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Jouni Laakso

Sensitivity of Ecosystem Functioning
to Changes in the Structure
of Soil Food Webs



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1998

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ABSTRACT

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Diss.

The main objective of this thesis was to assess the functionally important features in the detrital food web of coniferous forest soil by studying the role of top-down influences and species composition of trophic groups in the functioning of the food web. I manipulated food web structure in microcosms containing defaunated humus and litter, a birch seedling infected with ectomycorrhizal fungi, and a diverse microbial community. The faunal composition was also manipulated under N-poor and N-enriched conditions to assess whether the outcome of trophic interactions is sensitive to the availability of N. The role of wood ant *Formica aquilonia* Yarr. in the soil food web and system functioning was studied using field samplings and manipulations of wood ant density. In the laboratory experiments the biomasses of microbivorous and microbi-detritivorous grazers were effectively controlled by their predators. The influence of animal grazers on microbial biomass and respiration was weak and predators of grazers could exert only a weak positive influence on microbial biomass and activity. Field studies revealed that wood ants are negatively associated with other invertebrate predators and positively associated with earthworms. Feeding trials showed that earthworms have antipredatory defence against wood ants. However, the overall effect of wood ants on soil food web was weak outside the nest mounds. The presence of a diverse microbivore and microbi-detritivore community, and maintenance of nest mounds by wood ants increased species richness of soil fauna. N mineralisation, and plant growth and N uptake increased in the presence of microbivorous and detritivorous fauna but their predators generally had a weak influence on these processes. N-enrichment magnified the influence of food web structure on microbial biomass and plant N uptake, and modified the outcome of animal-microbial interactions. Wood ants did not influence N dynamics and plant growth outside the nest mounds. The weak propagation of top-down influences and high number of functionally redundant species suggest that ecosystem functioning is robust against changes in the structure of below-ground food webs.

Key words: Decomposition; food web; earthworms; nutrient cycling; primary production; silver birch; soil fauna; wood ants.

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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 performed most of the work.

- I Laakso, J. & Setälä, H. Population and ecosystem-level consequences of predation on microbial feeding nematodes. Manuscript (submitted)
- II Laakso, J. & Setälä, H. Primary productivity and functional redundancy in belowground food webs. Manuscript (submitted)
- III Laakso, J., Setälä, H. & Palojarvi, A. Control of primary production by decomposer food web structure in relation to nitrogen availability. Manuscript (submitted)
- IV Laakso, J. & Setälä, H. 1998. Composition and trophic structure of detrital food web in ant (*Formica aquilonia*) nest mounds and in the surrounding soil. *Oikos* 81:266-278
- V Laakso, J. & Setälä, H. 1997. Nest mounds of wood ants (*Formica aquilonia*): hot spots for litter-dwelling earthworms. *Oecologia* 111:565-569.
- VI Laakso, J. Short-term effects of wood ants (*Formica aquilonia* Yarr.) on soil animal community structure. Manuscript (submitted)
- VII Laakso, J. & Setälä, H. Impacts of wood ants (*Formica aquilonia* Yarr.) on the invertebrate food web of boreal forest floor. Manuscript (submitted)

1 INTRODUCTION

Havunneulanen, tuo metsämaamme pieni banaani

Janne Salminen

1.1 Soil food webs as a tool in linking population and community ecology

Population and ecosystem level phenomena are frequently studied separately although unification of these disciplines is often proposed to lead to significant advancement of ecological theory and its empirical testing (VanVoriss et al. 1980, O'Neill et al. 1986, DeAngelis 1992, Brown 1995, Grimm 1995, deRuiter et al. 1995, Zheng et al. 1997, Loreau 1998). Importantly, the knowledge covering both disciplines can be applied to pressing environmental problems caused by humans. For example, prediction of the consequences of declining biodiversity to ecosystem functioning (e.g. Tilman et al. 1996, McGrady-Steed et al. 1997), or manipulation of ecosystem productivity by inducing structural changes in food webs (Carpenter & Kitchell 1988) require a common language between the two disciplines.

Decomposer food webs are considered to be an important tool in the study of population–ecosystem interface due to their large contribution to energy and nutrient fluxes, and influences on structural properties of ecosystems (Bengtsson et al. 1995). Decomposer food webs are also qualitatively different from aboveground systems because the renewal rate of the primary resource, dead organic matter, is not directly affected by trophic interactions. Consequently, decomposer communities are regarded as “donor controlled” (Pimm 1982, Begon et al. 1990). However, there is an increasing amount of evidence that decomposers can exert an indirect control over their resource renewal by affecting the availability of growth limiting nutrients for the plants. Thus, besides bridging direct feeding interactions and ecosystem processes, the

indirect nature of decomposer–plant interactions makes decomposer food webs suitable to assess the importance of indirect or non-feeding interactions in communities.

Although soil ecology has a relatively long tradition in coupling population and ecosystem level processes, these relationships are in most cases studied without considering the interactions between decomposers and primary producers (e.g. Hunt et al. 1987, Setälä et al. 1991, Zheng et al. 1997). Besides providing a continuous supply of energy to the soil, plants can influence microbial community by competing for limiting mineral nutrients, and excrete growth regulating substances (Grayston 1997, Wardle 1992). These interactions have, in turn, a potential to modify animal–microbe interactions, suggesting that primary producers are influential enough to affect the outcome of food web interactions in soils.

Besides abiotic conditions and quality of the decomposing substrate (Williams & Gray 1974), the structure of decomposer food webs is considered to have a profound influence on decomposition and nutrient mineralisation (Verhoef & Brussaard 1990). In addition to the direct contribution of soil microbes and fauna to these processes, feeding interactions among soil organisms can regulate decomposition by affecting biomass and composition of the decomposer community (e.g. Swift et al. 1979, Visser 1985, Verhoef & Brussaard 1990). For example, microbivorous and microbi-detritivorous fauna is known to control microbial biomass and activity, and hence indirectly affect decomposition and nutrient mineralisation. In a similar way carnivores, albeit having a smaller biomass and hence a smaller direct contribution to nutrient and energy flows than their prey (Hunt et al. 1987, Persson et al. 1980), have a potential to indirectly affect excretion of N and microbial activity by controlling the biomass of detritivores and microbivores (e.g. Swift et al. 1979, Moore et al. 1988, Bengtsson et al. 1996).

1.2 Importance of top-down and bottom-up forces, and horizontal heterogeneity in food webs

Trophic dynamic theories (e.g. Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985, McQueen et al. 1986, Arditi and Ginzburg 1989) provide a starting point to assess the controlling role of feeding interactions, i.e. top-down forces on the biomasses of organisms. Recently this trophic dynamic framework has been used to bridge trophic structure and decomposition rate (Zheng et al. 1997), but this approach may still be immature because it lacks many features known to regulate decomposition processes, such as substrate quality (Williams & Gray 1974) and interactions with autotrophs (Grayston 1997, Wardle 1992). The predictions of trophic dynamic theories on the relative importance of top-down and bottom-up forces depend heavily on the type of interactions between the levels. Models assuming existence of strong top-down control and uniformly behaving trophic levels (Oksanen et al. 1981, Carpenter et al. 1985)

predict that the lowest levels of the food web, and hence the system functioning (Zheng et al. 1997) are strongly influenced by predators. In the opposite view, trophic levels are unaffected by the next adjacent levels (donor controlled interactions sensu Pimm 1982), which suggests that feeding interactions high up in the food chain have a minor role in system functioning (Zheng et al. 1997). In the latter case, the influence of soil fauna on C and N fluxes is predictable solely on the basis of organism biomasses and knowledge on the physiology of the organisms (Hunt et al. 1987). Significant top-down influences are known to exist in detrital food webs (e.g. Moore et al. 1988, Laakso et al. 1985, Mikola & Setälä 1998a), but the anti-predatory adaptations of soil fauna (e.g. Hopkin 1997), and refugia offered by the complex structure of the soil matrix (Elliott et al. 1980, Rutherford et al. 1992) can also reduce the strength of these influences. Moreover, it is an open question whether the complexity of real food webs can be successfully reduced to chain-like, homogeneously behaving entities assumed by trophic dynamic models: real food webs possess many features, such as omnivory and reticulatedness, that can confound trophic level dynamics (Strong 1992, Polis & Strong 1996, but see Hairston & Hairston 1997). Therefore, it is relevant to ask (i) whether the functional organisation of the food web can be described using large groupings of organisms, and (ii) what is the relative importance of top-down and bottom-up forces in regulating the functional groups (Menge 1992).

Besides feeding interactions, the characteristic response of ecosystem functioning to changes in the structure of the food web depends on the degree that species or groups of species can compensate for each other's roles in the system (e.g. Chapin et al. 1997). High number of functionally similar (competing) species can increase the stability of trophic level biomasses, and consequently promote the stability of system functioning to species deletion (Pimm 1982, King & Pimm 1983, Lawton & Brown 1994). Alternatively, if species within a trophic level are inflexible in their use of food resources, or have Heterogeneous responses to predators, the strength of trophic interactions (Leibold & Wilbur 1992, Abrams 1993) and system functioning (Lawton & Brown 1994) can be sensitive to species loss. Decomposer organisms are known for their widely differing dietary requirements (Siepel & de Ruiter-Dijkman 1993, Ponge 1991), life history traits (e.g. Hopkin 1997) and tolerance to disturbance (Salminen et al. 1997), which suggests that the functioning of the extremely species-rich decomposer communities is fragile to changes in species composition and diversity (Beare et al. 1995). An opposing hypothesis is that a complex and diverse soil biota is functionally highly redundant, and only few key species exist (Andrén et al. 1995).

In this thesis I aimed to assess the functionally important components and interactions in the detrital food web of boreal forest floor by manipulating the structure of soil food webs. To clarify the role of top-down forces in the food web, I manipulated the presence of

- microbi-detritivorous fauna (II, III)
- microbivorous fauna (I-III)
- predators of microbivores and microbi-detritivores (I-III)
- large invertebrate predators, i.e. wood ants (IV-VII)

As detritivorous and microbivorous fauna are known for their significant direct and indirect contributions to decomposition and nutrient cycling (Verhoef & Brussaard 1990), I also assessed the role of horizontal heterogeneity of this fauna by controlling

- the composition of microbivorous fauna at the level of trophic groups in the fungal and bacterial energy channels (I-III)
- the composition of fungivorous and microbi-detritivorous fauna at the level of species (II, III)

A general hypothesis throughout the study was following: strong top-down control in the food web should theoretically increase the sensitivity of system functioning to changes in the vertical structure of the community (sensu Oksanen et al. 1981, Carpenter et al. 1985, Zheng et al. 1997). Similarly, if species occupying the same trophic position are highly differentiated e.g. in their resource use, and hence unable to compensate each others roles (Beare et al. 1995), system functioning should also be sensitive to the variation in the horizontal structure of the food web.

2 METHODS

The organisms chosen for this study (Fig. 1, IV) are abundant components of the food web of boreal forest, and thus have a potential to be functionally important. Body size of the study organisms dictated whether the role of a particular species or trophic group was studied under laboratory conditions or in the field: micro- and mesofauna was studied under laboratory conditions, whereas macrofauna, i.e. wood ants were studied predominantly in the field. Although the generality of results obtained from laboratory experiments is frequently questioned (Carpenter 1996), comparisons of soil microcosm studies and field data have demonstrated that community and ecosystem processes can be closely mimicked using this approach (Verhoef 1996, Fraser & Keddy 1997). Moreover, the microcosms in this study are self-sustainable due to the presence of plants providing a continuous flow of energy and preventing unnatural accumulation of mineral nutrients in the soil; hence, the term "miniecosystem" instead of microcosm is boldly used in the text.

To test the relative importance variation at the level of species vs. trophic groups in the laboratory experiments, and to analyse the field data, I classified the soil organisms to coarsely-defined functional groups using the available and highly incomplete literature data on feeding preferences (for details see the original papers). It should be noted that this classification is only one tentative solution to the problem of aggregating species into functional groups, and the results should be viewed bearing this in mind.

The following two chapters contain an overview of methods applied in the experiments (I-VII).

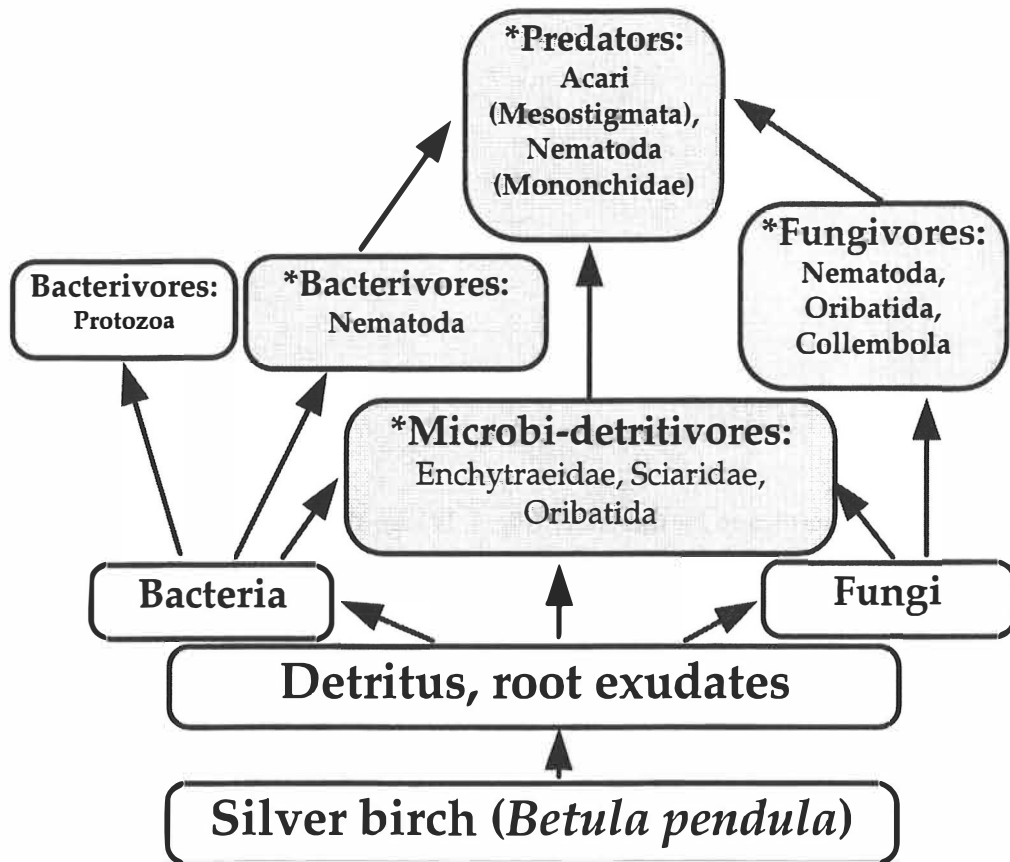


FIGURE 1 Schematic description of the detrital food web and feeding relationships in the laboratory food webs (I-III). Faunal groups marked with an asterisk were manipulated in the experiments. The microbial communities included mycorrhizal fungi and a diverse community of heterotrophic bacteria and fungi.

2.1 Miniecosystem experiments with soil micro-and mesofauna (I-III)

The miniecosystem experiments used semi-open, transparent containers (volume 1.5 L) in which birch seedlings (*Betula pendula*) infected with ectomycorrhizal fungi were growing in coniferous forest soil. The soil profile included defaunated litter and raw humus layers. All miniecosystems contained a diverse microbial community with bacteria, fungi and protozoa.

The experimental designs consisted of decomposer communities with varying faunal structure. The soil animal assemblages were constructed

hierarchically to obtain varying numbers of i) functional groups (I-III) and ii) animal species within each group (II and III). In experiment III the faunal treatments were also repeated under nitrogen-poor and N-enriched conditions to test whether the availability of N can influence the outcome of faunal and microbial interactions. The fauna used in the experiments was obtained from pure cultures (Nematoda and Sciaridae) or extracted from coniferous forest soil using large Tullgren funnels for microarthropods, and wet funnels for enchytraeids. Specimens extracted from soil were identified under dissecting microscope, stored in 2°C, and rinsed on nylon mesh to remove phoretic animals (e.g. Nematoda and microarthropods) prior to introduction to the miniecosystems.

The miniecosystems were incubated in a climate chamber with a daily cycle of 20 h light (photosynthetically active radiation $\sim 600 \mu\text{E}/\text{m}^2$), and with a temperature of 12-18°C during the summer, gradually decreasing to 0 h light and 1°C during the winter. After the second growing period for the birch, plant biomass and nitrogen uptake, composition of soil fauna, microbial activity and biomass, soil pH and water holding capacity, and 2 M KCl-extractable NH_4^+ and NO_3^- in the soil were analysed in each miniecosystem (I-III). In paper III also the structure of microbial community was determined by measuring concentrations of phospholipid fatty acids (PLFA) in soil. This paper also included measurements for NH_4^+ and NO_3^- , and numbers of nematodes in water leachates.

2.2 Field observations and experiments with wood ants (IV-VII)

The influence of wood ants (*Formica aquilonia* Yarr.) on the food web of boreal forest floor was first studied by mapping soil fauna, vegetation and soil properties at differing distances from wood ant nests and trails in a study area located in Konnevesi, Central Finland (IV). As this study revealed a previously unknown, positive association with wood ants and earthworms, and both are potential key taxa in the food web, the mechanisms allowing this association was further studied using wood ant colonies transferred to laboratory (V). In this study the behaviour of wood ants toward different species of earthworms and insect prey were monitored.

The next phase of the study included manipulation of wood ant density in the study area in a short-term field-mesocosm experiment (VI). The presence of wood ants was manipulated by placing mesocosms permeable to ants on ant trails, and outside the trails. The 1.8 l mesocosms contained litter and humus, and a diverse soil fauna typical in coniferous forest. While constructing the food webs, I put a special emphasis on two earthworm species by inoculating a known biomass of the epigeic lumbricids *Dendrobaena octaedra* (Sav.) or *Dendrodrilus rubidus* (Sav.) to the mesocosms. Soil animal densities were determined six weeks after the establishment of the experiment.

Finally, a long-term field experiment (VII) was established to study the impact of wood ants to the structure of the food web and to assess whether wood ants can induce changes in the system functioning. In this experiment wood ant density was manipulated by removing entire wood ant colonies from five areas and leaving five intact areas as a control. To reduce habitat heterogeneity, soil organic layer was removed from two circular plots (area 0.44 m²) at three meter distance from each of the nest mound under study. A new, homogenous soil profile was constructed on the plots, after which two spruce, pine and birch seedlings were planted on each of the plots. After the removal of wood ant colonies, changes in the invertebrate community in the homogenised plots, in the litter layer of the soil surrounding the patches, and on the nearby vegetation were monitored for three growing periods. Functional consequences of ant removal were addressed by measuring concentrations of mineral nitrogen in the soil of the homogenised patches five times during the experiment. At the destructive sampling microbial biomass, and plant N uptake and biomass were measured from the homogenised plots.

3 RESULTS AND DISCUSSION

3.1 Influence of vertical variation in the food web on organism biomasses and system functioning

Effective propagation of predatory influences down in a food web requires that prey at each trophic level is strongly influenced by their predators (DeAngelis 1992). As predators have usually a low biomass and thus little direct influence on system functioning (Persson et al. 1980, Hunt et al. 1987), a prerequisite for predator-induced changes in system functioning is that predators should have a control over high-biomass species (Moore et al. 1988). In this study, the biomasses of microbivorous and microbi-detritivorous grazers were generally effectively controlled by their predators (I-III), but the influence of animal grazers on microbial biomass and respiration was considerably weaker (I-III). These results are in general agreement with other works focusing on animal-animal (Martikainen & Huhta 1990, Setälä et al. 1991, Brussaard et al. 1995, Mikola & Setälä 1998a and b) and animal-microbe (Brussaard et al. 1995, Mikola & Setälä 1998a and b) interactions in soil food webs. However, that predators of microbivorous and microbi-detritivorous animals nevertheless exerted a weak positive influence on microbial biomass (III) and activity (I) suggests that trophic cascades (*sensu* Oksanen et al. 1981, Carpenter et al. 1985) can occur in soil food webs (see also Santos et al. 1981 for field data). Mikola & Setälä (1998a) suggested that excretion of nutrients (e.g. mineral N) by microbial grazers, and the subsequent increase in microbial activity (Hanlon 1981, Ingham et al. 1985) can be one of the main mechanisms preventing the occurrence of cascading effects to the level of microbes. The amount of mineral N in the soil of the autotrophic miniecosystems (I-III) was however very low in the current studies, which implies that microbial growth was N-limited (Wardle 1992, Breland & Bakken 1991) and thus more prone to be efficiently controlled by their grazers than microbes in previous studies in the absence of plants. This suggests that plant-induced limitation in the availability of N for the microbes can modify the

grazer–microbe interaction and serve as a mechanism that permits weak cascading effects on microbes to occur in autotrophic systems.

Manipulation of wood ant density in the field revealed a negative interaction between wood ants and invertebrate predators belonging to Araneae, Opiliones and Coleoptera (VI, VII). That the ant-induced reduction in the predator biomass was accompanied with positive effects on predatory mites and litter-dwelling earthworms suggests that cascading influences can also exist high up in the invertebrate food web. Although earthworms appear to be a potential prey for the ants, an antipredatory defence mechanisms by the earthworms seems to hinder the occurrence of predatory interaction: feeding trials in laboratory (V) showed that mucus secreted by earthworms is repulsive to wood ants. Apart from predators and earthworms, the majority of soil organisms did not respond to changes in the density of wood ants. This indicates that interactions between wood ants and other taxa are generally weak or that compensatory mechanisms exist in the food web, as suggested by the increased amount of other invertebrate predators under low wood ant density (VII).

Taking both laboratory and field experiments together, the magnitude and direction of faunal-induced changes in system functioning was inversely dependent on the trophic position that a species or a trophic group occupied. Microbivores and especially microbi-detritivores had a clear positive effect on N mineralisation, plant N uptake and growth, whereas predators of these fauna had a negligible or a negative effect on these processes (I-III). Moreover, the removal of wood ants (VII) did not reflect to system functioning. Thus, these experiments show that ecosystem functioning is most sensitive to changes close to the base of the decomposer food web.

The insensitivity of ecosystem functioning to changes at the top of the food web corresponds to my findings that predators have only a weak influence on the biomass of species other than their prey. Thus, the prerequisite for the occurrence of predator-induced changes in system functioning, i.e. strong top-down control of high-biomass trophic groups responsible for decomposition and N mineralisation, did not take place. The reasons for the weak role of top-down influences in soils are likely to include compensatory growth of microbes under grazing (Mikola & Setälä 1998a), antipredatory defences of soil animals (V, Hopkin 1997), complex spatial structure offering refugia (e.g. Elliott et al. 1980, Rutherford et al. 1992) in the soil matrix, and heterogenous responses of trophic groups to predators (Polis & Strong 1996). The weak propagation of top-down influences suggests that trophic-dynamic models emphasising donor-controlled (Pimm 1982) or ratio-dependent prey-predator interactions (Arditi & Ginzburg 1989) may better describe soil food webs than the models assuming strong top-down control (Oksanen et al. 1981, Carpenter et al. 1985). Moreover, that microbial biomass was clearly less affected by grazers than microbivorous and microbi-detritivorous fauna by their predators, suggests that models using different trophic functions for microbe-faunal and faunal-faunal interactions are required.

3.2 Influence of horizontal variation in the food web on organism biomasses and system functioning

Together with the vertical structure of the food web, the degree that species within a functional group differ in their properties – such as resource use and vulnerability to predators – can determine how other functional groups and ecosystem functioning respond to changes in the species composition (e.g. Abrams 1993, Lawton & Brown 1994). Moreover, the ability of species aggregates, such as trophic levels, to successfully simplify description of structure-function relationships in the ecosystem depends on the homogeneity of the functional groupings (Polis & Strong 1996).

The species composition of microbivorous and microbi-detritivorous fauna clearly affected the biomass and vulnerability of these groups to predators in the laboratory experiments (I-III). Moreover, diverse and high-biomass prey communities were able to sustain higher biomass and diversity of predatory fauna than communities with low species diversity and biomass (I, II). Despite these differences the responses of microbes and system functioning to species composition of microbivorous and microbi-detritivorous fauna were less clear. Variation in the composition of both microbivorous nematode community (I), and in the species composition microbivorous arthropods (II) had little influence neither on their microbial prey nor on system functioning. However, the species composition of microbi-detritivorous trophic groups proved to have an important role in the system functioning: the enchytraeid *Cognettia sphagnetorum* had an unproportionally large contribution to community biomass, and significantly enhanced N mineralisation, plant N uptake and growth, and affected the physical properties of the soil (II, III).

These observations demonstrate the importance of species composition and diversity of microbivorous and microbi-detritivorous fauna in controlling the biomass of upper trophic levels, and in modifying the strength of trophic interactions. That only one species (*C. sphagnetorum*) was functionally irreplaceable implies that functional redundancy among microbivorous and microbi-detritivorous fauna is high. Although the design of these experiments does not allow a strong test for species diversity-function relationship due to the limited number of species combinations (see Huston 1997) and trophic groups, the results nevertheless appear to support the redundant species hypothesis (Andrén et al. 1995). Further, the important role of *C. sphagnetorum* gives some support to the idiosyncratic response hypothesis (Lawton 1994) according to which species diversity has an irregular relationship with system functioning. The high biomass and important role in system functioning, together with the low abundance of other oligochaeta taxa in boreal forest soil (e.g. Persson et al. 1996) suggest that *C. sphagnetorum* warrants to be called as a keystone species in the system.

3.3 Influence of nitrogen availability on the outcomes of trophic interactions

The influence of decomposer fauna on nitrogen mineralisation and plant growth is suggested to be highest under N-poor conditions because N is generally limiting primary productivity (Elliott et al. 1979, Ingham et al. 1985). Results of experiment III appear to contrast this prediction: The relative importance of decomposer food web structure on plant growth was not smaller under N-enriched than under N-poor conditions. Interestingly, N-enrichment magnified the influence of food web structure on microbial biomass and plant N uptake; the effect of N enrichment on plant N uptake was 50% higher in miniecosystems with simple microbi-detrivore communities, than in communities with nematodes only, or in complex microbi-detrivore communities. Thus, under N-enrichment the food web structure appeared as a key determinant for the division of N between plants and the soil matrix.

It is possible that the N-enrichment did not fully remove N-limitation in the miniecosystems. However, this can only partially explain these results: the observed N-induced shift in the C:N-ratio and biomass of soil microbes, and in the structure of the microbial community suggest that the increase in faunal-induced variation in plant N uptake and microbial biomass in the N-enriched systems resulted from N-induced changes in the animal-microbe interactions. The mechanisms bringing about the change in microbial community are likely to include a direct enhancement of microbial growth and an alteration of competitive relationships between microbes by the increased level of N (e.g. Allen 1991, Wardle 1992). It is also possible that the observed faunal-induced changes in plant growth, and consequently in the production of root exudates, form a positive feedback in which faunal influences on microbes are indirectly magnified: in the presence of plants microbial growth can become increasingly N limited (Breland & Bakken 1991, Wardle 1992), and consequently lead into a situation in which stimulation of microbes by energy-rich root exudates can be magnified by nutrient additions (Breland & Bakken 1991). The key role of faunal structure in N fluxes and modification of animal-microbe interaction by N-availability shows that plants can be essential in assessing the role of trophic interactions in system functioning.

3.4 Wood ants and spatial heterogeneity in the soil food web

Although the correlative sampling (IV) and manipulations of wood ant density (VI, VII) suggest that wood ants have only a limited influence on soil fauna of the forest floor (IV, VI, VII), the nest mounds of wood ants proved to be distinct islands with unique abiotic conditions and faunal composition (IV). A large majority of the fauna inhabiting the upper layer of the nest mound belonged to non-myrmecophilous soil decomposer fauna so far largely overlooked in

studies on ant–invertebrate associations (Kistner 1982, Hölldobler & Wilson 1990). The abundance of fauna classified as nest specialists makes the nests unproportionally important for species richness of the forest floor; nest mounds harboured approximately 36 % of the taxa that are scarce in the adjacent soil (IV). Thus, the active maintenance of spatial heterogeneity and species diversity in the nest mound by the ants warrants this taxa to be called as a keystone one in maintaining species diversity of the forest floor.

Besides the unique species composition, the functional organisation of detrital community in the ant nest mounds differed from that of forest soil. Unlike in forest soil, basal resources for the food web in the nest mound are mainly provided by the ants collecting litter and prey from a large area. Nest mounds had a large microbial and animal compartment at the base of the food web, and few large predators – other than ants – at the top of the web. Further, there are some indications that the relative importance of food web compartments, or “energy channels” originating from bacteria and fungi (Moore & Hunt 1988) in the nest mounds differs from that of soil. The proportion of bacterivorous nematode fauna in the nest mounds was clearly higher than in the surrounding soil, which suggests that bacteria are more abundant than fungi (see Twinn 1974) in the former habitat, and that the energy flow starting from decomposing litter material is channelled mainly via the bacterial based food-web compartment. The ant-induced changes in the abiotic conditions of the nest mound (e.g. temperature; Rosengren et al. 1987), abundant basal resources, and negative interactions between wood ants and other predators are probably responsible for the characteristic community in the nest mounds (IV). Moreover, the control of wood ants over the structure of animal community is likely to cause secondary changes in the system: especially the high abundance of earthworms in the nest mounds may feed back to the physical structure of nest mound, affect decomposition rates, and increase the importance of bacterial energy channel in the system (Edwards & Bohlen 1996, Persson et al. 1996). Thus, I suggest the behavioral traits of wood ants responsible for the maintenance of the community organisation in the nest mound may feed back to the performance of the colony.

4 CONCLUSIONS

My studies show that both the vertical and horizontal structure of the detrital food web can influence ecosystem level processes, such as nutrient mineralisation and primary production. Thus, the ability of this community to influence the renewal rate and quality of their own resources emphasises the role of indirect or non-feeding interactions for the organisation and functioning of communities (Bengtsson et al. 1996, Loreau 1998). Moreover, this study demonstrates that the structure of soil food webs can have long term consequences to carbon balance of ecosystems (III). Although soil fauna generally increases N and C mineralisation (e.g. Huhta et al. 1991) and hence increases C loss from the system, the positive influence of the fauna on N-mineralisation and consequently on plant growth in the current study was able to overcompensate for the faunal-induced increase in C loss. I observed a similar phenomena, i.e. faunal-induced increase in miniecosystem C uptake in an experiment specifically designed to measure the influence of soil fauna on miniecosystem carbon balance using an automated measurement device (Laakso unpublished). The key role of faunal structure in C and N fluxes, and modification of animal-microbe interactions by N suggest that presence of plants can be essential in assessing the role of trophic interactions for the functioning of decomposer food web. Moreover, a close integration of population and ecosystem level processes in the ecological theory can be essential to fully understand the long-term consequences of pairwise interactions in the detrital food web.

Although the faunal composition had a clear impact on system functioning and species diversity, only few aspects in the structure of the food web proved to be functionally important. The weak propagation of top-down influences, and consequently the insignificant role of carnivores in system functioning implies that only species close to the base of the soil food web can significantly impact ecosystem processes. Further, only one species of microbivorous and microbi-detritivorous fauna, *Cognettia sphagnetorum*, was functionally irreplaceable. Thus, I suggest that the food web of coniferous forest soil contains a large amount of species that can be characterised as *functionally*

redundant (microbivores and detritivores) and species that are *functionally insignificant* (carnivores). This is in accordance with the hypothesis by Andrén et al. (1995), stressing the high number of species in soil food webs and recognition of functional differences between organisms. This view also agrees with the results of studies assessing diversity-function relationships in plant communities (Hooper & Vitousek 1997, Tilman et al. 1997, Wardle et al. 1997b). Although the existence of functionally redundant species can be important under disturbance (e.g. Lawton & Brown 1994, Andrén et al. 1995, Tilman et al. 1996), forest soil has been characterised as a relatively stable habitat (Bengtsson 1994), suggesting that disturbance may have a limited role in increasing the significance of biological diversity in system functioning. Moreover, although the generality of my results can be questioned due to the limited number of species combinations in the experiments I-III, the functioning of low-diversity communities should be most sensitive to variation in species composition (e.g. Tilman et al. 1996, Tilman et al. 1997, McGrady-Steed et al. 1997). Basing on my results, I propose that the efforts used to assess diversity-function, or structure-function relationships in decomposer food webs should be focused on the characteristics of species and trophic groups occupying the lowest trophic positions in the food web.

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YHTEENVETO

Ekosysteemin toiminnan herkkyys muutoksille metsämaan hajottajaravintoverkon rakenteessa

Väitöskirjatyössäni tutkin, millaiset muutokset hajottajaravintoverkon rakenteessa ovat merkityksellisimpiä ekosysteemin toiminnan kannalta. Tarkastelin saalistuksen ja trofiaryhmien sisäisen lajikoostumuksen vaikutusta hajotustoimintaan, ravinnekiertoihin ja kasvituotantoon metsämaaperässä.

Käytin tutkimuksessa laboratoriomikrokosmoksia (maaperän mikro- ja mesofauna; työt I-III) ja kenttätutkimuksia (*Formica aquilonia*-kekomuurahainen; työt IV-VII). Kaikissa mikrokosmoksissa (1.5 L muoviväastia) oli eläimettömäksi käsitelty kangasmetsämaannos, ektomykoritsalla infektoitu rauduskoivun taimi ja monimuotoinen maaperämikrobisto. Rakensin mikrokosmoksiin trofiarakenteeltaan ja lajistoltaan eroavia maaperäeläinyhteisöjä. Työssä III selvitin lisäksi, muuttaako typen saatavuus eläinyhteisörakenteen ja ekosysteemitoininnan välistä suhdetta. Kekomuurahaisten merkitystä metsämaan hajottajaravintoverkossa tutkin kartoittamalla maaperäeläimistön ja kasvillisuuden eri etäisyyksillä muurahaiskeoista (IV) ja manipuloimalla muurahaisten tiheyttä kenttäolosuhteissa (VI, VII).

Laboratoriokokeissa predاتورit kykenivät tehokkaasti säätelemään mikrobivorian ja mikrobi-detritivorian biomassoja, mutta mikrobivorian ja mikrobi-detritivorian vaikutus mikrobien biomassaan ja aktiivisuuteen oli heikko. Tästä huolimatta kokeissa havaittiin myös heikko mikrobilaiduntajia syövien petojen aiheuttama mikrobiaktiivisuuden ja biomassan muutos eli kaskadivaikutus. Kekomuurahaiset vähensivät muiden selkäranganpetojen mutta lisäsivät lierojen määriä, joiden tiheys oli suurin muurahaispesissä. Ravinnonvalintakokeet ja lierojen ja muurahaisten käyttäytymisen tarkkailu paljastivat, että lierot kykenevät puolustautumaan muurahaisten hyökkäyksiltä erittämällä muurahaisille vastenmielistä limaa. Kekomuurahaiset vaikuttivat muihin maaperäeläimiin lähinnä vain pesäkeoissa, joissa oli monimuotoinen ja trofiarakenteeltaan poikkeava hajottajayhteisö.

Mikrobivorit ja mikrobi-detritivorit lisäsivät typen mineralisaatiota, koivujen typenottoa ja kasvua, mutta mikrobivoreja ja mikrobi-detritivoreja syövien petojen vaikutus näihin prosesseihin oli yleensä heikko. Urea-typpilannoitus vahvisti eläinyhteisörakenteen aiheuttamia muutoksia mikrobistossa ja kasvin typenotossa ja muutti mikrobien ja eläinten välistä vuorovaikutusta. Kekomuurahaisten poistaminen ei vaikuttanut maaperän mineraalityypen määrään, kuusen typenottoon tai puuntaimien (koivu, kuusi ja mänty) kasvuun. Trofiaryhmien sisäisellä lajikoostumuksella ei ollut yleensä merkitystä ekosysteemin toimintaan; vain yksi laji, metsämaassa yleinen änkyrimato *Cognettia sphagnetorum* osoittautui poikkeuksellisen tärkeäksi typen mineralisaation ja kasvin kasvun kannalta. Kaskadiefektien heikkous sekä mikrobeja ja detritusta syövän eläimistön toiminnallinen samankaltaisuus viittaavat siihen, että maaperän hajotustoiminta ei ole herkkä hajottajaeläinyhteisön rakenteen muutoksille.

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Original papers

I

Population and ecosystem-level consequences of predation
on nematodes

by

Jouni Laakso and Heikki Setälä

Manuscript (submitted)

<https://doi.org/10.1007/s004420050859>

II

Primary productivity and functional redundancy in
belowground food webs

by

Jouni Laakso and Heikki Setälä

Manuscript (submitted)

<https://doi.org/10.2307/3546996>

III

Control of primary production by decomposer food web
structure in relation to nitrogen availability

by

Jouni Laakso, Heikki Setälä and Ansa Palojärvi

Manuscript (submitted)

<http://dx.doi.org/10.1023/A:1026534812422>

IV

Composition and trophic structure of detrital food web in
ant (*Formica aquilonia*) nest mounds and
in the surrounding soil

by

Jouni Laakso and Heikki Setälä

Oikos 1998 81:266-278

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V

Nest mounds of wood ants (*Formica aquilonia*): hot spots for
litter-dwelling earthworms

by

Jouni Laakso and Heikki Setälä

Oecologia 111:565-569

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VI

Short-term effects of wood ants (*Formica aquilonia* Yarr.) on
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by

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VII

Impacts of wood ants (*Formica aquilonia* Yarr.) on the
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