrlich 1992, Myers 1996). This concern has led, not only to the formation of several hypotheses of the relationship between ecosystem functioning and species richness, but also to extensive empirical experimentation. The first hypothesis, the "diversity-stability"-hypothesis, was introduced in 1955 by Robert MacArthur, who stated that every species is important for ecosystems to function properly. The "rivet-popper" (Ehrlich & Ehrlich 1981) and the "redundant species"-hypotheses (Walker 1992, Lawton & Brown 1994), in turn, acknowledge that ecosystems do have some redundancy built into them and that some species can be lost without apparent changes in ecosystem functioning (Ehrlich & Walker 1998). The most recent hypothesis, the "idiosyncratic"-hypothesis (Lawton 1994), suggests that taxon diversity affects ecosystem functioning. However, due to the complexity of interactions between organisms, increasing diversity can have either stimulating or retarding effects, but the direction of change can not be predicted (Lawton 1994).

Experiments aimed at elucidating on the relationship between species diversity and ecosystem function have resulted in supportive evidence for all the hypotheses mentioned above (see reviews by Schläpfer & Schmid 1999, Schwartz et al. 2000). Significantly, evidence is accumulating, which supports the idea that communities contain species that can be regarded as functionally replaceable (Lawton & Brown 1994, Andrén et al. 1995, Naeem 1998, Peterson et al. 1998, Walker et al. 1999, Nijs & Impens 2000a). Most of the work done in this field has been conducted in above-ground habitats by altering plant species richness (Schläpfer & Schmid 1999, Schwartz et al. 2000), but studies from aquatic (McGrady-Steed et al. 1997, Naeem & Li 1997, 1998, Jonsson & Malmqvist 2000, Norberg 2000, Emmerson et al. 2001, Engelhardt & Ritchie 2001, Ruesink & Srivastava 2001) as well as from soil systems (Salonius 1981, Degens 1998, Mikola & Setälä 1998b, Van der Heijden et al. 1998, Griffiths et al. 2000, Cavigelli & Robertson 2001, Jonsson et al. 2001) have also been reported.

Soil communities have been described as "the poor man's tropical rainforests" (Usher et al. 1979). This is a quite pertinent depiction because the diversity of soil organisms is high when compared that into other terrestrial habitats (Giller 1996): hundreds of microbial and faunal species can inhabit a handful of forest soil (Torsvik et al. 1994, Brussaard et al. 1997 and references therein). Although soils may be less sensitive to losses in biodiversity than e.g. above-ground habitats, the possibility that soil biodiversity is locally changed due to human activities can not be ruled out (see Wall 1999). Our knowledge of the significance of diversity in affecting soil function is still, however, scanty, and practically nothing is known about how species richness of soil fauna affects the processes in soils (but see Mikola & Setälä 1998b, Laakso & Setälä 1999).

### 1.3.1 Disturbance and the insurance hypothesis

Even though ecologists have been debating the importance of diversity begetting ecosystem stability over half a century (see McCann 2000 for a review), little is known about the relationship between species richness and a ecosystem's ability to resist disturbance and to recover from it (Yachi & Loreau 1999, Wardle et al. 2000). It has been suggested, that as increase in species richness apparently increase the odds of having functionally redundant species in a community (Walker 1992, 1995, Lawton & Brown 1994, Walker et al. 1999), ecosystem functioning should, due to functional compensation among species, be more stable in species rich than in species poor systems (Naeem & Li 1997, Naeem 1998, Yachi & Loreau 1999). In other words, species that seem to be redundant and have a small contribution to ecosystem processes under stable conditions, may become essential when a system faces a disturbance. This can take place either due to loss of formerly important species or due to the better ability of the hitherto "redundant" species in adjusting to new environmental conditions after perturbations. Therefore, high species richness is thought to act as an insurance against environmental uncertainty (Naeem 1998, Yachi & Loreau 1999, Ives et al. 2000).

## 1.4 Species identity and ecosystem function

In addition to functional complexity and species richness, species identity may also be important in regulating ecosystem functioning. In fact, it has been shown that deletion and/or addition of individual species to an ecosystem can cause dramatic changes both to community structure (Paine 1969, Estes & Palmisano 1974, Menge et al. 1994) and ecosystem functioning (Haimi & Boucelham 1991, Hooper & Vitousek 1997, Tilman et al. 1997a, Mikola & Setälä 1998b, Emmerson et al. 2001, Ruesink & Srivastava 2001). Such species, having disproportionate effects on the persistence of other species or having an influence on ecosystem function that is disproportionately large relative to its abundance, are called keystone species (Bond 1994, Power et al. 1996). Ecosystems that are influenced by the presence of one particular species should, thus, be susceptible to disturbances, because the loss of such influential species are likely to have a significant effect on the composition of the remaining species and ecosystem functioning (Brown et al. 2001 and references therein, Lepš et al. 2001). Thus, identification and protection of keystone (or key) species should deserve a high priority in contemporary ecological research (Wall 1999).

It has been suggested that in coniferous soils, the enchytraeid worm, *Cognettia sphagnetorum* (Vejdovský, 1877), fulfils the criteria set for a keystone species (Laakso and Setälä 1999). This species dominates the enchytraeid fauna in acidic coniferous forest soils (Nurminen 1967; Abrahamsen 1972) and comprises a considerable proportion of the total biomass of soil fauna (Persson et al. 1980). *C. sphagnetorum* stimulates decomposition processes (Setälä et al. 1988, Cole et al. 2000) and thus, enhances nutrient mineralisation (Williams & Griffiths 1989, Briones et al. 1998), ultimately having a positive influence on plant growth (Laakso & Setälä 1999, Setälä 2000). However, *C. sphagnetorum* is sensitive to both natural (Yli-Olli & Huhta 2000) and anthropogenic disturbances (Salminen & Sulkava 1996, Salminen & Haimi 1996, 1999, Haimi et al. 2000). It is thus likely that various perturbations of forest soils can negatively affect not only the survival of *C. sphagnetorum,* but also the vital processes this worm is known to carry out.

## 1.5 Aims of the thesis

In this thesis my main objective was to find out how community complexity (I), species richness (II), and identity (III, IV) of soil decomposer organisms affect soil processes, and to explore the susceptibility of these systems to long-term (wood ash) and to short-term (drought) disturbances. In addition, the influence of disturbances on soil decomposer organisms was assessed (I-V). The main hypotheses studied were:

- as community complexity and/or species richness increases, the rate of ecosystem processes will increase. However, the influence of species richness on the rate of ecosystem processes will saturate at high diversity levels [the "redundant species"- hypothesis (Walker 1992, Lawton & Brown 1994)]
- reduced species richness will impair the system's ability to resist disturbances [according to the "insurance" hypothesis (Naeem and Li 1997, Naeem 1998, Yachi & Loreau 1999)]
- wood ash, by altering and simplifying the community complexity of below-ground food webs and by decreasing survival of the enchytraeid *Cognettia sphagnetorum* (a potential key species), will have negative effects on ecosystem performance and the system's ability to withstand drought.

# 2 MATERIALS AND METHODS

## 2.1 Study site and experimental systems

The role complexity of soil faunal communities plays in affecting soil processes and the ability of soils to withstand disturbances was studied in field lysimeters and in laboratory microcosms. In addition, soil samples were taken from a field site.

### 2.1.1 The field site (I, V)

The field study was conducted in a 60-year old Empetrum-Calluna-type pine forest stand in Muhos, central Finland. Eight experimental plots, 30×30 $m^2$ in size, were established in this field site. Four of these plots were treated with 3000 kg of wood ash per hectare.

### 2.1.2 The lysimeters (I)

Twenty plastic lysimeters, containing mineral soil, humus, and litter layers, and a growing seedling of Scots pine (*Pinus sylvestris*, L.), were placed in the experimental plots at Muhos. The lysimeters were used to manipulate body size, and hence the functional complexity, of soil fauna in the systems by allowing either microfauna (lysimeters with 45 µm mesh) or micro- and mesofauna (lysimeters with 1 mm mesh) to enter the systems. Before the defaunated humus and litter materials were placed into the lysimeters, they were divided into two parts: one part was treated with wood ash by gently mixing it with the soil and the litter, whereas the other part was left as ash-free control soil. The amount of wood ash used corresponded to 5000 kg per hectare. Two to four lysimeters were planted on each experimental plot so that the ash-free lysimeters were situated on the control plots and the ash-treated lysimeters on the ash-treated plots (totally 10 lysimeters of both types: five lysimeters allowing the entrance of microfauna and five lysimeters allowing the entrance of micro- and mesofauna).

All lysimeters were disturbed with a 37 week long drought period created by preventing rainwater from entering the lysimeters. The response of the systems to drought was evaluated by comparing the biomass and abundance of soil biota before the disturbance to those after it and by analysing functional parameters, i.e. leaching of N and DOC, immediately after the drought.

### 2.1.3 The microcosms (II-V)

The microcosms used in these experiments were either acrylic cylinders (diameter 17 cm, height 30 cm) containing a seedling of silver birch (*Betula pendula*) (II), or plastic bottles (diameter 8 cm, height 28 cm), containing a seedling of silver birch (III, V) or Scots pine (IV). A simulated forest floor with mineral (II), humus (II-V), fragmentation (II) and litter (II-V) layers was created in the microcosms. The soil materials were defaunated either by heating (II, III, V) or by autoclaving (IV) before placing them in the microcosms. A portion of the microcosms in experiments III-V were treated with wood ash (corresponding to 5000 kg of wood ash per hectare) by mixing ash into the humus and litter (III-V) and by spreading it on the soil surface (IV).

The microcosms were reinoculated with microbes and microfauna either from soil-water-suspension (II, III, V) or from sterile pure cultures (IV) and after that with other fauna, i.e. microarthropods [mites and collembolas (II, III, V)] and *C. sphagnetorum* (III, IV). In experiment II, a diversity gradient of microarthropods, ranging from one to tens of species, was created in the microcosms. In experiments III and V, the introduced microarthropod community was similar among all microcosms. In experiments III and IV, *C. sphagnetorum* was introduced to half of the ash-free and ash-treated microcosms.

The microcosms were disturbed with drought by leading dry air to the airspace of the microcosms (II, III, V). In experiment II, each microcosm was disturbed by drought, but in experiments III and V, some of the microcosms were left undisturbed in order to shed light on the long-term effects of drought on the systems. The "short-term effects" of drought on the systems were evaluated with comparisons of samplings before and right after the drought. Wilting of the birch seedlings was used as an indicator of the severity of the drought. After the drought, the microcosms were irrigated to their original water content.

The microcosms were incubated in randomised order in a climate chamber for two growing periods for the birch (II, III, V) and pine (IV) seedlings. During the incubation, artificial autumn, winter, and spring (not in IV) were created.

## 2.2 Sampling procedures

Sampling during the experiments (I-III, V partially) followed the same general pattern (see Figure 1). After establishment of the experimental systems, the systems were allowed to stabilise before the first sampling was carried out. This sampling indicated a baseline state in the systems. After the first (or second in I) sampling, the experimental systems were disturbed with drought, after which the second (or third in I) sampling was conducted, giving an estimation of the effects of drought in the systems. Then, the experimental systems were allowed to recover from drought, and two more samplings were conducted in later phases of the experiments. The design of experiment IV differed from that of the other studies, in that the systems were sampled only twice and no drought-period was carried out. Duration of the experiments varied from about one year (II-IV, V partially) to almost three years (I, V partially).

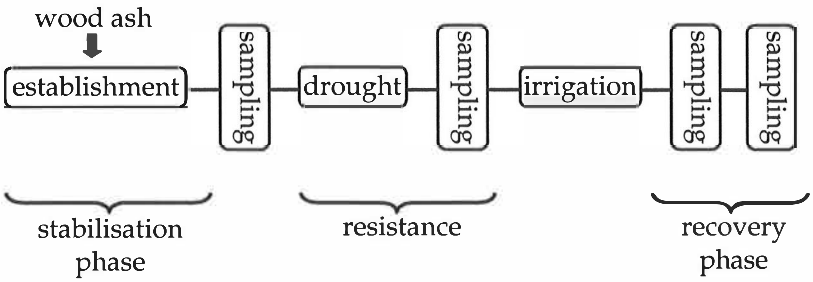

FIGURE 1 General desing of the experiments I-III and V.

## 2.3 Analyses

### 2.3.1 Physico-chemical-analyses

During these experiments, several physico-chemical-parameters that can have an impact on soil biota and that can be affected by soil biota were measured. At each sampling, soil moisture and pH were analysed from the field site and from the experimental systems. Nutrient content of the soil was not analysed, but the ability of the experimental systems to retain nutrients was analysed from leachate waters at the time of the samplings and, in the case of the lysimeters, monthly during the snow-free period of the year. The leachates were analysed for total N (I), $NH_4^+$-N (I-IV), $NO_3^-$-N (I-IV), and dissolved organic carbon (I, III). Cumulative losses were calculated by summing up the values obtained at the samplings (I-II).

### 2.3.2 Biological analyses

Soil fauna (nematodes, enchytraeids, and microarthropods) were extracted from the soil using appropriate extraction methods, and the numbers of individuals were quantified. Community composition of nematodes was analysed (I, III, IV), and microarthropods were identified to species level when possible (I-III, V). Biomass of enchytraeids (I, III, IV) and microarthropods (I-III) was also assessed.

Primary production in the experimental systems was analysed by measuring pine (I, IV) and birch (II, III) biomass production, root to shoot ratio (I-IV), root length (IV), and total N in the leaves or needles of the seedlings. The amount of other vegetation in the field lysimeters was also evaluated (I).

Microbial biomass and community composition were analysed from the humus soil using the PLFA (phospholipid fatty acid) -method of Frostegård et al. (1993) with modifications by Pennanen et al. (1999) (I-III). Biolog® Ecoplates with 31 carbon sources (Biolog Inc., Hayward, California) were used to measure substrate utilisation potential of the soil bacterial community (I, III). The number of the dominant fungal species was estimated by subjecting the purified total DNA of the organic soil (Pennanen et al. 2001) to PCR-amplification using 18S ribosomal DNA primer pairs and separating the resulting amplification products with denaturing gradient gel electrophoresis (DGGE) (Vainio & Hantula 2000) (II, III).

# 3 RESULTS AND DISCUSSION

## 3.1 Ecosystem functioning as affected by community complexity of soil decomposer organisms under disturbance (I)

The significance of community complexity, i.e. the importance of separate energy channels and functional groups of soil decomposer organisms, on soil system functioning was studied in the field lysimeters. Even though the manipulations of biomass, body size and species richness of soil microarthropods using different mesh sizes in the lysimeters, and manipulations of community composition of soil decomposers using wood ash were successful, effects of these manipulations on soil system functioning, measured as pine seedling growth and nutrient leaching, were relatively small. Wood ash had a greater impact on pine seedling growth than had the complexity of soil fauna. Also, pine growth was, unexpectedly, higher in the lysimeters with dense (45 µm) mesh than in those with coarse (1 mm) mesh. Nutrient leaching was practically unaffected by mesh size, whereas wood ash decreased leaching of $NH_4^+$-N during the experiment and increased leaching of $NO_3^-$-N after the drought. Wood ash did not change the ratio of fungal to bacterial biomass. This result contradicts the hypothesis that an abrupt increase in soil pH strengthens the relative importance of the bacterial-based energy channel in the decomposer food web.

In the lysimeters, the biomass of enchytraeids was high compared to that of other soil fauna, especially at the end of the experiment. Because the influence of soil fauna on soil processes is considered to be positively related to their biomass (Anderson et al. 1985, Verhoef & Brussaard 1990), and because the impact of enchytraeids on soil processes can exceed that of microarthropods and nematodes (Laakso & Setälä 1999, Setälä 2000), it seems that the differences in the microarthropod and nematode communities of the experimental treatments were not responsible for the results obtained. However, it is possible that changes at the base of the decomposer food web after wood ash application contributed to ecosystem functioning by decreasing availability of $NH_4^+$-N in the soil and by increasing nitrification rates after drought, thus decreasing the proportion of mineral nitrogen that is preferred by coniferous trees (Marschner et al. 1991, Flaig & Mohr 1992, Kronzucker et al. 1997). The stimulation of nitrification with increasing soil pH is consistent with findings of earlier studies (Paavolainen & Smolander 1998, Priha & Smolander 1999).

The fact that wood ash did not increase losses of $NO_3^-$-N until after the drought may indicate that changes at the base of the decomposer food web resulting from wood ash application can impair the system's ability to withstand other disturbances. In total, however, the results suggest that functioning of boreal coniferous soils is not driven by the community complexity of soil decomposer organisms, and that the community structure and biomass of soil organisms can be altered considerably without major consequences for the functioning of soils.

## 3.2 Ecosystem functioning as affected by species richness of soil microarthropods under disturbance (II)

Parallel to my hypothesis, the species richness of microarthropods was positively related to birch seedling growth and nitrogen availability in the soil. However, the impact of species richness on soil functioning was evident only at the species poor end of the diversity gradient. Hence, ecosystem functioning saturated when only a few microarthropod species were present in the system. This, indeed, supports the view that a large number of species within a "functional group" are functionally redundant (Lawton & Brown 1994, Andrén et al. 1995, Ettema 1998, Naeem 1998, Peterson et al. 1998, Laakso & Setälä 1999, Walker et al. 1999, Nijs & Impens 2000a, Ruess et al. 2001). Species richness of microarthropods was not related to either soil microbial biomass or to their community structure, even though grazing pressure was likely more intense in the diverse systems, since species richness of microarthropods and their biomass had a strong positive correlation in the microcosms. Thus, it seems that microbes were able to compensate for the grazed biomass (see e.g. Hedlund & Augustsson 1995), and, apparently, microarthropods were not strictly selective in their choice of microbial species, since no changes in community composition of microbes were observed (cf. Newell 1984, Maraun et al. 1998).

The positive relationship between species richness and ecosystem functioning can arise from three separate mechanisms: (i) sampling effect, (ii) complementary resource use, and (iii) facilitation (Lawton 2000, Nijs & Impens 2000b, Petchey 2000, Friedley 2001). The sampling effect refers to a situation in which an increase in diversity increases the probability that a system contains the most productive species (or those species best adapted to local conditions) in a particular species assemblage (Huston 1997, Tilman et al. 1997b). However, whether the sampling effect is just an artefact of experimental design or an analogue of an important natural process has been discussed in recent ecological literature (Aarsen 1997, Huston 1997, Tilman 1997,1999, Wardle 1999, Loreau 2000, Lepš et al. 2001). Complementary resource use, in turn, occurs when species richness increases with a concomitant increase in species with a variety of traits and, thus, the proportion of filled niches within an ecosystem. Hence, environmental resources are used more efficiently in species rich than in species poor communities (Hooper 1998, Loreau 1998). Finally, species in an ecosystem may have positive relationships, so that the presence of one species facilitates the performance of an other species in a community (see e.g. Hector et al. 1999, Loreau & Hector 2001). However, applicability of these mechanisms in soil microarthropod communities seems to be poor, because the curve denoting the relationship between microarthropod species richness and plant growth evened out when just a few microarthropod species were present in the microcosms (see paper II). It is probable that, since microarthropod species richness and their biomass were positively related, the differences observed in birch growth between the very simple and the diverse systems resulted not from species diversity *per se*, but from more intensive functioning of the microarthropod community in the diverse systems due to the higher faunal biomass in those systems (Anderson et al. 1985, Verhoef and Brussaard 1990).

The hypothesis that high diversity among functionally redundant species begets stability of communities and ecosystem functioning [the "insurance" hypothesis (Naeem and Li 1997, Naeem 1998, Yachi & Loreau 1999)] was not supported by this study. First of all, during the drought, the biomass of microarthropods decreased practically only in the diverse systems, and the reduction in the nematode and microbial biomasses was not related to the species richness of microarthropods. Furthermore, the recovery of decomposer organisms from the drought was not related to species richness of microarthropods. Secondly, the curve describing the relationship between plant growth and microarthropod species richness should have been steeper closer to the origin after the drought than before it, but the experiment showed no change in this relationship in contrast to the "insurance" hypothesis (see paper II).

Both empirical testing (McNaughton 1977, Tilman & Downing 1994, McGrady-Steed et al. 1997, Naeem & Li 1997, McGrady-Steed & Morin 2000; Mulder et al. 2001) and mathematical modelling (Yachi & Loreau 1999, Ives et al. 2000, Lehman & Tilman 2000) have shown that increasing species richness can increase the stability of communities and, consequently, ensure ecosystem functioning under and/or after disturbance. However, like this study, Wardle et al. (2000) found that increasing plant species diversity was not related to increasing system stability or rate of recovery. In fact, it has been shown that the ability of species poor systems to cope with disturbances can exceed that of species rich systems, if the dominant species in an assemblage respond 'favourably' to the disturbances in question (Sankaran & McNaughton 1999). Hence, it is possible that it is not diversity *per se* that begets stability, but the presence of certain species that survive or even benefit from perturbations (Sankaran & McNaughton 1999). In soils, a large proportion of faunal species are generalists in food choice (Walter 1987, Moore et al. 1988, Gunn & Cherrett 1993). Therefore, these species are more likely to be functionally substitutable.

Consequently, the loss of soil faunal species due to perturbations do not have major long-term implications on functioning of soils.

## 3.3 *Cognettia sphagnetorum*, ecosystem functioning and disturbance (III, IV)

The ability of the enchytraeid worm, *Cognettia sphagnetorum*, to retain its role in wood ash-stressed (III, IV), and later drought-disturbed soils (III) was studied in laboratory microcosms. *C. sphagnetorum* improved nutrient availability in the ash-free soils apparently by producing nutrient rich faeces (Didden 1993, Koutika et al. 2001). Microcosms with *C. sphagnetorum* showed increased amounts of N in the birch leaves (III) and in the leachate water (IV), as well as decreased root to shoot ratio of the pine seedlings (IV). However, previously observed positive effects of *C. sphagnetorum* on biomass production of tree seedlings (Laakso & Setälä 1999, Setälä 2000) were not detected in this study.

*C. sphagnetorum* had interesting influence on plant performance in the ash-treated soils. Wood ash in those microcosms without enchytraeids either increased (III; birch), or decreased (IV; pine) plant growth. The presence of enchytraeids counterbalanced the wood ash-induced effects either by decreasing plant growth (III) or by increasing it to the level of the control systems (IV). This happened even though the populations of worms, parallel to earlier findings (Huhta 1984, Haimi et al. 2000), decreased with increasing soil pH after wood ash application. The fact that *C. sphagnetorum* had a negative effect on plant growth in the ash-treated soil (III) was surprising and difficult to explain. However, as wood ash clearly changed microbial community composition, it is possible that the response of microbes to grazing by enchytraeids differed between the ash-free and ash-treated soil (Visser 1985). Differential functioning of the microbial communities may have led to different nutrient mineralisation rates in the ash-free and ash-treated soils. The positive influence of enchytraeids on plant growth in the ash-treated soils (IV), in turn, was likely related to feeding activities and faecal production of *C. sphagnetorum*. This study strongly suggests that the influence of *C. sphagnetorum* on soil processes, and perhaps that of soil fauna in general (Ingham et al. 1985, Sulkava et al. 1996, Laakso et al. 2000), is dependent on environmental factors, thus being context dependent.

The influence of a certain disturbance on communities and their functioning may depend on the nature and severity of previous perturbations (Hughes & Connell 1999, Fukami 2001). In this study, I hypothesised that wood ash decreases the ability of *C. sphagnetorum* to survive drought, and hence, that the functions of this species are impaired to a greater extent in the ash-treated soils rather than in the ash-free soils. Enchytraeids suffered from decreasing soil moisture, as evidenced by a drastic drop in their biomass during the drought-treatment (III), but after the soil was irrigated to its original water content, their populations recovered to pre-disturbance level. However, I found no indication that worms in the ash-treated soils were more sensitive to a second disturbance. This study indicates that short-term disturbances, such as drought, have small consequences to the overall functioning of soil ecosystems, even though they can temporarily decrease the biomass of soil biota, and probably impair their functions in soil (III). Long-term disturbances, such as increases in soil pH after wood ash-application, can have a significant effect on soil processes and plant growth, but the direction of that effect can change depending on environmental factors (III, IV).

## 3.4 Influence of disturbance on soil faunal communities (I-V)

In this study, the impact of wood-ash [disturbance with a long-lasting effect (Huhta 1984)] and drought (natural, short-term disturbance) on soil fauna was assessed when the two perturbations were separate and simultaneous. The impact of wood ash on soil fauna depended on the faunal group in question. Microarthropods, as a group, appeared to be resistant to the increase in soil pH resulting from wood ash application (I, III, V). However, some species of microarthropods [e.g. *Isotomiella minor* (Schäffer, 1896) and *Tectocepheus velatus* (Michael, 1880)] did suffer, resulting in decreased species richness, although no significant changes, according to PC-analysis, in community structure were observed (V). Enchytraeids, specifically the species *Cognettia sphagnetorum*, was sensitive to the wood ash application in the microcosms (III, IV, see above), but in the field site, enchytraeid populations increased after ash-application. It is possible that enchytraeid species other than *C. sphagnetorum* were present in this area and that these species might have benefited from the increased soil pH (I). Wood ash had both positive (I), neutral (IV), and negative (III) effects on soil nematodes, which emphasises the variety of responses that soil fauna can have to changes in their environment.

In general, soil faunal populations decreased during drought, but recovered to a original level when drought was terminated (I-III). Long-term effects of drought on soil fauna could not be distinguished, as neither faunal abundance nor their community composition differed between the drought-treated and untreated systems (III, V). Microarthropods appeared to be more resistant to the immediate effects of drought than enchytraeids (III, V). Interestingly, the response of soil faunal communities to drought did not differ between the ash-treated and ash-free soils (I, III, V).

Taken together, the results from the field and laboratory experiments suggest that soil fauna, in general, are resistant to disturbances (see also Setälä et al. 2000). Even though perturbations decreased soil microbial biomass (I-III), and changed their community composition (I, III), these changes, taking place at the base of the detrital food web, did not propagate to higher levels of the web (see also Siira-Pietikäinen et al. 2001). These results are consistent with earlier findings that soil fauna can withstand various disturbances (e.g. Haimi & Siira-Pietikäinen 1996, Hodkinson et al. 1996, Siira-Pietikäinen et al. 2001).

## 3.5 From methods to results

The choice of methods used in this study and how they may have affected the results deserves some consideration. Use of microcosms in ecological studies has been criticised (Carpenter 1996, Lawton 1999, Kampichler et al. 2001), and soil ecologists have been urged to move their studies from laboratory microcosms to the field and to field mesocosms (Verhoef 1996). Microcosms are closed artificial systems, with low spatial heterogeneity, bearing little resemblance to natural communities and processes in the field (see Kampichler et al. 2001). Moreover, studying the impact of disturbances on the soil biota and their functions can be problematic in the microcosms. For instance, when wood ash is applied to soil, e.g. via forestry practices, it is spread on the soil surface, from which it gradually percolates into deeper soil layers. In the lysimeters (I) and in the microcosms (III, V, but see IV) wood ash was, however, mixed into the soil. Thus, the impact of wood ash on soil processes and biota could have been overestimated. Also, the impact of drought can be less dramatic in nature than in the microcosms, e.g. due to higher availability of moist microhabitats in nature than in the microcosms or due to hindered vertical movement of soil biota in the microcosms. However, in this study, manipulation of soil faunal communities, such as the establishment of a diversity gradient of microarthropod species, and the creation of systems with or without enchytraeids, would have been practically impossible under field conditions. Despite methodological shortcomings, this study showed that soil fauna can resist disturbances and also recover from them rapidly. Thus, restrictions of the microcosms did not cause overestimates of the impact of disturbances on these systems.

The efficiency of different soil faunal extraction methods, depends on many factors e.g. on soil type. The methods used for faunal extraction in this study are known to be effective in humus soils (see e.g. Phillipson 1971), so I am confident that faunal extractions gave reliable results. The quantitative accuracy of the microbiological analyses in this study may also be questioned (see e.g. Hill et al. 2000, Widmer et al. 2001). However, as all three methods used, PLFA, Biolog, and DGGE, gave parallel results, they apparently revealed true treatment effects. Because the main interest of this study was to detect differences between the treatments, possible quantitative faults in the microbial analyses, will not affect the interpretation of my results.

# 4 CONCLUSIONS

This study gives evidence that community composition and species richness of soil fauna can change considerably without evident changes in soil processes and primary production. It seems that, due to omnivorous feeding habits, functional redundancy among soil invertebrates is high, and hence, a species rich community of soil fauna is not essential for the proper functioning of soils. However, the loss of some important species or groups of fauna, such as the enchytraeid *Cognettia sphagnetorum*, can cause significant changes in soil processes. Predicting the direction of this change is difficult, as the impact of soil fauna on soil processes is shown to be dependent on environmental conditions.

This study further showed that soil fauna are well adapted to short-term environmental perturbations, such as drought: albeit their populations might decrease, at least some of the species are able to recover rapidly after such disturbances. Thus, the influence of short-term, "pulse" disturbances on the functions of soil fauna is likely to be small. However, long-lasting depression of soil biota, e.g. after wood ash application, can have far-reaching consequences on ecosystem functioning, which can ultimately affect even ecosystem productivity.

## *Acknowledgements*

First of all, I would like to thank my supervisors Heikki Setälä and Jari Haimi for their excellent guidance, everlasting patience and encouraging attitude during the years I have worked with my thesis. You had time to listen and help me with my real and sometimes less real problems and I can truly say that this thesis would have never been completed without you two. Besides Heikki and Jari, co-authors of the papers are truly worth acknowledging. Taina Pennanen and Hannu Fritze introduced me a fascinating world of soil microbes, and without their contribution the scientific value of several papers in my thesis would have been significantly lower. Katja Ilmarinen, who did her master's thesis in our group, is thanked for all the hard work she did in establishing, sampling and analysing one of the experiments. I am also grateful to other, former and present, members of soil group: Mustapha Bouchelham, Veikko Huhta, Jouni Laakso, Tuomas Lukkari, Esko Martikainen, Mary Ann McLean, Juha Mikola, Jouni Nieminen, Riikka Ojala, Minna-Liisa Rantalainen and Mika Räty. Interesting scientific and, probably more often, non-scientific conversations in our old coffee room in Freda and recently in new laboratory-like coffee place in Ylistönrinne were nice breathing spells during the days of hard work. In our group meetings you gave me valuable comments on my manuscripts, and I want to especially thank Veikko and Juha for their constructive critics on some of the papers. I also thank Veikko for helping me with identification of mesostigmatid mites and Mary Ann with oribatid mites. Moreover, I am thankful to Matty Berg and Rauni Strömmer for commenting the earlier version of the thesis. During these four years that I have spent with my thesis, trainees, Jenni, Johanna, Leena, Marja, Nipa, Olli, Saana, Tarmo, helped me in different phases of my experiments and I thank each of you for your work contribution. Emily Knott kindly checked the language of the summary. I thank Päivi Tikka and Anneli Rautiainen for helping with microbiological analyses and Kari Nissinen and Harri Högmander for statistical assistance. I am also grateful to fellow researchers as well as to other people working in department for ensuring that our department has been a pleasant place to work in.

This theses was financially supported by the Academy of Finland and the Finnish Forest Federation Industries.

Of course life is more than just work... Arto, my brother and discussions with him, my mother and her delicious lunches on our Sunday trips and my father (together with Ulla, Jorma and Arja) and hilarious parties in summer cottage really helped me to forget all reading and writing I had ahead of me at work. Besides my family, I am grateful to all of my friends for giving me something else than work to think about and keeping me in touch with "the real world". And last, but definitely not least, I thank my dear husband, Sami, for his love and support during all of these years we have been together.

# YHTEENVETO

## Maaperän hajottajaeliöstön monimuotoisuuden merkitys metsäekosysteemin toiminnassa ja häiriönsiedossa

Maaperäeläinten on havaittu vaikuttavan maan prosesseihin, kuten orgaanisen aineksen hajotukseen ja ravinteiden mineralisaatioon ja siten myös perustuotantoon. Väitöskirjatyössäni tutkin, miten maaperäeläinyhteisön monimuotoisuus vaikuttaa sekä metsämaaperän prosesseihin ja kasvien kasvuun että metsämaaperän kykyyn sietää häiriöitä. Lisäksi selvitin, miten häiriöt (puuntuhka ja kuivuus) vaikuttavat maaperäeläinpopulaatioiden runsauteen ja niiden yhteisörakenteeseen.

Kokeita tehtiin sekä maastossa että laboratoriossa. Maastoon, jossa oli sekä puuntuhkalla käsiteltyjä että käsittelemättömiä koeruutuja, sijoitettiin 20 puolisuljettua lysimetriä, joista puolessa oli puuntuhkalla käsiteltyä humusmaata ja puolessa tuhkalla käsittelemätöntä maata. Lisäksi jokaiseen lysimetriin istutettiin männyntaimi. Lysimetrien sivussa oli joko 45 µm:n tai 1 mm:n verkko, jonka avulla manipuloitiin maaperäeläinten pääsyä lysimetreihin niiden koon perusteella ja siten maaperäeläinten toiminnallista monimuotoisuutta systeemeissä. Kokeen aikana maanäytteitä otettiin sekä lysimetrien sisäpuolelta että niiden ulkopuolelta. Laboratoriokokeet tehtiin mikrokosmoksissa, joissa kasvoi joko rauduskoivun- tai männyntaimi kangasmetsän humuksessa, josta eläimet oli aluksi tapettu kuumentamalla. Tämän jälkeen jokaiseen mikrokosmokseen lisättiin maaperän mikrobisto, mikrofauna ja tietyt maaperäeläimet kunkin kokeen tavoitteiden mukaisesti. Maaperäeläinten lajirikkauden merkitystä metsämaaperän toiminnassa ja häiriönsiedossa tutkittiin luomalla mikrokosmoksiin punkkien ja hyppyhäntäisten lajidiversiteettigradientti siten, että mikrokosmoksen lajilukumäärä vaihteli yhdestä useaan kymmeneen mikroniveljalkaislajiin. Änkyrimadon, *Cognettia sphagnetorum*in merkitystä häiriöitetyn metsämaan toiminnassa tutkittiin lisäämällä maahan puuntuhkaa. Lysimetrit ja mikrokosmokset häiriöitettiin myös kuivuudella, minkä jälkeen maa kasteltiin alkuperäiseen kosteuteensa. Osassa laboratoriokokeista viisi mikrokosmosta jätettiin kuitenkin häiriöttömiksi kontrolleiksi.

Maaperäeläinten toiminnallinen monimuotoisuus tai niiden lajirunsaus ei juurikaan vaikuttanut maan prosesseihin, kasvin kasvuun tai maaekosysteemin kykyyn sietää häiriöitä. Änkyrimadolla (*C. sphagnetorum*) oli kuitenkin merkittävä, joskin epäennustettava vaikutus koemaassa: tuhkattomissa mikrokosmoksissa änkyrimadolla oli positiivinen vaikutus ravinteiden saatavuuteen mutta ei kasvin kasvuun. Tuhkallisissa maissa änkyrimato joko vähensi tai lisäsi puunkasvua riippuen siitä, oliko kasvina koivu vai mänty. Tulokset viittaavat siihen, että suuri osa maaperäeläimistä on toiminnallisesti korvattavia ja siten maaperän toiminnassa ei tapahdu suuriakaan muutoksia lajien häviämisen myötä. Kuitenkin eräiden tärkeiden lajien, kuten *C. sphagnetorumin*, häviäminen voi vaikuttaa maaekosysteemin toimintaan ja sen häiriönsietoon, joskin vaikutus näyttäisi tutkimustulosten perusteella olevan riippuvainen ympäröivistä olosuhteista. Tämän seurauksena yksittäisten lajien, kuten esimerkiksi *C. sphagnetorum*in häviämisen vaikutuksien ennustaminen on käytännössä vaikeaa.

Häiriöt, puuntuhkan aiheuttama maan pH:n nousu sekä kuivuus, olivat luonteeltaan hyvin erilaiset, sillä tuhka oli häiriönä pitkäkestoinen, kun taas kuivuus oli kestoltaan lyhyt ja palautuva. Tässä tutkimuksessa sukkulamadot ja mikroniveljalkaiset sietivät keskimäärin hyvin häiriöitä, kun taas änkyrimato oli herkkä sekä maan pH:n nousulle että kuivuudelle. Kuivuuden jälkeen änkyrimatopopulaatiot palautuivat kuitenkin nopeasti. Lyhytkestoisilla häiriöillä, kuten kuivuudella, ei todennäköisesti ole suurtakaan vaikutusta maaperän toimintaan maaperäeläinten – kuten myös mikrobien – nopean palautumiskyvyn vuoksi. Pitkäkestoisella häiriöllä, kuten maan pH:n nousulla, voi sen sijaan olla maaperäeläinten toiminnan muuttumisen myötä vaikutusta aina perustuotantoon asti.

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## Original papers

### I

# Soil processes as influenced by the functional complexity of soil decomposer food webs under disturbance

by

Mira Liiri, Heikki Setälä, Jari Haimi,
Taina Pennanen and Hannu Fritze
Manuscript (submitted)

https://doi.org/10.1016/S0038-0717(02)00034-2

II

## Relationship between soil microarthropod species diversity and plant growth does not change when the system is disturbed.

by

Mira Liiri, Heikki Setälä, Jari Haimi,
Taina Pennanen and Hannu Fritze

Oikos (in press)

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http://dx.doi.org/10.1034/j.1600-0706.2002.960115.x

III

# Influence of *Cognettia sphagnetorum* (Enchytraeidae) on birch growth and microbial activity, composition and biomass in soil with or without wood ash

by

Mira Liiri, Heikki Setälä, Jari Haimi,
Taina Pennanen and Hannu Fritze 2001

Biology and Fertility of Soils 34: 185-195

https://doi.org/10.1007/s003740100397

IV

# The significance of *Cognettia sphagnetorum* (Enchytraeidae) on ecosystem processes in wood ash-treated soil

by

Mira Liiri, Katja Ilmarinen and Heikki Setälä

Manuscript (submitted)

**https://doi.org/**10.1023/A:1021515313890

V

# Community composition of soil microarthropods of acid forest soils as affected by wood ash application

by

Mira Liiri, Jari Haimi and Heikki Setälä

Manuscript (submitted)

https://doi.org/10.1078/0031-4056-00118