

# Soil Zoology

Abstracts from the  
11<sup>th</sup> Nordic Soil Zoology Symposium and PhD course

Akureyri, Iceland  
28 – 31 July 2006





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**Organizing Committee:**

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## Preface

The soil is a world unto itself, the home of millions of species and thousands of millions of organisms. The soil is a resource which man has exploited and used for ages, though in the beginning and long afterwards the role of living soil organisms was unknown to humans. Someone has said that today we have explored the sky and the universe better than the world of the soil beneath our feet. But we are now starting to know some of the species living there and to understand the processes that take place in the soil system.

Life in the Arctic and Nordic soils is surely not as diverse or as complicated as in the tropics, but it is special and also very fragile and prone to disturbances. Scientists and PhD students from the Nordic countries have gathered regularly for meetings on soil zoology since 1979, where they have exchanged experiences and presented the results of their research. These meetings have resulted in co-operative projects and strengthened soil zoology research in the Nordic countries. At the last meetings participants from Western Russia and the Baltic countries have also participated.

Now the meeting is held for the first time in Iceland, **The 11<sup>th</sup> Nordic Soil Zoology Symposium and PhD course**. It is held under the auspices of The Agricultural University of Iceland with the support of Samnordisk Skogsforskning (SNS), the Icelandic Department of Agriculture, The Agricultural Productivity Fund (Framleiðnisjóður landbúnaðarins), the City of Akureyri and the Akureyri Municipal Water and Power Company (Norðurorka). All these organizations deserve thanks for their support.

This publication contains abstracts of the papers and posters presented at the symposium. Thanks are also extended to Terry G. Lacy, for proofreading the English.

Bjarni E. Guðleifsson

# PROGRAMME

Friday July 28

08,00-09,00 Registration and poster mounting  
09,00-09,15 Welcoming address

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#### Theme II: Disturbance and resilience (e.g. agriculture, forestry, pollution, fire and flooding)

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##### Chairman: Heikki Setälä

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# Stable isotope techniques in soil animal ecology

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This paper comprises two parts. The first, introductory part outlines the principles of stable isotope techniques and sketches the approaches used in soil ecological research. The second part focuses on applications of isotope techniques in soil animal ecology and considers case studies as well as current and future developments.

## Part 1: Principles and overview

Stable isotope techniques are now a standard tool in (soil) ecological research (Fry 2006; Staddon 2004; West et al. 2006). They are so useful because they make it possible to trace and quantify flows of biologically important chemical elements including C, N and S in organisms and their environment. Isotope techniques can thus be applied to investigate and quantify ecological processes involving these elements, at various organizational, spatial and temporal scales, from cellular-level metabolism, trophic relations of animals, to past and present global biogeochemical cycles. The main strengths of these techniques in soil animal ecology are that they reflect assimilated, rather than ingested, dietary components, that they can be applied to study real, undisturbed food webs in the field, and that they can be used to quantify matter fluxes controlled by soil animals as functional processes.

Isotopes are atoms with a common number of protons but different number of neutrons; the isotopes of an element are chemically very similar but can be separated analytically. Stable isotopes do not undergo radioactive decay. The biologically most abundant light elements (H, C, N, O and S) have at least two stable isotopes. Isotope abundances are usually measured as the ratio of the heavy to the light isotope (e.g.  $^{13}\text{C}/^{12}\text{C}$ ,  $^{15}\text{N}/^{14}\text{N}$ ,  $^{34}\text{S}/^{32}\text{S}$ ) and expressed in a unit appropriate for the prevailing abundance level ('atom percent' for enriched tracers, 'delta per mille' [ $\delta$  ‰] relative to a standard for natural abundances). Isotope ratios at or near natural abundance level in biological bulk materials are usually determined in automated systems coupling an elemental analyzer with a continuous-flow isotope ratio mass spectrometer (CF-IRMS) that provide sufficiently large sample throughput, high precision, at a reasonable cost (Scrimgeour and Robinson, 2004). Sample size requirements for IRMS are not an issue for soil macro-fauna, but they pose problems for some mesofauna (Neilson & Brown 1999) and prohibit the analysis of microfauna.

Broadly, there are two approaches in the use of isotopes in soil ecological research, namely tracer addition and natural abundance methods. Traditionally, the less abundant, heavy isotope had to be enriched and added to soil-plant-animal systems for tracer studies, for example as a mineral  $^{15}\text{N}$  source or as  $^{13}\text{CO}_2$  gas. Nutrient cycling being such an important process in soils, tracer techniques have mainly been used to quantify the role soil animals play in this process, e.g. how much C or N they assimilate and excrete or how nutrient flows are altered when soil communities are manipulated. Advances in measurement techniques have given rise to natural abundance approaches that measure the ratios of naturally occurring stable isotopes, chiefly to reveal and quantify trophic linkages in soil food webs. This approach relies

on isotopic differences between potential food sources and known regularities in the changes (fractionation) in isotope ratios along food chains to infer food sources from C and S isotope ratios, which undergo little fractionation, and trophic positions of animals from their N isotope ratios, which increase along food chains in a step-wise fashion (Gannes et al., 1997; McCutchan et al. 2003).

## **Part 2: Applications and future developments**

Early stable isotope tracer applications included studies to quantify N flows from and to soil animals (e.g. Bouché & Ferrière 1986) and the effects of soil animals on C and N flows from plant litter (e.g. Zhang & Hendrix 1995; Setälä et al. 1996). While such approaches can suffer from a number of drawbacks (e.g. small scale, invasiveness) and potential pitfalls (e.g. non-homogenous tracer distribution), they provide a useful tool for quantifying specific elemental flows under controlled conditions. For example, improved protocols for generating earthworms with known isotopic tracer distribution in different tissues may aid studies of the fate of worm-derived C and N in the drilosphere (Dyckmans et al. 2005). A major advance was the development of mobile delivery systems for exposing plant-soil systems in the field to  $^{13}\text{CO}_2$  (Ostle et al. 2000). This tracer approach, which has produced novel insights into rhizosphere and soil microbial C processes (e.g. Bruneau et al. 2002), also has great potential for investigating rhizosphere-animal relationships under undisturbed field conditions.

The natural spacing in C isotope compositions between C3 and C4 photosynthetic plants has been exploited extensively to trace C flow from plants (or plant litter) into soil and estimate soil C turnover (Staddon 2004). Using such a C3/C4 approach (temperate C3 grass or cereals versus C4 maize), Martin et al. (1992) conducted a number of elegant experiments to quantify C assimilation by earthworms from different organic food sources and soil particle size fractions, while Briones et al. (2001) estimated C source contributions of short-term maize crops to earthworms. C3/C4 systems could potentially also be used to investigate movement of soil animals, feeding specialization and assortative mating (Malausa et al. 2005).

A related technique, natural abundance measurements of  $^{14}\text{C}$  (radiocarbon) by accelerator mass spectrometry (AMS) has been used to determine the age of assimilated C in to soil invertebrates. This approach, which exploits the decline in atmospheric  $^{14}\text{C}$  from nuclear weapons testing since the mid 1960s, can estimate the time of origin of organismal C younger than 40 years with a precision of about 1 year (Briones & Ineson 2002; Hyodo et al. 2006).

Natural isotopic differences between potential food sources in soil systems other than C3/C4 exist, but they have hardly been utilized for research purposes. Schmidt & Ostle (1999) traced animal slurry N, which was naturally elevated in  $\delta^{15}\text{N}$  after storage, into earthworms. Terrestrial and marine sources have different C and S isotope compositions which could be exploited for terrestrial-marine interface studies. For instance Maros et al. (2006) verified feeding by mole crickets on buried sea turtle eggs through C and N isotope measurements and Curry et al. (pers. comm.) have used seaweed fed to cattle as a natural source of  $^{34}\text{S}$  tracer in dung. Plants grown under experimentally high  $\text{CO}_2$  concentrations can also provide isotopically distinct biomass because industrial  $\text{CO}_2$  used in such experiments has a different C isotope composition from atmospheric air (e.g. Cotrofu et al. 2005)

Perhaps the most exciting development in the last 10 or so years has been the use of the isotopic measurements to identify the trophic position of soil invertebrates, independently of previous knowledge derived from conventional studies such as food choice tests, litter bags or gut analysis. Combined  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  analysis has proven useful to identify gradual soil and litter-feeding habits among sympatric species of earthworms (Schmidt et al. 1997, 2004) and termites (Tayasu 1998). A similar isotopic spacing between detritivorous or herbivorous invertebrates in field crops has recently been exploited by Wise *et al.* (2006) to reveal switching between prey by generalist predators. Schneider et al. (2004) found strong  $\delta^{15}\text{N}$  evidence for niche differentiation among 36 oribatid mite taxa in a forest soil, a group previously assumed to be generalist feeders. Measurements of  $\delta^{15}\text{N}$  alone or in combination with  $\delta^{13}\text{C}$  data were also used to analyse the trophic structure of entire forest soil animal food webs (Ponsard & Arditi 2000; Scheu & Falca 2000). The power of combining measurements of  $\delta^{15}\text{N}$  (to assign trophic levels) and of  $\delta^{13}\text{C}$  (to quantify recent C4-C plant inputs in a previously C3 system) for the analysis of an entire arable soil food web has been demonstrated convincingly by Albers et al. (2006).

Undoubtedly, future research efforts in soil invertebrate ecology can benefit from the developments in isotope ecology research in vertebrates which is generally more advanced. For instance, universally valid mixing models to calculate food source contributions from isotope data are now available (Lubetkin & Simenstad 2004), concepts for assessing trophic niche width in animals from isotopic data exist (Bearhop et al. 2004) and the feasibility of reconstructing the dietary history of animals through analysis of different tissues has been demonstrated for vertebrates (Phillips & Eldridge 2006) as well as insects (Gratton & Forbes 2006). Two technique developments capable of refining bulk tissue isotopic analysis that have already been adopted for the analysis of dietary C sources and assimilation by soil animals are the analysis of fatty acid compositions (Ruess et al. 2004) and the compound-specific analysis of isotope ratios in individual fatty acids (Chamberlain et al. 2004). Ecological stoichiometry (Moe et al. 2005) is another tool that could be combined with isotopic analysis in the future.

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## **Biotic interactions in the rhizosphere: Studies of soil food webs and their interactions with plants**

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The biotic interactions in the rhizosphere are very complex and variable. The principal effects resulting from carbon fluxes in multi-dimensional relationships between microbial populations (M), plants (P), soil fauna (F), organic matter (O) and exudates (E) may be summarized as follows:

- F → M      Soil fauna are known to be the important grazer of the microflora in terrestrial ecosystems, feeding selectively on certain soil microorganisms. This may stimulate growth of the less preferred species due to a reduced competition between species (Hedlund 1993).
- M → F      Microbes can play important roles in faunal-plant interactions, mediated by biologically active substances (Lynch 1990).
- E → M,F    Exudates provide carbon to soil microorganisms, which in turn provide nitrogen and phosphorus to the plant by mineralization and immobilization of organic matter. Exudates have been shown to increase the mass and activity of soil microbes and fauna (Butler 2003).
- O → M,F,P    Soil organic matter is formed by microbial action on plant litters and dead animals (Barea et al. 2004).
- M → P      A high diversity of microorganisms has been identified to have deleterious, beneficial or neutral effects on plants. Microbial populations can produce biologically active substances which affect plants either positively – growth promoting or negatively – growth inhibiting (Butler 2003).
- F → P      Soil biota directly influence plants by feeding on roots and forming different relationships with their host plants or indirectly (Wardle et al. 2004).
- P → M,F    The soil food web can control the successional development of plant communities both directly and indirectly, and these plant community changes can in turn influence soil biota (Bever 2003; Wardle et al 2004). Plants affect microbial populations both positive (Grayston et al 2001) and negative (Nehl et al 1996).

The study of trophic relationships is fundamental if we wish to understand the structure and function of floral and faunal communities. In terrestrial ecosystems many investigations have dealt with aboveground food webs because they are relatively accessible to different approaches. In contrast, soil food webs have received little attention, although soil invertebrates can have a great impact on the composition and structure of plant communities and directly or indirectly influence rhizosphere microbial communities.

Microorganisms play a very important role as food chain links between primary producers and animals. About 80-90% of the decomposition processes in soil are mediated by microorganisms (Brady 1990). This almost constitutes a blood system for the rhizosphere. Therefore the study of changes of the rhizosphere microbial communities helps the understanding of links between soil organisms and specific rhizosphere processes.

To determine these complex interactions in the rhizosphere we studied plants belonging to different functional groups: *Plantago lanceolata* (forbs), *Lotus corniculatus* (legume) and *Holcus lanatus* (grass). We used a combination of phospholipid fatty acid (PLFA) signatures of microorganisms, soil animals and plants, as well as detection of the  $^{13}\text{C}/^{12}\text{C}$  isotope ratio of the PLFAs signatures of these microorganisms and soil animals as an indicator of trophic levels. We used press perturbation experiments with increasing numbers of fungal and bacterial feeding soil animals to see how microorganisms will be affected (including bacteria, fungi and arbuscular-mycorrhiza fungi [AM]), as well as increasing the amount of root exudates in the soil as a potential carbon source for rhizosphere microorganisms.

The neutral fatty acid (NLFA) 16:1w5 is a signature for AM fungi (Olsson 1999). Degradation of neutral lipids in soil has not been studied, but it is likely that they are more persistent than the phospholipids (White et al. 1979). A recent study indicates that total  $^{13}\text{C}$  incorporation in AM fungal hyphae is correlated to that in 16:1w5 fatty acid (Olsson et al. 2005). Other PLFAs are signatures for rhizosphere bacteria (Frostegård & Bååth, 1996). Phospholipids are easily decomposed through enzymatic actions in soil and thus can be assumed to reflect the occurrence of living organisms (White et al. 1979). Consequently,  $^{13}\text{C}$  labeled signature fatty acids can be used to effectively track C flux from plants to the rhizosphere microorganisms (Olsson et al. 2002; Gavito & Olsson, 2003).

Soil microorganisms consume significant amounts of plant assimilated carbon, but this C flow has been difficult to quantify. The  $^{13}\text{C}$  pulse labelling of fatty acids that we used not only allows us to define C allocation but to quantify the flow of plant assimilated carbon to microorganisms. We measured the dynamics of the flow of newly assimilated C into AM fungi and rhizosphere bacteria and examined whether this differs between microbial communities from the rhizospheres of plants from different functional groups. Despite this, understanding of the role of rhizosphere microbial communities in C flow is still limited and little is known of roles of different members of the community in assimilating root exudates.

In soil a high number of species co-exist without extensive niche differentiation so that trophic relationships are unspecific with a broad overlap in resources and

ascribing soil animal species to trophic levels or feeding guilds is difficult. Soil animal diets are usually verified by analysis of gut contents (Jorgensen et al. 2005) or by observations of feeding behavior in laboratory experiments or with the help of C/N stable isotopes analyses (Ponsard & Arditì, 2000). We are interested to know the diversity of microorganisms in the guts of soil animals such as nematodes. To examine this, we will use a molecular technique based on the analysis of 16S ribosomal DNA sequences that is founded on the assumption that DNA from consumed organisms is not completely degraded during digestion and therefore could be amplified via PCR and analysed. We are going to detect DNA from bacteria and fungi in soil and gut contents of nematodes from the grassland site where faunal species diversity and other soil factors are very well known (Hedlund et al. 2003).

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# **Microorganisms and fauna in a cultivation system with leek and green manure**

## **- A food web study with $^{13}\text{C}$**

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The development of molecular methods and biomarkers for identification of soil microorganisms and sensitive analytical tools that can analyze the isotopic composition of a single soil animal has enabled detailed studies of the function of specific organisms in soil ecosystems. In this study, the stable isotope  $^{13}\text{C}$  was used as a tracer to link soil organisms in an agricultural field to different C sources; green manure amendments and the growing crop. Green manure is commonly used as a nitrogen source in organic crop production, especially on farms without livestock, and functions as a food base for soil organisms. The aim of this study was to increase the understanding of which organisms are active in and influence the rhizosphere, where they may have an important influence on plant health, and which organisms use dead organic matter as their primary food source and thus are responsible for decomposition and nutrient cycling. We hypothesized that green manure and growing crop support different microbial and faunal communities, i.e. that different microorganisms and soil fauna can be linked either to the green manure material or the growing crop through stable isotope probing (SIP).

### **Field trial with $^{13}\text{C}$ -labelled green manure and leek**

The field trial included three treatments replicated in four blocks; (A) labelled green manure (mean  $\delta^{13}\text{C}$  430 ‰) and unlabelled leek (mean  $\delta^{13}\text{C}$  -28 ‰), (B) unlabelled green manure (mean  $\delta^{13}\text{C}$  -26 ‰) and pulse-labelled leek (mean  $\delta^{13}\text{C}$  140 ‰ at end of experiment), and (C) unlabelled green manure and leek (control).

The green manure crop, red clover (*Trifolium pratense* L. cv. Vivi), was grown in a greenhouse and enriched with  $^{13}\text{C}$  through repeated pulse-labelling with  $^{13}\text{CO}_2$  (99%) prior to incorporation in the field. The fresh red clover was incorporated two weeks prior to planting of the leek (*Allium porrum* L. cv. Hilari). Pulse labelling of the leek was performed on three occasions during the growing season 4, 7 and 10 weeks after planting. On each occasion, the leek was subjected to pulses of  $^{13}\text{CO}_2$  for five days.

Soil samples for microbial analysis were taken after each labelling period, approximately 48 h after the last pulse, and at harvest of the leek. In these samples, phospholipid (PLFA) and neutral lipid (NLFA) fatty acids were extracted according to Frostegård & Bååth (1996) and the  $^{13}\text{C}$  isotopic ratios of the PLFAs were analysed by GC-c-IRMS. In total, 13 PLFAs were detected and identified.

Soil meso- and macrofauna were collected on two occasions during the growing season, in August and at harvest in October. Mesofauna (microarthropods and enchytraeids) were extracted from soil samples by standard Tullgren funnels or wet funnels. Macrofauna were sampled by hand sorting of soil. Arthropods were identified

mainly to family or genera level, enchytraeids were divided into size classes and earthworms were identified to species level and divided into age classes (adult or juvenile). The  $^{13}\text{C}$  isotopic ratio in the collected fauna was determined by IRMS.

### **Incorporation of green manure- or root-derived $^{13}\text{C}$ into microorganisms and fauna**

All PLFAs in the treatment with labelled green manure (A), except the bacterial marker cy17:0, were significantly enriched in  $^{13}\text{C}$  relative to the control ( $p < 0.05$ ). In the treatment with  $^{13}\text{C}$ -labelled leek (B), several PLFAs (various bacterial markers, the fungal markers 18:1 $\omega$ 9/18:2 $\omega$ 6,9 and the actinomycete marker 10Me18:0) were not enriched in  $^{13}\text{C}$  relative to the control on one or several sampling occasions ( $p > 0.05$ ). The fact that more lipids were enriched with  $^{13}\text{C}$  from the green manure than the leek could possibly be explained by a higher degree of enrichment in the green manure compared to the leek, or to specialization of the microorganisms producing the lipids. The AM fungal marker NLFA 16:1 $\omega$ 5 was strongly enriched in  $^{13}\text{C}$  from the leek on all sampling occasions, but to some extent also with  $^{13}\text{C}$  from the green manure. Different markers for gram-negative bacteria were both among the most enriched lipids (18:1 $\omega$ 7, 16:1 $\omega$ 7 and 16:1 $\omega$ 5) and those not enriched (10Me16:0, cy17:0 and cy19:0), irrespective of treatment. In contrast, the actinomycete marker 10Me18:0 showed a different response in the two labelled treatments. This lipid was one of the most enriched in the labelled green manure treatment, whereas it was not enriched in the labelled leek treatment. This suggests that actinomycetes are more strongly linked to decomposing green manure material than leek rhizodeposits.

In the treatment with labelled green manure, *Gamasina paragamasus*, *Gamasina spp.*, *Pseudosinella spp.* and *Rhodacharidae spp.* were significantly enriched in  $^{13}\text{C}$  relative to the control treatment ( $p < 0.05$ ). In the labelled leek treatment, only *G. paragamasus* was significantly enriched relative to the control ( $p < 0.001$ ). Enchytraeids, mainly of the genera *Henlea*, *Friedericia* and *Enchytraeus*, were enriched with  $^{13}\text{C}$  in the labelled green manure treatment, but statistically significant only in the smallest size class ( $< 2$  mm) ( $p < 0.05$ ). Although enchytraeids in the labelled leek treatment were slightly enriched in  $^{13}\text{C}$ , this trend was not significant compared to the control. Earthworms of the species *Aporrectodea caliginosa*, *A. longa*, *A. rosea* and *Alollobophora chlorotica* were analysed for their isotopic ratio. Due to large variations, no significant differences between the labelled treatments and the control could be found.

So far, we can conclude that  $^{13}\text{C}$  from both C sources, green manure and leek, is present in most microbial lipids and fauna. Some indications of specialization were found such as a stronger link to decomposing green manure by actinomycetes and, not surprisingly, a stronger link to the growing crop by AM fungi. Due to large variations in isotopic ratios for soil fauna, any observed trends were seldom statistically significant. This could possibly be due to heterogeneous tracer distributions.

Dual analysis of  $^{13}\text{C}$  and  $^{15}\text{N}$  in soil fauna give information on trophic shifts and whether direct or indirect (predation) feeding caused  $^{13}\text{C}$  enrichment. This could not be achieved in this study, but has proven successful in other studies (Albers et al. 2006). By combining SIP and molecular techniques, the function of microorganisms can be studied at higher resolution of taxonomy than is possible with the PLFA analysis. However, one advantage with the PLFA analysis is that it is quantitative and

we are currently investigating the extent of  $^{13}\text{C}$  incorporated into the biomass of different microbial groups (bacteria, fungi, actinomycetes and AM fungi). In contrast to previous studies on rhizosphere C flow involving SIP and PLFA analysis that have been biased towards recently fixed C (Butler et al. 2003; Treonis et al. 2004), the present study also includes the utilization of older fixed C.

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## **Stoichiometry for the collembologist, or time constraints, growth rate and response on food nutrient elements in arctic Collembola**

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I will here focus on the possible effect of food nutrient element on growth rate in arctic Collembola and its implication for thermal adaptation.

### **Time constraints**

A major direct effect of climate change in ectotherm organisms is the effect of temperature on growth rate. As time and size of first reproduction (development rate) are closely linked to fitness, one might expect a selection for increased efficiency of development rates within the thermal range usually prevailing during the growth season. The selective advantage of such an adaptation would depend on the rigidity of the species life cycle and phenology. In cold areas such as the High Arctic, a major challenge is to adjust growth and development rates to the decreased heat sum available for development.

### **Thermal reaction norms for growth**

Thermal adaptation in developmental processes (micro- and macro-evolution) may be tested from descriptions of how rates of different life history parameters vary across temperatures. Changes in such reaction norms may be obtained by qualitative or quantitative enzymatic changes. A structural change increasing enzyme efficiency at low temperatures (cold adaptation) is expected to occur at the expense of performance at higher temperatures, e.g. reduced efficiency or increased risk of heat stress at higher temperatures. Increased concentrations of enzymes, on the other hand, would increase reaction rates at all temperatures. In arctic Collembola, differences in micro-evolutionary patterns between species appears to be related to specific life cycle

patterns, which in turn affect the cost/benefit ratio for investing in increased growth rates. Inter-specific differences appear to be related to geographic range (phenotypic plasticity) and possibly also micro habitat occupation (nutrient availability).

### **Biological stoichiometry**

Biological stoichiometry is the study of the balance of multiple chemical elements in biological systems, in particular the C:N:P ratio. A central hypothesis in stoichiometry is the "Growth Rate Hypothesis", arguing that high P-content in biomass is caused by increased allocation to P-rich ribosomal RNA necessary to achieve rapid rates of protein synthesis (which in turn puts demands on N availability). Accordingly, the balance between ribosomal synthesis and protein synthesis is a major determinant of growth rate, and may lead to shifts between N and P limitation. This increased demand for nutrient elements represents a cost in increased growth rate. Also, species having evolved high growth rate lifestyles with high P (and N) demands are more likely to face ecological constraints (and possibly death) due to insufficient supplies of P (or N) from the environment, emphasizing another trade-off in the evolution of growth rate strategies. Similarly, species adapted to an environment with low availability of (one of) these nutrient elements is likely to possess mechanisms for efficient retention of the elements, which however may lead to incomplete physiological adaptations for excreting the same elements when offered nutrient-rich food, and thus run the risk of harmful accumulation of metabolic wastes (i.e. too much of a good thing may be harmful). Most of the basic studies in ecological stoichiometry have been done on fast growing invertebrates with a relatively well-defined life cycle, such as limnetic Cladocera (*Daphnia*) and rotifers and herbivore insects. An interesting question is whether this principle also is important for the relatively much more slow-growing Collembola with flexible life cycles.

In a series of studies on a set of closely related species (*Hypogastrura* spp.) that partly coexist on Svalbard, thermal adaptations in growth rates are linked to their life cycle strategies and its implication for time constraints, and the varying degree to which they differ in habitat occupancy and geographic range. Subsequently, these life history and habitat variables are considered when explaining these species' differential responses, both behaviourally (food preference) and growth rate, on variation in food element content.

Finally, contrasting patterns in micro-evolution in thermal adaptation along climate gradients from mild temperate to cold High Arctic are illustrated by *H. viatica*, *Xenylla humicola* and *Folsomia quadriculata*. Although the link between growth rate patterns and stoichiometry is still far from evident in these organisms, our studies so far have revealed some interesting patterns.

# **The significance of soil collembolans, protozoa and microorganisms and their interactions for soil fertility - A soil mesocosm approach**

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## **Introduction**

For sustainable land use there is an urgent need for a better understanding of the interactions between the different groups of organisms inhabiting the soil. Human effects on particular soil organisms may lead to changed conditions for other organisms below- and aboveground, which can then cause changes in both soil community composition and soil functioning. Soil fertility, which is a key concept in this discussion, is often defined vaguely or even ambiguously. Here, we refer to the view presented by Mäder et al. (2002), who suggested that fertile soils provide essential nutrients for crop plant growth, support a diverse and active biotic community, exhibit a typical soil structure and allow for an undisturbed decomposition.

The decomposition of organic matter and subsequent uptake of phosphorus by plants is an important soil function. Plants in phosphorus-deficient soils depend on arbuscular mycorrhiza (AM) fungi to supply them with phosphorus. External hyphae of AM fungi spread away from the colonized plant roots and take up phosphorus from outside the phosphorus depletion zone around the roots. AM fungal hyphae have no direct access to soil organic phosphorus, hence the phosphorus source for plants and AM fungi is mineral phosphate in soil solution or absorbed to soil particles. Thus, mineralization processes will govern AM uptake from organic phosphorus. Soil microorganisms and their predators facilitate this mineralization.

Collembola are a group of microarthropods that participate in the disintegration of particulate organic material, but also feed on various soil organisms depending on the morphology of the collembolan. The collembolan *Folsomia fimetaria* ingests a wide selection of fungi (Jørgensen et al., 2003), but the exact food specificity of this collembolan in soil is unknown. Protozoa feed mainly on bacteria though some also feed on fungal spores, other protozoa, algae or detritus. Predation on fungi has been sparsely investigated, but seems only to be essential for a small fraction of the protozoa (Ekelund, 1998). Saprotrophic bacteria and fungi also participate in the degradation of organic matter.

Fenpropimorph is a widely used sterol synthesis-inhibiting leaf fungicide used for the control of *Erysiphe graminis* (powdery mildew) and *Puccinia recondita* (cereal rust). Some soil protozoa are also sensitive to fenpropimorph at the recommended field dose (Ekelund, 1999), and this effect on protozoan numbers reduced the predation on bacteria at 10× the recommended dose (Thirup et al., 2000). Thus, we expect that the addition of fenpropimorph 10× the recommended dose can be used as a tool to change the soil community responsible for the decomposition of organic matter.

Here, we hypothesize 1) that moderate community composition changes induced by fenpropimorph will result in effects on soil fertility as measured by cycling of phosphorus from mesh bag soil only accessible to AM fungal hyphae and containing <sup>33</sup>P-labelled organic matter to phosphorus used for plant growth, and 2) that the presence of the collembola (*Folsomia fimetaria*) will stimulate organic matter mineralization and thus increase plant uptake of phosphorus via AM fungal hyphae from within the mesh bags. We monitored these changes by examining the effects on selected groups of soil organisms and plant growth in soil mesocosms.

### Experimental procedures

We grew barley (*Hordeum vulgare*) in pots in a P-deficient, defaunated soil that was divided into a rooting and a root-free compartment, with or without addition of the fungicide fenpropimorph and the collembolan *Folsomia fimetaria*. We harvested eight times. Each treatment was replicated four times. Soil inoculum of the AM fungus *Glomus claroideum* was mixed thoroughly into the soil.

The pots contained mesh bags (25 µm), which exclude roots but allows for passage of AM hyphae. The mesh bags contained soil mixed with 1% dried and ground subclover shoots labeled with <sup>33</sup>P. The soil in half of the mesh bags had been amended with the fungicide fenpropimorph. The resulting fenpropimorph concentration in the amended mesh bags was 12.5 mg fenpropimorph kg<sup>-1</sup> soil, which corresponded approximately to 10× the amount expected in the soil after application at the recommended field application dose (Thirup et al., 2000). We added 100 *Folsomia fimetaria* to half of the amended and unamended mesh bags. We sampled on days 1, 3, 7, 10, 16, 36, 70 and 99. Not all parameters were measured on all sampling days. We extracted *Folsomia fimetaria* from the mesh bags in a high gradient heat extractor of the MacFadyen type, collected them on plaster, and counted and measured them using an image analysis system (Krogh et al., 1998). The total number of **culturable bacteria** was obtained on 1/300 tryptic soy agar. **Protozoa** were enumerated using a "most probable number" (MPN) method (Rønn et al., 1995). We used tryptic soy broth (TSB powder 0.1 g l<sup>-1</sup>) as the growth medium. **Arbuscules and other AM structures** in the roots and **external hyphal** were assessed employing a line intersect method.

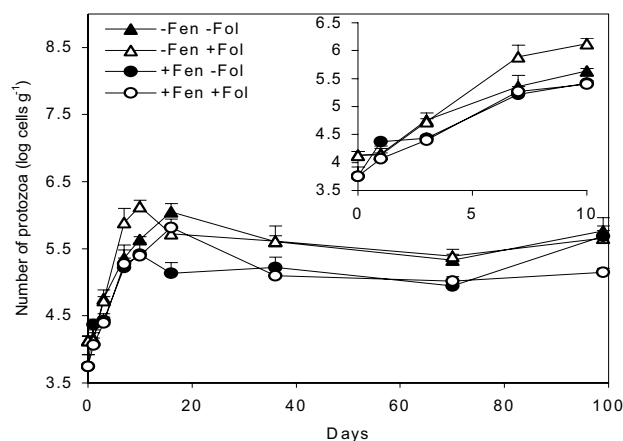
### Results

All parameters measured changed significantly with time. Surprisingly, addition of *Folsomia* had virtually no effect. Except for the effects discussed in more detail below (and a weak effect on juvenile *Folsomia*), fenpropimorph had no clear effects on the systems. During the first ten days, numbers of **protozoa** increased (Figure 1). Numbers of protozoa in amended pots were significantly different from (p=0.0315, log-transformed data), and almost consistently lower than those in unamended pots. Numbers in unamended pots stabilized at a level of about 2×10<sup>5</sup> cells g<sup>-1</sup> soil. The

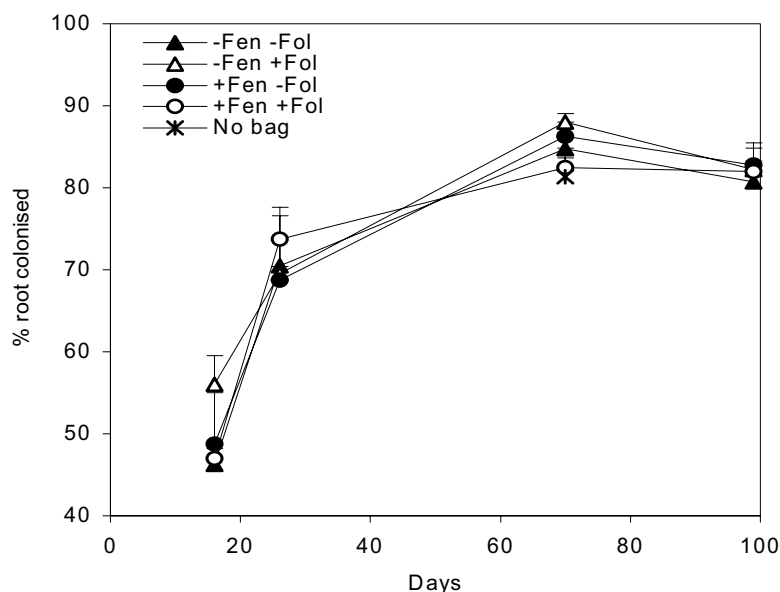
percentage of barley root length colonized by AM fungi (Figure 2) increased during the experiment, but we saw no treatment effects. Roots in pots without mesh bags were close to significantly less colonized by hyphae than roots in pots with mesh (one-way ANOVA,  $p=0.098$ ). The results of percent root length colonized by AM fungi with arbuscules were in accordance with the results presented in Figure 2 (data not shown).

## Discussion

Our data suggest that the mesh bags acted as sources of phosphorus in a phosphorus-poor environment. We used a phosphorus-deficient soil. All nutrients except for phosphorus were added to this mixture to give a non-limiting supply. During the experiment plants exhibited signs of phosphorus deficiency, and measured shoot P concentrations were well below reported values for severe phosphorus deficiency in barley (Jakobsen et al., 2005). Therefore, we find it justified to consider phosphorus to be the major limiting factor for plant growth in the experiment. A significantly lower shoot biomass production and higher root/shoot ratio in pots without mesh bags (Figure 3) further demonstrate the importance of the mesh bag soil as a phosphorus source. The root/shoot ratio increases when a certain nutrient is deficient.

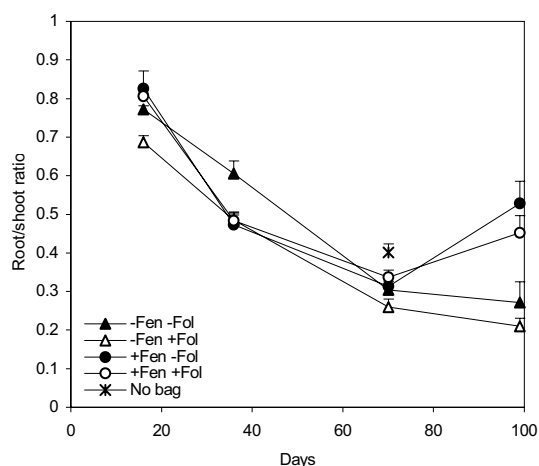


**Figure 1.** Numbers of protozoa feeding on indigenous soil bacteria in microcosms with defaunated soil during a 99 day period. Microcosms were with or without fenpropimorph treatment (Fen) and addition of *Folsomia fimetaria* (Fol). Points are mean values from four microcosms. Error bars represent 1 SEM.



**Figure 2.** Percent barley root length colonized by AM fungi in microcosms with defaunated soil during a 99 day period. Microcosms were with or without fenpropimorph treatment (Fen) and addition of *Folsomia fimetaria* (Fol). Three microcosms without mesh bags with organic matter were sampled on day 70 (no bag). Points are mean values from four microcosms. Error bars represent 1 SEM.

As expected, fenpropimorph altered the soil community composition. We observed effects on protozoa (Fig 1). Still, the effects of fenpropimorph were moderate, and it did not significantly affect the numbers of adult *Folsomia*, bacteria or FDA-active hyphal length. This moderate effect only on some key organisms in the system allows us to draw some general conclusions about undisturbed soil systems from the experiment.



**Figure 3.** Root/shoot ratio of barley plants (dw) in microcosms with defaunated soil during a 99 day period. Microcosms were with or without fenpropimorph treatment (Fen) and addition of *Folsomia fimetaria* (Fol). Three microcosms without mesh bags with organic matter were sampled on day 70 (no bag). Points are mean values from four microcosms. Error bars represent 1 SEM.



There was a striking effect of fenpropimorph on the root/shoot ratio. Root/shoot ratio of herbaceous plants generally decreases with age/size, which we observed for all treatments until day 70. However, after 99 days fenpropimorph-amended pots showed a marked increase to values below 0.4 characteristic of nutrient limitation, most likely of phosphorus. Probably due to some nutrient limitation in these pots, the root/shoot ratio in pots without fenpropimorph continued to decrease after day 70, albeit at a lower rate than previously. This confirms our hypothesis that moderate community composition changes induced by fenpropimorph would result in effects on soil fertility as indicated by transport of phosphorus from organic matter to plant growth.

Protozoa were the biotic component in the system that fenpropimorph affected most severely, in accordance with Ekelund (1999), who found that fenpropimorph had detrimental effects on the soil protozoan community even in very small concentrations. Protozoa generally stimulate plant uptake of mineral nutrients from soil organic matter (Bonkowski, 2004), including phosphorus (Cole et al., 1978). Hence, we suggest that reduced protozoan activity was a key factor responsible for the increased root/shoot ratio in the pots with fenpropimorph.

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## Soil animals and plant-soil interactions

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Nitrogen availability limits primary production in most terrestrial ecosystems and plants are under strong selection for developing features that enhance their nitrogen acquisition ability. Among these features, one conceivable option for plants is to try to manipulate soil decomposers in a way that leads to higher net nitrogen mineralization

in soil. It has also been postulated that when attacked by aboveground herbivores and in need of resources for compensatory shoot growth, plants could improve their nitrogen uptake by stimulating soil decomposers. Since soil animals, such as microbial and detritus feeders, have a major role in soil nutrient mineralization, it is reasonable to hypothesize that if plants are able to improve their nitrogen uptake by manipulating soil decomposers, soil animals are likely to have a significant role in this process. In our research group, we have recently tested whether the amount of nitrogen taken up from dead organic matter by plants is related to the way different plant species affect soil decomposers. We have also examined how removal of plant shoot tissue affects soil food webs, both in the short and long term, and whether changes taking place in the soil can further influence plant nitrogen uptake. In my presentation I will summarize results from these experiments with especially focusing on the role of soil animals in plant-soil interactions.

## **Effects of decomposer, fungivore and predatory soil fauna on microbial biomass and C/N mineralisation in forest soil microcosms**

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Decomposition and mineralization processes are controlled by environmental factors like temperature and substrate quality and by the structure of the decomposer community. Decomposer soil animals can speed up decomposition of organic matter by comminution of litter, providing favourable conditions for enzyme and microbial activities inside the gut, and intermixing topsoil and subsoil materials. Microbivorous soil animals can affect decomposition rates by regulating the microbial community and mobilizing nutrients from soil organic matter. Even predators have the potential to indirectly affect microbes by controlling the microbivore community.

The prime aim of this presentation is to evaluate to what extent functional and taxonomic groups of soil animals in the forest soil food web will contribute to carbon and (net) nitrogen mineralization and relate these effects to changes in organic matter, microbial biomass and prey animals. We hypothesized that different functional groups of soil fauna contribute differently to C and N mineralization. Presence of decomposer soil fauna feeding on high C/N substrates should result in low net N mineralization, microbivorous soil fauna feeding on moderately low C/N substrates should result in high net N mineralization, and predatory soil fauna feeding on low C/N preys should result in extremely high net N mineralization per unit of animal biomass.

The present compilation is a summary of a number of microcosm studies performed in the laboratory under controlled temperature (15 °C) and soil moisture (60% WHC) with addition or removal of soil animal groups at the start of the experiments, and with heterotrophic respiration (CO<sub>2</sub> evolution rate, C mineralization rate),

accumulation of inorganic N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) and microbial estimates as dependent variables.

The first study (Persson 1989), performed at two temperatures and three moisture levels, indicated that presence of microarthropods (mixed community of collembolans and mites) did not affect C mineralization but stimulated net N mineralization. At a soil moisture of 60% WHC, total net N mineralization was about three times higher at 15 °C as at 5 °C in the arthropod-free microcosms, and the extra stimulation by soil arthropods was about 10% at both temperatures. Net N mineralization was clearly lower at lower soil moisture levels, but the arthropod effect on mineralization seemed to be independent of soil moisture. Consequently, the arthropod contributed relatively more (45-100%) to net N mineralization in dry soil (15% WHC) than in mesic (30% WHC) or moist (60% WHC) soil indicating that soil fauna might be the dominant producer of inorganic N during dry soil conditions, whereas the faunal role for net N mineralization is less pronounced during mesic/moist conditions that are favourable for microbial activity.

The second study (Lenoir et al. 2006) tested the hypothesis that meso- and macrofaunal soil predators can regulate fungivore populations and, thereby, cause a top-down cascade effect on fungal biomass and decomposition/mineralization processes in boreal forest soils. The study was performed as a microcosm experiment in the laboratory with two contrasting soils (humus layers), one poor and one rich in N, and with different combinations of fungivore and predator soil fauna added to “defaunated” soil. In comparison with control microcosms lacking mesofauna (but with nematodes and protozoans), presence of a diverse (20 species of Collembola and 30 of Oribatida) fungivore community significantly reduced (FDA method) or tended to reduce fungal biomass (ergosterol method) in the N-poor humus, but no clear effect could be detected in the N-rich humus. Fungivores as well as fungivores plus predators (gamasids, spiders, beetles or a complete predator community) reduced C mineralization and increased net N mineralization in both soils. Presence of predators (particularly gamasid mites) reduced collembolan numbers, and alleviated the negative effect of fungivores on fungal biomass in the N-poor soil. In the N-rich soil, presence of predators increased fungal biomass (ergosterol) in relation to the “defaunated” soil. To understand this, we assumed that fungivore grazing resulted in compensatory growth and that this compensation was larger in the N-rich than in the N-poor soil.

In the third study, enchytraeids (*Cognettia sphagnetorum*) were added to defaunated microcosms containing the same humus materials as in the former study. Presence of enchytraeids with the same density as in the field reduced FDA-active fungi in N-poor humus had no effect on C mineralization and increased net N mineralization. After 100 days, presence of enchytraeids had increased net N mineralization by 75-80% in relation to defaunated microcosms, which can be compared with an increase of 15-35% when microarthropods were added. Consequently, the microbi-detrivore *C. sphagnetorum* had a similar effect on fungal estimates, a smaller effect on C mineralization and a stronger effect on net N mineralization than the fungivorous microarthropods.

In the fourth study, the earthworm *Dendrobaena octaedra* and the enchytraeid *Cognettia sphagnetorum* were added to defaunated microcosms, either alone or

together with each other. To obtain a similar biomass, two juvenile earthworms and 100 enchytraeids were added to jars containing 16 g (dry wt) sieved humus layer. Presence of *D. octaedra* or *C. sphagnetorum* or both together increased bacterial biomass and reduced fungal biomass, and the presence of *D. octaedra* also had a tendency to reduce the number of amoebae. C mineralization increased by 10 (*C. sph*), 13 (*D. oct*) and 24% (*C. sph* + *D. oct*) in relation to microcosms without animal addition, and net N mineralization became 2, 2.5 and 3 times than in the animal-free microcosms, respectively.

The studies indicate that animals feeding predominantly on dead organic matter under decomposition (microbi-detritivores) have a tendency to increase C mineralization and a pronounced capacity to increase net N mineralization. Fungal-feeding soil fauna (collembolans and oribatid mites) seem to decrease C mineralization and increase net N mineralization. Predatory soil fauna had no clear effect on C mineralization but had a slight stimulating effect on net N mineralization. Possible explanations will be discussed during the presentation.

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## **Oribatid mite response to reduced mycorrhizal biomass - A field experiment**

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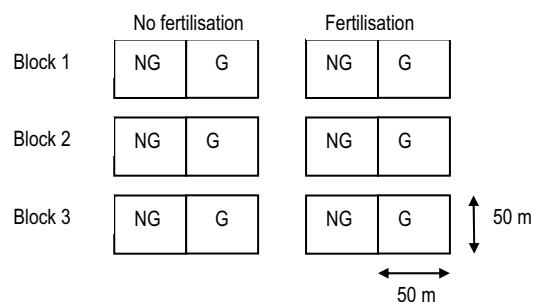
Populations of oribatid mites (Oribatida, Acarina,) are decreased by forest management practices like clear felling (Huhta, 1976), liming (Hågvar and Amundsen, 1981), and nitrogen fertilisation (Axelsson et al., 1973). Changes can also be observed among mycorrhizal-forming fungi (Bakker et al., 2000; Fransson, 2000; Jones et al., 2003) which constitute a large proportion of the fungal biomass of boreal forests. Oribatid mites are commonly regarded to be detritus or fungal feeders, and since both the mycorrhizal fungi and the oribatid mite community change due to forest management practices, there might be a connection between the two organism groups; the mites could for example feed on the fungi.

In order to investigate the relationship between the mites and the mycorrhizal-forming fungi, sites with reduced mycorrhizal biomass were studied, in this case plots within a large-scale tree-girdling experiment. On a girdled tree a broad band of the bark is stripped off the stem to the depth of the xylem, which prevents photosynthates from reaching the roots and the mycorrhizal fungi. The girdling treatment reduces the biomass of ectomycorrhizal (EM) fungi (Högberg and Högberg, 2002), which is the most common mycorrhizal symbiosis in coniferous forests. The fungi are strongly

dependent on assimilates from the tree, and Högberg et al. (2001) found that tree girdling eliminated EM-fruited bodies and reduced soil respiration by 54%. The study site is also part of a long-term fertilisation study, and therefore the additional effects of fertilisation on the mites were also studied.

The aim of this study was to determine the effects of a reduced EM community on soil-living oribatid mites in order to detect species that interact with EM fungi. The hypothesis was that oribatid mite species that are decreased after the girdling treatment are specialists feeding on EM fungi.

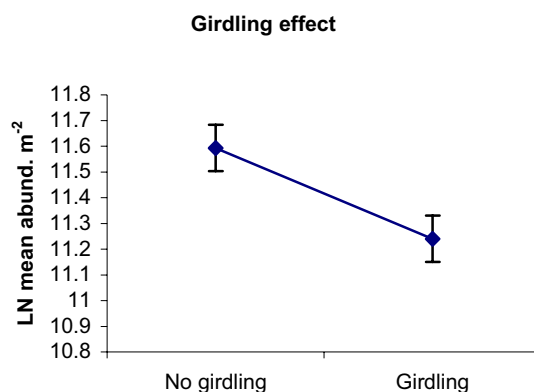
The sample site was a 40-year old Norway spruce *Picea abies* (L.) forest at Flakaliden N. Sweden (64° 07' N, 19° 27' E). Girdling took place in 2002 and sampling was carried out in October 2003 and 2004. The experiment had a randomised block design with three blocks, each containing four treatments: girdling, fertilisation, girdling plus fertilisation, and control. The fertilised plots had been treated with solid NPK fertilisers during the period 1987-2001 with a mean N dose of 75 kg ha<sup>-1</sup>.



**Figure 1.** Sketch of the plot design at Flakaliden seen from above. NG=no girdling and G=girdling.

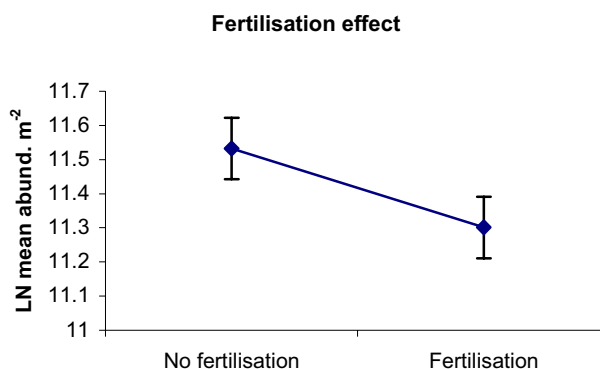
Soil samples of the organic layer were collected using a 100 cm<sup>2</sup> metal frame that was pressed into the forest floor down to the mineral soil.

Altogether at least 55 species of oribatid mites were found at the study site. The total number of individuals of oribatid mites was higher in the non-girdled than in the girdled plots (P=0.0053).



**Figure 2.** Overall effects of girdling on total number of individuals, including fertilisation/no fertilisation and year. LN mean abundance (S.E.) m<sup>-2</sup> in Flakaliden 2003-2004 (n=6).

There were also a higher number of individuals in the non-fertilised plots than in the fertilised plots ( $P=0.049$ ).



**Figure 3.** Overall effects of fertilisation on total number of individuals including girdling/no girdling and year. LN mean abundance (S.E.) m<sup>-2</sup> in Flakaliden 2003-2004 (n=6).

The mean number of species was lower in the girdled plots than in the non-girdled plots. There were also a significant difference between the years, with a higher abundance of mites in 2004 than in 2003 ( $P= 0.0109$ ).

Only two species had a significantly lower abundance in the girdled than in the non-girdled plots: *Oppiella nova* and *Lauropia maritima*. There were no oribatid mite species that showed a significant increase after the girdling treatment.

Both *O. nova* and *L. maritima* belong to the genera of Oppiidae which commonly are regarded to feed on fungi. The decrease of two fungivorous species in plots with reduced ectomycorrhizal biomass could indicate feeding preferences for EM fungi. However, *O. nova* occur in high numbers in agricultural fields where EM fungi are lacking. This contradicts the hypothesis that *O. nova* is a feeding specialist on EM fungi. *O. nova* is also found at heavily disturbed sites, e.g. post-industrial dumps, where the abundance of EM fungi is presumably low. The girdling experiment did not answer the question as to whether oribatid mites are feeding specialists on ectomycorrhizal fungi, but the treatment did have a significant decreasing effect on two species and several more were affected, indicating an interesting interaction between oribatid mites and EM fungi.

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## Management of corky root disease of tomatoes using composts and fungivorous nematodes

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Tomato is the dominant single crop of Swedish organic greenhouse production. The soil-borne disease corky root (causal agent *Pyrenochaeta lycopersici* Schneider and Gerlach) causes the most serious problem of organic tomato production. In this project, we have focused on biological control of corky root disease by using fungivorous nematodes and composts. Fungivorous nematodes puncture fungal cell wall with their mouth stylet, withdraw the cell contents, kill the fungus and thus fungivorous nematodes may have a biological control potential for certain plant parasitic soil fungi (Ishibashi & Choi, 1991). Compost has also been reported to protect plants from soil-borne root pathogens when used as a soil amendment (Noble & Coventry, 2005). Microbial communities in the compost can suppress the pathogen by competition, antibiosis, parasitism/predation and systemic induced resistance of the host plant (Hoitink & Boehm, 1999). Pathogen-specific antagonists cannot always be expected to be present in the early stage of composting. Therefore, it is recommended that specific antagonists be added to the compost to increase the disease suppression activity (Segall, 1995). In the present study, we conducted three different greenhouse trials in which soil naturally infested with *P. lycopersici* was used to grow tomato plants and the separate and combined effects of compost amendment and fungivorous nematodes on corky root disease were evaluated. Our hypotheses were: 1) Compost amendment and fungivorous nematodes would decrease corky root disease infection; 2) The disease suppressive effect of the compost would increase with fungivorous nematode enrichment.

Four different types of compost: Green manure compost, Horse manure compost, Garden waste compost 1 and Garden waste compost 2, and two fungivorous nematodes: *Aphelenchus avenae* Bastian and *Aphelenchoides* spp. were used. Three different greenhouse trials were conducted with soil naturally infested by *P.*

*lycopersici*. Composts were mixed (20% compost by volume) with the infested soil. Fungivorous nematodes were propagated on a fungus (*Pochonia bulbillosa* W. Gams and Malla) culture grown in agar plate for four weeks and thereafter extracted by the Baermann Funnel method. Three-week old tomato seedlings were transferred to plastic pots (5 l volume) in the greenhouse. Each pot contained a single seedling. Fungivorous nematodes were inoculated in the soil and soil-compost mixture one day after the transplanting of tomato seedlings. The nematode inoculation rate was 23 and 33 nematodes/ml substrate for *A. avenae* and *Aphelenchoides* spp., respectively. A low inoculation rate (3 nematodes/ml substrate) of both nematodes was also included to compare the effects of low and high inoculation rates of *A. avenae* and *Aphelenchoides* spp. on the infested soil. The greenhouse experiments were terminated after ten weeks and disease was measured from infected roots after harvesting. Total fruit weight and both fresh and dry weights of roots and shoots were measured. The nematodes were extracted and counted to ascertain the final population.

*Aphelenchus avenae* significantly reduced the disease in the infested soil in the absence of the composts at two different inoculation rates (3 and 23 nematodes/ml substrate). *Aphelenchoides* spp. did not suppress the disease at any inoculation rate (3 or 33 nematodes/ml substrate), either in the presence or the absence of the compost. It is possible that *P. lycopersici* was not as palatable to *Aphelenchoides* spp. nematodes fulfilling their nutrient requirements, while *A. avenae* could use this fungus successfully as food. A study by Ikonen (2001) indicated that *A. avenae* and *Aphelenchoides bicaudatus* Filipjev and Schuurman Stekhoven have different nutritional requirements. Another possibility is that the tested *Aphelenchoides* spp. perhaps changed their food preferences temporarily in the soil and selected other soil fungi as their food source. The results from an *in vitro* study by Ruess et al. (2000) support this idea, as they observed a change in food source of an *Aphelenchoides* sp. when an alternative was available. According to them, the possible reason for this change in eating behaviour was to avoid undesirable toxic compounds in the food source. The only compost that had a suppressive effect on *Pyrenochaeta* was Garden waste compost 1. This effect was lost when it was combined with fungivorous nematodes. It may be that fungivorous nematodes used the beneficial fungi as a food source that was present in Garden waste compost 1 and was responsible for disease suppression. Further research is needed to establish whether beneficial fungi were involved in disease suppression and whether fungivorous nematodes preferred these fungi. In all experiments, both *A. avenae* and *Aphelenchoides* spp. failed to maintain their initial population level. One factor that causes reductions in nematode populations is food scarcity. Our greenhouse experiment continued for ten weeks and the amount of substrate available was perhaps not sufficient to supply food for fungivorous nematodes for this long a period. In our study, disease suppression by Garden waste compost 1 was not positively correlated with root and shoot dry weight and total fruit weight. Disease suppression by *A. avenae* was not always positively correlated with root and shoot dry weight and total fruit weight. This could be because of the short experimental period and early harvesting.

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## **Enhancing the capacity of nutrient and pollution retention in urban soils by manipulating aboveground plant communities**

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### **Introduction**

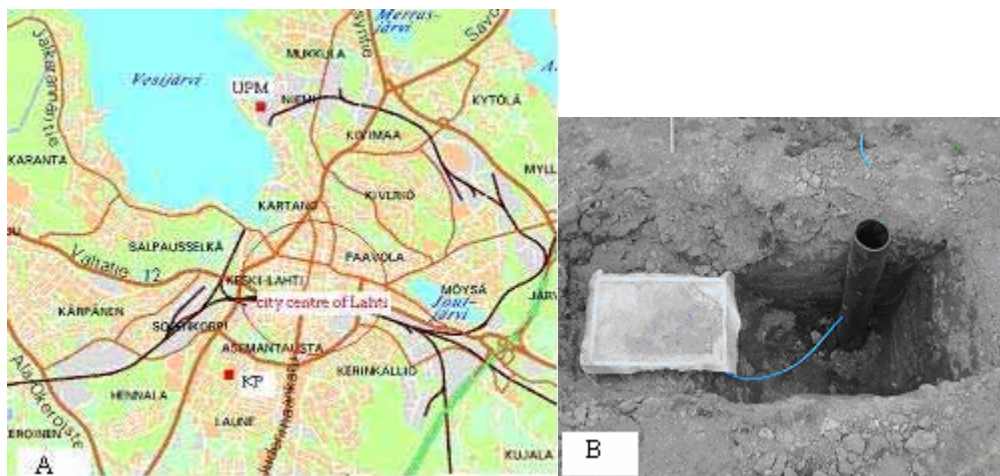
Urbanization has led to remarkable changes in land use causing drastic alterations in plant communities, biogeochemical cycles, biological diversity, and losses of soil organic matter and nutrients (e.g. Shochat et al., 2006; Pickett et al., 2001). The ability of disturbed soils to retain nutrients, organic matter and harmful chemicals can be, at least in theory, improved by manipulating the plant-soil system to absorb and conserve the substances more efficiently. The aim of this study is to find out how manipulation of aboveground plant communities affects functions of the closely associated soil food webs in the plant rhizosphere. To study the mechanisms of aboveground plant-community manipulation, plants with different functional characteristics (based on for example litter type quality, mycorrhizal symbionts and growth strategies) were included in the experiments. The plant species (representing different functional plant traits) studied in the experiments were: *Holcus lanatus* (grass), *Lotus corniculatus* (legume, herb), *Calluna Vulgaris* and *Picea abies* (shrub and tree).

### **Experimental set up**

The study consisted of two separate field experiments (named as KP and UPM), both located near the city centre of Lahti (in Southern Finland) (Figure 1.A). Field trials were established in 2004. Both sites have 5 experimental plots of each functional plant trait (each 1 m<sup>2</sup> in area), 5 plots with mixed culture of all the traits and 5 plots lacking the vegetation cover (bare ground controls) (Figure 2.). To collect water (including nutrients and harmful chemicals) leached through the different rhizospheres, lysimeters were constructed underneath each plant community (Figure 1.B).

The questions of interest were: I) Does manipulation of the aboveground communities cause changes in the belowground decomposer community? II) Do different functional plant traits promote the growth of different saprophytic microorganisms and establishment of either a bacterial- or fungal-based energy-channel in

rhizosphere? III) How is the retention of nutrient, organic matter and pollutants affected by changes in the decomposer community?



**Figure 1.** (A.) The field experiments (KP and UPM) were located near the city centre of Lahti. (B) The lysimeter system collected the water leaching through each plant community.



**Figure 2.** The field experiments consisted of 1m<sup>2</sup> plots of different functional traits of plants: A) grass *Holcus lanatus*, B) herb, legume *Lotus corniculatus*, C) coniferous tree *Picea abies* and shrub *Calluna vulgaris* and D) bare ground (plant free control). In both field trials there were also mixed cultures of all the plant traits.

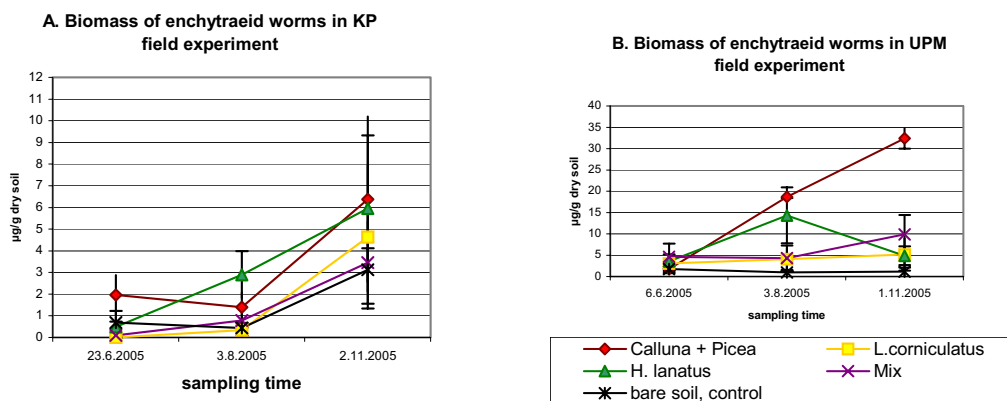
In previous studies a fungal-based energy-channel has been shown to be more effective in conserving nutrients in the soil (e.g. Moore & Hunt, 1988, Williamson et al., 2005) compared to a ‘leaky’ bacterial-based energy channel. Conifer trees and shrubs create a fungal-based decomposer food web in nature, while the energy channel of herbs and grasses should be bacteria-dominated. We hypothesize that the plant traits creating fungal-based energy channels in urban soils are also more

efficient in conserving the extra nutrient load from atmospheric deposition when compared to plant traits having a bacteria-based belowground energy channel.

To study the effects of different plant traits on soil biota the following parameters were analyzed from soil samples: number/biomass of soil animals (nematodes, enchytraeids, microarthropodes), microbial community composition (PLFA analysis), microbial activity (soil respiration) and amount of nutrients (inorganic nitrogen and phosphorus). From lysimeter water samples we measured the amount of inorganic nitrogen and phosphorus and total organic carbon (TOC). Decomposition of the litter of different plant traits was studied in a reciprocal litter placement experiment.

### Preliminary results (in 2005)

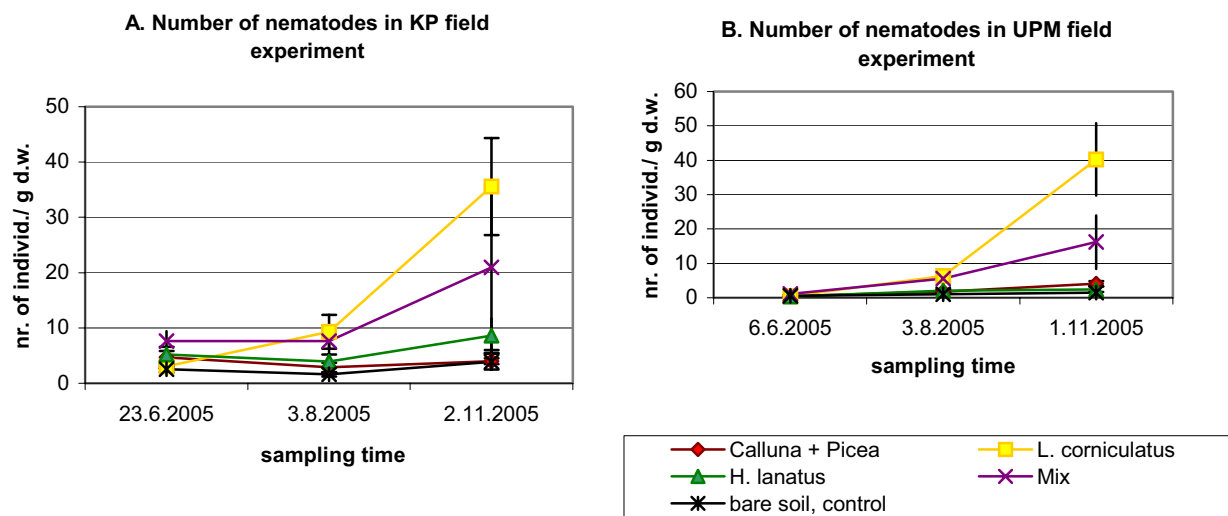
Here I present results from 2005. Soil samples were collected in June, August and November. Lysimeter samplings in KP were done in August and November and in UPM in August and October. Data were analysed with ANOVA of repeated measurements and a pair-wise comparison with the Tukey test. The biomass of Enchytraeidae worms was calculated from all soil samplings in 2005. The biomass of enchytraeids increased in the *Picea* and *Calluna* treatments from June to November, but there was no significant effect of plant treatment (UPM  $p=0.074$ , KP  $p=0.431$ ) (Figure 3).



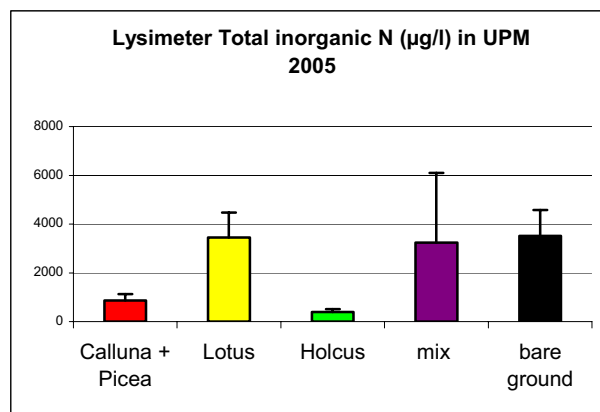
**Figure 3.** The biomass of Enchytraeidae worms ( $\mu\text{g/g}$  dry soil  $\pm$  St. Dev) in June, August and November samplings in 2005 in (A) KP and (B) UPM field experiments. Different line colors indicate different plat treatments (the box above).

The number of nematodes was counted in the same soil samples as Enchytraeidae worms (Figure 4.). The plant traits had a significant effect on the number of nematodes in UPM ( $p=0.0001$ ) and in KP ( $p=0.004$ ). The number of nematodes in *Lotus corniculatus* treatments in UPM was significantly higher than in *Holcus lanatus* treatment ( $p=0.01$ ), in *Picea abies* and *Calluna vulgaris* treatment ( $p=0.01$ ) and in bare ground treatment ( $p=0.001$ ). In KP *Lotus corniculatus* treatment differed significantly from the *Picea abies* and *Calluna vulgaris* treatment ( $p=0.014$ ) and bare ground treatment ( $p=0.007$ ).

Plant treatment did not have a significant effect on inorganic nitrogen (nitrate and ammonium) nor on phosphate concentrations of lysimeter waters leached through different plant treatments in UPM or KP field experiments in 2005 (Figure 5.).



**Figure 4.** The number of nematodes (nr. of individuals/g dry soil  $\pm$  St. Dev.) in June, August and November samplings in 2005 in (A) KP and (B) UPM field experiments. Different line colors indicate different plant treatments (the box above)



**Figure 5.** Inorganic nitrogen concentrations of lysimeter waters leached through different plant treatments (*Calluna + Picea*, *L. corniculatus*, *H. lanatus*, mix and plant free) in the UPM field experiment in 2005.

## Conclusions

The preliminary results of two field experiments indicate that different plant traits may rapidly influence the composition of belowground food webs. The majority of free-living nematodes are bacterial feeding (Yeates, 2003), which indirectly indicates the greater role of a bacterial-based energy channel in the rhizosphere of an herb (*Lotus corniculatus*) compared to other plant traits included in the study. Plant traits did not have significant effect on the biomass of enchytraeidae worms, but in the November sampling of the UPM experiment the biomass was seemingly higher in *Calluna* and *Picea* plots. This could suggest a growing importance of fungal-based energy channel as the system matures.

At the early stage of the experiment, the function of different plant-soil systems to retain the nutrients in the soil did not differ significantly. However, the trend of increasing leaching of inorganic nitrogen compounds (ammonium and nitrate) through *Lotus*, mixed and no plant treatments was clearly visible in both field trials. At the same time we also established a laboratory experiment with the same plant traits to further look at the nutrient dynamics of the systems.

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## **Do different plant traits promote dissimilar decomposer communities?**

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The planet we are living on consists of numerous types of terrestrial ecosystems, such as forests, grasslands, heath lands, fens, and deserts. As a matter of fact these ecosystems not only vary in their composition of plants, but also in the biota they harbor belowground. In an established and well functioning ecosystem, the nutrient cycling processes between the aboveground vegetation and the belowground decomposer community are usually in balance. Plants are producing organic matter, which is returned as litter to the soil, where it is degraded by the decomposer food web. According to Wardle (2002) this is how most soil biologists tend to see the aboveground vegetation, as a source of carbon, without considering the interactions between these two compartments. Similarly plant ecologists usually do not pay much attention to the belowground biota.

In our investigations we included the aboveground biota in our soil studies to address the main question whether different functional traits of plants promote dissimilar types of decomposer communities. Different plant traits are herein defined by the variation in the given resources (litter) and the differences in the root symbionts.

The abovementioned difference in litter quality is mainly due to its chemical properties. While leaves of fast growing, perennial grasses and herbs contain cellulose or hemicellulose as the dominating structural polysaccharide, the leaves and stems of trees and shrubs contain lignin and in addition often phenolic compounds. Both bacteria and fungi produce cellulose systems to degrade the more labile cellulose, but only some fungi are able to break down recalcitrant lignin (de Boer et al., 2005).

Not only litter has a strong influence on the belowground community, but also the root symbionts. According to Timonen et al. (2004) ectomycorrhizae have negative effects on the number of culturable Protozoa in the rhizosphere because the hyphal mantle reduces root exudation and consequently the growth of bacteria, which results in a decreased number of bacterial feeding Protozoa. In addition the external mycelium of this type of root symbiont has been shown to reduce the number and activity of bacteria in pine litter (Olsson et al., 1996 in Timonen et al., 2004). This leads to the assumption that plants without the ectomycorrhizal hyphal mantle exude more and hence the rhizosphere is more suitable for Protozoa.

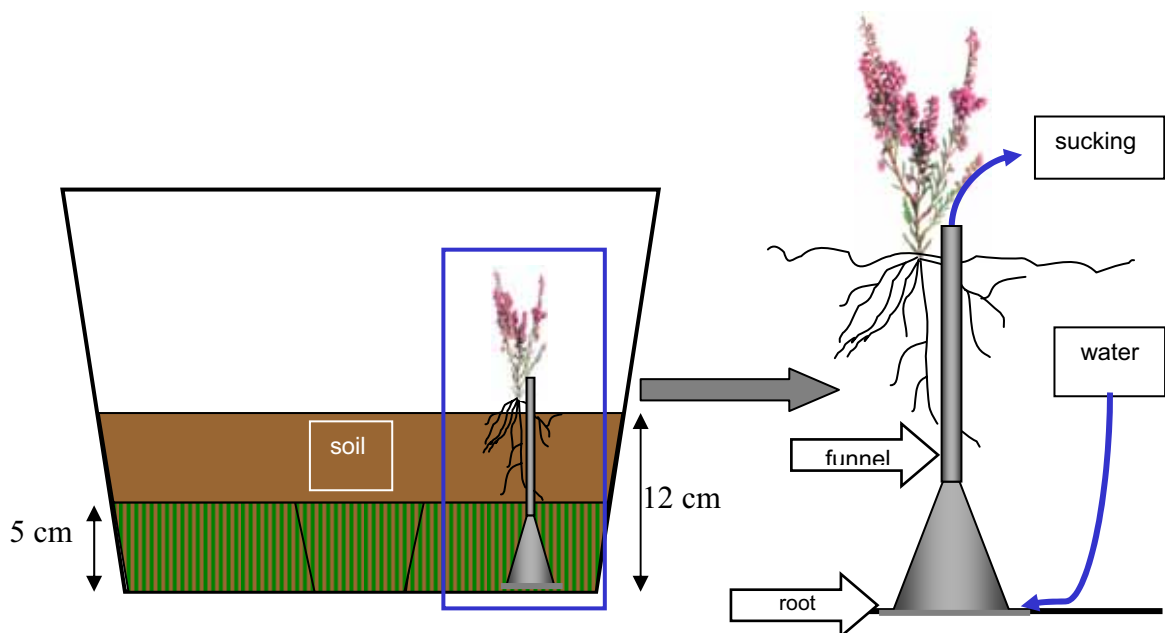
As a consequence we assume different plant traits to be the main driving force for the establishment of a specialized belowground decomposer community, with a fungal-dominating energy channel below recalcitrant plants and a bacterial-dominating under the labile plant traits. The fungal dominated energy channel consists mostly of fungi such as dominating microorganisms, fungal feeding microarthropods (Collembola, oribatid mites) and their antagonists (predatory mites). In contrast, we assume bacteria as the predominating microorganism, more bacterial feeding Protozoa and nematodes, as well as their antagonists (predatory nematodes) under the labile plant traits. Furthermore the nutrient composition of leachates is expected to vary considerably due to the fact that the decomposer communities differ in their ability to retain the nutrients in the soil and their dependence on doing so.

To explore whether the theory is confirmed we established a novel experimental approach differing from the traditional “flowerpot” ones. The main disadvantage of small pots is the limited ability for soil biota to select their desired “niche”. Our ecosystems were large buckets with a diameter of 50 cm, where 5 cm high plastic walls were glued on the bottom to separate different “plant regions” from each other, yet allowing soil biota to choose the desired plant rhizosphere (see Figs. 1 and 2). These walls should prevent the plant roots spreading around in the unwanted sectors. Before adding the soil (30 kg in total, depth 12 cm, sorted to remove stones, earthworms, caterpillar larvae and plant parts) with its initial soil biota, a lysimeter system was adjusted to collect water leachates at the bottom of each section (Fig. 1). The plants *Picea abies* (seedlings) and *Calluna vulgaris* (seedlings) as recalcitrant, and *Holcus lanatus* (seeds) and *Lotus corniculatus* (seeds) as labile functional traits, were placed each in one of the outer sections, while the inner compartment remained as unplanted controls. With these plants we aimed to cover the most common root symbionts, with ecto-, ericoid- and arbuscular mycorrhiza as well as nitrogen fixing bacteria.

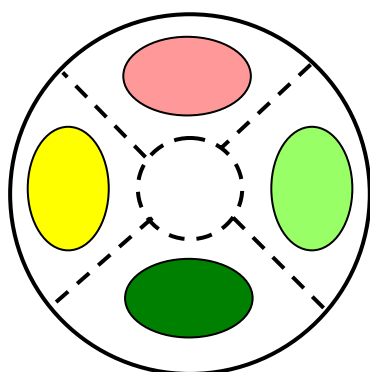
The experiment was placed in a cool water bath to prevent the soil from overheating. In addition we create artificial growing seasons with appropriate illumination and temperature. After each “summer” the experiment will be sampled by taking soil cores from the rhizosphere of each plant and the plant free section. The soil will be

analysed for the composition of phospholipid fatty acid (PLFA), relative microbial activity (basal- and substrate induced respiration SIR), number of culturable Protozoa, number and composition of nematodes, number of enchytraeids, and number and composition of soil microarthropods. To screen the possible physico-chemical differences in the rhizospheres due to the different plant groups, we analyse the leachates taken from under each section for phosphate, nitrate and ammonium concentration.

Again, the aim of this macrocosm set-up is to give the soil fauna the possibility to move freely to find the most suitable environment for their requirements. There is evidence that soil animals, such as nematodes (Griffith & Caul, 1993) and Collembola (Bengtsson et al., 1994), migrate actively in search of the preferred habitat. Is this seeking activity and establishment controlled by specific properties in the plant rhizosphere?



**Figure 1.** Experimental setup (side view) with lysimeter system.



**Figure 2.** Experimental setup (top view), dashed line = 5 cm barriers, pink = *Calluna vulgaris*, dark green = *Picea abies*, light green = *Holcus lanatus*, yellow = *Lotus corniculatus*, middle section = unplanted, N = 8.



So far two samplings have been done and the first results show a significant difference in the relative microbial activity between the different functional traits after the first growing period (basal respiration:  $p = 0.02$ ; SIR:  $p = 0.03$ ). This is not surprising, for microorganisms are the fastest to react to changing conditions. Also we found a higher leaching of nitrate and after the second growing season significantly more nematodes in sections where *Lotus corniculatus* was growing. From the first impression of the results the legume seemed to be the most “active” plant in changing the rhizosphere.

In this presentation I will give a detailed description of the set up and first results after two samplings.

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## The influence of ecological conditions of alluvial soils genesis on the dynamics of soil invertebrate communities

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Soil biota are the basic component of the functioning and evolution of terrestrial ecosystems. The processes of litter transformation, synthesis and mineralization of humus in soils, accumulations and migrations of substances in landscapes are closely connected to soil biota activity. Questions about the specific diversity and dynamics of soil invertebrate communities and also features of alluvial soil genesis are rather poorly investigated in floodplain forests of the European North-East, although floodplain ecosystems represent unique habitats that can be studied to further understand the youth, dynamism and high density of a biota.

The aspen-birch forest generated on the floodplain terrace of the Sysola River (Komi Republic, middle taiga) has served as the site and object of our research. Plots that differ sharply as to the ecological conditions of soils genesis were chosen: ridge summit (S1), leveled site of floodplain terrace (S2), and inter-ridge depression (S3). Standard methods of soil-zoological research were used for studying specific composition, structure of the population and the dynamics of a number of soil invertebrates. Soil of 0.0025 m<sup>2</sup> and 0.0625 m<sup>2</sup> were sampled in 10-fold frequency monthly during the summer-autumn of 2003-2004.



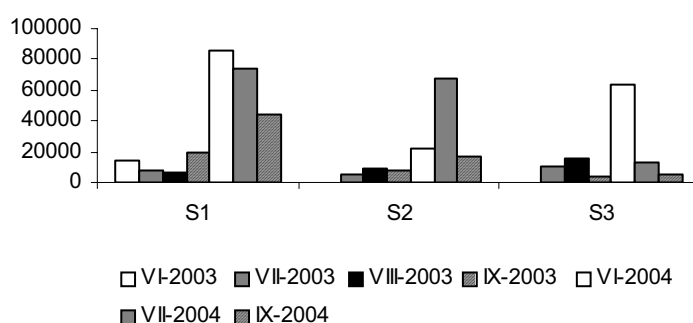
As a result of the research it was established that in floodplain forests, in contrast to meadows, the horizon of well expressed litter-enriched humus had been formed in the soil profiles. The capacity of the litter, without dependence on an element of the floodplain relief and soil type, on the average was about 3-5 cm. Significant stocks of energy (328.1-383.5 million in kcal/ga), nitrogen (1.64-1.74 t/ga), carbon (36.8-43.0 t/ga) and other elements were accumulated in the forest litter. The horizons of litter (A0) in alluvial soils were most dynamic in relation to humidity parameters. The litter on the ridge summit was characterized by the least humidity (20-40% of total moisture capacity). The litter in the inter-ridge depression was characterized by the greatest humidity. However on such plots, depending on a freshet mode and weather conditions for the year, a decrease in litter humidity to optimum parameters (40-60% of total moisture capacity) in the middle or the end of summer was marked. Mineral horizons (A1) of this alluvial soil remained up to the end of the vegetation period with the greatest humidity (80-90% of total moisture capacity).

The alluvial soils were sour and nonsaturated by bases, with a sharply decreasing profile distribution of organic carbon (at a depth of 20-30 cm the maintenance of organic carbon is 0.5-0.9%, whilst in organic horizons its size varied from 4.5-4.8% (S1, S2) up to 3.0 (S3)). Running from the ridge summit to the inter-ridge depression an essential increase in acidity in the organic horizons was observed, the level of subsoil waters raised and depth and a degree of warming were reduced. During the autumn period, due to receipt fresh leaves, the decrease in acidity in the organic horizons of the alluvial soils at the research plots was observed, that is accompanied by splash in number of microorganisms. Thus, ecological conditions of soil biota habitats changed from ridge summit to inter-ridge depression.

As a result, in alluvial soils 53 species of Collembola from 36 genera and 11 families were registered. Isotomidae (18), Neanuridae (10), Onychiuridae (6), Hypogastruridae (5) and Entomobryidae (4) prevailed in species amount. Other families were represented by one or two species. A total of 43 species were found at the ridge summit, seven species were found only here (*Shoettella ununguiculata*, *Xenylla mucronata*, *Agrenia riparia*, *Anurophorus laricis*, *Desoria blekeni*, *Vertagopus sp.*, *Entomobrya nivalis*); 35 species were found on a leveled site of floodplain terrace, *Arrhopalites secundarius* and *Sminthurinus igniceps* were met only here. A total of 38 species were found in the inter-ridge depression, and seven species were registered only here (*Mesaphorura krausbaueri*, *Stenaphorura quadrispina*, *Brachystomella parvula*, *Friesea claviseta*, *Folsomia sp n. aff. bisetosa*, *Isotomurus fucicolus*, *Marisotoma teunicornis*). The prevalence of the family Isotomidae is the characteristic feature of Collembola fauna in taiga forests. Collembola groups of alluvial soils are polydominant: mass species consisted of 88.6 - 93.4% of the total species amount. On each plot an abundance of forest species *Folsomia quadrioculata* and *Isotomiella minor* was high, and the share of *I. minor* increases with the increase in humidifying. On the ridge summit and in the inter-ridge depression the greatest number of species, characteristic only for these habitats, was marked. The similarity of specific composition of Collembola in alluvial soils was 0.73-0.82 (index of Chekanovskii-Sierensen). The taxonomic structure of Collembola in alluvial soils was stable on 2003-2004.

In alluvial soils 44 species of large invertebrates (Lumbricidae, Lithobiidae, Geophylidae, Carabidae, Staphylinidae, Elateridae, Diptera larvae) were registered. The maximal specific diversity of large invertebrates was revealed on a high (S1) and on an average (S2) level of floodplain terrace. The diversity of large invertebrates decreased in the inter-ridge depression (S3). Constant dominant species were absent in communities of large invertebrates, as against Collembola groups. During the different periods *Lumbricus rubellus*, *Monotarsobius curtipes*, *Geostiba circellaris*, *Selatosomus impressus*, *Athous niger*, *S. aeneus* carried out the role of dominant species on the ridge summit, *Monotarsobius curtipes* and *S. impressus* – on the leveled site of the floodplain terrace, *Octolasion lacteum*, *G. circellaris* in the inter-ridge depression. Despite of distinctions in specific structure, the set of the basic groups of macrofauna varied nonsignificantly for the summer-autumnal period, and for the two years of 2003-2004. Changes are shown in a numerical ratio of groups. Mesogyrophil species mainly occupied the leveled site of the floodplain terrace (S2). Mesophil species were better represented on the ridge summit (S1), where mesogyrophil and even gyrophil species were met. Gyrophil species preferred the alluvial soils in the inter-ridge depression (S3).

It has been shown that the number of invertebrates varies with the season and the year. A greater degree of Collembola is determined by weather conditions of the vegetative period (Kaczmarek, 1975; Кузнецова, 1984), genesis of soils and character of a freshet mode. In 2003 with cold and humid early summer, the late high water number of Collembola was low. There were corresponding changes in different alluvial soils. The reduction in the number of Collembola number was observed in July – August on the ridge summit. The peak number of Collembola number was marked in August (with a nonsignificant decrease in July and September) at the leveled site on the floodplain terrace and in the inter-ridge depression. In 2004, in contrast, year with warm weather and moderate humidity during the first half of summer, an early high water number of Collembola increased on practically all plots in all terms of selection with a peak in July. The soil in the inter-ridge depression at the end of summer and in the first half of September was sharply humidified, a condition that caused a decrease in the number of Collembola (Figure 1).



**Figure 1.** Number (N, ind./m<sup>2</sup>) of Collembola in alluvial soils in 2003-2004.

All Collembola were concentrated in the litter (A0) and in the humus horizon (A1) of the alluvial soils. The number of Collembola in the horizons changed during the vegetative period. In 2004 the great amount of Collembola on the leveled site of the floodplain terrace was been concentrated in the litter during all vegetative periods.

Continuing until September the increase in the number of Collembola in the litter (in comparison with horizon A1) was marked and reflected the index of vertical distribution ( $K = N_{A0}/N_{A1}$ ,  $N_{A0}$  and  $N_{A1}$  – number in litter (A0) and humus horizon (A1) respectively). In alluvial soils on the ridge summit and in the inter-ridge depression a small "deepening" of Collembola groups was marked. The number of Collembola was high, not only in the litter, but also in horizon A1 (table 1).

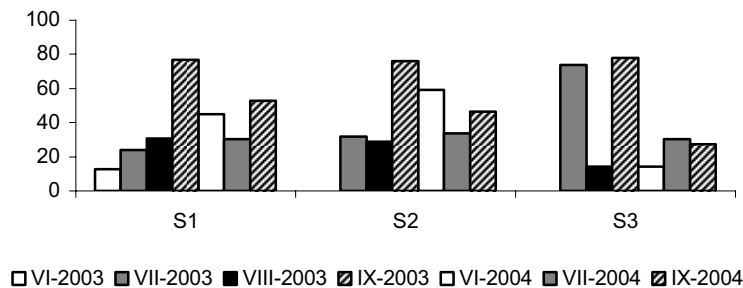
**Table 1.** Number (N, ind./m<sup>2</sup>) and index of vertical distribution (K) of meso- and macrofauna in alluvial soils in 2004.

	S1			S2			S3		
	N <sub>A0</sub>	N <sub>A1</sub>	K	N <sub>A0</sub>	N <sub>A1</sub>	K	N <sub>A0</sub>	N <sub>A1</sub>	K
	Mesofauna (Collembola)								
June	36060	50220	0.7	18260	3220	5.7	30000	33540	0.9
July	45400	29260	1.5	55440	12120	4.6	6380	6140	1.0
September	31920	12720	2.5	16860	640	26.3	2000	2900	0.7
	Macrofauna								
June	24.0	20.8	1.2	46.4	12.8	3.6	11.2	3.2	3.5
July	11.2	19.2	0.6	16.0	17.6	0.9	25.6	4.8	5.3
September	51.2	1.6	32	43.2	3.2	13.5	11.2	16.0	0.7

In alluvial soils the number of Collembola depended on ecological conditions of soil formation as determined by various factors. At the ridge summit the number of Collembola was connected to the activity of bacterial flora (factor of correlation  $r=0.52$ ), temperature capacity of the litter ( $r=0.58$ ), amount of acting deposits ( $r=-0.53$ ). On the leveled sites of the floodplain terrace the number of Collembola correlated with soil temperature ( $r=0.89$ ), number of macrofauna ( $r=-0.50$ ) and soil humidity ( $r=-0.42$ ). In the inter-ridge depression the number of Collembola correlated with the number of macrofauna ( $r=-0.42$ ) and the amount of acting deposits ( $r=0.49$ ).

A greater number of large invertebrates is determined by the temperature. A rise in temperature causes a real decrease in the number of macrofauna in the middle of summer due to their migration from the litter in the mineral horizons of alluvial soils (factor of correlation  $r=-0.77$ ,  $r=-0.76$ ,  $r=-0.51$  for plots S1, S2, S3 respectively). The second important factor, influencing number of macrofauna, is total number of microorganisms ( $r=0.64$ ,  $r=0.77$ ,  $r=0.69$  for plots S1, S2, S3 respectively). The soil humidity plays a smaller role in the number of Collembola. There was no linear connection between the number of meso- and macrofauna number at the ridge summit (S1). There was no linear connection between the number of large invertebrates number and soil humidity in the inter-ridge depression. It is caused by specific taxonomic structure of macrofauna on these plots.

In 2003 the number of macrofauna in soils of various elements on the floodplain relief increased from June to September. Thus in the inter-ridge depression there was a sharp decrease in the number of macrofauna in August whereas the number of Collembola was high. In 2004 a similar increase in the number of macrofauna by September on all plots was observed. Thus optimization of the water-air and thermal modes of alluvial soils in the inter-ridge depression, connected with a decrease in the subsoil water level to the end of the summer, caused an improvement of conditions for the existence of large invertebrates that lead to an increase of their number (Figure 2).



**Figure 2.** Number (N, ind./m<sup>2</sup>) of macrofauna in alluvial soils in 2003-2004 years.

Large invertebrates, as well as Collembola, were not met deeper than 20 cm from the surface of the ground. The majority of representatives of this functional group were concentrated in the litter on all plots. However the index of vertical distribution of large invertebrates was higher at the ridge summit and on the leveled sites of the floodplain terrace in September, and in the inter-ridge depression in July. Basically it is possible to speak about the tendency to "deepening" of macrofauna groups in alluvial soils on the ridge summit and in the inter-ridge depression. However, large invertebrates were more active than Collembola, and their number on the soil horizons varied more considerably (Table 1). By the end of the vegetative period, in connection with some optimization of humidity conditions in soils in the inter-ridge depression, an increase in the number of macrofauna in the organic horizons and expansion of their specific structure were observed.

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## Lichen-oribatid mite associations in the high mountains of Himalaya and Norway

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We will present the results of oribatid mites research extracted from samples of lichen species collected from the Gyama valley and Nyenchentanglha glacier foreland of Tibet (4000 m to 5500 m a s l) in 2004. We also present results of gradient samples of *Xanthoria elegans* collected from Nyenchentanglha glacier foreland (4900 m to 5600 m a s l). Oribatid mites were also extracted and have been studied from different lichen samples collected from the Gangapurna glacier foreland, Nepal (3500 m to 4000 m a s l) in 2004. In addition, we will discuss some preliminary results of lichen-mite associations of the glacial foreland of Midtdalsbreen (1300 m to 1400 m a. s. l.) in Finse, Norway, deglaciated since the "Little Ice Age".

# The effects of land reclamation and afforestation on soil fauna in Iceland

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## Abstract

The abundance of mites and collembola was studied in a chronosequence study of larch and birch in East Iceland and sitka spruce, lodgepole pine and birch in West Iceland. In both areas, grazing seemed to have negative effect on soil fauna abundance. In East Iceland there was a negative correlation between age of larch stands and density of soil fauna, but similar tendencies were not found for different age classes of sitka spruce and lodgepole pine in West Iceland. Mites were dominating in all birch habitats, in lodgepole pine and young larch and young spruce. As the spruce and larch forests grew older collembola density increased.

**Keywords:** Afforestation, land reclamation, chronosequence, collembola, mites

## Introduction

It has been estimated that at the time of settlement, around 870 AD, 65% of Iceland was vegetated and that woodland, primarily downy birch (*Betula pubescens*), covered 25% - 40% of the total land area. Presently ca. 25% of the country is vegetated and birch woodlands cover only ca. 1% of the total land area (Arnalds 1987). Significant efforts have been made in Iceland in recent decades to revegetate eroded areas and to increase forests in the country. The species used are both indigenous - such as downy birch, tea-leaved willow *Salix phylicifolia* and lyme grass *Leymus arenarius*, and exotic - such as siberian larch *Larix sibirica*, sitka spruce *Picea sitchensis*, lodgepole pine *Pinus contorta* and alaskan lupin *Lupinus nootkatensis*. The effects of revegetation and afforestation on soil biology have been studied by Óskarsson (1984) and Oddsdóttir (2002). Other studies on soil fauna in Iceland concern different habitats (Sigvaldason 1973, Hallgrímsson and Sigvaldsson 1974, Hallgrímsson 1975, 1976, Sigurdardóttir 1991, Gudleifsson 1998). In the present paper we will present studies from the "ICEWOODS" project.

## Experimental set-up

The study sites were in East and West Iceland. In East Iceland soil samples were taken from 5 age classes of larch (16, 22, 23, 40 and 54 years old) and 2 different stands of birch. One of the birch stands grew up after the land was protected from grazing in 1979. The other stand has been protected from grazing since 1905. In West Iceland samples were taken from 16 and 47 year old lodgepole pine; 3 different stands of sitka spruce; one 11 year old stand and two 45 year old stands, one thinned and the other unthinned; and 2 different stands of birch, one grazed and the other protected from grazing since 1964. The control was grazed heathland.

Within each study area, five 50 m long study transects were randomly selected. In East Iceland soil samples were taken on June 3<sup>rd</sup>, July 13<sup>th</sup> and September 14<sup>th</sup>, 2004.

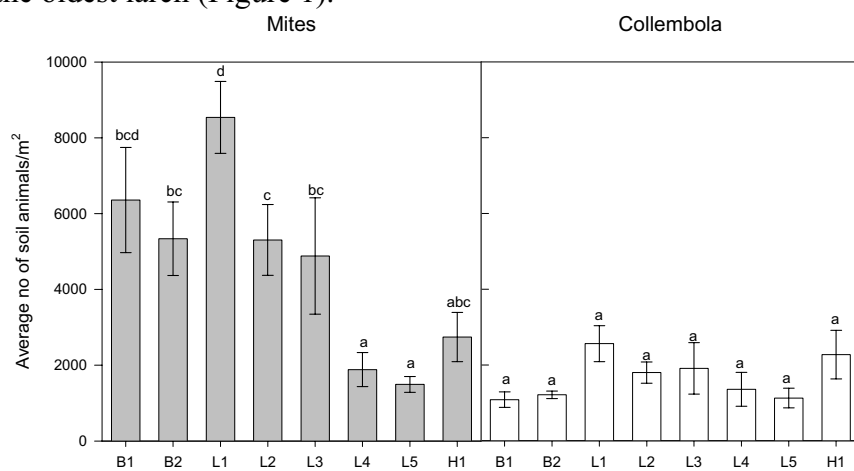
Samples were taken at two randomly selected sites on each transect with a core sampler 5 cm in diameter and at three depths: 0-5 cm, 5-10 cm and 10-15 cm. As very few individuals were found in the lower depths the 10-15 cm sample was omitted on September 14<sup>th</sup> and 4 samples per transect were taken at a depth of 0-5 cm. In West Iceland soil samples were taken on June 9<sup>th</sup>, July 27<sup>th</sup> and September 8<sup>th</sup>, 2005. At each sampling time samples were taken at three depths: 0-5 cm, 5-10 cm and 10-15 cm. Soil fauna were extracted from the samples with a MacFayden high-gradient extractor, using standard methods described by Petersen (1978) and identified to families and subclasses as in Oddsdottir (2002). Collembola will be further identified to species, but no further identification of mites is planned.

## Results and discussion

Abundance of soil fauna was highest in the topmost soil (0-5 cm) and few individuals were found in samples from below 5 cm at both study sites. In the topmost soil, the abundance of soil animals increased during the summer in all habitats. During the first two samplings at both study sites, numbers of individuals were similar but increased dramatically during the latest sampling.

In East Iceland the abundance of mites in the topmost soil (0-5 cm) was highest in the youngest larch (planted 1990) but reduced steadily as the larch grew older, and the lowest abundance was found in the oldest larch (planted 1952). A significant difference in number of mites was detected between habitats ( $F= 5.99, p<0.001$ ). A similar, but not significant, tendency was seen for the collembola ( $F=1.67, p=0.15$ ).

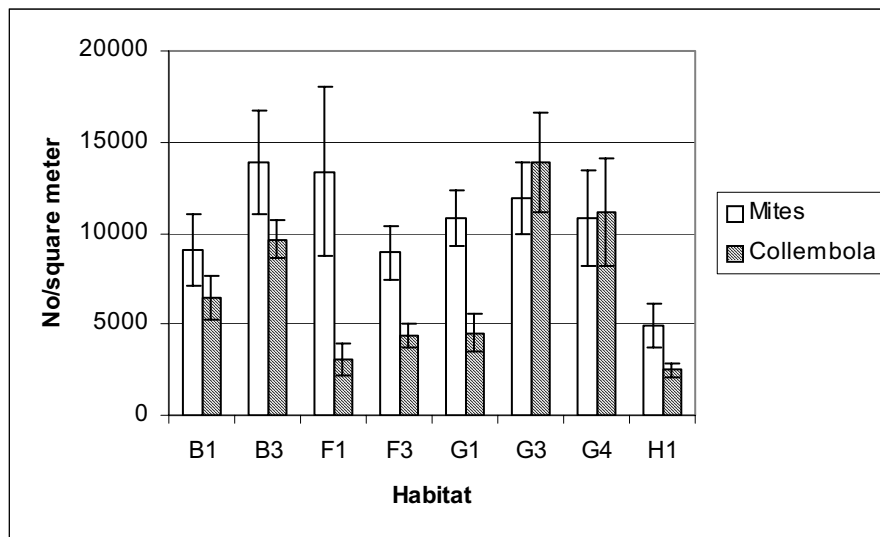
The abundance of both mites and collembola in young birch (B1) was very similar to that of old birch (B2). In the birch forests the abundance of mites was similar to that of larch planted in 1983 and 1984, but the abundance of collembola was similar to that of the oldest larch (Figure 1).



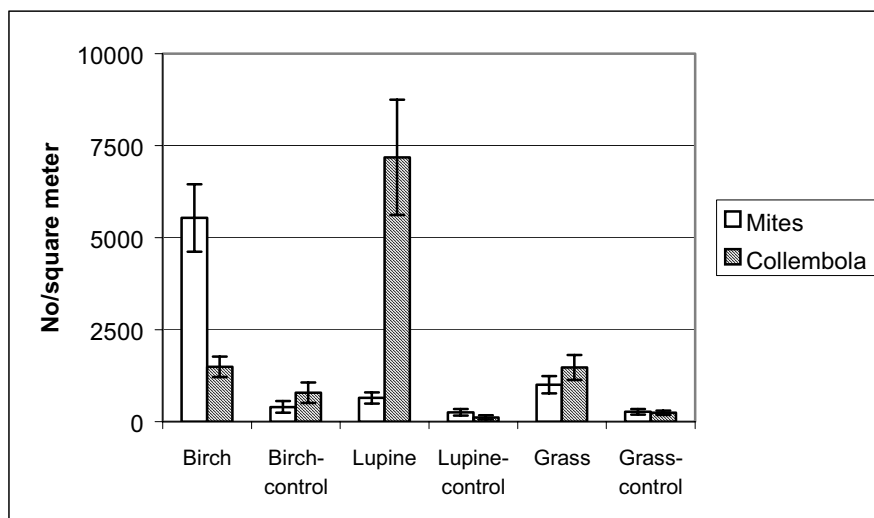
**Figure 1.** East Iceland. Average number of mites and collembola/m<sup>2</sup> in the topmost soil of different habitats at all sampling dates. B1 and B2 are different age classes of birch, 27 and 101 years old, respectively. L1, L2, L3, L4 and L5 are different age classes of larch, 16, 22, 23, 40 and 54 years old, respectively. H1 is grazed heathland. Vertical bars show StE. Columns marked with same letter are not significantly different.

In East Iceland there was a significant negative correlation between average number of mites and leaf area index (LAI).

In West Iceland the abundance of mites in the topmost soil (0-5 cm) was highest in the ungrazed birch (B3), but lowest in the grazed heathland (H1). The abundance of collembola was highest in G3 but lowest in the grazed heathland (Figure 2).



**Figure 2.** West Iceland. Average number of mites and collembola/m<sup>2</sup> in the topmost soil of different habitats at all sampling dates. B1 = grazed birch, B2 = ungrazed birch. F1 = 16 years old lodgepole pine, F3 = 47 years old lodgepole pine. G1 = 11 years old sitka spruce, G3 = 45 years old unthinned sitka spruce. G4 = 45 years old sitka spruce, thinned in 1995. H1 is grazed heathland. Vertical bars show StE.



**Figure 3.** Average number of mites and collembola/m<sup>2</sup> in the topmost soil of areas revegetated with birch, Alaskan lupine and grass. Control is disturbed adjacent areas. Vertical bars show StE. Based on Oddsdóttir 2002.

In East Iceland numbers of soil animals were reduced as the larch forest grew older and denser. This was not observed in West Iceland. The reasons for these differences are unknown, but other studies under the ICEWOOD project show great differences in forest ecosystems between East and West Iceland (Elmarsdóttir & Magnússon 2006, Ólafsson & Ingimarsdóttir 2006). On both study sites the total number of soil animals

increased after afforestation. This can most likely be attributed to the increased plant biomass available for degradation after the areas were protected from grazing. This may also be the reason for the lower abundance of soil animals in the grazed birch forest in West Iceland (B1) than in the ungrazed forest (B3). Studies in South Iceland on the effect of revegetation on soil fauna have also shown that the density of soil animals was highest on the most productive areas that were revegetated with birch and lupine, but lowest on areas revegetated with grass (Oddsdóttir 2002) (Figure 3). In general, afforestation and revegetation seems to have positive influence on soil animal abundance in Iceland. There are clear differences in the response of soil animals to revegetation with different species. Mites dominated in all birch habitats, in lodgepole pine and young larch and young spruce. As the spruce and larch forests grew older collembola density increase. In the Alaskan lupin collembola was clearly dominating.

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## Are soil animals killed by shooting?

### A case study at a shooting range area contaminated by lead

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## Introduction

Heavy metals, such as lead, may affect the species composition in an ecosystem, either due to direct toxic effects or by altering food availability and interactions



between the species. In soils, such changes in the food web may lead to reduced decomposition rate and nutrient cycling. This may, in turn, affect the aboveground ecosystem, e.g. by reducing plant biomass production.

The Hälvälä shooting range area in Hollola, Finland, has been in active use for decades. However, despite the excessive contamination of the soil by lead pellets, there are no obvious signs of stress in the aboveground pine forest ecosystem. Therefore, we asked whether the structure and function of the soil food web is altered after all due to excessive lead contamination. Here, a part of our ecosystem scale analyses is presented.

## Materials and methods

Three study sites in the same pine forest in the shooting range area were studied:

- 1) New (in active use since 1985) contaminated site where the lead pellets are evenly distributed in the organic horizon of the soil.
- 2) Old (shooting terminated in 1987) site where the lead pellets are generally deeper in the organic horizon of the soil because of the accumulation of new litter.
- 3) Control site, an uncontaminated site near the contaminated sites.

Nematodes, enchytraeid worms, microarthropods and soil microbes were sampled at twenty locations at each site along a lead concentration gradient in October 2005. In addition, soil lead concentrations and general soil characteristics were analysed, and the study sites were found to be similar as regards moisture and organic matter content.

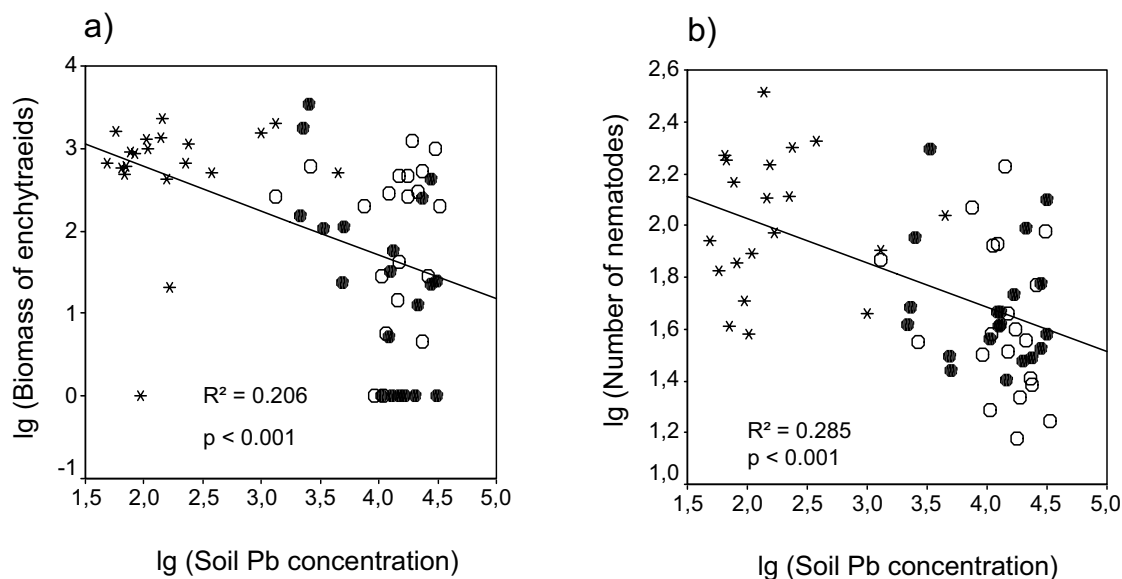
**Table 1.** The relationships between analysed variables (biomass of the enchytraeid worm *Cognettia sphagnetorum*, soil nitrate and ammonium concentrations, number of nematode individuals and number of nematode individuals in different feeding guilds) and soil characteristics (soil Pb concentration, pH, moisture and soil organic matter (SOM)) analysed by stepwise multiple regression.

<i>Variable</i>	<i>Multiple linear regression equation</i>	<i>R<sup>2</sup></i>	<i>p</i>
lg( <i>Cognettia sphagnetorum</i> )	- 4.352 - 0.520(lg(Pb)) + 4.66(lg(moisture))	0.275	< 0.001
lg(NO <sub>3</sub> <sup>-</sup> )	- 2.910 + 0.554(lg(Pb)) + 0.352(pH)	0.727	< 0.001
lg(NH <sub>4</sub> <sup>+</sup> )	- 1.364 + 1.899(lg(moisture))	0.353	< 0.001
lg(nematodes)	2.367 - 0.171(lg(Pb))	0.285	< 0.001
lg(bacterivorous nematodes)	5.250 - 0.881(pH)	0.335	< 0.001
lg(herbivorous nematodes)	1.312 - 0.254(lg(Pb))	0.209	< 0.001
lg(omnivorous nematodes)	- 0.208 - 0.385(lg(Pb)) + 1.375(lg(SOM))	0.515	< 0.001
lg(predatory nematodes)	0.407 - 0.088(lg(Pb))	0.088	0.021
lg(Shannon-Wiener diversity)	0.838 - 0.099(pH)	0.093	0.018

## Results

At our study sites, lead affected the nematode community and trophic structure by reducing the total number of individuals, especially omnivores, but also herbivores and bacterivores (Figures 1b & 2, Table 1). In addition, enchytraeid worm biomass decreased with increasing lead concentration (Figure 1a, Table 1). The microarthropod data is still to be analysed. Of the soil characteristics measured, soil

pH ( $R^2 = 0.181$ ,  $p = 0.001$ ) and nitrate concentration (Table 1.) increased with increasing lead concentration in the soil.



**Figure 1.** Relationships between total Pb concentration in the humus (mg/kg [soil dry mass]) and a) the biomass of the enchytraeid worm *Cognettia sphagnetorum* ( $\mu\text{g/g}$  [soil dry mass]) and b) the number of nematodes (individuals/g [soil dry mass]).

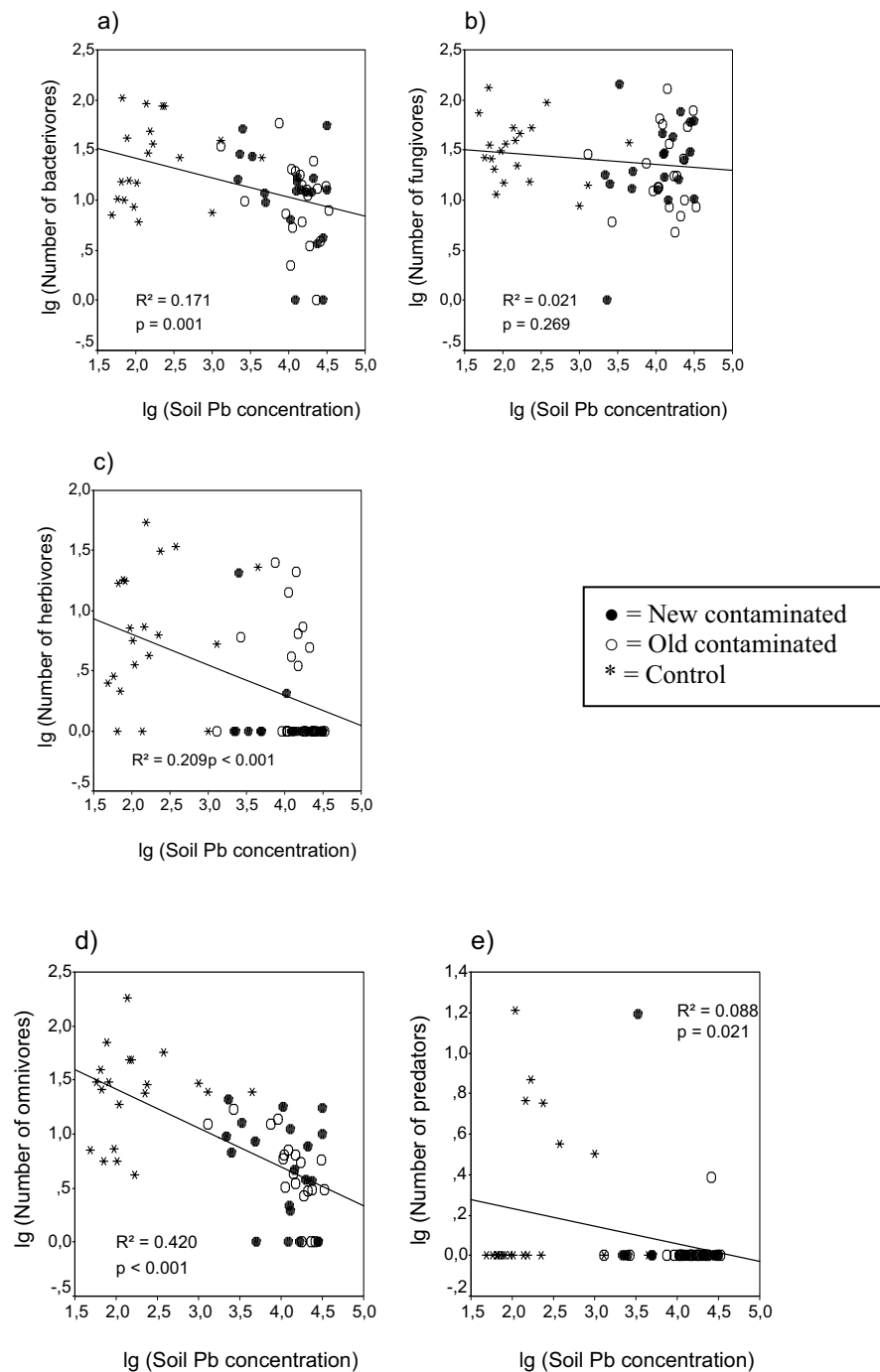
## Discussion

Our results agree with observations of other studies (Korthals et al. 1996; Shukurov et al. 2006) that omnivorous nematodes are sensitive to heavy metal exposure (Figure. 2d, Table 1.). This sensitivity may result from the long generation time and more permeable cuticle of this group as compared to bacterivores, fungivores or herbivores (Korthals et al. 1996).

Contrary to other studies (Korthals et al. 1996; Shukurov et al. 2006), we found a negative relationship between the number of bacterivorous nematodes and soil pH (Table 1). However, since pH and lead concentration are positively correlated in this study, the effects of lead and pH cannot be entirely distinguished. Negative effect of lead on bacterivores, but not on fungivores (Figures 2a & 2b) may indicate either differences in sensitivity of these groups or indirect effects of lead. It is possible that lead affects the microbial community structure by decreasing bacterial biomass, but not the biomass of fungi. Thus, lead would indirectly affect the bacterivores, but not the fungivores. However, we did not find any effects of lead on microbial activity measured as basal respiration and SIR.

With respect to enchytraeid worms, the results of this study support the findings of previous investigations at this shooting range area that soil contamination by lead pellets has negative effects on enchytraeid worms (Salminen *et al.* 2002). Since enchytraeids are considered as keystone species in coniferous forest soils, the decline in their population densities may disturb nutrient cycling and decomposition of organic matter.

The effects of lead on enchytraeids and nematodes could have been more dramatic, if there had not been a positive relationship between lead concentration and pH. Increasing pH has been found to reduce the bioavailability and toxicity of lead e.g. to earthworms (Bradham et al. 2006) and humans (Navarro et al. 2006). Although the bioavailable lead concentrations have not yet been analysed in this study, Turpeinen et al. (2000) found a water soluble form of the lead to be less than 0.3 % of total Pb concentration in soil from the Hälvåla shooting range area.



**Figure 2.** Relationships between Pb concentration in the humus (mg/kg [soil dry mass]) and number of nematodes individuals/g [soil dry mass] in the different (a-e) feeding guilds.

Increased soil pH may also explain the increase in soil nitrate concentration (Table 1.), since increasing pH may stimulate the nitrification potential in soils (Sauve et al. 1999; Stuczynski et al. 2003). Sauve et al. (1999) found that nitrification in soils contaminated with lead and copper was even more sensitive to soil pH than to metal contamination. Thus, it is possible that nitrification is stimulated more by increased pH than inhibited by lead exposure.

### **Conclusions**

Nematode community and trophic structures were affected, enchytraeid worm biomass reduced and pH and nitrate concentration increased by raised lead concentration in the soil. Some of these changes may have resulted from indirect effects of lead, e.g. decrease in bacterivorous nematodes by a possible decline in the bacterial biomass in the soil, and increased nitrate concentration by increased soil pH. Thus, lead contamination affected the food web structure and nutrient dynamics of the soil in the shooting range area. However, the functioning of the aboveground system is apparently highly resistant to changes in the below ground system, as the forest in our study site did not show any apparent signs of stress.

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## **Soil macrofauna recovery from wildfires in a Scots pine forest in Central Sweden**

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Soil macrofauna recovery was studied in 2001-2005 after wildfires in Tyresta National Park (Sweden). A large fire happened in 1999, a small one in 2001. Soil samples were collected with a 100 cm<sup>2</sup> soil corer along the transects crossing the burned areas. Diversity and abundance of soil macrofauna was the highest in the unburned forests (up to 3820 indiv. m<sup>-2</sup>). In the burned areas, abundance varied from 140 to 1360 indiv. m<sup>-2</sup>. Fire severity influenced recovery the most. Deep soil layer inhabitants were found first in the burned areas. Neither pronounced edge effect nor effect of the size of burned areas on soil macroinvertebrates was observed during the colonization process. Fast colonization was supplied with mobile taxa, mostly flies (Chironomidae, Cecidomyiidae), which possibly experienced a lack of predation during the first stages of colonization. With the development of mosses and post-fire vegetation, the assemblages of soil macrofauna became dominated by plant feeding groups like aphids, cicadellids and thrips. Even two years after the fire, almost no soil-living predators developed in the burned area, which demonstrates the lack of resources for them. A 5-year period was insufficient for macroinvertebrates to recover to the pre-fire level.

## **Effects of fire severity on survival and recovery of soil fauna after a clear-cut burning**

**Anna Malmström, Tryggve Persson**

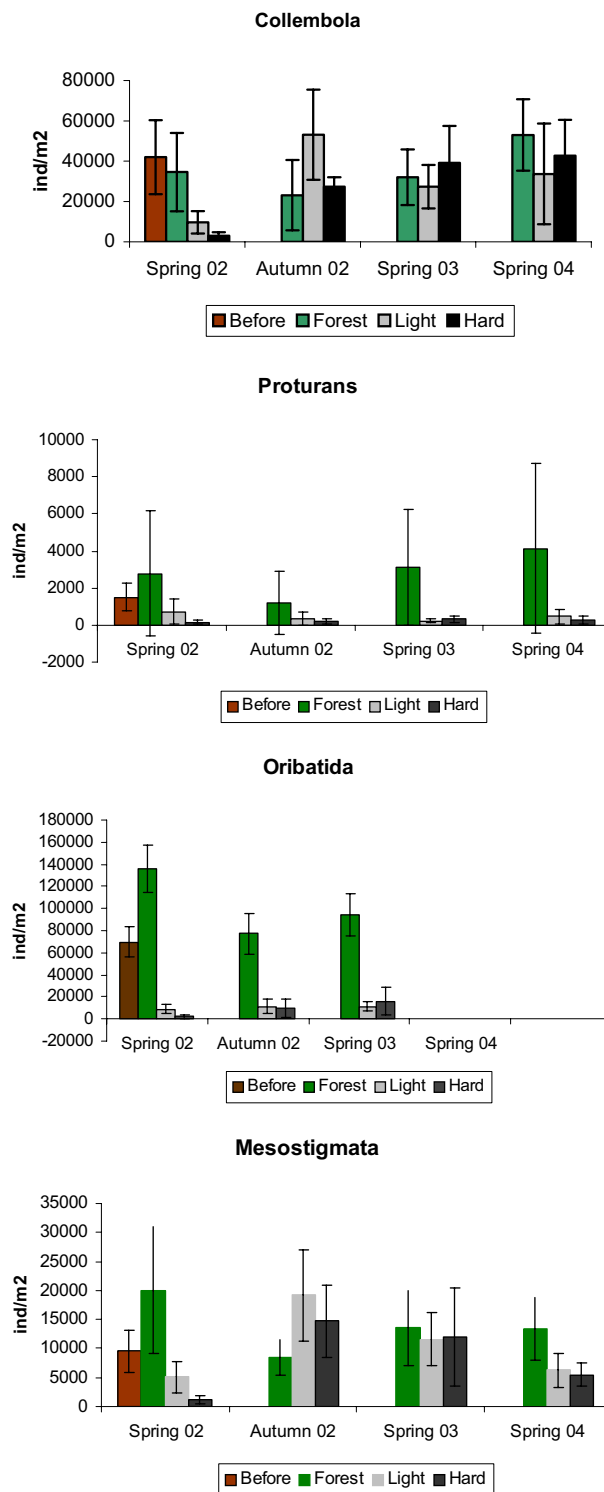
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The number of microarthropods is known to decrease after fire (Heyward & Tissot 1936; Pearse 1943; Huhta et al. 1967; McCulloch et al. 1998; Tamm 1986; Karpinnen 1957). The time it takes for them to recover differs from only a few weeks to several years. These differences could probably be explained by variations in fire severity, but very few studies take this factor into account. Also, very little is known about the first phase after a fire, since almost all studies have been made at least a few months after the burn.

We investigated the direct effects of fire and the effect of different fire severity on both the total amount of microarthropods and species composition. To do this we investigated the soil fauna at a clear-cut that was burnt in May 2002. To manipulate fire severity, harvest residues were added as fuel or were entirely removed from the experimental plots. Samples were taken one week before and one week after the fire as well as the autumn of the same year. Samples were also taken the following two springs (2003 and 2004). Collembolans and oribatid mites were counted and determined to species level, while mesostigmatid mites were only determined to family. Proturans were counted as a group. Simpson's diversity index and Simpson's evenness measure were calculated, as well as the mean number of species. Rarefaction was used to adjust for differences in sample size between the treatments.

All animal groups responded to fire with a direct decrease in abundance (Figure. 1). The abundances of Collembolans were lower in the hard burnt plots (7% of the control) than in the lightly burnt plots (23%). The same was true for oribatid mites

(3% in hard burnt and 13% in light burnt) and mesostigmatid mites (13% vs. 53%). There were less proturans in the hard burnt plots than on both the unburnt clear-cut and the light burnt plots, but no difference could be detected between the light burnt treatment and the control.



**Figure 1.** Effects of different fire severity on survival and recovery of Collembolans, Proturans, Oribatid mites and Mesostigmatid mites. The figure shows the total abundances of animals (+SE) one week before the fire one week, 5 months, 1 and 2 years after the fire.

The number of species decreased in the burnt treatments, with fewer species found in the more severe treatment. Rarefaction analysis showed that this was not only due to smaller sample size. The diversity of collembolans decreased in the burnt plots compared with the unburnt compared to the unburnt clear-cut and the forest.

Several species of both Collembola and oribatid mites responded to burning. Most of the species that decreased an equal amount in both burnt treatments were surface living species, while the species that were found in low abundances in the hard burnt treatments were soil living species to a greater extent. Many mesostigmatid mites responded to fire, but the majority of species only responded to the hard-burnt treatment. Only *Pergamasus* sp. decreased in both fire treatments.

After the first decrease in animals no difference could be seen between the hard burnt and the light burnt plots. The only Collembola species that showed any differences between the different fire treatments was *Bourletiella hortensis*, which occurred in higher numbers in the hard burnt plots in 2004.

This study shows that the effects of fire on soil microarthropods are immediate. One week after the fire the number of animals was severely reduced, and the effect was more pronounced in the hard-burnt treatment than in the light-burnt treatment. Wikars and Schimmel (2001) report a similar result after studying immediate effects of fire severity on soil invertebrates.

Surface living species did not react to fire severity, whereas soil dwelling species did to a higher extent. This is probably because species living in the vegetation and in the upper soil layer will suffer from the fire regardless of fire intensity. The risk of being consumed by the fire is great, and the heat at the surface is several hundred degrees (DeBano et al. 1998). For animals living in the soil and that are able to migrate downwards during fire the fire intensity becomes of increasing importance. A more intense fire will release more heat into the soil (Steward et al. 1990). Humus-living microarthropods are killed at around 40 °C (Malmström et al. in manuscript) and temperatures of that magnitude are often reached in the soil during a fire (Steward et al. 1990, Busse et al. 2005, Schimmel and Granström 1996). That soil animals are killed by temperature are supported by Wikars and Schimmel (2001) who found that taxa living in the mosses and the litter layer were more affected by fire than those living deeper down in the soil. Vlug and Borden (1973) also found that the influence of both logging and slash burning was greater at the surface and decreased deeper down in the soil.

No effect of fire severity could be seen over time in this study. Wet and cool weather conditions resulted in a light intensity fire where the humus layer stayed intact. No measurable differences could be seen on humus consumption between the different treatments. We strongly believe that the initial differences in animal abundances are due to increased heat transfer into the soil in the hard burnt plots. Microarthropods are able to come back fast after a disturbance (Lindberg & Bengtsson 2006) provided that the habitat is suitable. Since the humus layer was left intact after the fire the microarthropods were probably able to recover.

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## Influence of volcanic ash on the community of oribatid mites in a peat land in Espenberg, Alaska

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There is a current discussion considering the climatic impact of large volcanic eruptions and the sedimentation of volcanic ash. Analyses of climatic parameters in sediments formed prior to and after earlier eruptions are essential in the study of these dynamics.

About 3400 years BP, a large volcanic eruption formed the Aniakchak Caldera on the Alaska Peninsula. In large areas of Western Alaska, the tephra from this eruption forms a distinct layer in the sediments. It has been suggested that this eruption was large enough to impact the climate (Begét et al. 1992).

The material for this study was collected at Cape Espenberg, 1500 km north of Aniakchak. The identification of this tephra has been confirmed by radiocarbon dates.



A core of sediments was taken from peat land, and 7 cm of the core, 3.5 cm above and below the tephra layer was investigated. This material has been sedimented over approximately 700 years. All remains of oribatid mites were hand picked out of the samples. Approximately 3000 adults and 1750 juveniles were picked out. All adults were identified to 14 species. The juveniles were not identified due to difficulties with identifications and their different taphonomy, as the difference between how well the species are preserved is much larger in juveniles than adults. The multivariate analyses DCA, PCA and RDA were used to statistically investigate the results.

As expected of an oribatid community in peatland, hydrophilous species were plentiful. Among the species found, *Malaconothrus*, *Trimalaconothrus*, *Hydrozetes*, *Limnozetes* and *Ceratozetes* were common. There was a clear development in the community as time progressed.

In general, there is an increase in the number of oribatids we found. The most striking feature is, however, the rise and fall of *Ceratozetes parvulus* prior to and after the tephra layer. Popp (1962) classifies this as a true bog species, it is however linked to the tussocks. This is supported by the environments where Behan-Pelletier (1985) found this species in North America, including Alaska. At the decline of *C. parvulus*, the abundance of *Trimalaconothrus maior* and *Hydrozetes* sp. peaks. As these species are known to inhabit wet habitats, we believe that this is due to a humification of the peat land. This is further supported by the *Limnozetes palmerae* appearance in the upper part of the core. This species is known to be linked to wet, well developed *Sphagnum* bogs (Behan-Pelletier 1989).

In conclusion, this community develops over time, but there does not seem to be any large influence by the tephra. The statistical tests also support this hypothesis.

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## Recolonization after disturbance - Is this a key to the resilience of soil communities?

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Soil communities are generally regarded as resilient to changes, as seen by the existence of stable communities following disturbance and in a number of experiments where the functioning of communities seems to have been restored even

at low levels of community diversity. Disturbances to the soil system can arise as a direct action on the soil, or indirectly from effects on the aboveground plant community. The temporal scale of disturbance might be a very short time (minutes), such as carbon turnover in the rhizosphere, or large, as when dealing with changes in the climate.

How then do disturbed communities recover so quickly from the disturbance?

First, the functions that we measure as processes in the soil community are usually resistant as the several different species have the ability to cover the functions/resources that were used by a different species before the disturbance.

Secondly, soil communities are generally heterogeneously distributed, which allows the coexistence of otherwise potentially competing species and also allows a high species diversity to coexist in the soil.

Thirdly, soil communities under change can be regarded as transient systems which do not rely on equilibrium interactions between competing species or trophic levels. In disturbed communities (non-equilibrium states) the importance of dispersal in space and time should be higher than in more stable communities that are more dependent on competition between species. The high redundancy which is usually seen in soil community functioning is thus probably dependent on a very high ability of dispersal of soil organisms, especially in time but probably also in space.

There is currently very little knowledge of how the dynamics of soil organisms in space and time can recolonize a habitat after disturbance. Clearly, many soil organisms can disperse in time, resulting from their ability to form resistant, resting structures as a response to the highly dynamic nature of substrate availability in soil. This means that with a dynamic spatial and temporal response to disturbance soil organisms are more resilient to disturbance on a larger scale. However, this will increase a stochastic development of the interacting organisms on a local scale.

The means by which soil organisms are dispersed are not really known today. In considering passive dispersal mechanisms the high frequencies of passively dispersed soil organisms, e.g. in Arctic communities, have been noted and we can at least conclude that dispersal is a plausible factor making soil organisms resilient.

Studies of recolonization and dispersal will be discussed in the presentation.

## **Effects of moss cover removal on collembolan communities in a Scots pine forest based on a five year study**

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The feather mosses *Hylocomium splendens* and *Pleurozium schreberi* are the most common and widespread moss species in pine forests in Latvia. They form a distinct

spatial structure on the forest floor. Many studies have shown that soil Collembola also have a distinct pattern of aggregated distribution. The aim of this study was to investigate the relationship between vegetation and a soil Collembola community structure in a Scots pine forest in northern Latvia.

An experiment was set up in order to study the role of feather mosses as a contributor to soil biodiversity. The study was carried out in nine experimental plots (100m<sup>2</sup>) with three treatments – damaged (upside-down), removed and undamaged moss cover of forest floor – located in a Scots pine forest that was about 80 years old. Soil and moss samples were randomly collected from each sampling plot twice a year in June and October between 2001 and 2005. Manipulations with moss cover were made after the first sampling in June 2001. Structure and spatial distribution of Collembola communities have been studied. Fifty-two species of Collembola were recorded during the study period. The highest number of species (42 species) was observed in control plots, whereas the lowest (33 species) was in the plots with the moss cover removed. Species richness tended to decrease gradually in the plots with the moss cover removed throughout the study period. The effect of several ecological factors such as soil moisture, thickness of humus layer, and treatment type on the distribution of soil Collembola are discussed.

## **Recovery of soil fauna after experimental summer droughts**

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Disturbances like fire and droughts are common in most ecosystems. The persistence of species and maintenance of diversity depends on species being able to survive disturbances or to recolonize disturbed patches from surrounding habitats (Bengtsson 2002). There are many studies that have examined the effects of various disturbances on soil fauna, but much fewer that have subsequently studied the recovery of the communities. We examined the recovery of Collembola, Oribatid mites and Mesostigmatid mites after experimentally imposed summer droughts for 6 years. This was done in a pre-established experiment in a Norway spruce *Picea abies* stand at Skogaby in southern Sweden in which roofs had excluded the main part of the precipitation during summer from 1990 to 1996. The recovery plots were compared to adjacent plots in which the roofs were still in place during 1997-99. We included both predators (Mesostigmata) and fungivores/detritivores (Collembola, Oribatida) to examine whether recovery ability differed because of differences in trophic position, dispersal ability and reproductive strategies. Within the two latter groups, we also examined if species with different habitat preferences or life history traits differed in the rate of recovery.

All three groups had been negatively affected by the drought treatment in 1991-96. Total abundances of all three groups were similar in recovery and control plots after 3 years, but species richness, the Shannon-Wiener diversity index  $H'$ , and community composition recovered more slowly, particularly among the Oribatid mites. There was

a tendency for the two more mobile groups to recover faster than the slow-moving oribatids.

Surface-living species tended to have a narrow habitat width and were less negatively affected by the drought. However, among species negatively affected by the drought, species with larger habitat widths tended to recover faster after the drought. Parthenogenesis was more common among the oribatid species that recovered after the drought than among those that did not. Collembola species generally recovered faster than Oribatida, and several Oribatid species had not recovered 3 years after the drought treatment had been terminated.

Our results suggest it is not useful to examine total abundance of higher taxonomic groups when measuring community recovery, and that community composition is more relevant than species richness when discussing recovery of communities. The results also show that differences in life history traits like habitat preferences and reproductive mode are related to the rate of recovery of populations of different species. Finally, our results indicate the importance of dispersal ability for the resilience of soil communities. However, the small scale of the plots (500 m<sup>2</sup>) makes it difficult to extrapolate our results to the large-scale disturbances that will be imposed by the predicted increased drought with climate warming. However, it is likely that the results of large-scale disturbances will be larger (rather than smaller) than those observed in this study.

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## Primary succession of Oribatid mites near a receding glacier (Hardangerjøkulen), South Norway

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The Hardangerjøkulen glacier in central South Norway has been shrinking during the last 250 years. In the study area at Finse, it has been retracting about 600 m only during the last 70 years. The Oribatid fauna were studied in 25 plots along a gradient from newly exposed soil to 8000 year old soil. All soil samples were taken in *Salix herbacea* vegetation (at 0-3 cm depth) to standardize the habitat. The gradient was divided into four zones. Zone A: Close to the glacier, age of soil 30-45 year; only scattered, small plots of vegetation, and 0-1 mm organic layer. Zone B: Age of soil 50-70 years; vegetation patchy, but some mats of *S. herbacea* and mosses, organic layer usually only 1-2 mm. Zone C: Age of soil 70-250 years; vegetation still not continuous, but *S. herbacea*-mats with up to 1-2 cm thick organic layer. Zone D:

About 8000 years old soil, usually with more than 3 cm deep organic layer; soil pH fell from about 6 close to the glacier to about 4.5 in old soil.

Both adults and juveniles were identified to species level. The number of Oribatid species increased with soil age. Zone A contained 3 species, zone B 8 species, zone C 13 species and zone D 19 species. Pioneer species were two small “generalists”: *Tectocepheus velatus* and *Liochthonius sellnicki*. Six species were only found in the oldest soil. Very few earlier studies exist on the primary succession of Oribatids in a glacier foreland. The gradual colonization is discussed according to the ecology of each species. The succession pattern is also compared with pioneer succession in industrial dumps.

Collembola species were more rapid colonizers, and were also caught numerous in pitfall traps close to the glacier.

## **Effects of climatic manipulations on soil fauna in European shrublands**

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Fauna studies under the multi-disciplinary EU-sponsored ecosystem research project “VULCAN: Vulnerability assessment of shrubland ecosystems in Europe under climatic changes” ([www.vulcanproject.com](http://www.vulcanproject.com)) were based on samplings from 6 shrubland sites, i.e. Calluna heathland (Denmark, Wales, Netherlands), maquis (Sardinia and Catalonia) and poplar shrubland on inland dunes (Hungary), representing large-scale North-South (cool to warm climate) and East-West (dry to wet climate) gradients in Europe. Manipulations of temperature and precipitation were carried out in the same way at all sites, i.e. by covering experimental plots with automatically working curtains resulting in reduced heat radiation at night and reduced precipitation in critical seasons of the year. In each site each of the treatments (warming, drought and control) were replicated in 3 replicate plots 4 x 5 m<sup>2</sup>.

The object of the faunal part of the multi-disciplinary study is to elucidate the effect of long-term climatic changes on quantity and composition of the terrestrial invertebrate fauna of shrublands in different climatic regions and the relationship between effects on fauna and other ecosystem components. The data include population density and biomass on group and species level as well as estimates of biodiversity.

The fauna samplings were carried out from April to July 2003 in the sequence: Capo Caccia (Sardinia), Garraf (Catalonia), Fülöphaza/Kiskunsag (Hungary), Mols (Denmark), Oldebroek (the Netherlands) and Clocaenog (Wales) and included suction samples from above-ground vegetation and soil surface and soil cores treated in high-gradient extractors. Five subplots were chosen for fauna sampling within each of the experimental plots. The position of the subplots was selected to represent the most dominant plant species of the respective sites.

More than 70 families or other larger taxonomic groups of arthropods representing several hundred species were identified and counted. Analysis to species level was done for Collembola and Acari. Comparisons of faunal abundance show several examples of significant differences between sites and between treatments within sites for broad fauna categories such as total invertebrates, total insects, plant feeders and Detritus/microbial feeders (mainly soil fauna) as well as whole fauna groups such as Acari (mites), Collembola (springtails), leaf hoppers (cicadas), plant bugs, aphids, wasps, ants and spiders.

Compared to other sites the Danish site was characterized by a very high number of mostly small mites in all treatments, but decreasing from the control (550,000 m<sup>2</sup>) through the warming treatment to the drought treatment (330,000 m<sup>2</sup>). It is speculated that this may be a result of the earlier mowing of all plots at the Danish site to improve regeneration of *Calluna* after a heather beetle attack.

Whether the responses of population density to manipulated drought and warming were negative, positive or non-significant depended on taxonomic group and site. Negative responses compared with the control dominated in the drought treated plots while a more equal share of positive and negative responses was found in the warmed plots. However, the statistically significant comparisons showed that most individual taxonomic groups responded in the same direction at all sites, i.e. mostly negatively, to both types of climatic manipulations, whereas several examples of opposite reactions in different sites were demonstrated for the composite assemblies of taxa: total insects, total fauna, plant-feeders and detritus/microbial feeders. Especially, several composite fauna groups responded positively to the treatments at the Spanish site. It is interesting that in the rather humid Welsh site no significant differences were found between control and climate manipulated treatments for any of the taxonomic or composite trophic fauna groups. On the other hand, it seems that for some fauna groups significant responses may be found at the species level.

Further analysis of the data showed that the cover percentage of individual plant species within the subplots interacted with the treatments so that in some cases opposite effects on fauna populations were observed depending on vegetation type. Thus, in the Danish site subplots with high cover percentage of *Holcus mollis* the plant feeders were most abundant in the drought treatment, while in the subplots dominated by *Deschampsia flexuosa* the number of plant feeders was lower in the drought treatment than in the control treatment.

Detailed analysis of the micoarthropod taxa Acari and Collembola further demonstrated that different species may respond differently to the heating and drought manipulations resulting in altered species composition and diversity due to the treatments. Comparison at the species level of collembolan populations revealed examples of different reactions to treatment of closely related species. Thus, at the Welsh site the population of the collembolan *Folsomia quadrioculata* reacted positively to the drought treatment while no significant difference in abundance could be shown between treatments in the populations of *Folsomia brevicauda*. This may be an example of altered competition between two related species due to climate-induced changes in the environment. On the other hand, examples of opposite reactions of one collembolan species at different sites were also observed.

Biodiversity (number of species) in the soil and soil surface layer of Collembola, mites and other arthropods was highest in the Spanish site and lowest in the Hungarian site. In most sites the drought treatments contained fewer species than the control while the effect of warming on biodiversity is more complex.

The distribution between sites and treatments of crude biomass estimates based on average individual weights borrowed from the literature differed considerably in composite taxa from distributions based on abundance values. This difference was the result of a large variety in size found between the fauna groups composing these taxa. Less crude biomass estimates were based on measurement of the actual size distribution within the fauna groups. Average weights were calculated from linear body dimensions (e.g. length and width) of individuals representative of the populations. The average weights were then multiplied with abundance to obtain biomass per m<sup>2</sup>.

## **The huge biodiversity of soils: Can it be saved?**

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### **Soil: A biotic frontier**

About 1.8 million species have so far been described in the world. Estimates about the real species number vary greatly, from 5 to 100 million. Together with this uncertainty, we are rather certain that a lot of species disappear each year, and much faster than we are able to collect and describe them. In fact, we will never know how many species lived together with man. But what we can do is to try to save as many as them as fast as possible. And in this work, the biodiversity of soils must be included.

Traditionally, the global focus of biodiversity has been the tropical forest canopy. As many as 30 million arthropod species have been estimated to live in this “first biotic frontier” (Erwin, 1983), but other estimates are lower. In marine environments, tropical coral reefs have long been known as biological hot spots. But after that, a large unknown diversity of deep-sea benthic invertebrates was discovered. It has been indicated that deep-sea areas may contain tens of millions of animal species, representing a “second biotic frontier” (Grassle & Maciolek, 1992). Still more recently, soil zoologists and microbiologists have shown that soils contain many more species than anticipated. Therefore, soils can be regarded as the “third biotic frontier”, where a considerable part of the globe’s biodiversity remains to be discovered (André et al. 1994; Lawton et al. 1996).

In fact, nowhere in nature are species so densely packed as in soil communities. Soils also contain a high “phylogenetic diversity”, represented by a large number of animal phyla and a very diverse microflora. The species richness in soils comprises a

considerable part of any country's biodiversity, and Usher et al. (1979) described soil communities as "the poor man's tropical rainforest".

*Suspended soils: Combining two biotic frontiers*

Earlier Wallwork (1976) had already pointed to the fact that a rich and specialized "soil fauna" could exist high up in trees. Often, decomposing material accumulated in various microhabitats in trees, for instance in connection with epiphytes, creating "suspended soils". Such habitats represent one of the most interesting and least explored soil communities. Especially in tropical rainforests, the first and third biotic frontiers (canopy and soil) are combined in these suspended soils.

According to Walter & Behan-Pelletier (1999), mites usually exceed all other arthropods in abundance in forest canopies, and they are second in species richness only to canopy insects. In lowland rain forest in Peru, Wunderle (1992a) compared the oribatid fauna in ordinary soil with that in epiphytes 15 m above ground. Among 205 species, 22 % lived only among the epiphytes. Suspended soils may also be interesting outside the tropics. In canopies of Sitka spruce trees in British Columbia, Winchester et al. (1999) found thirty species of Oribatida in moss vegetation covering the branches, and twelve of these were canopy specific. Also in temperate regions without a heavy rainfall, many species of oribatids live in different microhabitats on trees. Wunderle (1992b) has demonstrated this well in a beech forest in SW Germany.

*How many species, and how densely packed?*

Even when we look at rather well-studied groups of soil animals, like Collembola and Oribatida mites (at least the majority of species in these groups are soil-living), we have no good estimates about the real species number. About 8,000 Collembola species have been described (Fjellberg, pers. comm.), but even specialists do not dare to estimate the real number (examples of very uncertain guesses are 16,000 and more than 50,000 species). According to Walter & Proctor (1999), 11,000 species of Oribatida have been described, and "guesstimates" vary from three to ten times that number. Another mite group which is mainly soil-living is Uropodina with 2,500 known species, and guesstimates range from four to ten times that number. In a compilation, Brussaard et al. (1997) presented the following number of described soil-living species within various groups: 18-35,000 fungi, 1,500 Protozoa, 5,000 Nematoda, more than 600 Enchytraeidae, about 30,000 mites, about 40,000 root herbivorous insects, 2,000 termites, 8,800 ants and about 3,600 earthworms. Several species-rich groups of soil animals, as for instance Nematoda, are badly known, and global estimates of numbers of total species cannot be given. In other words, even experts are unable to tell us the order of magnitude for the total number of soil animal species.

The dense packing of soil organisms is a fascinating ecological feature. One square metre of forest soil may contain over 200 arthropod species (Usher & Parr, 1977), and altogether up to 1,000 species of soil animals (Anderson, 1975). Mature forest soils appear to have a phylogenetic diversity greater than any other habitat, with the possible exception of coral reefs (Behan-Pelletier & Bisset, 1992). An astonishing biodiversity can be observed even in very small soil samples. In a Cameroon near-primary forest, Lawton et al. (1996) found 204 nematode species in five soil samples covering together 14.2 cm<sup>2</sup>, and they anticipated finding more than 1,000 species,



most of them new to science. Torsvik et al. (1990) found 4,000 different microbial genomes in a single gram of soil.

### **Endemism in soil fauna**

Several species and groups of soil animals are endemic. For instance, the Giant Gippsland Earthworm, *Megascolides australis*, is endemic to Australia. On this continent and on Tasmania, certain localities also contain a highly endemic Collembola fauna. Many of these Collembola species are now restricted to small fragments of their original soil and vegetation type (Greenslade & Rusek, 1996; Rodgers & Greenslade, 1996). In the Pyrenees, Deharveng (1996) found an endemic element among Collembola species in semi-natural beech forests, and this group of species was threatened due to conifer plantations. According to this author, there is a general need for a systematic inventory and protection of forests with endemic soil biota. In the USA, Hendrix (1996) called for protection of certain deadwood-rich forest ecosystems to protect the nearctic earthworm fauna.

### **Why preserve soil biodiversity?**

Many arguments have been summed up by Hågvar (1994, 1998) and others, and only some main points will be presented here. They can be divided into ecological, utilitarian and ethical arguments.

*Ecological arguments.* Soil biota are important in many ecological processes, like decomposition, energy flow, nutrient cycling and water availability, etc. Many microorganisms live in symbiotic relationships with animals and plants. For instance, more than 1,000 ectomycorrhizal fungi on tree roots make northern coniferous forests possible (Allen et al. 1995). If soils suddenly became sterile, all terrestrial ecosystems would collapse rapidly.

*Utilitarian arguments.* In agriculture, we rely upon the processes described above, and soils have been described as our most precious non-renewable resource. Penicillin and cyclosporin are two famous medicines extracted from fungi, and further possibilities are large. Many basic ecological questions can be studied in soil, as nutrient webs, predation, competition and niches overlap. Not to forget, soil biodiversity fascinates man through the beauty of many organisms.

*Ethical arguments.* All species and communities can be said to have an intrinsic value. This ethical value is independent of whether or not the biodiversity or system has a direct advantage to man.

### **Can we save it?**

Soil biodiversity is threatened for a number of reasons: Fragmentation and loss of habitats, modern agriculture with strong use of chemicals, pollution, climatic change, etc. The protection of this diversity is achieving increased interest in conservation biology. A useful overview was presented by Collins et al. (1995), and a special number of *Biodiversity and Conservation* has been issued (vol. 5, no. 2, February 1996). Although there is a great need for further registrations, description of new species and education of more taxonomists, we know enough to start conservation work for soil biodiversity. The following guidelines are suggested:

- Sites for endemic species or higher taxa should be mapped, and the need for protection considered.
- Rare soil types or rare nature types should generally be protected. Research should be started to identify the possible uniqueness of the soil community in such sites.

- Countries which have very little area of soils left undisturbed by man should preserve these sites.
- Pristine or little-influenced forest sites are good candidates for having very species-rich soil communities, and should be preserved.
- In landscape planning, one should include patches of forest in the agricultural landscape, as surviving sites for soil organisms and sources for dispersal.
- Secondary successions on abandoned agricultural land should be allowed to reach the local climax stage (usually forest), at the same time as all successional stages are preserved. Restoration should preferably occur close to existing forest patches, which may serve as sources for species colonization.
- When transforming natural habitats to agricultural land, some areas of the original habitats should be left as untouched as possible.
- Sites unusually rich in species should be preserved.
- Unique environments tend to have a specialized soil fauna. These may be for instance very dry and adverse sites (e.g. Greenslade 1995). Sea-shore habitats tend to have a unique and highly specialized microarthropod fauna (Fjellberg, pers. comm., André et al., 1994). This may be due to the long history and continuity of shore habitats, together with needs to adapt both to a steep gradient, to harsh environments, and special habitats as sand dunes or the tidal zone (Fjellberg, pers. comm.). Shore habitats could be the aim of systematic soil community studies and conservation measures.
- The application of fertilizers and pesticides in agricultural soils should be kept to a minimum.
- In the preservation of microflora diversity, ex situ preservation in cultures will probably also be part of the strategy.
- Transport of soil should be controlled in order to avoid harmful introduction of soil organisms.

When protecting areas, one should aim at preserving whole ecosystems, ensuring a natural climate and the continued production of natural litter. The areas must be large enough to support viable populations and to withstand stress factors as edge effects and activities within the area. Often, soil biodiversity arguments will exist together with other conservation arguments. But one should be willing to establish nature reserves on the basis of soil biodiversity alone.

### **An international initiative**

At an international colloquium in Dublin in 1996, a declaration was agreed with the following text:

*To: The Signatory Nations of the Rio Biodiversity Convention*

*From: The Members of the XIIth International Colloquium on Soil Zoology*

#### **PROTECTION AND SUSTAINABLE USE OF THE BIODIVERSITY OF SOILS**

*The Biodiversity Convention has concentrated upon the visible world, but a considerable part of biodiversity is situated in the soil. Soil contains some of the most intricate and species rich communities of the globe. Its fauna and microflora represent a major part of our natural heritage but are often neglected in conservation management plans. Yet soil biological processes are fundamental for the functioning of natural and managed ecosystems and so are vital for human needs. Consequently consideration of the biodiversity of soil must be included in national plans drawn up*

to comply with the Biodiversity Convention. (Signed by Professor Dennis Parkinson, Chairman Subcommittee D (Soil Zoology), International Society of Soil Science.)

Following this initiative, “soil organisms” was included in the recommendations from the third meeting of the signatory nations later in the same year. However, consciousness about soil biodiversity as an important element in a country’s natural heritage is still low in most countries. Soil biologists can contribute to increase this awareness.

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## Soil invertebrates of spruce geobiocoenoses in Belarus

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Nowadays a lot of problems concerned with preservation and maintenance of coniferous forests are very real. A forest is a system which intercepts solar energy under the control of climatic, weather and edaphic factors and the genetic properties of trees and other organisms (particularly, soil invertebrates) occupying forest habitats.

A full 90 % of all species of animals live in the soil, and this fact shows the importance of studying soil fauna. Soil mesofauna play a very important role for successful development of forest geobiocoenoses. It is essential that each type of forest soil possesses a unique complex of soil fauna. The interlinks among these organisms are dynamic, and this is the key for successful management of forests ecosystems because of our knowledge about the soil mesofauna can help to retain coniferous forests in their natural station (Kellomaki, 2000).

The area of the spruce forests (*Picea abies* (L.) Karst.) is about 11% of the total forest area of Belarus. There are many problems connected with the maintenance of stability of this type of geobiocoenoses. The use of soil invertebrates to indicate the formation processes of spruce forests and to assess their stable state has great significance in modern ecological studies for bioindication or in monitoring an environment and climate change.

The aim of the present study was to investigate and to compare the pedocomplexes in spruce stands of an oak-dark coniferous geobotanical area and to explain observed differences on the basis of environmental conditions in each geobiocoenoses.

A total of six spruce forests sites were investigated. The invertebrate complexes of sod-podzolic and peat-podzolic soils in spruce forests of different ages (from 12 to 80 years) were studied. The following types of geobiocoenoses were studied in the territory of the Minsk district:

1. Age – 55 years old: Piceetum coryloso-oxalidosum (PCO 55), Piceetum pleurozioso-pteridiosum (PPP 55), Piceetum hylocomioso-oxalidosum (PHO 55).
2. Age – 12, 80 years: Piceetum coryloso-oxalidosum (PCO 12, PCO 80).

We compared all obtained data from these forest stands with results from the spruce forest (*Piceetum coryloso-oxalidosum*, age 55 years old – PCO BG) which is situated in the territory of the Botanical Garden of the National Academy of Sciences of Belarus.

The soil invertebrates were collected by using pitfall traps (Ghilyarov, 1941) over the whole snow-free seasons in 2004–2005. The pitfall trap is made of plastic glass (diameter 72 mm, volume 250 ml). The fifteen pitfall traps were placed (in each spruce stand) approximately 5 m away from each other. The traps were filled with 4% formalin and they were in operation from May till the end of October. All collected soil invertebrates were identified to species.

To compare communities of soil mesofauna from different spruce stands we used species richness of various groups of pedobionts, relative abundance of groups and species. We compared the communities of millipedes by using cluster analysis. Some differences in the organization and composition of the invertebrate community were obtained. Yearly and seasonal differences were discussed. The results of investigation of the most numerous and diverse groups of pedobionts are presented in this paper.

More than 80,000 individuals of pedobionts were collected during the period of investigation. The quantity of various groups and species of pedobionts was higher in PCO 55 PCO 80. The maximum number of soil invertebrates was recorded in July–August, but in PPP 55, PHO 55 we sampled a maximum amount of pedobionts in September–October. We found 2 types (Annelida, Arthropoda), 6 classes (Oligochaeta, Crustacea, Arachnida, Diplopoda, Chilopoda, Insecta), 7 orders and 31 families of soil invertebrates over the period of investigation. The maximum quantity of pedobionts was found out in PCO 55, PCO 80. The most numerous classes in all of the investigated stands were Arachnida and Insecta. The orders Coleoptera and Aranei had the largest variety of species among all invertebrates.

The most varied composition of Insecta species belonged to the family Carabidae. Every spruce geobiocoenosis had different number of carabid species: PCO 12 (26 species), PCO 55 (29 species), PCO 80 (29 species), PPP 55 (29 species), PHO 55 (25 species), PCO BG (24 species). The type of geobiocoenosis, age of forest stand and environmental conditions have a great influence on structure and composition of ground beetles. Thus, PCO 80 was characterized by optimal soil-climatic conditions for pedobionts, which is why their composition and species richness was the most varied and unusual. The most diverse genera among the carabid beetles were *Carabus* (Linnaeus, 1758) - 11.4% of the total number of all carabids, *Pterostichus* (Bonelli, 1811) 17.1% of the total amount of carabids. The leading position in all study sites belonged to forest carabids (51% of the total quantity of carabid beetles). The structure of domination was different in all geobiocoenoses. We can describe it as polydominant because there were 3–5 dominant species in each spruce forest (except PCO 80, where there were only 2 dominants: *Pterostichus oblongopunctatus* (Fabricius, 1787) and *Carabus nemoralis* Muller, 1764). Five species of carabids were dominants in PCO BG: *Pt. niger* (Schaller, 1783), *Pt. melanarius* Illiger, 1798, *Pt. oblongopunctatus*, *C. nemoralis*, *Calathus micropterus* (Duftschmid, 1812).

We also examined such families from the order Coleoptera as Staphylinidae, Curculionidae, and Elateridae. Communities of Staphylinidae, Curculionidae were

more diverse and numerous in PCO 55, PCO 80, PCO BG, PPP 55. On the basis of obtained data we can conclude that zoophages were the dominant group in all spruce forests. This fact shows depression of spruce geobiocoenoses and it points out the negative processes in these stands. Saprophages did not prevail in study sites. The processes of decomposition of organic substance and inserting it in food chains of study stands progresses very slowly.

Among the Lumbricidae were revealed 7 species of earthworms: *Lumbricus rubellus* Hoffmeister, 1843, *L. terrestris* Linnaeus, 1758, *L. castaneus* (Savigny, 1826), *Aporrectodea rosea* (Savigny, 1826), *Denrobaena octaedra* (Savigny, 1826), *Octolalasius lacteum* (Orley, 1885), *A. caliginosa caliginosa* (Savigny, 1826). These species are usual for the oak-dark coniferous geobotanical zone. The relative abundance of this group of soil invertebrates among other pedobionts was 0.1-1.8%. The earthworms from genus *Lumbricus* predominated in samples during the whole period of the study. *L. rubellus* was dominant in PCO BG. The average value of dynamic density of Lumbricidae in PCO BG was 1.32 ind./100 trap-days. We found only 3 species of earthworms in PCO 12: *L. rubellus*, *D. octaedra*, *Ap. rosea*. *L. rubellus* also was dominant in this geobiocoenosis. Such poor composition of earthworms in PCO 12 can be justified on the basis of the high degree of density of the forest canopy. This fact was the reason for the weak development of the herbage in PCO 12 and for the absence of normal conditions for earthworms. The species richness of Lumbricidae was different in more mature geobiocoenoses. We discovered 2 species (*L. rubellus* (53% of the total number of earthworms), *D. octaedra* (27% of the total quantity of earthworms) in PCO 55 and 5 species in PCO 80. The average dynamic density in PCO 80 was 1.73 ind./100 trap-days. *L. rubellus*, *D. octaedra*, *A. rosea*, *L. terrestris* were found in PPP 55; *D. octaedra* prevailed in samples. Only 2 species of Lumbricidae were detected in PHO 55: *L. rubellus* (80% of the total number of earthworms in PHO 55) and *A. rosea* (20% of the total number of earthworms). For the whole period of examination the quantity, species richness of Lumbricidae, and the presence or absence of one or another species of earthworms greatly depended on soil-climatic conditions in each of the investigated stands.

Two species of Crustacea (Isopoda, Oniscoidea) were discovered. The species composition of Crustacea (Isopoda, Oniscoidea) in all spruce forests (except PCO 80) included only 1 species from the family Ligiidae Brandt, 1883: - *Ligidium hypnorum* (Curvier, 1792). The quantity of this species was low in all study stands except PCO BG where the value of dynamic density consisted of 53.3 ind./100 trap-days. In addition to *L. hypnorum* 1 specimen of *Cylosticus convexus* (De Geer, 1778) (family Cylisticidae Verhoeff, 1949) was found in PCO 80.

The structure of communities of Myriapoda had differences in every study site; 20 species of millipedes from the 5 families (Paradoxosomatidae Daday, 1889, *Julidae* Leach, 1814, *Blaniulidae* Koch, 1847, *Polydesmidae* Leach, 1815, *Mastigophorophyllidae* Verhoeff, 1899) registered during 2004-2005. We also discovered 5 species of Chilopoda from 2 families (*Henicopidae* Pocock, 1901, *Lithobiidae* Newport, 1844). The most diverse composition of millipedes was discovered in PHO 55, PCO 80 – 16 species. *Strongylosoma stigmatosum* (Eichwald, 1830), *Leptoiulus proximus proximus* (Nemec, 1896), *Polydesmus complanatus* (Linne, 1758), *Mastigophorophyllon saxonicum* Verhoeff, 1897, *Ommatoiulus sabulosum* (Linne, 1758) dominated in these geobiocoenoses. Only 8

species of Diplopoda were found in PCO BG and *M. saxonicum* was the most numerous species in this forest stand. The composition of millipedes in PCO 12, PCO 55 included fewer than 16 species: (13 species of Diplopoda) and in PPP 55 (14 species). The results of the cluster analysis of the species composition in such spruce stands as PCO 12, PCO 55, PCO 80 and PCO BG illustrated the maximum similarity of species composition between PCO BG and PCO 80. The community of Diplopoda species in PCO BG had a considerable number of characteristics that distinguished them from other complexes of millipedes and formed a separate cluster.

We recorded 5 species of Chilopoda: *Lamyctes fulvicornis* Meinert, 1868, *Lithobius forficatus* (Linnaeus, 1758), *Monotarsobius curtipes* C.L.Koch, 1847, *Lithobius erythrocephalus* C.L. Koch, 1847, *Lithobius lucifugus* L. Koch, 1862. Four species of Chilopoda were discovered in PHO 55 and 3 species were found in PPP 55. *M. curtipes* predominated in all geobiocoenoses.

Spiders (Aranei) and harvestmen (Opiliones) were the most varied groups of the soil invertebrates in all spruce forests; 68 species of spiders (from the 14 families) and 8 species of harvestmen (from the 3 families) were recorded during the period of investigation. *Linyphiidae* was the most diverse family. It included 36 species or 53% of all investigated species of *Aranei*. We found 41 species (11 families) of spiders in PCO BG. *Linyphiidae* (59.1% of total number of spiders), *Lycosidae* (10.4% of the total number of spiders), *Thomisidae* (25.8% of the total amount of spiders) dominated in PCO BG. Among the *Linyphiidae* of PCO BG *Diplocephalus picinus* (Blackwall, 1841), *Tenuiphantes tenebricola* (Wider, 1834) were dominants. Only 1 species (*Trochosa terricola* (Thorell, 1856)) was the most numerous among *Lycosidae*. At the same time such spiders as *Oziptila praticola* (C. L. Koch, 1837), *O. trux* (Blackwall, 1841) prevailed among *Thomisidae*. We discovered that the families *Araneidae* (*Araneus sturmi* (Hahn, 1831)), *Clubionidae* (*Clubiona caerulescens* L. Koch, 1867, *C. lutescens* Westring, 1851, *C. sp.*) *Gnaphosidae* (*Haplodrassus soerenseni* (Strand, 1900), *H. signifer* (C. L. Koch, 1839), *H. sp.*), *Salticidae* (*Pseudeuophrys erratica* (Walckenaer, 1826)), *Agelenidae* (*Tegenaria atrica* C. L. Koch, 1843), *Philodromidae* (*Philodromus aureolus* Sundevall, 1833), *Theridiidae* (*Enoplognatha ovata* (Clerck, 1757), *Steatoda grossa* (C. L. Koch, 1838)) were not numerous. A total of 50.6% of all spiders from PCO BG were juvenile individuals. We identified 8 species of Opiliones: *Leiobunum rupestre* Latreille, 1802 (*Sclerosomatidae*), *Lacinius ephippiatus* (C.L.Koch, 1835), *Mitopus morio* (Fabricius, 1779), *Opilio dinaricus* Silhavy, 1938 *Lophopilio palpinalis* (Herbst, 1799), *Phalangium opilio* Linnaeus, 1758, *Paraplathybunus triangularis* Simon, 1872 (*Phalangidae*), and *Nemastoma lugubre* (O. F. Muller, 1776) (*Nemastomatidae*). *L. ephippiatus* was the single dominant and it prevailed in samples in all of the study sites.

The composition of families in PHO 55 consisted of *Linyphiidae*, *Lycosidae*, *Thomisidae*, *Clubionidae*, *Gnaphosidae*, *Salticidae*, *Theridiidae*, *Tetragnathidae*. The number of species in this spruce forest was 31. *Linyphiidae* prevailed in samples. The composition of dominants of *Linyphiidae* was the same as in PCO BG, but the structure of subdominants was the following: *Abacoproeces saltuum* (L. Koch, 1872), *Diplostyla concolor* (Wider, 1834), *Palliduphantes pallidus* (O. Pickard-Cambridge, 1871), *Walckenaeria atrotibialis* O. Pickard-Cambridge, 1878. The composition of Opiliones included 8 species.

We recorded 6 families of spiders in PCO 12, 8 families of Aranei in PCO 55 and 4 families in PCO 80. The most diverse community of Aranei was in PCO 55, where we collected 27 species of spiders. On the other hand, only 14 species of Aranei were found in PCO 80. Opiliones were numerous in all of mentioned the study sites.

In spite of the nearness of the location of PHO 55 and PPP 55 their structure and composition of Arachnida distinguished them from each other. We registered 20 species of Aranei in PPP 55 in contrast to 31 in PHO 55: Theridiidae (*Robertus lividus* (Blackwall, 1836)), Linyphiidae (*Agyneta ramosa* (O. Pickard-Cambridge, 1863), *Diplocephalus latifrons* (O. Pickard-Cambridge, 1863), *D. picinus*, *D. concolor*, *Erigonella hiemalis* (Blackwall, 1841), *Gongylidium rufipes* (Linnaeus, 1758), *Linyphia triangularis* (Clerck, 1757), *P. pallidus*, *Micrargus herbigradus* (Blackwall, 1854), *Microneta viaria* (Blackwall, 1841), *T. tenebricola*, *W. atrotibialis*, *W. obtusa* Blackwall, 1836), Lycosidae (*Pardosa lugubris* (Walckenaer, 1802), *Pirata hygrophilus* Thorell, 1872), Gnaphosidae (*H. soerenseni*), Thomisidae (*O. praticola*, *O. trux*), and Salticidae (*P. erratica*).

To summarise, the communities of soil invertebrates were relatively similar at all study sites. Age of geobiocoenoses, their type and soil-climatic conditions influenced the structure and composition of pedobionts. The abundance and species richness of the soil invertebrates from PCO BG were low in comparison with other sites. It was noted that in more mature spruce stands the species diversity was higher than in young spruce geobiocoenoses.

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## Soil mezofauna in the different biogeocenoses in Belarus

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The conservation and use of biological diversity as the basis for sustainability and stability of the ecosystems has become clearly defined. The decrease in biological diversity is considered one of the basic global ecological problems that mankind faces today.

The knowledge about biodiversity and about reasons for and laws of dynamics of soil mesofauna and population diversity of soil invertebrates has exclusively important (rather applied, or theoretical) significance for soil science.

The goal was to quantify the abundance, specific richness and biodiversity of soil mesofauna in the different biogeocenoses and places (including several national parks and reserves).



“Pripyatsky” National Park- It is situated in the south of Belarus, located in the Pripyat River valley between its tributaries Stviga and Ubort. The relief is not homogeneous and includes boggy low places and channels.

“Beloviezhszkaya puscha” National Park- It is situated in west Belarus and Poland.

Berezinsky State Biospheric Reserve– It is situated in the northern part of Belarus. Deciduous bog forests make up 33.4% of the woodlands, coniferous forests 56.2%.

Polesky State Radio-Ecological Reserve– The reserve was founded in 1988 and set out in a 30 km evacuation zone (in the Gomel region, within 30 km of the Chernobyl Nuclear Power Plant).

The specimens were collected according to generally accepted method by M. Ghilyarov (Ghilyarov, 1941) and by using pitfall traps. The pitfall traps were plastic glasses 72 mm in diameter and were situated some metres away from each other. The traps were filled with 4% formalin. The collected animals were identified to species. Soil samples were 0.25 m<sup>2</sup> and animals were extracted from samples by sifting and by hand sorting. The communities of soil invertebrates of forest and meadow biogeocenoses from different parts of Belarus were compared. The specimens collected were separated to males, females and juveniles, based on their genital features.

The specific richness and biodiversity of the invertebrate community were investigated over a period of several years in Belarus. Some changes in the organization and spatiotemporal composition of the invertebrate community were identified. Yearly and seasonal differences were discussed.

The faunal composition described by the presence or absence of species, indices of species similarity or by relative species abundance, has been widely used as a tool to compare different habitats and measure the effects of habitat modification. The fauna of fields is likely to be influenced by the sequence of crop types grown over time (crop rotation).

The fauna of soil invertebrates in Belarus includes 3 types (*Annelida*, *Mollusca*, *Arthropoda*), 8 classes (*Hirudinea*, *Oligochaeta*, *Gastropoda*, *Crustacea*, *Arachnida*, *Diplopoda*, *Chilopoda*, *Insecta*), 18 orders, and 61 families. *Insecta* is the dominant class with the dominant order *Coleoptera*. The order *Coleoptera* had the largest variety of species among arthropods, thus beetles represent a considerable portion of species diversity in biogeocenoses.

Most of the *Coleoptera* species belonged to the families *Carabidae*, *Staphylinidae*, *Chrysomelidae*, and *Curculionidae*. There were invertebrates of 4 trophic groups: saprophages, zoophages, phytophages and myxophytophages. Zoophagous were dominant. Many groups of saprophages and zoophagous animals were identified as “surface dwellers”; more than 90% of their zoomass occurred in the A-layer and surface soil to a depth of 10 cm. Species composition was more diverse in pine forests (242 species) and in the meadows (143 species). Litter- and litter-soil-dwelling forms dominated, with the zoophages the most numerous. In summer the soil invertebrate population was concentrated in the litter (from 60 to 75 % of the total number).

We studied the earthworms in the soils of fields, meadows and forests. Earthworms are known to have an essential impact on soil fertility. In ecosystems they are the most important members of soil mesofauna and take part in the nutrient cycling process and decomposition of organics. In field soils, the mean number of earthworms was  $42.7 \pm 11.1$  individuals per  $m^2$ . 5 species of earthworms were found. The individuals of the most common species *Aporrectodea caliginosa* comprised 65% of the total abundance. In conventionally managed field the total number of earthworms was  $54.1 \pm 10.3$  ind./ $m^2$ , the number of species was 6.5% of all earthworms were individuals of species *A. caliginosa*. It can be concluded that ecological tillage creates better conditions for earthworms as well as a higher content of organic matter in soil.

Three species of *Lumbricidae* have been identified in the radioactive-contaminated site (Polessky State Radio-Ecological Reserve). They were: *Octolasion lacteum* Oerley, 1885; *Lumbricus rubellus* Hoffmeister, 1843; *Dendrobaena octaedra* (Savigny, 1826). In the control areas (National Park "Pripyatsky"), in contrast, 6 species were found (Maksimova, 2002).

The number of different species and groups of epigeic fauna were higher in broad-leaved forests. The number of *Coleoptera* was the highest at the beginning of summer and decreased in the middle of summer, whereas in autumn the number again increased.

In pine and spruce forests the number and biomass of earthworms and soil mesofauna as a whole were generally lower than in the deciduous broad-leaved forests. The earthworms were not important in the differential formation of humus types. The total number of earthworms was 4.6 ind./ $m^2$ , *Diplopoda* – 9.0 ind./ $m^2$ . Insects (especially *Coleoptera*) were dominant in the biogeocenoses investigated.

Earthworms and millipedes were dominant in alder forests. Among earthworms *Octolasion lacteum* and *Aporrectodea caliginosa* were numerous. The total number of *Lumbricidae* was 105.6 ind./ $m^2$ .

In birch forests *Insecta* and *Lumbricidae* were dominant. In the order *Coleoptera* the imago and larvae of *Curculionidae* were numerous. The mean number reached 95 individuals per  $m^2$ .

In oak forests *Insecta* (almost 80 % of the total abundance) were dominant. Among *Insecta*, *Coleoptera* and *Diptera* were numerous. The species diversity of *Staphylinidae* was higher (26 species) than one of other *Coleoptera* families.

All of 25 *Diplopoda* species and 8 *Chilopoda* species were recorded in the habitats studied in total. Study sites differed in their species composition and in the total number of myriapods. The litter-inhabiting millipedes were active in litter in the period of feeding activities, copulation and migration. The abundant species of *Chilopoda* was *Monotarsobium curtipes* C.L. Koch. *Diplopoda* consisted of 3 subclasses: *Penicillata*, *Pentazonia* and *Helminthomorpha*. *Penicillata* included only 1 order *Polyxenida* with one species *Polyxenus lagurus lagurus* (Linne, 1758). *Pentazonia* included only 1 order with 1 species *Glomeris connexa* Koch, 1844. *Helminthomorpha* included 4 orders: *Polyzoniida*, *Chordeumatida*, *Polydesmida*,

*Julida*, *Glomerida* and *Chordeumatida* were met only in the west of Belarus. Representatives of *Polydesmida* and *Julida* (15 species) dominated. *Polydesmus complanatus* L., *Leptoiulus proximus proximus* (Nemec, 1896), *Ommatoiulus sabulosus* (Linne, 1758) were found to be the dominant species. Among *Polydesmida*, *Polydesmus complanatus* L. was dominant, found in all biogeocenoses. The activity of millipedes was greatest in May and October. During the summer months *Diplopoda* specimens began to disappear from the soil traps. This was the start of the decline in activity. The males disappeared at the end of May or beginning of June. The females almost disappeared in the middle of July. At the beginning of autumn activity began to increase. Up to July adults were most frequent in different biogeocenoses, and declined to almost zero during the subsequent 4 weeks. Subadults, absent all summer, made their appearance in the autumn and dominated the population by October. All 12 species of *Diplopoda* have been identified in the contaminated biogeocenoses (compared to 20 in the control group). Altogether, 12 *Diplopoda* species were collected in the radiocontaminated forest biogeocenoses, i.e. almost 50% of the total 25 diplopod species presently known from Belarus. In the control area the fauna of *Diplopoda* were represented by 20 species. A list of the *Diplopoda* of National Park "Prypiatski" has been published (Maksimova, Khotko, 1997). The species common in both control and radio-contaminated biogeocenoses were *Polydesmus complanatus*, *Nopoiulus kochii* (Gervais, 1847), *Megaphyllum sjaelandicum*, *Proteroiulus fuscus*, *Cylindroiulus coeruleocinctus* (Wood, 1864), *Julus terrestris*, *Leptoiulus proximus proximus*, *Microiulus l. mierzeyewskii*, *Ommatoiulus sabulosus* (Linnaeus, 1758) and *Rossiulus kessleri* (Lohmander, 1927).

In the territory of the Berezinsky reserve *Coleoptera* were dominant. The four families of *Coleoptera* were numerous; *Staphylinidae*, *Carabidae*, *Elateridae* and *Scarabaeidae*. In the territory of the "Pripyatsky" National Park *Coleoptera* were dominant. The 5 families of *Coleoptera* were abundant; *Staphylinidae*, *Elateridae*, *Curculionidae*, *Carabidae*, *Scarabaeidae*. The species composition of invertebrates of the Polesky State Radio-Ecological Reserve was published in 1998 (Maksimova, 1998).

These investigations form part of a long-term research program including investigations of animal biodiversity of Belarus.

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# **The Development of Lhalu Dhamra, a Marshland in Lhasa, Tibet**

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The study on the ecology and development of Lhalu Dhamra was carried out from 2000 to 2002 in Lhasa Tibet. The Lhalu Damra marshland lies at 29° 39' 46.3'' to 29° 41' 05.5''N, 91° 03' 48.5'' to 91° 06' 51.4''E, 3648 m a s l in the northwest part of Lhasa, about 3 km to north of the Kyichu River. It is a relatively well-preserved alpine natural wetland ecosystem and its current total area is about 6.2 km<sup>2</sup>. It plays a very important role in maintaining and retaining the biodiversity, increasing the air moisture, and influencing the climate of Lhasa City. It also provides an important habitat for various animals that live there.

This study presented the reconstruction of the local vegetation history and environmental changes of the Lhalu Dhamra marshland, Lhasa. This has been done by means of plant macrofossils (mainly seeds and fruits), micro-faunal remains of chironomid larvae head capsule and Oribatid mites, sediment stratigraphic analysis and loss-on-ignition measurements. This is the first time such palaeo-ecological reconstruction has been done in Tibet. A more detailed and complete picture of vegetational and environmental changes of the marshland can therefore be developed showing that the basin had four pronounced phases in its vegetational succession, including both periods before and after the formation of the marshland.

1. The feature of sediment stratigraphy and absence of both plant and animal remains in the sediments at the bottom indicated that the basin could have been an ancient river course, and that virtually no plants and soil animals were in the basin.
2. The river course might have been diverted slightly to the south by regional environmental changes and created a large riverside depression. It seems that the riverside depression was filled rapidly by fluvial and alluvial sedimentation with high-energy water flow, which created a well drained sandy ground. There was still no vegetation in the depression but we found some fossil seeds of terrestrial plants, charcoal fragments and typical cold and flowing water-living chironomids. These remains are considered to have been transported by water into the depression and redeposited in the riverside depression.
3. The riverside depression still received a slower water flow, and started to develop compact and poorly drained sandy silt ground. Plant colonization into the riverside depression began at this phase, which induced changes in hydrological conditions in the basin and caused an accumulation of peat so that the vegetation in the basin might now be dominated by terrestrial and waterside plant elements and some weeds. Due to the plant production in the basin, the conditions in the basin became more suitable for invertebrates, and the oribatid mites, standing water-living Chironomids and some other invertebrates also started to colonize the basin.
4. The silty ground of the basin was replaced by a marshland and during the formation and development of the marshy peat, the basin experienced strong fluctuations in water level. This is evidenced by the mixed plant macrofossil assemblage of submerged, semi-emergent and waterside plants. However, the marshland was constantly under moist conditions throughout the peat developmental

process since a large amount of less decomposed vegetative parts were found in the sediments and most of the oribatid mites and chironomids were very abundant in the upper part of the sediments. The vegetation during this phase was dominated by both aquatic (*Chara*, *Hippuris*, *Zannichellia* and *Potamogeton*) and wet meadow (*Carex*, *Scirpus*, *Eleocharis*,) plant species in the marshland.

This study also analysed data on the present-day vegetation composition of the marshland using the multivariate techniques of TWINSPAN, DCA and CCA. TWINSPAN was applied for present-day local vegetation data to classify the samples (plots) on the basis of the species abundance values and this classification is used to obtain a classification of the species and DCA was used to display the TWINSPAN classification groups in a low-dimensional space. CCA was applied to analyse the relationship between plant species and environmental variables.

## **Icelandic Oribatid mites revisited**

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In 1994, Peter Gjelstrup, Århus, and I published a paper in “The Zoology of Iceland” on the known records of oribatid mites and their habitat in Iceland, based on extensive field work by both of us and a control of all previous records where material was available and preserved. We recorded a total of 159 species, some new to science and many new to Icelandic fauna.

In my talk I want to summarize our findings, especially on habitat selection compared with new information from other Nordic countries and how oribatid remains from Icelandic wetlands and lakes can be used in palaeo-ecological reconstructions.

## **Some characteristics of the Icelandic Collembola fauna**

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### **1. Introduction**

Increased efforts in studies of the Icelandic soil fauna over the last few years have raised the number of known Collembola species from 77 (Olafsson 1991) to more than 140 (Fjellberg unpubl.). The low number of Icelandic species among larger insects like butterflies, bumble bees and dragon flies, is probably caused by the isolated geographical position, the dispersal capacity of these insects and the prevailing humid and chilly climate. Apparently the soil mesofauna are far better off and species numbers are comparable to those from mainland Scandinavia. Accumulated species lists of Collembola from different Icelandic habitat types

indicate a general reduction in species number in areas affected by humans. This is further discussed below.

## 2. Material and methods

The present study is based on 77 samples which were collected during four visits to Iceland by the author during 2004-2005, mainly from localities in the south, west and north. The samples were of different size, and were transported in plastic bags to the lab for extraction in open Tullgren funnels heated by light bulbs. In a given habitat type (Table 1) samples were taken so as to uncover all species present in the different microhabitats. Samples were not quantitative, only presence/absence of species was recorded. The species were further classified either as generalist or specialists according to their nich specificity (author's accumulated experience).

## 3. Results and discussion

### 3.1. Habitats and the species inventory

Table 1 summarizes the number of species found in 5 main habitat types. The highest number of species was found on seashores, in old birch forest and in stream banks. The lowest numbers were in lava fields and degraded (eroded, only patchy vegetation) habitats as well as in grasslands (pastures, meadows) and heaths (herbs, dwarf bushes).

**Table 1.** Accumulated species numbers in different habitat types.

A: Seashores, sand dunes (affected by wind/waves/salt/ input of organic material)

B: Inland stream banks (affected by flood and input of organic debris)

C: Mature birch forest (probably with a long continuity back in history)

D: Conifer plantations (various species and ages)

E: Grasslands, heaths (closed vegetation)

F: Lava fields and degraded habitats (disrupted vegetation)

	A	B	C	D	E	F
Samples (N)	30	6	14	11	5	11
Generalists	53	30	37	30	25	22
Specialists	18	4	5	1	0	0
All species	71	34	43	31	25	22

A higher number of samples and presence of strictly halophilous species was certainly reflected in the particularly high number of species (71) from the coastal seashore habitats. However, the presence of 30 species in 6 stream bank samples probably reflected a real difference in the 22 species in 11 samples from lava fields and degraded habitats. The 43 species found in old birch forest matched the 36 species recorded in a birch forest in North Norway just south of the Arctic Circle (Fjellberg et al. in press). Corticole species were not surveyed in N Norway. These would have added another 4-5 species to the list. Also 31 species from coniferous plantations were comparable to 34 species found in plantations of Norway spruce and Sitka spruce in North Norway (Fjellberg et al., op. cit.).

Another obvious trend was the reduced proportion of specialists going from seashores-stream banks-birch forest to habitats which are man-made or degraded. At first view wave-exposed seashore or a flooded riverbank may appear as a very unsafe

place to live, but Collembola apparently thrive here. Seashores - the contact zone between land and ocean - are amongst the oldest landscape elements on the earth with an unbroken continuity in history. Even if the physical impacts are violent, they are predictable and repeated again and again. Collembola have adapted to this environment by specialization to the many microniches existing in the gradient from the littoral to sand dunes and open meadows. Stream banks are also old landscape elements and many collembola species have adapted to the special physical conditions, which, apart from lower salinity, resemble those of the seashores.

The interesting case of the Icelandic birch forest calls for further studies. Unlike seashores and stream banks, the historic extent of the birch forest has been greatly reduced and the present fauna associated with birch may be regarded as relic. During a postglacial maximum at about 4000 - 2500 B.P. the birch forests may have covered 40-50% of the land surface, in contrast to the fragmented 1% of the present day (Einarsson 1963). It is likely that some species of the forest Collembola were lost from Iceland during this reduction, even if the above comparison with North Norway indicates that the fauna are fairly complete.

The Collembola of the present day birch forest may serve as a source for the new fauna developing in coniferous plantations. The exclusively corticole species *Vertagopus cinereus* (Nicolet, 1841), which is frequent under bark on dead birch, was established under bark on conifers both at Skorradalur and at Haukadalur.

### 3.2. *The benefits of being small, living in the soil*

Small euedaphic Collembola with high population densities are probably better adapted for passive dispersal and more ready to establish viable populations than large surface forms with low densities. Some of the major genera of euedaphic Collembola are well established in Iceland, like *Willemia* (5 spp.), *Protaphorura* (13 spp.), *Mesaphorura* (9 spp.) and *Folsomia* (14 spp.). These genera have a complete or almost complete inventory of species compared with the fauna of Norway and Sweden. In contrast, large forms which live on the surface are not well represented in Iceland. The genus *Desoria*, with 17 species in Norway/Sweden, only has 5 known representatives in Iceland.

### 3.3. *Biogeography of Icelandic Collembola*

The list of Icelandic Collembola is clearly of West European character. Nearctic elements are absent, so are High Arctic species which are more or less circumpolar and present in Greenland and the Norwegian Arctic islands. The only exception is *Willemia similis* Mills, 1934 which is present in Spitzbergen and absent from the Scandinavian mainland. The recently described European species *Mesaphorura arbei* Simon et al., 1994 appear to be established in Icelandic pioneer communities (streambanks, sandy lava fields) and is so far not recorded from the other Nordic countries. *Marisotoma canaliculata* Fjellberg, 1997 belongs to a western Atlantic element and is present in the Faroe Islands, Iceland and the west coast of Norway. A limited but characteristic group of species is expected in the thermophilic communities associated with volcanism in Iceland. Only a few samples have been investigated, but the recorded *Folsomia onychiurina* Denis, 1931 and *Proisotoma subminuta* Denis, 1931 definitely belong here.

### 3.4. Future expansion of the Icelandic species list

While the number of Collembola species in most Nordic countries is stabilized or slowly increasing, with about 200-300 species per country, the Icelandic list is still apt to be rapidly increased. Some major habitat types, like the high alpine, have not been examined in Iceland. Alpine Collembola form a distinct element in the Scandinavian mountains and are probably also present in Iceland, though not yet examined. The alpine flora, as we know it from Scandinavia, is widely distributed in Icelandic mountains (Steindórsson 1963). So why not Collembola?

Species living in compost and other organic debris associated with human settlements are only sporadically known from Iceland. A systematic search will certainly uncover new species. Thermophilic species which become established in compost may serve as a source for species colonizing the natural geothermal habitats in Iceland, or the other way around - depending on what comes first.

### 4. Conclusion

The presence of a diverse Collembola fauna with a high proportion of specialized species in long-term stable habitats like seashores, stream banks and birch forest indicates that Iceland has a species-rich soil mesofauna which was well established long before the arrival of the first settlers. Parts of this fauna have been lost with the reduction of the birch forest in historic times and replaced with a species-poor assemblage of generalists in grasslands and degraded and secondary habitats. The planting of conifers may offer alternative habitats for species that were formerly present in birch forest.

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## Archaeological excavation at Kvitevoll, Halsnøy Island, Western Norway, 2004. Results from the mite analysis

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This is a work done in collaboration with the archaeological survey carried out for the building of the road connection between Halsnøy Island and the mainland in the Kvinnherad community in Sunnhordaland County, western Norway. The scope of the work was to reconstruct the local environment surrounding the human settlement and to identify the possible changes in the landscape due to human influence.

Oribatid mites were used as indicators of the environment at the archaeological excavation of Kvittevoll. Several series of samples were taken at different sites. Only samples obtained from a monolith yielded enough subfossil oribatid mites to support the analysis. This might easily be explained by the fact that most of the samples analysed, besides those from the monolith, were rather mineral and it seems that they had oxic conditions. Thus, possible remains were already decomposed.

Radiocarbon dates for the monolith samples showed an age of  $3905 \pm 90$  years BP at the top of the sequence and  $7740 \pm 155$  years BP at the bottom of the sequence, which corresponds to the late Neolithic. The high number of oribatid mites recovered identified to the species level (93%) makes the reconstruction rather reliable.

The method used to analyse the samples for oribatid mites was similar to the method used to analyse samples for plant macrofossils described by Birks (2001). In our case, the sediments were not from a lake but from a drained mire. Identification of the different specimens was usually done following keys from Pérez-Íñigo (1993; 1997); Subías and Arillo (2001), Balogh and Mahunka (1983), Gyliarov (1975) and personal experience. Nomenclature was according to Subías (2004).

The sequence studied was divided into two periods, “moist woodland zone” and “wet woodland zone”, according to the change in the number of subfossil oribatid mites recovered. Woodland was clearly present during both periods; at the bottom of the sequence (first zone) remains of *Caleremaeus monilipes* were found, which according to Schatz (1989) is an oribatid associated with trees, and of *Liebstadia humerata*, which lives under the bark of trees and in the subalpine birch forest (T. Solhøy pers. com.).

At the top of the first zone there were found remains of the oribatid mite species *Oribatula exilis* and *Phauloppia lucorum*, both associated with lichens, where they live and which they feed on (Knülle, 1957; Seyd & Seawards, 1984). Most of the other species of mites found with *O. exilis* and *P. lucorum* indicate tree presence, as *Cultroribula juncta*, which is an indicator of old deciduous forest (T. Solhøy pers. com.). Therefore, it is probable that *O. exilis* and *P. lucorum* lived in lichens on trees. Besides the oribatid species indicating wooded areas, there were also found fossil oribatid mites indicating moister and more open areas: *Moritzoppia neerlandica* and *Suctobelbella similis* were two examples. Knülle (1957) considered both species as inhabitants of moist and open areas, although never wet or soaked.

Along the second zone, “wet woodland zone”, the number of oribatid remains found was indicative of increasingly open and wet areas. The increase in *M. neerlandica* was remarkable, which indicated wet habitats. There was also an increase in *Transoribates lagenula*, which is also a species preferring wet areas, but usually with tree presence (Popp, 1962; Weigmann & Miko, 2002). Although this species has been found before in Scandinavia (Lindberg et al, 2004), this was the first record in Norway. Along the

second zone there was also a further increase of the oribatids remains indicative of trees/woodland. There were also found several species not found in the preceding zone: two of them were *Suctobelbella perforata* and *Dometorina plantivaga*. According to the findings of Knülle (1957), Cadwalladr (1969) and Hammer (1972) the former is a species found mainly in moist forest litter. The latter species, *D. plantivaga*, is considered to be associated to lichens living on trees (Grandjean, 1950; Travé, 1963; Gjelstrup, 1978).

At the top of the second zone appeared the species *Fuscozetes fuscipes*. This is considered a species with preference for wet surfaces of peat and acid swampy forest soils (Knülle, 1957). T. Solhøy (pers. com.) and Riva-Caballero (2003) consider this species as typical of wetland in western Norway. Besides *F. fuscipes*, indicating a wetter habitat or water logged soil, at the top of the sequence there were also found several oribatid species indicating forest, for example, *Furcoppia dentata*, *Liacarus acutidens*, *L. splendens* all of them species associated with old deciduous forest (T. Solhøy per. com.). *Odontoceoheus elongatus* has been found in different occasions in the litter layer of forests within Scandinavia (Dalenius, 1950; Gjelstrup, 1978).

There was a large increase in oribatids associated with trees/woodland and wet and open areas at the top of the sequence, which have been due to an increase in precipitation and, therefore, a lower rate of decomposition. Oribatid mites associated with trees and forest increased steadily during the whole period. However, oribatid mites associated with wet habitats also increased gradually during the whole period. It may be possible that mire was developing in the area.

In conclusion, the most likely evolution of the landscape at Kvitevoll was from a more or less big forested area encircling patches of open areas towards less forested area with big open spaces of wet grassland with tree groves remaining in the drier areas. None of the oribatid subfossils found were indicative of any cultivation process. The existence of a mosaic of forested and open areas at Kvitevoll was constant during the whole sequence. It does not seem that the landscape has changed substantially since the first human settled in the area.

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## Long-term changes in species richness of oribatid mites in pine forest ecosystems of Ziemelvidzeme biosphere reserve

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In 1992 – 1997, investigations of oribatid mites were performed in Scots pine forests of the Ziemelvidzeme Biosphere Reserve. Permanent sampling plots were selected at three sites: young (30-40 years old), middle-aged (50-70 years old), and old (150-200 years old) pine forest. Sampling took place every year at the end of August/beginning of September. One hundred soil samples were taken by soil sampler (5 cm<sup>2</sup> x 10 cm) at each forest site. A modified high gradient extractor was used for extraction of soil mites. Soil moisture, acidity, and other edaphic factors were investigated. The meteorological data from the nearest meteorological station in Rujiena were used.

The highest average numbers of oribatid mites (3400 ind/m<sup>2</sup>) were found at the old forest site. The middle-aged and the young forests did not differ much in numbers of mites (2220 – 2270 ind./m<sup>2</sup>). The highest total numbers of species - 38 was recorded at the young forest site. Species richness in the young and middle-aged forest was similar – 36 species. All the sites had the same dominant species: *Ceratozetes gracilis*, *Carabodes spp.*, *Adoristes ovatus*, *Fuscoribatula furcillata*.

During the period of investigations statistically significant trends of increases in species richness were recorded for the middle-aged and the old pine forest sites ( $r=0.823$ ,  $P<0.05$ ;  $r=0.858$ ,  $P<0.05$ ). The trend for the young forest was not significant

( $r=0.782$ ,  $P>0.05$ ). An increase in species richness of oribatid mites was a result of certain shifts in species composition. Mostly groups of recedent and subrecedent species with relative abundance less than 4% and 1% were affected. The number of species such as *Eremaeus* spp., *Phthiracarus* spp., and *Euphthiracarus* spp. entering the community during the period of investigation, was higher than the number of species (*Damaeus subverticillipes* and *Oribatei* spp.) leaving it. A slight increase in mean August air temperatures and a decrease in precipitation and soil moisture was recorded in 1992-1997. It should be noted that a similar analysis of soil collembola data (Jucevica, Melecis, 2002) showed a decrease in species richness, so the reaction of these two groups of soil microarthropods were opposite. Oribatid mites are known to be more drought resistant than Collembola. The changes observed in the community of soil microarthropods appeared to be the result of drought induced competition.

## **Spatial structure and soil ecology**

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Spatial structure is ubiquitous in soils as in all ecosystems. In soils, spatial heterogeneity may be caused by abiotic factors like soil structure, topography, etc., but also by biotic factors. Plants influence both abiotic factors and resources for soil organisms, bioturbators and ecosystem engineers like earthworms or ants create structures and spatial variation, etc. In this talk, I will discuss how spatial structure in soil communities at local sites may be influenced by plants and soil fauna, giving examples of plant species effects on soil fauna, of ant effects, and probably some other examples. I will also briefly discuss how to measure spatial structure, and the factors that influence whether spatial variation in soil communities is small or large.

## **Habitat fragmentation, dispersal ability, community assembly and biodiversity patterns - Using bryophyte-associated soil fauna as a model system**

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### **Introduction**

Human exploitation and alteration of natural habitats is today considered to be the major causes of species extinction and community relaxation (Collinge, 1996; Hoyle & Gilbert, 2004). This process is formally known as habitat fragmentation. The mechanisms of biotic responses following habitat fragmentation are recognized as drastic changes in microclimate and inhibited migration abilities of extant species caused either by isolation or the appearance of an inhospitable matrix (Saunders et al.

1991). The inflated effect of stochastic processes when populations become smaller following deterministic extinctions is also stressed.

Species extinctions and the loss of populations (relaxations) are thought to reassemble and impoverish food webs in ecological communities. It has been shown that species loss may influence important functions regarded as properties of ecosystems e.g. biomass production (Gonzalez & Chaneton, 2002). However species extinctions and ecosystem function relationships are not straightforward and several authors stress the importance of further research (Hooper et al. 2005). At the same time it is alarmingly clear that we still lack a detailed understanding of how ecological communities are organized and structured, especially when they are subjected to spatial reconfigurations.

The recognition of spatial aspects in ecology has successfully explained biodiversity patterns on islands (MacArthur & Wilson, 1967), dynamics of colonization and extinctions of individual species in networks of habitat patches (Hanski & Gilpin, 1997). More recently, ecologists have incorporated multispecies interactions to the dynamics of spatially subdivided communities in a cluster of theories formulating the concept of metacommunities (Leibold et al. 2004).

The realization of metacommunity study has raised the level of complexity in theoretical thinking by adding entire sets of species, their potential interactions and relative abundance into discrete biological networks. However challenging for experimentalists, the enhanced level of realism also promises advances in understanding the dynamics of ecological communities in spatially subdivided habitats.

Although, in its present form, metacommunity theory assumes networks of habitat patches, the theory allows for a broader definition, including mainland-island metacommunities (Leibold & Miller, 2004). This concept of assuming a focal species pool, the mainland, is clarifying the study of important biological activities in relation to habitat fragmentation such as: Colonization processes, and assembly and stability of communities following habitat fragmentation.

Food webs, the trophic interactions between species, have been used to describe the structure of communities (Pimm, 1982). Existing theory on the relationship between food webs and habitat fragmentation predicts that predators at the top of food chains (which could be viewed as collapsed linear food webs) are more susceptible to extinctions in the fragmentation process. This phenomenon has also been shown experimentally (Davies et al. 2000). However, whether such changes at the top of the food web cascades down and thereby influence system functioning is not known.

How the process of habitat fragmentation is working on biodiversity has been considered extensively in many theoretical aspects and its detrimental effects have often been shown for single species. However experimental investigations where natural multi-species communities are used are scarce. Existing experiments often display synthetic and ill represented levels of diversity, trophic structure or relevant temporal aspects (Gonzales & Chaneton, 2002). The rationale is simple, natural large-scale communities are unmanageably complex and diverse. Constituent species have long generation times that preclude extinction or colonization observations. These

obstacles can be overcome using natural micro-ecosystems such as moss-cushions (Srivastava et al. 2004). Moss-cushion on rocky outcrops contains a diverse fauna with a short generation time and a relatively broad trophic representation. The moss-cushion systems have, for example, been used successfully studying species-area relationships (Gonzalez, 2000) and the usefulness of corridors in mitigating species extinctions (Gonzalez et al. 1998).

### **Material and methods**

In this study we used moss-cushions from rocky outcrops and their constituent soil and litter fauna to study how differences in dispersal rates and species traits such as body size, abundance, trophic position and taxonomic integrity could be related to community assembly and biodiversity patterns at different degrees of isolation, size and heterogeneity of the habitats. We use three experimental approaches.

In the first experiment the aim was to study the assembly of communities of varying degree of fragmentation. We constructed micro-landscapes at Tvärminne field station in southern Finland by sweeping the rocks clean of moss. By using templates, we created moss patches of three different sizes, which were positioned at three different distances from a continuous moss bed acting as a mainland (species pool). Moss patches were completely defaunated before being designated to an experimentally fragmented moss-landscape. Variation in dispersal ability between species has been suggested to promote non-random biodiversity patterns. We therefore created an elongated defaunated moss-peninsula attached to the mainland allowing species to disperse in natural vegetation. Moss cushions, controls from the mainland and the sections of the peninsula were thereafter destructively sampled and the fauna were extracted using established methods. The collection composed of collembolans, Acari, Araneae and nematodes were thereafter determined, if possible, to species level.

The second experimental approach, where we aimed to investigate the disassembly process, had a setup that was similar to the first except for the absence of a peninsula, but most importantly, that the moss patches had from the start an intact and present fauna.

In the third experimental approach the mainland was also excluded, and all patches in this experiment had the same size but the within-patch heterogeneity and distances between patches varied. The moss fauna in this setup were also intact and we aimed to study how isolation and heterogeneity of the fragmented habitats alters biotic interactions such as predation, and if this change has any cascading effects on species richness within and between trophic guilds. The third experimental setup was placed on the roof-top of the department facility in Lahti to avoid the effect of unwanted dispersal sources. As a measure of ecosystem functioning we focused on degradation of organic material, which in our experimental case was degradation of cellulose. To each patch in all three experiments a cellulose strip of known weight was designated to all patches and the weight loss was then recorded at the time of each sampling.

### **Results**

Preliminary results from the first experiment showed that, during the early stages of community assembly, the pattern in species richness followed the predictions of island-biogeography, i.e. both size and degree of isolation of the habitats affected the species richness. Although species richness was higher in large and more connected

habitats, species abundance per habitat area tended to be higher for a subset of species in more isolated and smaller habitats. This could be explained by either absence of predation, which would allow species to be competitively dominant (Terborgh 2001) or, alternatively, this pattern of hyperabundance was ephemeral and was a reflection of the variation in dispersal ability among species. In the latter case this pattern of counterintuitive species abundance will with time fade away. However, initially top predators such as spiders and Mesostigmata mites seemed less abundant in more fragmented patches, which indicated support for the first explanation. We have also noted that functional food-chain lengths are top-down truncated in small and isolated habitats. A deeper analysis will reveal if community structure is altered by fragmentation and if this alteration could be related to ecosystem functioning and performance.

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## Geographic variation and adaptation to climatic stress in the springtail *Orchesella cincta*

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Knowledge of environmental adaptation is important in predicting how and which populations will be affected by climatic change. However, only a few studies have been published on adaptation to climatic gradients for soil invertebrates. This is rather surprising as soil invertebrates are important components of soil ecosystems and play an important function in the soil (Petersen & Luxton 1982). Soil mesofauna, such as springtails, are grazers of bacteria and fungi and are thought to stimulate microbial decomposition rates (Hedlund & Ohrn, 2000). A number of studies have shown that soil fauna increase nitrogen mineralization with up to 25% (e.g. Verhoef & Brussaard, 1990). It therefore seems inadequate that our understanding of how climatic changes will affect community structure in soil ecosystems is based on model organisms such as *Drosophila*.

We therefore investigated multiple traits of stress resistance in different populations of the epedaphic springtail *Orchesella cincta*. Second generation adults from five laboratory populations were compared with respect to resistance to extreme temperatures and desiccation, and traits relevant to climatic adaptation. Populations were collected along a 2000-km latitudinal gradient ranging from Denmark to southern Italy and reared under the same standard laboratory conditions. Traits investigated were resistance to high and low temperature, desiccation resistance, body size and water loss rate (WLR). Results showed genetically based differences in resistance to high and low temperature, desiccation, WLR and size between populations. Individuals from the most northern population had the highest desiccation and cold shock resistance, and the lowest heat shock resistance. Females were significantly more desiccation resistant than males. The results of cold shock resistance showed a positive increase with lowest environmental temperature recorded at the sites of population origin, whereas heat shock resistance showed a positive increase with highest recorded temperature at the sites of population origin. Desiccation resistance increased towards the most southern and northern populations, suggesting that both low and high temperature extremes affect desiccation resistance. Body mass and WLR showed interpopulation as well as sex specific variation. This provides evidence for geographical variation in stress resistance of springtails related to climatic conditions.

A number of physiological adaptations can explain the observed geographical patterns in the resistance traits. Among those are molecular chaperones that are important in the protein control system and become increasingly important when organisms are exposed to stress. Heat shock proteins are molecular chaperones that have an



important function for the organism when exposed to environmental stress. Traditionally these proteins have been shown to be important when exposed to heat stress (Sørensen *et al.*, 2005). We have shown that Hsp70 is upregulated in individuals of *Orchesella cincta* exposed to heat stress (unpublished results). Desiccation protective proteins that might affect both desiccation and cold shock resistance are the LEA proteins, that is, late embryogenesis abundant protein, that have been shown to be induced by desiccation and cold shock in anhydrobiotic organisms (e.g. Goyal *et al.*, 2005). LEA proteins have been proposed to act as molecular chaperones or a molecular shield that helps prevent the formation of damaging protein aggregates during water stress (Goyal *et al.*, 2005). Preliminary analysis suggest the presence of LEA-like protein in *Orchesella cincta* (unpublished results: Tunnacliffe, A., McGee, B., Bahrndorff, S.). This suggests that protein expression patterns are highly relevant for stress resistance in springtails and should be included in future population studies looking at climatic adaptation and population differences in soil ecosystems.

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## Species – area relations and island distribution of carabid beetles (Coleoptera, Carabidae) on small islands off the coast of western Norway

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### Aim

The study explores carabid beetle communities on small islands to assess distribution patterns in terms of stochastic and non-random mechanisms.

### Location

The study was carried out on 14 small islands in Øygarden, an island archipelago 30 km north-west of Bergen, western Norway. The islands studied are all on the west side of Øygarden, exposed to the North Sea. All these islands are characterized by a discontinuous and patchy vegetation cover and most of them are bare rock. The dominant vegetation was *Calluna vulgaris* heath.

## Methods

Sampling was carried out with 83 pitfall traps operating continuously from May 30 to November 14, 1983. Log-linear regression was applied for analysing the data.

## Results

The pitfall trapping yielded 29 species and 6139 specimens of ground beetles (Coleoptera, Carabidae). The island area was less significant than the habitat size in determining the species diversity. An island further away from the source area contained a higher proportion of species with the ability to fly than did islands close to the source area. There were a few characteristic species: *Amara ovata* was only found on the smallest islands, islands with gull colonies and islands heavily exposed to wind and waves. *Amara lunicollis* Schiødte, *Carabus problematicus* Herbst, *Harpalus latus* (L.), *Pterostichus niger* (Schaller) and *P. nigrita* (Paykull) were all species that were found on the larger islands with grasses and *Calluna* heath. The larger species were found in the larger habitat patches, and this association was significantly correlated. Islands exposed to the action of wind and waves were inhabited by species with adult hibernation. Species with later larval hibernation were significantly inversely correlated with the degree of vegetation cover in terms of species as well as individuals. The immigration rate of *Carabus problematicus* Herbst was probably very low, leading to a certain degree of genetic isolation, expressed by differences in size between islands.

## Main conclusions

Carabid beetles from small islands of the coast of western Norway were non-randomly distributed according to habitat size and distance from source areas. The present study clearly showed the importance of habitat patches and migration. It also showed that extreme conditions, like small islands, can alter the species assemblages in a profound way.

**Keywords:** Carabid beetles, Carabidae, hibernation strategies, dispersal, genetic isolation

## The latest news from Norway on the invasive Iberian slug, *Arion lusitanicus*

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Since 2002 we have studied aspects of population fluctuations, growth, feeding and beetle predators of this slug in western Norway, and the main results up to now will be presented.

There will also be presented some distribution data and preliminary data on the genetic and fatty acid analyses of selected populations of *A. lusitanicus*, *A. arter* and of the possible hybrid between the two species. Some results from ongoing studies on how to control the Iberian slug by colleagues at the Norwegian Plant Protection Institute will also be presented.

## POSTERS

### **Does defoliation alter N dynamics in the soil on a short time scale?**

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It has been shown for several plant species that defoliation leads to a peak of rhizodeposition within a time span of 48 hours and also increases N content compared to non-defoliated plants. This increase might be mediated either by an increase in the N uptake capacity of the roots or by a greater availability of N in the soil in the short term. Since it has been shown that some more active micro-organisms were found under defoliated systems and since it is also known that heterotrophic micro-organisms are the main drivers of N dynamics in the soil, the main question we address in this work is: does a punctual input of C, as it may be observed in the case of a defoliation, alter the soil microbial loop to an extent that can explain an increase in N in the plant?

We grew *Plantago arenaria* for 49 days in microcosms. After 40 days of growth half of the plants were cut to a 2 cm height. A first harvest was done 2 days after defoliation and a second 9 days after defoliation. Then we measured different parameters such as the number of CFUs, the MPN of protozoa and the SIR.

The first results showed that the number of organisms in the rhizosphere and their basal respiration were not modified by the defoliation. But at the same time, it appeared that the N-induced respiration was higher in the rhizosphere of the non-defoliated plants than in the rhizosphere of the defoliated plants.

These results indicate that the effect of defoliation was probably too weak to impact significantly the number of micro-organisms in the soil and their basal respiration. However this defoliation might be sufficient to induce the transfer of N from a recalcitrant pool to a more labile one which may explain that micro-organisms are less N-limited in the defoliated systems.

# **Abundance and diversity of earthworm communities in flooded semi-natural meadows**

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Floodplain and coastal meadows are semi-natural landscapes rapidly disappearing in Europe due to changes in land use. The uniqueness, environmental value and cultural importance of these landscapes have become evident too late: most previously semi-natural communities are today overgrown, afforested or cultivated. Today the species diversity of semi-natural areas is influenced by the continuity of extensive management (mowing, grazing); historical management influences the formation of both plant communities and soil characteristics (reduced fertility). Soil organisms are an integral part of meadow ecosystems, especially in food chains and the process of decomposition.

The aim of this study was to determine the abundance and species composition of earthworm communities in the soil of coastal and floodplain meadows in West Estonia, to find out how the flooding of meadows influences earthworm communities, and to investigate how earthworm communities' abundance and diversity are related to floods and the salinity gradients of grasslands.

## **Material and methods**

The investigation area was selected to represent grasslands temporarily flooded with freshwater or saline water or both (coastal grasslands, floodplains, or intermediate transient meadows where fresh or saline water extent is indistinct). The flood duration is approximately one month in spring with shorter periods in autumn and summer. Earthworm and plant communities were studied on 11 flooded meadows in Matsalu National Park (West-Estonia) which are mown annually (floodplain meadows) or grazed at low intensity (coastal meadows), and the intermediate grasslands are mown or grazed.

At each site five soil blocks (50 x 50 x 40 cm) were examined by hand sorting or using mustard solution as a vermifuge (Meyer, 1996; Gunn, 1992). Species were identified (Graff, 1953; Timm, 1999) and individuals were counted. The mean number of individuals per m<sup>2</sup> of soil surface and standard error (SE) were calculated. Moisture content (105<sup>0</sup>C), pH (KCl), organic matter (in muffle furnace at 360<sup>0</sup>C), nitrogen concentration (Kjeldahl method) and soluble phosphorus concentration (lactate method), K and Na concentration (flame photometer) were determined for each composite soil sample.

We calculated soil ecological parameters obliquely, using plant species Ellenberg's indicator values (salt, water, reaction, and nitrogen demands in soil for plant communities using a small scale qualitative list of species and coverage of each species). In addition, to, we estimated soil and plant communities' species richness and analysed the ecological structure of mutually adapting communities (Table 1).

**Table 1.** Characterization of investigated vegetation categories (distinguished according to moisture regime and salinity gradient). For majority of characteristics has given gradation over categories (from 1 (min. value) to 4 (max. value)), and also statistically relevant differences between four types compared (Kruskal-Wallis ANOVA,  $p < 0.05$ ).

General vegetation categories/ Characteristics	I. Wet floodplain grassland	II. Fresh floodplain grassland	III. Transient grassland	IV. Coastal grassland
Transects (study areas)	Kelu, Kloostri I, Kloostri II	Kasari I Kasari II	Suitsu I, Suitsu II, Lõpe	Salmi I Salmi II
<b>VEGETATION</b>				
Community types (by Krall <i>et al.</i> , 1980)	Wet floodplain grasslands with tall sedge or floodplain fens: <i>Caricetum distichae</i> , <i>Caricetum acutae etc</i>	Moderately moist floodplain meadows, sometimes described as dry impoverished floodplain grasslands	Species-rich paludified grasslands: <i>Scorzonero- Caricetum pallescentis</i> , on grazed sites <i>Deschampsio- Ranunculetum acris</i>	From saline to suprasaline paludified grassland: <i>Junco-Glaucetum</i> , <i>Deschampsio-Caricetum nigrae</i>
Herb layer characterization, dominant and/or character species	High and lush, sometimes lodged <i>Carex disticha</i> , <i>Carex acuta</i> <i>Deschampsia cespitosa</i>	Lush and dens, rather species-rich, high diversity of vegetation associations and variants; <i>Lychnis flos-cuculi</i> , <i>Sesleria coerulea</i> , <i>Geum rivale</i> , <i>Filipendula ulmaria</i>	Medium and species-rich (comparable to boreo-nemoral grasslands), on grazed sites, lower, poorer and tufted. <i>Scorzonera humilis</i> , <i>Ranunculus acris</i> , <i>Deschampsia cespitosa</i>	Variable, from low and sparse to high and lush; <i>Juncus gerardii</i> , <i>Glaux maritime</i> , <i>Triglochin maritimum</i> ; <i>Carex nigra</i> , <i>Potentilla anserina</i> <i>Festuca sp.</i>
Mean vegetation coverage per 1m <sup>2</sup> ±SE (%)	79.3±2.5 1. (different from 3 and 4)	94.5±2.2 4. (1)	92.1±2.5 3. (1)	88.5±2.8 2.
Small scale species richness (mean sp no per 1m <sup>2</sup> ±SE)	6.6±0.5 1. (different from 3 and 4)	13.4±0.9 3. (1)	16.4±0.9 4. (1 and 2)	10.6±0.8 2. (4)
<b>ECOLOGY:</b> Ellenbergs' indicator values (Ellenberg 1991; Lindacher 1995)				
Demand for continentality (mean ±SE)	0.6±0.2 1. (different from 3 and 4)	2.2±0.2 3. (1)	2.6±0.3 4. (1 and 2)	0.8±0.2 2. (4)
Demand for moisture (mean ±SE), moisture regime	8.1±0.3 4. (1 and 2) Long-lasting fresh water overflow, poorly drained to saturated or permanently saturated	7.2±0.2 3. (1 and 2) Fresh water overflow, regularly flooded, well drained	5.5±0.4 2. (3 and 4) Occasional and short-term flooding. Area where fresh and salted water flow together	4.9±0.4 1. (3 and 4) Regular saline water overflow, highly fluctuating moisture regime
Demand for salinity (mean ±SE)	0.04±0.02 1. (3 and 4) Affected by fresh water	0.08±0.03 2. (4) Affected by fresh water	0.13±0.03 3. (1) Affected by fresh and saline water at the same time	2.44±0.78 4. (1 and 2) Affected by saline water
Demand for nitrogen (mean±SE)	4.2±0.2 4. (1 and 2)	4.0±0.2 3. (1)	2.8±0.2 1. (3 and 4)	3.2±0.3 2. (4)

All earthworm and vegetation data were analysed using the non-parametric dispersion analysis of Kruskal-Wallis.

## Results and discussion

Flooded grasslands of different type (Table 1) differed by soil characteristics and plant communities. Abundance of earthworm species differed as well, depending on habitat conditions. To describe the habitat we used Ellenbergs' indicator values of cover forming plant species and some parameters determined directly from the composite sample of study sites. Light, temperature and soil reaction values did not differ statistically significantly between meadow types and were not analysed.

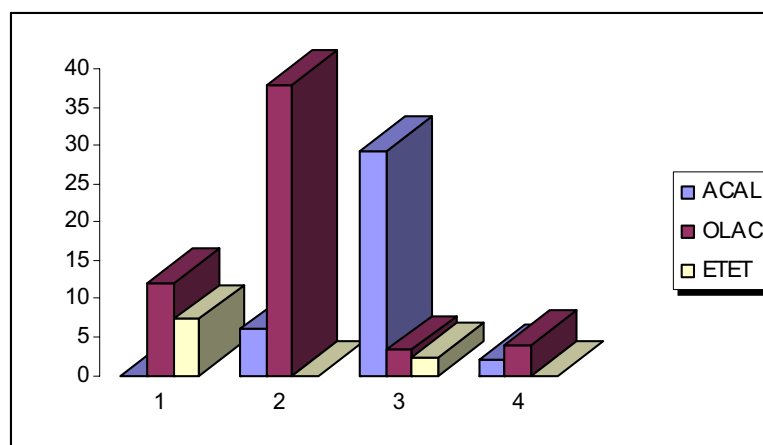
Wet floodplain grasslands vegetation is classified as tall sedge meadows or even floodplain fens. Dominating community types are *Caricetum distichae* and *Caricetum acutae*. Ellenbergs' values indicate flooded and poorly drained soil. The quantity of sediment, its physical and chemical properties as well as flood duration are the main factors that determine the soil and vegetation types on floodplains (Truus & Tõnisson, 1998). Soil moisture is high ( $62.6 \pm 4.0\%$ ) even in a period without flooding and limits the abundance of most earthworm species except semi-aquatic ones. Organic matter and nitrogen contents were high because of poorly decomposed sediments; Ellenbergs' value of nitrogen demand showed temporary nitrogen-rich soil. Total abundance of earthworms ( $40 \pm 22$  individuals per  $m^{-2}$ ) and number of species are low. Though common in all habitats in Estonia the species *Aporrectodea caliginosa* and *Lumbricus rubellus* were missing because of high moisture; anecic species were missing because of the high groundwater table. The dominant species was semi-aquatic *Octolasion lacteum*, and there was a high abundance of semi-aquatic epigeic *Eiseniella tetraedra* as well; additionally we found individuals of species *Lumbricus castaneus*, *Aporrectodea rosea* and *Dendrobaena octaedra*. The composition of earthworm communities was characterized by semi-aquatic species or species which like conditions of high soil moisture.

Moderately moist (fresh) floodplain meadows were more suitable habitat for earthworm: soil moisture  $44.0 \pm 4.5\%$  was high but did not limit the presence of common species. The rate of decomposition was higher because of better aeration of soil resulting in lower organic matter and nitrogen content of soil. The total number of earthworms per  $m^{-2}$  was  $81 \pm 26$ . Endogeic semi-aquatic *Octolasion lacteum* dominated the community, and species that were tolerant of the conditions of the habitat, namely *Aporrectodea caliginosa*, *Aporrectodea rosea* and *Lumbricus rubellus*, were presented as well. Anecic species were missing. We also found some individuals of the epigeic species *Dendrodrilus rubidus* and *Dendrobaena octaedra*.

Transient grasslands are located between floodplain and coastal grasslands and are flooded by fresh and marine water. A very low content of marine water in flooding was not detectable but it obviously influenced the specific structure of community. Soil characteristics (pH, moisture, organic matter content) were similar to the characteristics of moderately wet grasslands, Ellenbergs' values of plant communities indicated less acidic soil conditions, less wet and poorer in nitrogen. Earthworm communities are less abundant but more diverse (58.8 individuals, 4.7 species). The species most tolerant to ecological conditions species, namely *Aporrectodea caliginosa*, dominated and *Lumbricus rubellus* was relatively abundant. The community was diverse: species with various demands were represented – tolerant *Aporrectodea rosea*, and typical for wet habitat *Octolasion lacteum*, *Eiseniella tetraedra*, *Lumbricus castaneus*, epigeic *Dendrobaena octaedra*.

Coastal grasslands are meadows under the direct influence of the sea, i.e. flooded at least by storm waves. Very low abundance of earthworms ( $6.0 \pm 5.0$ ) was characteristic of coastal grasslands; only two endogeic species were present, *Aporrectodea caliginosa* and *Octolasion lacteum*. Marine water was a limiting factor despite the fact that the salinity of water in Matsalu bay was very low (5-6‰). This type of grassland is not suitable for earthworms; overflooding and a high content of  $K^+$  and  $Na^+$  ions in the soil, especially in the floor layer, are strongly limiting factors for earthworms. In saline zones close to the coastline no earthworm were found. Ellenberg's value indicated concentrations of chloride ions in soil of 0.05-0.3%. Real soil moisture (measured in August) was high ( $61.2 \pm 3.75\%$ ) and in the period between overfloodings the upper layer of coastal soil can dry off. This is an additional limiting factor for earthworms and was reflected in Ellenbergs' value of demands for moisture (Table 1).

The most abundant earthworm species on flooded grassland are semi-aquatic *Octolasion lacteum* and *Eiseniella tetraedra* or *Aporrectodea caliginosa*, which is tolerant of unfavorable ecological conditions. The abundance of species depends on the moisture content of the soil – semi-aquatic species react positively to this parameter and other species negatively (Figure. 1). Flooding by fresh water is a positive factor for semi-aquatic earthworms and negative for all others. The salinity of flooding sea water is an additional negative factor for all species of earthworms as well as the temporary drying of the thin coastal soil.



**Figure 1.** Mean abundance (individuals per  $m^2$ ) of *Aporrectodea caliginosa* which is tolerant to ecological factors, and semi-aquatic species (*Octolasion lacteum* and *Eiseniella tetraedra*) in different types of grasslands (1 – wet floodplain grasslands; 2 – fresh floodplain grasslands; 3 – transient grasslands; 4 – coastal grasslands).

### Conclusion

The meadows differed in terms of soil and communities' characteristics. Ellenbergs' indicator values were valuable to define characteristics of habitat conditions, integrating the changes in different seasons. Flooding of soil by fresh water was a limiting factor for earthworm abundance and diversity except for semi-aquatic species. Flooding of soil by marine water limited the abundance of all earthworm species as well as the temporary drying of the thin soil layer.

### Aknowledgements

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## ***Pterostichus vulgaris* (L.,1758)(=*melanarius* (Illiger, 1798)) and *Harpalus pubescens* (Müll.,1776) in agricultural fields**

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More than 40.000 species of ground beetles (*Carabidae*) have been described so far; nearly 2.700 are known in Europe (Ekschmitt et al., 1997; Lövei & Sunderland, 1996) and nearly 300 are known in Estonia (Haberman, 1968). Ground beetles are probably the most diverse in habitat and structure of all soil-inhabiting insects. The ground beetles with their long legs are well adapted to running over the surface of the soil (Kromp, 1999). Frequently only five to six species are dominant in a particular crop field, making up 90% of the total number of carabid individuals. Among the more important genera from agricultural perspectives are *Carabus*, *Pterostichus*, *Harpalus*, *Agonum*, *Calathus*, *Amara*, *Brachinus*, *Bembidion*, *Trechus*, *Clivina* and *Dyschirius*.

*Pterostichus vulgaris* and *Harpalus pubescens* are nocturnal autumn breeding carabids; during the day they hide under grass or stones. These carabids prefer open habitats and are rather favoured by agriculture. As in many ground beetles, *P. vulgaris* has a very unspecific diet; both larvae and adults are predatory, preying on slugs and aphids (Fournier, Loreau, 2002; Fournier, Loreau, 2001); *H. pubescens* feed on seeds or strawberries (Haberman, 1968).



Agricultural activities change the diversity of the ecosystem directly, influencing the survival of individuals, or indirectly, changing the level of resources (Neher, Barbercheck, 1999). Agricultural activities such as soil tillage, turning the soil while ploughing, fertilization, using pesticides, planting hedges, tree lines or a small forest etc influence the soil biota, affecting the organisms living on the surface of the soil as well as belowground (Paoletti et al., 1991).

One important reservoir for carabids may be the vegetation that borders an agricultural field. Field borders may benefit carabid populations by providing refuge from agricultural practices such tillage and pesticide use and a stable microhabitat for overwintering. Field borders with a well-established thick vegetative cover and a stable microhabitat such as hedgerow (or shelterbelt) have been shown to increase overwintering success compared with the bare, open ground of an agricultural field (Varchola, Dunn, 1999). The aim of the research is to evaluate the influence of soil types, crops and borders on ground beetles in the soil of different agricultural landscapes in Estonia.

### **Methods**

Twenty-four study areas of the three most widespread soil types (pebble rendzinas, typical brown soils and pseudopodzolic soils) all over Estonia were selected. In each group of soil type, eight fields with different management practices were selected for studies in 2003-2004. To collect samples of ground beetles on the soil pitfall-traps were used (Meyer 1996). Depending on the purpose of the research, the traps were put in the middle of the border of the selected fields 1m outside of the border of the field (in case there is a field bed) and 5m, 10m and (15m) 20m inside of the border of the field and in the middle of the field. Depending on the methods, the distance between traps was 1m and the traps were emptied after 5 days. Each different community bordering the field constituted one border, thus the number of borders was different for different fields. The traps were filled up to ¼ with 20% salt solution. The traps were covered with covers in order to avoid rainwater getting in the traps.

In all composite soil samples moisture content (at 105 °C) was determined.

### **Results**

The mean abundance of *H. pubescens* and *P. vulgaris* did not show a significant preference for soil types and for soil moisture (Table 1). The same result applied to borders. We estimated 11+1 different types of borders but all were without significant preference. These 11+1 different field borders were: hedge, pasture, cereal, hay, road, forest, clover, corn, rape, heap of stone, melilotus and middle of field.

**Table 1.** Characteristics of soil of studied fields (mean value  $\pm$  SE) and mean abundance of *P. vulgaris* and *H. pubescens* in different soil types. Pbr= pebble rendzinas, Tbs= typical brown soils, Pps= pseudopodzolic soils.

Time	Type of soils	Soil moisture %	<i>P. vulgaris</i>	<i>H. pubescens</i>
Summer 2003.	Pbr		2.4 $\pm$ 1.0	<b>5.0 <math>\pm</math> 1.5</b>
	Tbs	-	<b>4.7 <math>\pm</math> 2.7</b>	2.2 $\pm$ 0.5
	Pps		1.6 $\pm$ 0.5	3.1 $\pm$ 0.8
Autumn 2003.	Pbr	13.18 $\pm$ 2.06	0.3 $\pm$ 0.1	0.8 $\pm$ 0.3
	Tbs	14.80 $\pm$ 0.82	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1
	Pps	<b>16.93 <math>\pm</math> 1.12</b>	0.4 $\pm$ 0.1	2.0 $\pm$ 1.0
Summer 2004.	Pbr		2.9 $\pm$ 1.6	2.8 $\pm$ 0.6
	Tbs	-	<b>3.5 <math>\pm</math> 1.3</b>	3.2 $\pm$ 0.7
	Pps		1.8 $\pm$ 0.3	<b>4.7 <math>\pm</math> 2.7</b>
Autumn 2004.	Pbr	20.04 $\pm$ 2.96	0.8 $\pm$ 0.3	2.6 $\pm$ 1.0
	Tbs	17.73 $\pm$ 0.98	1.4 $\pm$ 0.5	0.9 $\pm$ 0.3
	Pps	<b>20.48 <math>\pm</math> 3.41</b>	2.6 $\pm$ 0.7	0.8 $\pm$ 0.2

The mean abundance of *H. pubescens* and *P. vulgaris* was the highest in cereal or cereal/clover fields and in fields of rape (Table 2).

**Table 2.** Mean abundance of *P. vulgaris* and *H. pubescens* in different culture fields.

		Cereal	Cereal/clover	Clover	Rape	Hay
<b>Summer 2003.</b>	<i>P. vulgaris</i>	<b>3.4 <math>\pm</math> 1.3</b>	1.8 $\pm$ 1.3	1.1 $\pm$ 0.5	1.6 $\pm$ 0.7	2.5 $\pm$ 1.0
	<i>H. pubescens</i>	3.6 $\pm$ 0.9	<b>4.8 <math>\pm</math> 1.0</b>	3.0 $\pm$ 0.6	1.2 $\pm$ 1.0	1.8 $\pm$ 0.5
<b>Autumn 2003.</b>	<i>P. vulgaris</i>	0.2 $\pm$ 0.0	<b>0.7 <math>\pm</math> 0.1</b>	0.0 $\pm$ 0.0	<b>0.7 <math>\pm</math> 0.7</b>	-
	<i>H. pubescens</i>	0.8 $\pm$ 0.3	<b>3.7 <math>\pm</math> 2.2</b>	0.3 $\pm$ 0.3	0.3 $\pm$ 0.3	-
<b>Summer 2004.</b>	<i>P. vulgaris</i>	2.2 $\pm$ 0.8	4.1 $\pm$ 2.1	1.5 $\pm$ 0.8	<b>5.6 <math>\pm</math> 2.7</b>	-
	<i>H. pubescens</i>	<b>4.6 <math>\pm</math> 1.6</b>	2.0 $\pm$ 1.6	2.7 $\pm$ 1.2	1.6 $\pm$ 1.1	-
<b>Autumn 2004.</b>	<i>P. vulgaris</i>	1.8 $\pm$ 0.5	1.9 $\pm$ 0.7	0.4 $\pm$ 0.2	<b>2.4 <math>\pm</math> 1.2</b>	-
	<i>H. pubescens</i>	1.6 $\pm$ 0.6	<b>3.0 <math>\pm</math> 1.0</b>	0.6 $\pm$ 0.2	0.4 $\pm$ 0.2	-

## Discussion

Arable land forms approximately a quarter of Estonian territory. The pebble rendzinas form 9.0% of Estonian arable land, typical brown soils form 9.7% of arable land and pseudopodzolic soils form 15.1% of arable land (Kõlli, Lemetti, 1999). Pebble rendzinas soils are characterised by a high humus and nutrient content but sensitive to drought and these soils are largely cultivated. Typical brown soils are the most productive agricultural soils in Estonia; these soils have high soil biota activity. Pseudopodzolic soils are characterized by medium humus content and relatively high soil acidity and these have also largely been cultivated (ESTONICA, 2006).

Soil texture may be of critical importance for carabids. Many species obviously prefer fields with clay soil to those with sandy soil. The greater abundance in clay soil is probably due to the combined effect of higher moisture, denser vegetation cover and higher productivity of organic substances which ensure a better food supply (Ekschmitt et al., 1997). While our three different types of soils are characterized by

quite good humus content and productive agricultural soils, probably soil type does not play such an important role in abundance of *P.vulgaris* and *H.pubescens*.

Insects are ordinarily not affected directly by normal precipitation but indirectly through the effect of precipitation on humidity and soil moisture (Ross, 1956). Different species of carabids strongly differ with respect to their preferred humidity range and generally carabids are well adapted to the drought conditions (Ekschmitt et al., 1997). According to Table 1, there was no preference between species of carabids and soil moisture %. Thus, soil moisture was not a critical factor in our research in terms of affecting the abundance of *P.vulgaris* and *H.pubescens*.

As described by Lövei and Sunderland (1996), habitat and microhabitat selection are influenced by temperature or humidity extremes (especially of overwintering sites), food availability, presence and distribution of competitors and the type of life history and seasonality. Lower population densities of carabids have generally been more often encountered in root crops than in cereals (Ekschmitt et al., 1997). Plants affect soil biota directly by generating inputs of organic matter above- and belowground and indirectly by the physical effects of shading, soil protection and water and nutrient uptake by roots (Neher, Barbercheck, 1999). Field ground beetle species prefer warm and dry sites (Kromp, 1999) whereas polyphagous *Harpalus spp* aggregate in crops and *P.vulgaris* moved from winter wheat to a weed strip within a wheat field where feeding conditions were better (Lövei, Sunderland, 1999) as in this research where mean abundance of *P.vulgaris* and *H.pubescens* was highest in the fields with cereal, cereal/clover or rape (Table 2).

Many species of ground beetles overwinter in the field margins and many ground beetles disperse into cereal grains from field edges; other species may remain near edge areas. Species are classified as habitat generalists or soft edge species, habitat specialists or hard edge species and as edge species (French, Elliott, 1999). Several studies showed that *P.vulgaris* avoids bare areas because of this microclimate constraint (Fournier, Loreau, 2001). In our research there was no significant preference between mean abundance of carabids and borders. The abundance of carabids was probably influenced by other factors such as age of edge, mowing, herbicide etc.

According to Lövei and Sunderland (1996), carabids can and have been used as indicator organisms for assessment of environmental pollution, habitat classification for nature protection, characterization of soil-nutrient status in forestry or description of landscape mosaic parts (Paoletti *et al*, 1991); *P.vulgaris* is a good bioindicator species for conventional cultivation (Kromp, 1999).

## **Conclusions**

Agricultural fields are heterogeneous communities depending on soil types, vegetation, climate, agricultural management etc. Investigating the fields by using ground beetles as bioindicators is difficult as the beetles are influenced by several other factors at the same time. Probably the most important factor affecting carabids are chemical compounds and agricultural management but these require further investigation.

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## ***Beauveria bassiana*: an exciting soil dwelling fungus infecting insects**

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*Beauveria bassiana* Vuillemin is a naturally occurring generalist entomopathogenic fungus. *B. bassiana* can be isolated from the soil, leaf surfaces, infected hosts etc. using different isolation techniques such as bait, selective media, etc.

*B. bassiana* has been researched for control of soil borne insects. Many soil insects, however, may have a natural tolerance to this pathogen, which is not exhibited in many foliar pests. Therefore, commercial development of this fungus for biological control has primarily been targeted against foliar feeding pests. The infection process of *B. bassiana* in insects has been investigated but so far no *in vivo* visualization has been done of the infection process. The purpose of a currently running Ph.D. project is to make a stable *gfp*-transformant of *B. bassiana* and visualize the infection process of the fungus in insects *in vivo* using confocal laser scanning microscopy.

## **Soil fauna and soil properties after wildfires in Tyresta and Petrozavodsk – A comparison**

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Two small wildfire plots in pine forests by rocks covered with podsol-peat soils and separated by a distance of 930 km were selected to check the following hypotheses: Wildfire impact should be increased in the west-east direction; Traits of soil fauna recovery should be similar for ‘west’ and ‘east’ plots; Losses of diversity and decrease of population number should be observed in the west-east direction. The ‘west’ plot was chosen in Tyresta National Park, Sweden and the ‘east’ plot near Petrozavodsk, Karelia, Russia. There are obvious differences between the ‘west’ and ‘east’ plots in animal assemblage composition after three years of recovery after wildfires. Climate differences play the main role because a share of ‘resident’ groups is lower in the soil of the ‘east’ plot in the comparison with the ‘west’ one. Diversity and population number of animals are higher in soil of the west plot although some groups found in the east plot were not found in samples of the west plot. ‘Continentality’ leads to reduction of differences between burned and unburned plots due to substitution of ‘resident’ groups by ‘mobile’ ones.

## **Spatial distribution of soil microfauna in peat soils at rocks at White sea coast**

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Peat soils over rocks under pine stands are widely distributed by the White Sea. The study was carried out in August, 2000 in the vicinity of the Biological Station of Moscow State University (WSBS). We took 144 samples of 100 cm<sup>2</sup> each. The depth was limited by the rock layer (about 15-20 cm). The number of animals was 174 per

m<sup>2</sup>. The soil macrofauna were highly aggregated. The coefficient of variation for the number of animals was 85%, but for separate groups from 115% (spiders) to 400% (all other groups). A low correlation of possibility of meeting separate groups in the same samples was observed ( $r$  fluctuated in limits 0.3-0.4). Evidently, such distribution explains the relatively low meetability and understated estimations of quantity and biomass by standard investigations on large soil invertebrates. The thickness of soil and litter levels played an important role in the distribution of dominating animals. The influence of soil pH, which varies from 2.92 to 3.76, was noticed only for distribution of hemipterans and beetles. The high acidity of the soil can also be a factor, confining migration of species from less acid soils, for example from podzolic soils, encountered at WSBS. The study was supported by RFBR grant 06-05-64902 and the Russian Science Support Foundation.