

Communities of nematodes, enchytraeids and earthworms in anthropogenous birch stands in central Finland

Mika Rätty



SUONENJOEN TUTKIMUSASEMA
Suonenjoki Research Station

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Faculty of Mathematics and Science
University of Jyväskylä

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The Finnish Forest Research Institute
Suonenjoki Research Station

Supervisors	Professor Veikko Huhta Department of Biological and Environmental Science University of Jyväskylä Finland
	Dr. Jari Haimi Department of Biological and Environmental Science University of Jyväskylä Finland
Reviewers	Dr. Visa Nuutinen MTT Agrifood Research Finland Environmental Research Jokioinen, Finland
	Professor Tryggve Persson Department of Ecology and Environmental Research Swedish University of Agricultural Sciences Uppsala, Sweden
Opponent	Professor Jari Kouki Faculty of Forestry University of Joensuu Finland
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Abstract

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The aim of the study was to compare the communities of Nematoda, Enchytraeidae and Lumbricidae in anthropogenous birch stands of different origin with each other and with naturally developed broad-leaved forests at the same latitude in Finland. A total of nine forest sites were investigated: three birch stands (*Betula pendula*) planted *ca.* 30 years prior to the study after clear-cutting of mature spruce stands, three birch stands established *ca.* 30 years earlier on arable soil, and three naturally developed (not planted) deciduous forests. Vegetation and soil characteristics were analyzed to explain the community differences, and two laboratory experiments were conducted to test hypotheses brought about by the field observations. The faunal communities differed markedly between birch stands of different origin, and between these and naturally developed coniferous and deciduous forests, but even more between replicates of equally managed forests. Total numbers and species diversity of nematodes were lowest in former agricultural soils. Relative proportions of bacterial feeders and omnivores were higher and that of plant feeders lower in birch stands established on spruce forest soil than in natural deciduous forests. Total numbers and populations of most enchytraeids were lower in former arable soils than in birch stands established after spruce forests. *Cognettia sphagnetorum* was the dominant enchytraeid in all birch stands cleared from spruce forests, and in one natural deciduous stand. The clearest differences were found in the earthworm communities. The most diverse and abundant community was found in one of the naturally developed forest, while in another they were totally lacking. *Dendrobaena octaedra* composed a single-species community in one of the birch stands with spruce forest origin, while the two others harboured also *Aporrectodea caliginosa* and three *Lumbricus* species. All of these species were also present in birch stands on arable soil. Laboratory experiment revealed that both *A. caliginosa* and *L. terrestris* were able to live and reproduce in the soil of the deciduous forest where they were absent. Soil characteristics could only partially explain the variation in the communities. Dispersal ability is a crucial factor in determining, which species have invaded deciduous forests located far from source populations. Active dispersal by land is limited in edaphic animals, many of which depend on casual transport by man in their distribution. Burrowing earthworms, once established their populations, alter the soil properties and suppress the populations of enchytraeids and nematodes. In conclusion, the structure of the faunal communities in different forests is an outcome of interplay between edaphic factors, site history, colonisation, and interspecific interactions.

Key words: Nematoda, Enchytraeidae, Lumbricidae, birch, deciduous forest, dispersal, forest soil

Correspondence: Mika Räty, The Finnish Forest Research Institute, Suonenjoki Research Station, FI-77600 Suonenjoki, Finland. Tel. +358 10 2114857, Fax +358 10 2114801. E-mail: mika.raty@metla.fi

Preface

This study is a part of the research project “Decomposer community structure, its causal relationship and functional implications in anthropogenous birch stands within the coniferous forest biome”, being conducted by the University of Jyväskylä and the Finnish Forest Research Institute. I thank Heikki Smolander, head of Suonenjoki Research Station, for providing excellent working facilities in METLA. The study was financed by the Academy of Finland and the foundation Metsämiesten Säätiö. I express my thanks for the financial support.

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Finally I want to express my gratitude to my family. My parents and my sister Katja have been interested in my work in every step, and your support in various part of my life has been overwhelming. I would like to express my deepest thank to my wife Heli, for giving me space and freedom to enable to accept manifold challenges of my life, particularly those beyond the science. I dedicate this thesis to our children Vilma and Alekski.

Suonenjoki, 5th May 2004

Mika Rätty

Abbreviations

List of abbreviations and symbols used in the text. Journal names are abbreviated according to instructions of the ISI Journal Abbreviation Index and the International Organization for Standardization, International Serials Data systems, CIEPS Paris 1985, ISBN 2-904938-02-8.

BAS	basal respiration
SIR	substrate induced respiration
C/N ratio	carbon/nitrogen ratio
GC	gas chromatography
erg	ergosterol
<i>e.g.</i>	<i>exempli gratia</i> , for example
s.s	sensu stricto
s.l	sensu lato
<i>i.e.</i>	<i>id est</i> , that is
<i>in situ</i>	in place
SOM	Soil organic matter
CI	channel index
EI	enrichment index
H'	Shannon diversity index
J	Shannon equitability
γ	Simpson diversity index
E	Simpson equitability
PPI	plant parasites index
SI	structure index
SR	species richness
ΣMI	maturity index
D_b	Bulk density (g cm^{-3})
Md	mean particle size, mm
S_0	degree of sorting (Q_3/Q_1)
%SA	percentage of water stable aggregates
WHC	water holding capacity
S_t	total porosity (%)
Ψ	matric potential (kPa)

List of original articles

This thesis is based on the following articles, which are referred to in the text by Roman numerals **I–V**. The published articles are reprinted with permission of the publishers.

- I** Rätty, M. and Huhta, V. 2003. Nematode communities of anthropogenous birch stands in central Finland. *Nematology* 5 (4): 629–639.
- II** Rätty, M. and Huhta, V. Communities of Enchytraeidae (Oligochaeta) in planted birch stands as compared with natural forests in central Finland. Manuscript (submitted).
- III** Rätty, M. and Huhta, V. 2004. Earthworm communities in birch stands with different origin in central Finland. *Pedobiologia* 48 (3): 283–291.
- IV** Rätty, M. and Huhta, V. 2003. Earthworms and pH affect communities of nematodes and enchytraeids in forest soil. *Biology and Fertility of Soils* 38: 52–58.
- V** Rätty, M. Growth of *Lumbricus terrestris* and *Aporrectodea caliginosa* in an acid forest soil, and their effects on enchytraeid populations and soil properties. *Pedobiologia*. (In press).

The studies in papers **I–III** were conducted mainly by M. Rätty. The research design and establishment of field studies were carried out in collaboration with V. Huhta, J. Haimi and M.A. McLean, while M. Rätty performed most of the faunal and soil analyses. The experimental design in papers **IV** and **V** was planned by M. Rätty and V. Huhta in collaboration. Experiments and analyses in papers **IV** and **V** were carried out by M. Rätty. M. Rätty is responsible for writing and interpretation of the results in papers **III–V**. Papers **I** and **II** were drafted by V. Huhta in collaboration with M. Rätty.

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1 Introduction

Due to Quaternary glaciations, endemic soil fauna is lacking in Fennoscandia. The species present are thus post-glacial immigrants that have colonized the area after the latest glacial period, either spontaneously or by vector dispersal. On the other hand, ice-free refuges with arctic vegetation may have harboured some cold-adapted components of soil fauna during glaciation, and these may have dispersed during the preboreal era, as virgin soil gradually emerged (Stöp-Bowitz 1969, Terhivuo 1988a). From this phase onwards until the Litorina period, broad-leaved forests dominated in the subboreal area, and in association with favourable edaphic conditions, dispersion of soil fauna was presumably efficient with the aid of zoochory and other stochastic events. According to Willis *et al.* (1997), the dispersion of deciduous trees was closely associated with pedogenesis, by which podzolic soils were transformed to brown earth. This favoured the colonization of soil fauna. Later, from the end of the Litorina period, coniferous forests gradually occupied the landscape, resulting in impairment of the soil conditions (Rankama and Vuorela 1988). However, natural disturbances and human influence, such as wildfires and slash-and-burn agriculture, led to changes in tree species composition in favour of deciduous trees. During early successional phases, pioneer deciduous trees dominated the landscape before gradual recolonisation by conifers. Despite the temporary character of the pioneer phase, different successional stages have composed a continuum of more favourable habitats for soil fauna, enabling the expansion of new species.

Nordic coniferous forests have undergone several changes due to human influence. Slash-and-burn agriculture was virtually the only cultivation technique as late as the 19th century, and it was applied in most fertile forest sites (Heikinheimo 1915). Burn beating was abandoned in the 20th century, and was replaced with more intensive forestry which tended to grow conifers in monocultures. This reduced substantially the proportion of deciduous or mixed stands. During the last two decades an opposite tendency has prevailed, and a 10–30 % mixture of deciduous trees (mainly silver birch, *Betula pendula* Roth) is generally recommended in practical forestry (Metsätalouden kehittämiskeskus 2001, Valkonen *et al.* 2001). In addition, abandoned fields are usually reforested with birch, resulting to young birch stands of homogeneous age structure. The agricultural policy of the European Union will cause an adjustment in agriculture, which will release ca. 25 million hectares of arable soil to forestry or recreational use (Hytönen and

Polet 1995). The increasing value of hardwoods both in forestry and in landscape ecology will favour their use in reforestation. In the future, the expected warming of the global climate will probably further contribute to the change of boreal forests in favour of broadleaved trees (Kellomäki *et al.* 1996).

The boreal forest soil harbours an abundant and diverse decomposer community. Soil fauna, particularly ‘macrodecomposers’ such as earthworms, are among the key components in forest ecosystems due to their essential functions in decomposition, nutrient cycling and soil formation (Abrahamsen 1990, Edwards and Bohlen 1996, Baker 1998, Lavelle and Spain 2001). Composition of the soil communities is determined by various factors, including soil properties, (micro)climate, dispersal abilities and biotic interactions. As a result, the soil faunal assemblages differ in different habitats.

Due to decreasing importance of natural disturbances, human intervention has become an important factor in forest habitat dynamics. Human activities, particularly material transports, facilitate the colonization of soil fauna to new habitats. In the viewpoint of forest ecosystem functioning, it is essential to know more about biological changes in forest soils in association with changes in stand composition. Although the soil fauna of boreal coniferous forests is relatively well known, quantitative studies in deciduous forests are scarce and casual, particularly those that include more than one major faunal group.

The present thesis is a part of a study on the decomposer communities in anthropogenic deciduous forests in central Finland. Other papers outside of this thesis are: Ojala and Huhta 2001, Huhta 2002, McLean and Huhta 2002, Huhta and Niemi 2003, Huhta and Rätty unpublished, Huhta *et al.* unpublished).

2 Aims of the study

The aim of the present study is to describe and compare the faunal communities of planted birch stands of different origin with those of naturally developed deciduous forests at the same latitude, and to explain the observed differences on the basis of soil characteristics, site history and biotic factors.

The first section (**I–III**) considers whether the communities of Nematoda, Enchytraeidae and Lumbricidae in coniferous forest soil after replanting with silver birch come to resemble those of deciduous forests, does the community of a birch stand established on arable soil change towards a forest soil community, and do the communities of planted birch stands of different origin become similar in the long run, or do they rather retain their original composition. The second section (**IV–V**) is experimental, and is aimed to test the interactions between the studied faunal groups, in order to explain the differences in community composition between the study sites.

3 Methods

(For details, please refer the original articles I–V)

3.1 Field sites

A total of nine forest sites were investigated. Three of these were silver birch (*Betula pendula* Roth) stands planted 28 to 33 years prior to the study after harvesting the original spruce stands (“Birch after Spruce”, symbol BS). Three sites were silver birch stands established 26 to 43 years earlier on arable soil (originally cleared from spruce forest) that had been under cultivation (leys and cereals) for decades or centuries until reforestation (“Birch after Field”, symbol BF). Three stands were naturally developed (*i.e.* not planted) deciduous forests with diverse assemblages of broad-leaved trees (“Natural Deciduous”, symbol D). Silver birch was the dominating tree species even in the D sites, but up to ¼ of the stand density was covered by other species. It must be noticed that virtually all deciduous forests at this latitude are under human influence to a greater or lesser extent, and this holds also for the present D sites. Coniferous forests were not included in the study, since relevant data for comparisons are available in earlier studies. Schematic presentation of the study sites and their succession is provided in Figure 1.

3.2 Vegetation and soil analyses

The ground vegetation was analyzed in July 1998 by estimating the coverage of all plant species from ten random 1 m² plots at each study site. Site quality was classified according to Cajander (1949) and Tamminen (2000), using indicator plants along with soil properties and characteristics of adjacent stands. Tree species composition was determined, stand age was measured by increment borer, and breast height basal area by the angel-gauge method.

The following soil variables were determined from three samplings in 1998 (May, August and October), separately for the depths 0–3 and 3–6 cm: Soil pH_{H₂O} was measured in soil–water suspension (1:2, v/v), dry matter and water contents were measured by drying the samples for 18 h at 80°C, and organic matter content by ignition for 4.5 h at 550°C. Mineral nitrogen (NH₄⁺ and NO₃⁻) was extracted in 2-M KCl and measured according to SFS standard 3032. The rate of carbon mineralisation was determined

by aerobic laboratory incubation, and soil microbial biomass with the substrate-induced respiration method (SIR) described by Anderson and Domsch (1978). An infrared carbon analyser (Unicarbo EQ92) was used for the CO₂ measurements. Maximum respiration was achieved with glucose addition of 20 mg ml⁻¹ of soil water (WHC 80 %). Fungal biomass was estimated using the ergosterol method of Nylund and Wallander (1991).

The following soil variables were determined only once and on different dates: Particle size distribution was determined by dry sieving down to 0.2 mm, and smaller fractions using SYMPATEC diffraction spectrophotometer. Soil texture was classified according to Haavisto (1983). Soil water holding capacity (WHC) was determined using pressure plate chambers at potentials -0.3, -1, -5, -10 and -100 kPa. Retention at -10 kPa was used to illustrate the approximate water retention characteristics at field capacity. Total porosity (%) of mineral soil was calculated from the bulk density (D_b), and mean particle density (D_p) ($S_t = (D_p - D_b) \times D_p^{-1}$) using mean particle densities of 2.65 Mg m⁻³ for mineral soil (Heiskanen 1992). Soil structure was analysed by determining the content (% weight) of water-stable aggregates using wet and dry sieving methods (Hillel 1982).

3.3 Faunal analyses

Soil faunal samples were taken in May, August and October 1998 for nematodes and May, August and October 1999 for enchytraeids. Lumbricids were sampled in May and October 1999, at the time of maximum activity and lowest variation in populations (Nordström and Rundgren 1973). The soil samples, each consisting of six sample units, were taken separately for each animal group, and randomly from the same representative area of 30 x 30 m independently of the total size of the similarly managed area. The samples for nematodes and enchytraeids were taken with cylindrical steel corers (area 10 cm² for nematodes and 25 cm² for enchytraeids). The soil cores were divided into 0-3, 3-6 and 6-9 cm layers and treated separately. Subsamples for nematodes, each representing 1.5 cm³ of soil volume *in situ*, were weighed for extraction (wet funnel method of Sohlenius 1979). Intact sample units for enchytraeids were extracted using wet funnels with O'Connor's (1962) heating regime. Samples for lumbricids (25 x 25 cm) were taken with a steel spudder, and the layers 0-5 and 5-10 cm were treated separately. Earthworms were extracted using modified wet

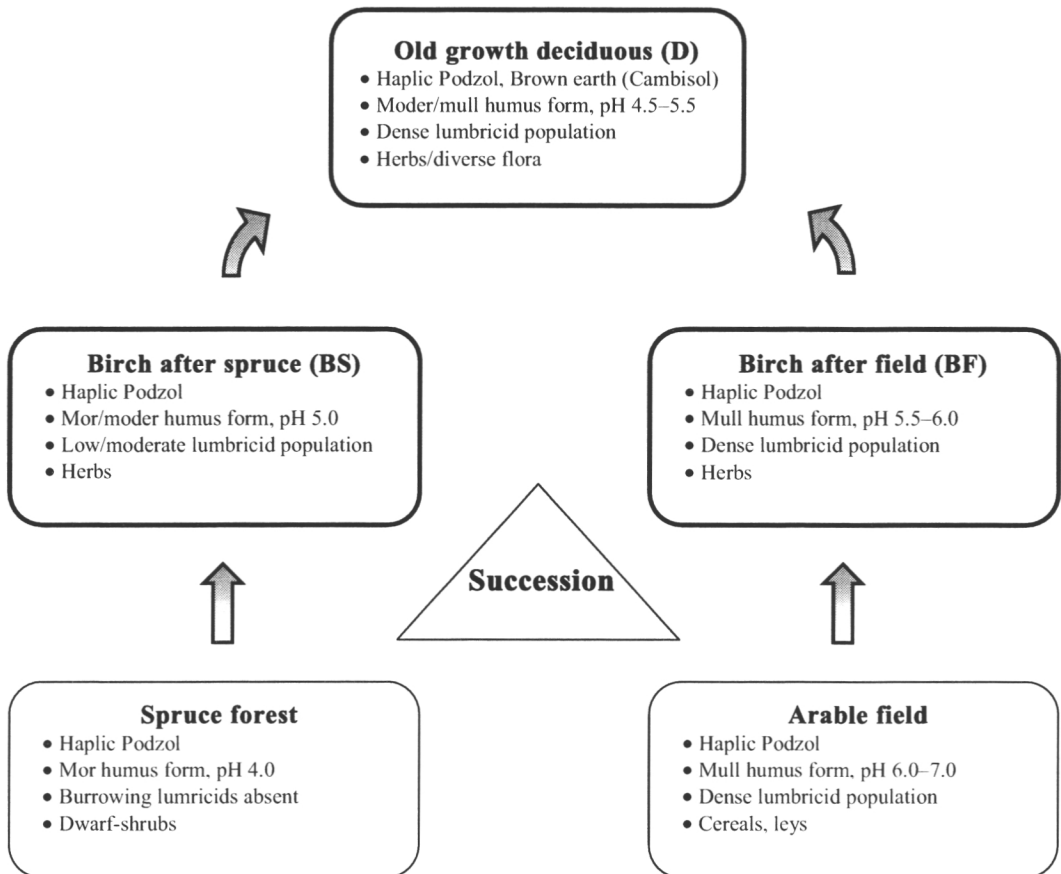


Figure 1. Schematic presentation of the succession from mature spruce forest or arable field towards the old growth deciduous forest.

funnels as described by Huhta and Koskenniemi (1975). In addition, formaline extraction (Daniel *et al.* 1992) was separately applied (2.5 ‰ and 5 ‰ solutions consecutively) for the deep burrowing species *Lumbricus terrestris*.

Nematodes were identified to genus when possible. Identification and nomenclature are mainly based on Bongers (1988). Feeding groups were determined according to Yeates *et al.* (1993), and allocation to c-p groups (ΣMI) after Bongers (1990). Nematode biomasses were estimated on the basis of body volume as described by Huhta and Koskenniemi (1975). Enchytraeids were identified to species level, but immature specimens of several genera could be identified only to genus. Identification and nomenclature are based on Nielsen and Christensen (1959, 1961, 1963). Abrahamson's (1973a, 1973b) equations of body volume and density were used to calculate the biomasses of different species. Because the immature specimens of *Fridericia* could not be identified, the genus was treated as one unit and assigned to Abrahamson's class D. Lumbricids were identified to species level according to Stöp-Bowitz (1969), except immature specimens of *Lumbricus* spp., which were identified to genus. Earthworms were divided into three functional guilds (epigeic, anecic and endogeic) according to Bouché (1977). Earthworms were weighed fresh after 48 h storage on moist paper to empty their guts. Weights were transformed to dry weights based on a dry mass content of 16 %.

3.4 Laboratory experiments

Two laboratory experiments (IV, V) were carried out to test hypotheses that were brought about by the field observations. The first experiment tested the interactions between different faunal components, and the importance of soil pH in modifying the community structure. Specimens of *Aporrectodea caliginosa* and *Lumbricus rubellus* together with a mixed community of enchytraeids were inoculated into "mesocosms" containing forest soil with original or adjusted (limed) pH levels. The soil included the natural biota of microflora and -fauna. Animal populations and microbial biomass were analysed after 32 weeks' incubation. The second experiment tested survival and growth of *A. caliginosa* and *L. terrestris* in the soil of one "natural deciduous" forest site (D1) where no earthworms were found in the field survey. Soil materials (mineral subsoil, humus and partially decomposed topsoil) were arranged in plastic containers in layers as in the field. Lumbricid and enchytraeid populations were analysed and several soil characteristics were measured after 60 weeks' incubation from each soil layer and *L. terrestris* middens.

3.5 Statistical analyses

Animal numbers and soil variables were tested by analysis of variance. Significant differences were separated by Tukey's test (**I–III**, **V**) and LSD (**IV**). *Ln*-transformation was applied to the faunal density data before statistical tests, since the log-normal distribution generally prevails in soil animal communities (Debauche 1962). Multivariate data were analysed with the aid of Non-Metric Multi-dimensional Scaling (NMS), using the PC-ORD software (McCune and Mefford 1999).

Several indices describing the nematode and enchytraeid communities were calculated (Pielou 1975): species richness $SR = (s-1)/\log_e N$ (**I**, **II**, **IV**), Shannon-Weaver diversity index $H' = -\sum p_i \log_e p_i$ (**I**, **II**, **IV**), Shannon's equitability $J = -\sum p_i \log_e p_i / \log_e S$ (**I**, **IV**), Simpson's index of dominance $\gamma = \sum p_i^2$ (**I**, **IV**), and Simpson's equitability $E = 1 / \sum p_i^2 S$ (**I**). In addition, nematode communities were analysed using the "maturity index" $\sum MI = \sum v p_i$ (**I**), ratio of bacterial to fungal feeders $B / (B + F)$ (**I**), and ratio of plant parasites to predators (PPI) (**I**) (Yeates 1984; Bongers 1990). Indicator guild weightings described by Ferris *et al.* (2001) were applied to evaluate food web conditions (**I**). Enrichment (*EI*) and structure indices (*SI*) were used to describe faunal profiles along the "structure and enrichment trajectories" (**I**). Further, the channel index (*CI*) provided information on the predominant decomposition pathways (Ferris *et al.* 2001).

4 Results

4.1 Site characteristics

The flora differed markedly between the birch stands established on forest soil and on arable soil (Table 1). Grasses, e.g. *Deschampsia flexuosa* and *Calamagrostis arundinacea* were characteristic to the “Birch after Spruce” sites, followed by some common forest herbs such as *Melampyrum sylvaticum*, *M. pratense*, *Rubus saxatilis* and *Maianthemum bifolium*. Dwarf-shrubs that dominate in coniferous forest were found only sporadically. In the “Birch after Field” sites, *Agrostis capillaris* was most abundant. All other predominant plant species in BF were herbs of cultural origin, e.g. *Silene dioica*, *Fragaria vesca*, *Geum rivale*, etc. Silver birch formed the canopy in the BS and BF sites and dominated also in the “Natural Deciduous” forests, but in the latter the tree species composition was more diverse, including *Populus tremula*, *Picea abies*, *Alnus glutinosa*, *Pinus sylvestris* and *Salix* spp. (Table 1). *Juniperus communis* was present in sites BS1 and BS2. All study sites were characterized as rich deciduous forest types with grass-herb vegetation.

Organic matter and soil water content in the deeper soil layer were higher in “Birch after Field” than in “Birch after Spruce”, indicating more even distribution of the organic fraction. pH was also higher in the BF sites (Table 1). Clay content and fine fraction of mineral soil was higher in the BF sites, which reflects the fact that soils with fine texture have been preferably taken for cultivation in comparison with coarse soils. Contents of mineral nitrogen varied considerably between replicates, but the average NO_3^- content was higher in BF than in BS. Content of water stable aggregates was much higher in BF. Some of these characteristics indicate the original site conditions, while some, such as pH and organic matter distribution reflect the previous cultivation in BF, and some others, such as soil aggregation, are of biological origin and result from earthworm activity.

The three “Natural Deciduous” forest sites (D) differed considerably from each other with respect to several soil characteristics (Table 1, I–III). In particular, site D1 deviated from D2 and D3 having much lower pH and clay content in the humus layer. The texture of the mineral soil in D1 was fine silt covered by a thick (30–40 cm), layered organic horizon of mull type (Table 1). The content of water-stable aggregates was particularly high in D3,

Table 1. Soil characteristics of the field study sites (Papers I–III).

Site	Soil characters, pH ^d	Total N ^e	NH ₄ ⁺ (NO ₂ ⁻ +NO ₃ ⁻)-N ^d	SOM ^f	SIR ^d	ERG ^d	S ₀	Md	Fine fraction	% SA ^g	S _i	WHC ^h	Ground vegetation (%)	Tree species composition
BS1 Birch after spruce Limattala, Äänekoski 62° 40' N 25° 47' E	Haplic Podzol Sandy till Mor/moulder, 5.1	0.28	31 0	15.7	17.37	42.5	4.6	0.22	27.5	20	0.72	29.2	<i>Deschampsia flexuosa</i> 58, <i>Melampyrum sylvaticum</i> 20, <i>Oxalis acetocella</i> 7, <i>Maianthemum bifolium</i> 12	<i>Betula pendula</i> (18), <i>Juniperus communis</i> (< 1), 35 yr
BS2 Birch after spruce Limattala, Äänekoski 62° 41' N 25° 49' E	Haplic Podzol Sandy till Mor/moulder, 4.9	0.34	38 0	17.6	18.19	93.5	4.4	0.36	22.1	10	0.67	25.8	<i>Agrostis capillaris</i> 42, <i>Calamagrostis</i> <i>arundinacea</i> 22, <i>Rubus saxatilis</i> 17	<i>Betula pendula</i> (11), <i>Juniperus communis</i> (< 1), 32 yr
BS3 Birch after spruce Iitsalo, Äänekoski 62° 48' N 25° 57' E	Haplic Podzol Sandy till Mor, 5.4	0.43	55 0	16.0	24.74	132.5	6.2	0.26	29.3	18	0.68	26.3	<i>C. arundinacea</i> 24, <i>M. bifolium</i> 9 (total herbs 38)	<i>Betula pendula</i> (10), 32 yr
BF1 Birch after field Uurainen, Oikari 62° 23' N 25° 30' E	Haplic Podzol ^a Fine sand Mull, 6.2	0.32	52 20	11.0	10.69	21.0	4.5	0.06	52.8	30	0.65	38.6	<i>A. capillaris</i> 28, <i>Silene dioica</i> 14 (total herbs 53), mosses 23	<i>Betula pendula</i> (12), 26 yr
BF2 Birch after field Ilmolahti, Viitasaari 63° 0' N 25° 52' E	Haplic Podzol ^a Fine sandy till Mull, 5.4	0.44	65 5	15.1	11.86	80.6	15.5	0.37	38.8	28	0.69	32.3	<i>Deschampsia caespitosa</i> 13, <i>Veronica chamaedrys</i> 10 (total herbs 50)	<i>Betula pendula</i> (14), 42 yr
BF3 Birch after field Ilmolahti, Viitasaari 62° 58' N 25° 51' E	Haplic Podzol ^a Fine sandy till Mull, 5.6	0.29	37 0	13.0	14.05	57.4	13.2	0.18	44.7	26	0.74	35.4	<i>A. capillaris</i> 11, <i>Filipendula ulmaria</i> 8 (total herbs 55)	<i>Betula pendula</i> (15), 33 yr
D1 Deciduous forest Rutajähti, Leivonmäki 61° 57' N 25° 58' E	Brown earth ^b Fine sand Mull, 4.7	1.38	53 47	62.3	8.46	75.1	3.5	0.07	55.2	3	0.86	45.2	<i>M. bifolium</i> 13, <i>Viola palustris</i> 13 (total herbs 47), <i>Athyrium filix-femina</i> 10 (ferns)	<i>Betula pendula</i> (12), <i>Populus tremula</i> (3), <i>Picea abies</i> (1), <i>Alnus glutinosa</i> (1), <i>Salix</i> sp. (< 1), 65 yr ^c
D2 Deciduous forest Oittila, Korpilahti 61° 56' N 25° 44' E	Haplic Podzol Sandy till Moder/mull, 5.2	0.39	54 11	20.0	19.52	64.6	8.0	0.23	37.5	13	0.72	32.4	<i>Matteuccia struthio- pteris</i> 27, (total herbs 22), <i>Vaccinium myrtillus</i> 13 (ferns)	<i>Betula pendula</i> (12), <i>Alnus</i> sp. (4), <i>Populus tremula</i> (1), 90 yr ^c
D3 Deciduous forest Kuokkala, Jyväskylä 62° 13' N 25° 45' E	Brown earth ^b Fine sandy till Mull, 5.6	0.22	63 11	12.3	16.40	16.9	12.7	0.09	54.2	34	0.69	46.3	<i>Oxalis acetosella</i> 26 (total herbs 50), <i>Equisetum sylvaticum</i> 13, <i>O. acetocella</i> 26, mosses 37	<i>Betula pendula</i> (8), <i>Pinus sylvestris</i> (4), 75 yr ^c

Soil characters (solum, humus form, texture, pH_{H2O}^d), total nitrogen (% of d.m.), ammonium and nitrate N ($\mu\text{g g}^{-1}$ o.m.), loss of ignition (SOM, % of d.m.), Substrate Induced Respiration, SIR (Mg Cmc g⁻¹ o.m.), ergosterol ($\mu\text{g g}^{-1}$ o.m.), degree of sorting ($S_0 = \sqrt{(Q_3/Q_1)}$), mean particle size (mm, Md = Q2), fine fractions (%), < 0.006 mm), percentage of water stable aggregates (%SA), total porosity ($\text{m}^3 \text{m}^{-3}$), water retention at 10 kPa (WHC), dominating plant species in the ground vegetation (percent coverage), proportional distribution of tree species (stand basal area, m²/ha) and stand age (yr) in the study sites. ^aDisturbed, ^bnot permanent, ^cdominant age class, ^d0–3 cm (F/H/A), ^e0–5 cm (F/H/A).

which is a result of earthworm activity (III). High water content and water holding capacity indicate good water availability in D1 and D3. The nitrate level was markedly higher in D1 than at any other site.

4.2 Faunal communities in different forests

4.2.1 Nematoda

Total numbers and biomass of nematodes in the “Birch after Spruce” sites were higher than those reported earlier from coniferous forests (Huhta and Koskeniemi 1975) (Figure 2). The community structure in BS was rather similar to coniferous forest soils (Huhta *et al.* 1986), but the relative proportions of the functional groups were different. The proportion of bacterial feeding nematodes was 50 % or less in BS, while in coniferous forests it is higher (Huhta *et al.* 1986).

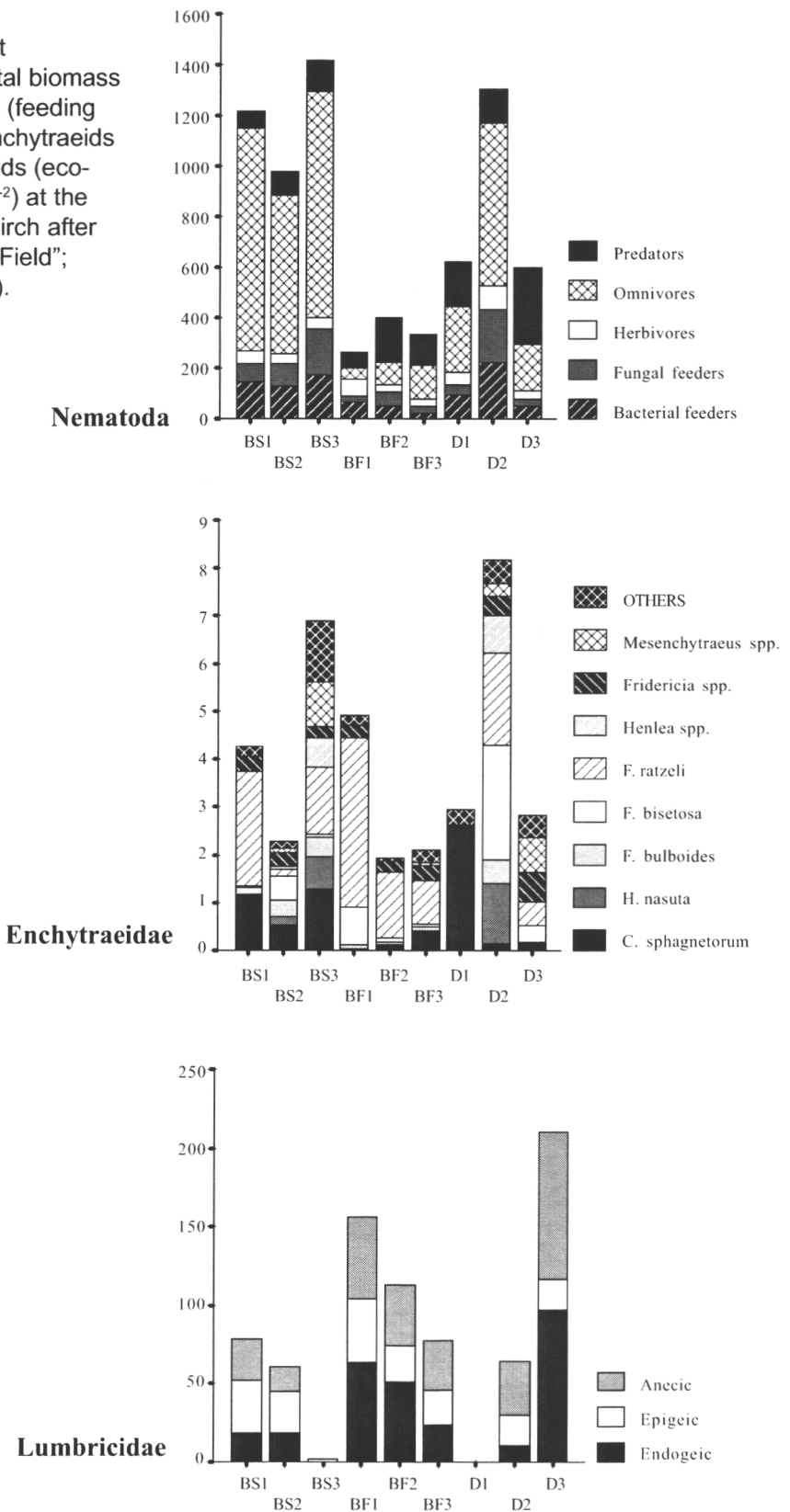
The total numbers of nematodes in the “Birch after Field” sites were roughly one third of the average in BS (II). Most genera and functional groups were less abundant in BF than in BS, and the same holds for taxonomic diversity (I). Hence the community in the “Birch after Field” sites could be characterized as similar but impoverished in relation to “Birch after Spruce”. In arable soils the nematode densities may be in the range of two to nine millions per m² (omitting extreme values), based on several studies (*e.g.* Sohlenius *et al.* (1988) and Hansson *et al.* (1990)). Thus the nematode densities in BF remain at the lower range of soils under cultivation.

The differences between the replicates of the “Natural Deciduous” sites hamper the conclusion whether the nematode communities of planted birch stands have become similar to those of naturally developed deciduous forests. According to Petersen and Luxton (1982), the nematode populations in deciduous forests tend to be greater than in coniferous forests. However, the average populations of several taxa were clearly lower in D than in BS, but in D2 with a high total abundance some taxa were even more abundant than at any BS site.

The Maturity Index (Bongers 1990) describes the position of a nematode community in successional time series, or enables to monitor its disturbance or recovery from a disturbance. The index value (MI) did not differ between the site treatments, but it differed within the treatments. The same was the case with the ratio of

Figure 2.

Contribution of the most abundant taxa to the total biomass of identified nematodes (feeding groups, mg f.m. m⁻²), enchytraeids (g f.m. m⁻²) and lumbricids (ecological groups, g f.m. m⁻²) at the nine study sites (BS, "Birch after Spruce"; F, "Birch after Field"; D, "Natural Deciduous").



bacterial feeders to fungal feeders, which tended to increase after addition of easily available food resources such as manures and organic amendments (Ettema and Bongers 1993). The index values within the treatments (ΣMI , $B/(B+F)$) did not correlate with pH, ergosterol or microbial biomass. The “Channel Index” (Ferris *et al.* 2001) provides a more sophisticated method to evaluate the predominant decomposition pathways. The index value (CI) revealed clear differences, with certain exceptions, between former arable soils (including D3) and forest soils. It was significantly higher in BS, D1 and D2 than in BF and D3. This suggests that the predominant decomposition pathways of former arable soil might be bacterial-mediated, which can be evident still several decades after afforestation. Site BS3 deviates from the others, having a lower CI value, probably due to higher pH associated with the absence of ‘geophagous’ lumbricids. The nematode faunal profiles along the ‘richness’ and ‘structure’ trajectories (Ferris *et al.* 2001) were clearly clustered in the quadrat D, which indicates ‘degraded’ food web conditions at all study sites, including natural deciduous forests. This suggests that anthropogenic birch stands or their nematode communities are not more disturbed or less ‘mature’ than those in natural deciduous forests.

4.2.2 Enchytraeidae

Enchytraeid communities also differed considerably between replicates of similarly managed forests. However, it was evident that still 30 years after reforestation the communities of birch stands established on spruce forest soil and on arable soil differ markedly from each other. Mean abundances were higher in “Birch after Spruce” than in “Birch after Field”, with a dominant position of *Cognettia sphagnetorum*, the superdominant enchytraeid in coniferous forests (Nurminen 1967, Abrahamsen 1972a). In former arable soils (BF) *C. sphagnetorum* was less abundant or totally absent, and *Enchytronia parva* was dominant instead. Despite the fact that the communities were clearly different between BS and BF, species richness (SR) and Shannon diversity (H') did not differ.

Within the BS sites, BS1 was the most similar to the spruce forest community, and within BF, BF1 was least similar to it (II). The three “Natural Deciduous” forests differed strongly from each other. The community in D1 resembled that in spruce forest soil, with *C. sphagnetorum* comprising 89 % of the total numbers, and also the two next abundant species *C. glandulosa* and *Bryodrilus ehlersi* were in common with coniferous forests (Nurminen 1967). D1 and D2 harboured the most dissimilar communities, located at

opposite extremes in the NMS ordination (II). The community of D2 was the most diverse in terms of species richness, with a total abundance roughly three times that in D3 (the latter was rather similar to the BF sites).

Enchytraeid communities in coniferous forest soils in cold and temperate climates are simple and strongly dominated by *C. sphagnetorum*, though the total numbers are often high (Nurminen 1967, Lundkvist 1982, Didden 1993). On the contrary, in deciduous forests and even in more fertile spruce forests the species diversity is much higher, and clear dominance of a single species is not observed. Kairesalo (1978) recorded 21 and 18 species in two rich deciduous forests in southern Finland, and Abrahamsen (1972a) 7 to 21 species in herb and fern-dominated spruce forests in southern Norway. In the present study, 34 species were recorded in total. 18 species could be characterized as common, and 15 of these were found in the most diverse sites BS2, BS3 and D2.

4.2.3 Lumbricidae

Numbers of earthworms were lower in "Birch after Spruce" than in "Birch after Field" (III). Deciduous forests typically harbour the most diverse lumbricid communities at the boreal latitudes (Terhivuo 1989). However, there was an extreme variation within three "Natural Deciduous" sites, D3 having an abundant and diverse community, and D1 totally lacking earthworms. The endogeic *A. caliginosa* was a typical species at most study sites, dominating in numbers the communities in D3 and all BF sites. However, in terms of biomass, the anecic *L. terrestris* reached or exceeded the importance of *A. caliginosa* (Figure 2). Within the BS sites the most typical species was the epigeic *D. octaedra*, the only species found in BS3. Other epigeic species, *Lumbricus rubellus*, *L. castaneus*, *Dendrodrilus rubidus* and *Octolasion tyrtaeum* were found in low densities in BS1 and BS2, but the burrowing species *L. terrestris* and *A. caliginosa* were also present. This suggests that the earthworm communities at sites BS1 and BS2 have considerably changed during the 30 years' influence of birch. Earthworm communities in coniferous forest soils are generally poor; if any, only sparse populations of the acid-tolerant species *D. octaedra*, *D. rubidus* and *L. rubellus* are found under the spruce canopy; at higher latitudes only *D. octaedra* and *D. rubidus* (Terhivuo 1988a). On the contrary, the community structure at the BF sites resembled that in arable soils, suggesting that the lumbricid communities have not changed after afforestation. According to Terhivuo (1988), most species of arable soils also inhabit deciduous forest soil.

The vertical distribution of earthworms was more uniform in former arable soils (BF and D3) than in “Birch after Spruce”, where the biomass was strongly concentrated in the upper 5 cm (excluding *L. terrestris* that was collected by formalin extraction). This pattern was largely due to distribution of the endogeic *A. caliginosa* and organic matter in the soil profile.

4.3 Laboratory experiments

4.3.1 Faunal interactions

An antagonistic relationship between earthworms and other soil biota was demonstrated in the laboratory experiment (IV): *A. caliginosa* and *L. rubellus*, either together or both species separately, suppressed the populations of nematodes and enchytraeids, and affected their community structure.

In all, 18 nematode genera were recorded in the experimental soil. Bacterial feeders dominated, while numbers of herbivores and fungal feeders were low, and no predators were found. The presence of earthworms decreased the total abundance of nematodes and depressed the diversity of the nematode community. Total numbers of nematodes were substantially greater at higher pH, and omnivores were found almost exclusively in limed soil. However, pH did not affect the diversity indices except that the number of taxa was higher in limed soil. The ratio of bacterivorous to fungivorous nematodes was markedly higher in limed soil, but only in the absence of earthworms. The nematode Maturity Index (ΣMI) was lower in unlimed soil and in the presence of *A. caliginosa* or *L. rubellus* separately, while no differences were found when both earthworms were present, nor in the limed treatments.

The presence of earthworms clearly depressed the numbers and biomass of enchytraeids (IV). In unlimed soil, no enchytraeids were found in the presence of earthworms. In the absence of earthworms, *C. sphagnetorum* and *B. ehlersi* were found in low densities. In limed soil, *E. bucholzi*, *H. nasuta*, *C. sphagnetorum* and *E. parva* were able to maintain their populations even in the presence of earthworms. *E. parva*, *E. bucholzi*, *Fridericia* spp. and *C. sphagnetorum* were the dominant species in limed soil, where the densities in the absence of earthworms were manifold compared to those in unlimed soil.

A similar inverse relationship between earthworms and enchytraeids was shown by the second experiment (V) where the presence of earthworms depressed the enchytraeid numbers roughly

to one fifth of the initial density. Most of the decline was due to *C. sphagnetorum*, whereas *B. ehlersi* and *Fridericia* spp. were able to maintain their populations. In the absence of earthworms, abundance and biomass of enchytraeids remained unchanged and their community structure resembled the initial composition. In addition, *Enchytraeus albidus* was found only in *L. terrestris* middens, where it formed a dense one-species community. *E. albidus* was not native in the experimental soil, and thus it was probably accidentally introduced together with earthworms.

In experiment IV *A. caliginosa* decreased the microbial biomass (SIR) in unlimed soil, while in limed soil and in the presence of *L. rubellus* no significant effects were found. Instead, microbial biomass responded to liming in all treatments by increasing substantially (IV). No significant treatment effects were found in long-term CO₂ evolution, though the average respiration was somewhat lower in the control without earthworms.

4.3.2 Survival of lumbricids in forest soil

The experiment (V) revealed that *L. terrestris* and *A. caliginosa* can maintain their populations in the acid forest soil taken from site D1 where lumbricids were completely absent. *L. terrestris* became well established, and by its activity the litter layer was rapidly consumed, middens were created, and the initially homogeneous and poorly structured soil developed a crumb structure during the 60 weeks' incubation. The mean biomass of adult and immature *L. terrestris* remained unchanged, but in some replicates the biomass increased considerably. Numbers and biomass of mature *A. caliginosa* decreased during the incubation, while those of immatures remained unchanged. The average individual weight of *A. caliginosa* did not change during the experiment.

The presence of earthworms caused a clear increase in the pH of topsoil and humus. pH was also elevated in the *L. terrestris* middens. In the absence of earthworms, pH remained unchanged during the incubation in all soil layers. Organic matter concentration increased in the humus layer by the activity of earthworms. In the middens, the OM concentration was lower than in the bulk soil due to translocation of mineral soil from subsoil to middens.

5 Discussion

5.1 Edaphic factors

Soil acidity is one of the principal factors in determining the community composition of soil fauna. Most enchytraeid species are intolerant to low pH and prefer semi-acid to neutral soils. In productive deciduous forest soils their densities are lower but species diversity higher than in coniferous forests (Nielsen 1955; Abrahamsen 1972a, Didden 1993). Standen (1980) and Nowak (2001) found a positive correlation between pH and species diversity of enchytraeids. However, some species, *e.g.* *C. sphagnetorum*, reach their highest densities in raw humus soils with low pH (Standen and Latter 1977, Hågvar and Abrahamsen 1980).

For earthworms, acid coniferous forest soil is an extreme habitat. Most species, endogeics and anecics in particular, are sensitive to acidity, absent in acid soils (pH<3.5) and sparse in soils with average pH below 4.5 (Stöp-Bowitz 1969, Curry 1998). Lumbricids are commonly absent in dry pine forest floor, and even in more fertile spruce forests their densities remain low. *Dendrobaena octaedra* is the most common earthworm species in the Nordic countries, typically forming more or less single-species communities in coniferous forests (Terhivuo 1989). Instead, meadows, herb-rich forests, and cultural habitats such as arable soils and pastures, may harbour dense and species-rich communities even at northern latitudes, where lumbricids are almost entirely associated with human settlements (Terhivuo 1989). In fertile soils earthworms form the dominant component of the total biomass of soil fauna (Abrahamsen 1972b, Huhta and Koskenniemi 1975), and probably exceed the importance of enchytraeids in the soil processes (Huhta *et al.* 1998).

As the BF sites and the D sites 2 and 3 had higher soil pH than the BS sites and D1, the species richness of enchytraeids and lumbricids should be higher in the former. However, the species diversity of enchytraeids did not show correlation with pH, and hence acidity alone cannot explain all variation in the communities in the present case. Although the pH of site D1 was lower (4.5–4.7) than at the other D sites, it was well within the range for burrowing earthworms (Curry 1998). The laboratory experiment (V) revealed that *L. terrestris* and *A. caliginosa* maintained their populations in the soil taken from the site and caused an increase in the soil pH. Thus the absence of earthworms at site D1 was not

because of soil acidity. There is also other evidence that earthworms by their positive influence on decomposition increase the soil pH in microcosms (Lee 1985, Haimi and Huhta 1990). However, it is unlikely that earthworms alone can have a substantial effect on pH in natural systems.

Soil texture and structure may be important factors for soil fauna due to their role in soil water economy (Hillel 1982). Several studies have aimed to find relations between soil fauna and physical properties of the soil matrix. However, few of them have demonstrated that the distribution of soil fauna depends on soil physical properties. Nordström and Rundgren (1974) found a positive relationship between clay content and e.g. *A. caliginosa* and *L. terrestris*. Baker *et al.* (1992) found a positive interaction between clay content and numbers and biomass of *Aporrectodea* spp., and Khalaf El-Duweini and Ghabbour (1965) reported an inverse relation between sand and gravel fractions and abundance of *A. caliginosa*. Pawluk (1987) and Thompson *et al.* (1990) reported that the physical structure of humus affects enchytraeid populations, and Hunt (1993) found a relationship between soil texture and nematode communities. In the present study, the clay content in the topmost soil layer at the D sites correlated positively with earthworm abundance, while it was inversely related at the BF sites. The former agricultural sites (BF) showed a smaller particle size and than the forested sites. However, water holding capacity among the study sites was relatively homogenous. In all, clay content or soil physical properties do not explain the soil faunal communities in the present case.

5.2 Resource quality and soil fertility

Birch has a legendary reputation in forestry due to its ability to improve soil fertility (Gardiner 1968). Dimpleby (1952) demonstrated that birch trees on heather moorlands turn raw humus soil into mull within 60-100 years, due to their influence on pH and associated increase in earthworm populations. Sactre *et al.* (1999) considered that birch litter may be the most important factor causing differences in faunal composition between different forest. Therefore, the effect of birch as “soil conditioner” is associated with positive feedbacks between birch litter, earthworm populations and soil (Sactre *et al.* 1999).

Coniferous forest soil and litter are favourable habitats for numerous soil animals, e.g. Oribatida, Collembola, some enchytraeids and the earthworm *Dendrobaena octaedra*. Most of the species

inhabiting acid mor humus are either fungivores or consumers of dead organic matter with fungal growth inside (Luxton 1972, Springett and Latter 1977, Latter and Howson 1978). According to Swift *et al.* (1979), the amount and quality of organic matter are important determinants for the fungal-based soil food web. On the other hand, low-phenolic litter of herbs and deciduous trees is more palatable or even essential for many soil animals such as most earthworms, diplopods and isopods. Their populations are thus often limited by the poor quality of litter rather than its quantity (Satchell and Lowe 1967, Swift *et al.* 1979, Boström and Lofs-Holmin 1986, Curry 1998). As there are considerable differences in food preferences among soil fauna, resource quality is expected to contribute to the faunal composition in different habitats. On the other hand, vegetation has also a significant influence on several soil characteristics through litter production and root exudates. Its effects on soil are manifold, comprising both physico-chemical and biological characters. Differences in plant communities at earlier stages of succession may be crucial for further site development (Graham *et al.* 1995). The most dramatic influences exerted by vegetation may be secondary, through the activities of soil fauna. For instance, the contribution of earthworms to soil fertility and physico-chemical soil properties is widely known (Lee 1985).

Enchytraeids, due to their ecological resemblance with lumbricids, can be expected to have similar food requirements and preferences. This was demonstrated by Dózsa-Farkas (1976). Kurt (1961) also showed that litter type influenced the enchytraeid populations. While the resource requirements of enchytraeids and earthworms overlap, enchytraeids are better adapted to extreme conditions, particularly acid soils and harsh environments, where they are capable to compete with earthworms. In these conditions, enchytraeids may compose simple, often one-species communities (Didden 1993). In the present study, the vegetation in the different forests (BS, BF, D) was relatively similar (herbs and deciduous trees), and therefore litter quality can not explain the different earthworm and enchytraeid communities.

The quantity and quality of resources also control nematode populations (Yeates 1981a). The distribution of various soil nematode taxa is influenced by edaphic factors associated with vegetation (Boag and Yeates 1998). In a broad sense, vegetation types, *e.g.* grasses versus woody plants, exert a decisive influence. Nematode fauna in boreal coniferous forests is composed mainly of bacterial and fungal feeders (Sohlenius 1979, Huhta *et al.* 1986), while in deciduous forests at the same latitudes herbivores may be the dominant or sub-dominant component in their assemblages (I). Several studies indicate that meadows, deciduous and mixed forests have the greatest species diversity (Wasilewska 1979, Háněl

1993, Boag and Yeates 1998). Fertile soils associated with diverse plant communities provide a wide range of host species for root feeders, but also for fungal feeders due to more diverse litter materials. Vegetation may thus partly explain differences in species diversity between coniferous and broad-leaved forests, but it does not explain the differences between the site replicates of the present study, since their plant communities were relatively homogeneous. On the other hand, vegetation can affect edaphic factors and microbial communities, which in turn may exert influence on the structure of nematode communities. For instance, the Channel Index (CI) revealed differences between former arable soil and forest soil (I). This suggests that the predominant decomposition pathways of former arable soil is more bacterial-mediated, which can be evident decades after reforestation. This in turn may favour bacterivorous nematodes. However, BS3 was different, having low index value, which is probably due to higher pH associated with absence of geophagous earthworms.

5.3 Dispersal ability

Enchytraeid and lumbricid assemblages in coniferous forest soils are typically species-poor, lacking most species that occur in more fertile forests as well as in cultural landscapes. After a favourable habitat change, such as a birch stand established in an earlier spruce forest, dispersal ability, geographical isolation of the site, and possible dispersal barriers are factors that control the colonization of potential new species, and consequently the structure of the whole community.

In general, a wide variety of dispersal strategies have been found among soil animals. Dispersion by land is typical for most epigeic beetles and spiders, while many mites have capacity for phoretic dispersal. Terrestrial nematodes spread efficiently by vector dispersal (Nicholas 1983), but aeronautic dispersal is also possible in cryptobiosis. In all, passive means of dispersal obviously prevail in soil fauna, and thus colonization of new habitats is often accidental.

Within the present “Natural Deciduous” forests, site D1 was the most isolated from cultural environments; it was bordered by lake, brook, cliff and spruce forest. The enchytraeid community on the site was very poor (only species of coniferous forests present), and earthworms were totally lacking. The experiment (V) revealed that *L. terrestris* and *A. caliginosa* are able to maintain their populations and reproduce in the soil taken from this site. Within the “Birch after Spruce” sites BS3 was the most isolated, surrounded

by coniferous forest from all sides. *D. octaedra* was the only earthworm species present here, but the enchytraeid community was the most diverse among the BS sites. Isolation most probably explains the absence of burrowing lumbricid species at sites D1 and BS3, while the presence of several acid-intolerant enchytraeids in BS3 needs another explanation.

Anthropochory is an important mode of dispersal in earthworms (Lee 1985). As enchytraeids are similar in their biology, it can be assumed that they share the same dispersal strategy. However, there is a difference in their mode of dispersal by man: enchytraeids are only accidentally transported together with soil, while earthworms are carried as fish baits and released intentionally. Possibly the enchytraeids in BS3 have arrived in the wheels of forestry machines. (In this case, cocoons rather than active worms are more likely to be transported.) Active dispersal over long distances seems unlikely in enchytraeids; in laboratory *C. sphagnetorum* has been observed to spread only a few centimetres per week (Sjögren *et al.* 1995, Salminen and Sulkava 1996). Unfortunately, virtually nothing is known about dispersal in Enchytraeidae.

The eurytopic earthworm *D. octaedra* has a key position in the lumbricid communities in a number of habitats due to its wide habitat spectrum, including relatively harsh environments (Terhivuo 1989). The species has capability for dispersal without human aid, and it is tolerant to substantial variation in habitat conditions and resource quality (Terhivuo 1988b). In addition, the wide morphological and genetic variation of the species in Fennoscandia (Terhivuo 1988b, Terhivuo and Saura 1990) indicates that it is able to colonize new habitats more efficiently than most other lumbricids. Thus *D. octaedra* can be considered a pioneer species, which by improving soil conditions may enable other species to invade the site (Terhivuo and Valovirta 1978, Burtelow *et al.* 1998). *D. octaedra* is commonly associated with large-scale earthworm invasions in North America, resulting in changes in soil physical and biological characteristics (McLean and Parkinson 1997a, 1997 b, 2000).

5.4 Interspecific interactions

An inverse relationship was observed in the abundance of earthworms and other soil animal groups in the field communities. The study sites differed markedly with respect to their earthworm populations: in former arable soil (BF and D3) the abundance and biomass of earthworms were high, whereas nematode populations were low and their communities less diverse. Similarly, enchytraeid

populations were less abundant in association with high biomass of earthworms, although in biomass one large species *Fridericia ratzeli* partially masked this relationship. In the former spruce forest soils (BS), nematodes and enchytraeids were most abundant in BS3 were lumbricids were virtually lacking. Site D2 with high abundance of nematodes and enchytraeids was mainly inhabited by *L. terrestris* that feeds on litter, and thus probably interacts less with other fauna than does the geophagous *A. caliginosa*.

In the field it is difficult to reveal interspecific competition, but several correlative and experimental studies, including the present study (IV, V), have given evidence that earthworms depress populations of nematodes and enchytraeids. An inverse relationship between earthworms and nematodes was observed by Yeates (1981b). Hyvönen *et al.* (1994) suggested that by feeding on their substrate, earthworms may accidentally consume microfauna as part of their diet. Dash *et al.* (1980) suggested that such feeding may also be selective. Cole *et al.* (2000) concluded that the inverse relationship between earthworms and nematodes is probably due to predation rather than to food competition. Dead nematodes have also been found in the digestive track of lumbricids (Munt'yan *et al.* 1969, Dash *et al.* 1980). On the other hand, Elliott *et al.* (1980) reported that earthworms can compete for food with bacterial-feeding nematodes. However, Hyvönen *et al.* (1994) found no suppression of bacteria in the presence of earthworms; instead a slight increase was observed. Also in the present experiment (IV) lumbricids did not decrease the microbial biomass; however the numbers of nematodes decreased. Thus it may be concluded that the decline of nematodes in the presence of dense lumbricid populations is due to accidental or selective predation rather than to food competition. Comparable antagonism between enchytraeids and nematodes has not been reported. Hyvönen *et al.* (1994) reported that *C. sphagnetorum* did not affect nematode populations. Although enchytraeids resemble earthworms in their biology and nutrition, their smaller body size probably excludes nematodes from their diet, though occasionally dead nematodes can be found in the digestive tract of enchytraeids (Dash 1973, Rätty unpublished).

The enchytraeid *C. sphagnetorum* has been reported to be sensitive to competition with the earthworm *D. octaedra* (Huhta and Viberg 1999). Hyvönen *et al.* (1994) demonstrated that *D. octaedra* reduced the numbers of *C. sphagnetorum* in limed soil. Schaefer and Schauer mann (1990) reported that in a German beech forest the abundance and biomass of lumbricids and enchytraeids were inversely related. Both enchytraeids and earthworms are regarded as microbi-detritivores, which makes it likely that they compete for the same resources. Competition for food is probably the main factor that reduces the enchytraeid abundance in soils with dense

lumbricid populations. Although antagonism obviously prevails between earthworms and enchytraeids (IV, V), positive relations have also been observed. Zachariae (1967) reported that some enchytraeid species may consume excrements of lumbricids, and hence they benefit from a dense lumbricid population. Correspondingly, Dózsa-Farkas (1978) reported more enchytraeids (*Fridericia galba* and *Stercutus niveus*) in earthworm burrows than in the surrounding soil. Also in the present study, high numbers of *Enchytraeus albidus* were observed to inhabit *L. terrestris* middens (V).

Interspecific competition presumably prevails in earthworm communities, but coexistence is possible among species with different feeding habits (Curry 1998). Due to ecological differences between species in the three ecological categories (epigeic, endogeic, anecic), their habitat requirements only partially overlap, thus enabling their coexistence. However, Terhivuo (1989) showed that only few species co-occur in high frequencies and that negative relationships prevail in lumbricid communities in fertile soils, whereas in extreme environments, either positive or negative interactions are insignificant. Kretzschmar (1998) suggested that earthworms may not have a constant ecological function, but rather a dynamic character to change their ecological role as habitat conditions change.

Conclusions

It became evident that the soil faunal communities of planted birch stands established on coniferous forest soil and on arable soil differ markedly from each other still 30 years after reforestation. They also differ significantly both from the communities of coniferous forests and from those of naturally developed deciduous forests. The extreme variation within the “natural deciduous” forests hampers the conclusion whether the communities in anthropogenic birch stands come to resemble those of natural deciduous forests even after several decades. There are also differences between animal groups in the degree of “community specialisation”. Communities of earthworms and enchytraeids may be fundamentally different in similarly managed forests, whereas the community structure of nematodes is more similar.

The soil physico-chemical characteristics can only partially explain the variation observed in the faunal communities. The capacity to colonize new localities appears as crucial factor in determining which species have invaded the earlier inhospitable coniferous forest sites after reforestation by birch. Active dispersal by land is limited in many edaphic animals, lumbricids and enchytraeids in particular, and several of them rely on vector dispersal. Based on human transport, cultural habitats are populated by fauna from more fertile environments and often from more southern latitudes, serving as sources of these species to the surrounding environment. However, isolation may prevent from colonization of forest sites far from human settlements. Burrowing earthworms, once established, alter the soil structure and acidity, and either directly or indirectly suppresses the populations of enchytraeids and nematodes. Thus the structure of the faunal communities is an outcome of an intricate set of factors, in which soil characteristics, site history, dispersal ability and interspecific interactions are involved.

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Nematode communities of anthropogenous birch stands in central Finland

Mika RÄTY^{1,*} and Veikko HUHTA²

¹Finnish Forest Research Institute, Suonenjoki Research Station, 77600 Suonenjoki, Finland

²Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35 (Ambiotica), 40351 Jyväskylä, Finland

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Summary – This study compared the nematode communities in anthropogenous birch (*Betula pendula*) stands of different origin with each other and with natural forests and arable soils at the same latitude in Finland and Scandinavia. Nine forest sites were investigated in central Finland: three birch stands planted *ca* 30 years prior to the study after the clear-cutting of spruce stands (BS), three birch stands planted *ca* 30 years earlier on arable soil (BF) and three natural deciduous forests (D). There were clear differences between the birch stands established after spruce forest and after arable cropping, and between these and deciduous forests, but even more between replicates of similarly managed forests. Total numbers, species diversity, and populations of most taxa and feeding groups were the lowest in BF sites. The relative proportion of bacterial feeders and omnivores was higher and that of plant feeders lower in BS than in D sites. The BS sites were relatively similar in community structure to natural deciduous forests, and BF were dissimilar to both, although one deciduous site was similar to one BF site. Non-metric multidimensional scaling ordination placed the three BS sites in one cluster, while the BF sites were clearly separated from these and from each other. Several environmental variables related to soil moisture and acidity contributed to explain the variation in community structure. A hypothesis is suggested that the presence of burrowing earthworms plays a role in regulating populations of nematodes.

Keywords – *Betula pendula*, community structure, earthworms, forest soil, interactions.

Nematodes are among the most important organisms in decomposer communities. Their numbers are generally between one and ten million per m² in virtually all kinds of soils. In spite of a relatively low biomass, their direct and indirect contribution to energy flow and nutrient mineralisation is comparable with other major soil animal groups (Wasilewska, 1979; Petersen & Luxton, 1982; Freckman, 1988).

Nordic coniferous forests have undergone many changes due to human influence. During the 20th century, the proportion of deciduous and mixed forests decreased at first after the abandonment of slash-and-burn agriculture, and then decreased further, after the adoption of intensive forestry practice that tended to grow spruce or pine in monocultures (Finnish Forest Research Institute, 1993). During the last two decades an opposite tendency has prevailed and a 10-30% mixture of deciduous trees (mainly silver birch, *Betula pendula*) is generally recommended in practical forestry. In addition, abandoned fields are usu-

ally reforested with birch, as a result of which young birch stands of homogeneous age structure are commonly seen. Further, agricultural policy in EU countries will promote expeditious changes in the operational environment of agriculture. In the future, it is estimated that 25 million ha of agricultural land will be replaced by forestry (Hytönen & Polet, 1995). The expected warming of the global climate will probably contribute further to a change of boreal forests in favour of broadleaved trees (Kellomäki *et al.*, 1996).

The aim of the present study was to compare the soil nematode communities of anthropogenous birch stands of different origin with those of natural forests and arable soils at the same latitude. This is one in a series of papers, each dealing with different animal groups (Huhta, 2002; Huhta & Niemi, 2003). We also discuss and explain the observed differences and similarities between the communities. Laboratory experiments for testing several

* Corresponding author, e-mail: mika.raty@metla.fi

Table 1. pH, loss on ignition (OM, %) (0–3 cm layer), degree of sorting of soil particles ($S_0 = Q_3/Q_1$), mean soil particle size ($Md = Q_2$), percentage of water stable aggregates (%SA) and dominating plant species in the ground vegetation (percent coverage) in study sites. Site symbols as Fig. 1.

Site	pH	OM	S_0	Md	%SA	Plant species
BS1	5.1	16	1.8	2.3	20.4	<i>Deschampsia flexuosa</i> 58, <i>Melampyrum sylvaticum</i> 20, <i>Maianthemum bifolium</i> 12
BS2	4.9	18	1.7	2.5	10.2	<i>Agrostis capillaris</i> 42, <i>Calamagrostis arundinacea</i> 22, <i>Rubus saxatilis</i> 17
BS3	5.4	16	1.9	2.3	17.6	<i>C. arundinacea</i> 24, <i>M. bifolium</i> 9 (total herbs 38)
BF1	6.2	11	2.0	1.8	30.3	<i>A. capillaris</i> 28, <i>Silene dioica</i> 14 (total herbs 53), mosses 23
BF2	5.4	15	4.3	2.6	28.2	<i>Deschampsia caespitosa</i> 13, <i>Veronica chamaedrys</i> 10 (total herbs 50)
BF3	5.6	13	4.7	1.9	26.2	<i>A. capillaris</i> 11, <i>Filipendula ulmaria</i> 8 (total herbs 55)
D1	4.7	62	1.8	2.2	3.0	<i>M. bifolium</i> 13, <i>Viola palustris</i> 13 (total herbs 47), <i>Athyrium filix-femina</i> 10
D2	5.2	20	2.3	2.3	13.2	<i>Matteucchia struthiopteris</i> 27, total herbs 22, <i>Vaccinium myrtillus</i> 13
D3	5.6	12	4.1	1.7	34.0	<i>Oxalis acetosella</i> 26 (total herbs 50), <i>Equisetum sylvaticum</i> 13, mosses 37

hypotheses were carried out simultaneously with the field study (Rätty & Huhta, 2003).

Materials and methods

SITE DESCRIPTION

A total of nine forest sites were investigated. Three of these were birch (*Betula pendula*) stands planted 28–33 years prior to the study, after the clear-cutting of spruce stands (birch after spruce, symbol BS). Three of them were birch stands planted 26–43 years earlier on arable soil (originally cleared from spruce forest) that had been under cultivation for decades or centuries until reforestation (birch after field, BF). Three stands were 'natural deciduous' forests (D), though one of the sites (D3) had been under cultivation in the 19th century (all deciduous forests at this latitude are under human influence to a greater or lesser extent). Birch is also the dominant tree species in the D sites but up to 25% of the stand density is covered by other species. Natural coniferous forests and cultivated soils were not included in the study, since relevant data for comparisons are available in earlier studies. pH, loss on ignition (0–3 cm layer, OM%), soil texture and dominating plant species in the ground vegetation (% cover) are shown in Table 1.

The BS sites are characterised by lower pH and a higher organic matter content than the BF sites. Site D1 has a very high organic content and low pH compared with the other D sites; D3 is in the range of the BF sites and D2 in between. There is a large biomass of burrowing earthworms (*Lumbricus terrestris* and *Aporrectodea caliginosa*) in all BF sites and in D3. Both species are also present in BS1, *L. terrestris* only in BS2 and D2

and neither in BS3 and D1 (Rätty & Huhta, unpubl.). All study sites are located in central Finland, the BS and BF sites 30–90 km north of the town of Jyväskylä, D1 and D2 ca 40 km south of Jyväskylä and D3 in the town area (62°13'N 25°45'E).

SAMPLING, IDENTIFICATION AND MEASUREMENTS

Three samplings were made, in May, August and October 1998. The samples, each of six units, were taken randomly from the same representative area of ca 30 × 30 m, independent of the total size of the similarly managed area. The soil samples, including the litter layer (A₀₂–A₃ horizons) were taken with a cylindrical steel corer (area 10 cm²), into which plastic rings (3 cm deep) were inserted. The soil cores were cut between the rings and the 0–3, 3–6 and 6–9 cm layers were treated separately. Subsamples representing 1.5 cm³ of soil volume *in situ* were weighed for extraction by the 'wet funnel' method (Sohlenius, 1979).

Nematodes were identified to genus whenever possible. Identification and nomenclature are mainly based on Bongers (1988). Feeding groups were determined according to Yeates *et al.* (1993), and allocation to c-p groups after Bongers (1990). The data from the three layers (0–9 cm) were summed, except when vertical distributions were compared, and the results were transformed into numbers per m².

Several environmental variables were determined from the same (August and October) or separate (May) samples, for each soil layer separately: pH_{H₂O}, water content (after drying overnight at 80°C), loss of ignition (after 4.5 h at 550°C), mineral nitrogen (NH₄⁺ and NO₃⁻; 2-M KCl; SFS standard 3032) and microbial biomass

(SIR method; Anderson and Domsch, 1978; Nordgren, 1988). The content (% weight) of water-stable aggregates (determined by Viljavuuspalvelu Ltd, Mikkeli, Finland, using wet and dry sieving methods (Hillel, 1982)), total porosity (S_t), water holding capacity (WHC) and the particle size distribution of mineral soil (dry sieving down to 0.2 mm, smaller fractions using a SYMPATEC diffractometer (Sympatec GmbH, Germany)) were measured only once and on different dates. Water retention was determined by using a pressure plate chamber at potentials -0.3 , -1 , -5 , -10 and -100 kPa. The environmental data were only used in ordination analyses; detailed results will be reported in another paper.

STATISTICAL TREATMENTS

Several indices describing the nematode communities were calculated for each sample unit (Pielou, 1975; Bongers, 1990; Yeates, 1994): species richness $SR = (s - 1) / \log_e N$, Shannon-Weaver index $H' = -\sum p_i \log_e p_i$, Shannon's equitability $J = -\sum p_i \log_e p_i / \log_e S$, Simpson's index of dominance $\gamma = \sum p_i^2$, Simpson's equitability $E = 1 / \sum p_i^2 S$, total densities of each feeding group, maturity index $\Sigma MI = \sum v_i p_i$, ratio of bacterial to fungal feeders $B / (B + F)$, plant parasite index PPI , and ratio of plant parasites to predators PP/P . Indicator guild weightings described by Ferris *et al.* (2001) were utilised to evaluate food web conditions. Enrichment (EI) and structure indices (SI) were used to describe faunal profiles along the structure and enrichment trajectory. In addition, faunal analyses utilising the channel index (CI) provided further evaluation of the predominant decomposition pathways (Ferris *et al.*, 2001). These variables and the most abundant taxa were analysed using ANOVA. \ln -transformation was routinely applied to the nematode density data before statistical tests, since the log-normal distribution generally prevails in soil animal communities (Debauche, 1962). The tests were carried out separately for the taxa densities and for other variables listed above. At first a multivariate ANOVA was applied in order to test the overall significances, after which two-factor (site, date) ANOVA were applied to each taxon or index. The differences in population densities between the site treatments (BS, BF, D) and treatment replicates (1, 2, 3) were tested by two-way Analysis of Variance (site, date). The tests between site treatments (BS, BF, D) were carried out on sample averages of each site and date ($n = 3$), while each group of treatment replicates (BS1, 2 and 3, etc.) was tested on original data ($n = 6$). There were few significant time effects or time \times site interactions and, as

these factors are unimportant in the present context, they are not presented. Vertical distributions (separate data for 0-3, 3-6 and 6-9 cm layers) were tested with total numbers by three-way (site, date, layer) ANOVA, and a significant site/layer interaction was interpreted as a significant difference in distribution. The tests were performed using the SPSS for Windows.

Community ordinations on the identified material (all taxa included) were carried out with the aid of Non-Metric Multidimensional Scaling (NMS), using the PC-ORD programme (Version 4, 1999; McCune & Mefford, MjM Software Design, Gleneden Beach, OR, USA). It was run in NMS Autopilot mode, using the Sørensen (Bray & Curtis) index as a distance measure. The data were \ln -transformed prior to the analyses. The choice of these options was based on the experience of Huhta (1979) and see also the PC-ORD manual. The ordinations were applied to all the data but, as this resulted in too many sample points in the graphs, they were also run with sample averages. As the population data of the whole sample depth (0-9 cm) were combined and the environmental variables of different depths were not additive, only the physio-chemical measurements of the 0-3 cm layer were used for the analyses since the top soil layer was considered more descriptive the study sites. However, mineral nitrogen was calculated per m^2 including 0-6 cm depth and particle size distribution was measured from mineral soil below the organic horizon. Percentage Similarities (Renkonen's (1938) index) were also calculated between all sites on pooled total data after \ln -transformation.

Results

POPULATION DENSITIES

The abundances of most taxa differed significantly between different kinds of forests (MANOVA, Wilk's lambda: $F = 137.1$, $P = 0.007$). The general trend was that average population densities were lowest in BF sites. This also refers to the total numbers of nematodes that were 2.6 times higher in BS and 2.3 times higher in D, on average (Table 2; Fig. 1). *Rhabditis*, *Tylenchus* and *Prionchulus* had the lowest populations in BS sites, but *Clarkus* was the only taxon in which the average densities were higher in BF than in D forests. However, there were also considerable differences between replicates of the same site treatments. Of the 19 taxa tested, ten differed significantly within BS, 15 within BF and 17 within D sites. The total numbers were roughly equal within BF

Table 2. Numbers ($10^3/m^2$) of common taxa, feeding groups and various community indices of nematodes (total in 0-9 cm soil depth; averages of three samples: May, August and October). Column 'P' indicates differences between site treatments, asterisks in columns '3' of each treatment those between replicates. Letters after taxa refer to feeding groups. Site treatment symbols as in Fig. 1.

Site treatment	P	BS			BF			D		
		1	2	3	1	2	3	1	2	3
Replicate										
<i>Acroboloides</i> (b)	0.005**	309	294	380	134	90	34	98	240	14***
<i>Cervidellus</i> (b)	0.099*	48	26	55	76	7	0***	0	174	0***
<i>Prismatolaimus</i> (b)	0.005**	8	71	30***	0	5	4***	16	54	2***
<i>Plectus</i> 1 (b)	<0.001***	661	277	706***	63	249	44***	221	540	158***
<i>Teratocephalus</i> (b)	0.001**	37	16	24	0	5	4***	20	86	4***
<i>Rhabditis</i> (b)	0.101*	30	28	166***	174	189	132	53	81	383**
<i>Cephalobus</i> (b)	<0.001***	39	53	96	28	7	8	11	8	0***
<i>Monhystera</i> + f4 (b)	<0.001***	45	38	24	0	5	3**	12	18	7
<i>Aphelenchoides</i> (f)	0.002**	154	112	158	72	16	7***	21	149	16***
<i>Tylencholaimus</i> 1 (f)	0.038*	95	179	535***	2	180	38***	60	436	37***
<i>Ditylenchus</i> (f)	0.018*	64	46	62	15	3	39**	30	123	11***
<i>Tylenchus</i> e-type (f)	<0.001***	24	38	26	92	18	82	105	435	87***
<i>Malenchus</i> d-type (r)	0.024*	18	130	62***	59	0	3***	37	18	3*
<i>Filenchus</i> (r)	0.022*	148	101	286***	154	3	121***	206	224	333*
<i>Paratylenchus</i> (r)	0.006**	213	54	137***	0	13	129***	237	625	71***
<i>Helicotylenchus</i> c-type (r)	0.581	0	0	71***	0	0	57***	64	0	17***
Dorylaimidae spp. (o)	<0.001***	153	195	379***	23	44	69***	135	330	93***
<i>Prionchulus</i> (p)	0.008**	35	44	44	22	102	79***	109	80	194**
<i>Clarkus</i> (p)	0.048*	9	38	65*	32	22	0***	4	5	2
Bacterial feeders	0.002**	1258	902	1587*	565	592	245***	547	1427	610***
Fungal feeders	0.010**	453	533	808***	188	230	173	246	1172	177***
Root feeders	0.003**	438	302	560*	282	50	313***	555	937	432**
Omnivores	<0.001***	269	265	404*	23	47	69***	135	330	93***
Predators	0.103	49	84	114	54	126	78***	118	91	198*
Total Nematoda	<0.001***	2468	2086	3473*	1113	1044	878	1601	3958	1511***
Number of taxa	<0.001***	25.0	25.2	22.9	13.4	17.4	15.3***	19.3	24.1	15.7*
Species richness SR	<0.001***	3.938	4.070	3.396***	2.405	3.172	2.774***	3.211	3.464	2.673***
Shannon diversity H'	<0.001***	2.591	2.799	2.530***	2.235	2.163	2.241	2.413	2.608	2.099***
Shannon equitability J	0.422	0.808	0.871	0.812***	0.868	0.760	0.824***	0.817	0.821	0.771
Simpson diversity γ	0.002**	0.118	0.085	0.116***	0.149	0.183	0.167	0.135	0.109	0.189**
Simpson equitability E	0.431	0.358	0.491	0.397***	0.540	0.342	0.473***	0.406	0.423	0.399
Ratio bact./fung. feeders B/(B+F)	0.345	0.724	0.600	0.640**	0.757	0.704	0.579**	0.640	0.556	0.684*
Maturity index ΣMI	0.559	2.199	2.419	2.524***	1.983	2.553	2.332***	2.402	2.370	2.342
Plant parasites index PPI	0.026*	2.134	2.079	2.140	2.280	2.606	2.187***	2.112	2.119	2.073
Plant parasites to predator PP/P	<0.001***	10.243	5.269	7.668**	4.809	0.458	5.379***	12.851	12.243	2.251***
Enrichment index EI	<0.001***	12.030	17.735	12.868***	25.900	20.420	34.884**	19.794	18.029	33.434***
Structure index SI	<0.001***	15.295	26.058	29.141***	10.843	33.449	35.087***	33.191	23.407	38.104***
Channel index CI	<0.001***	60.161	67.731	44.629***	38.253	28.103	42.942	60.787	75.200	37.212***

while, within D stands, D2 had about 2.5 times more nematodes than D1 and D3 (Table 2; Fig. 1).

The vertical distribution of total densities differed significantly between the site treatments (ANOVA, site

× layer interaction: $F_{[4]} = 4.795, P = 0.002$). The BF sites had the highest proportion in the deepest (6-9 cm) horizon. The D sites differed from each other, D3 having the highest and D2 the lowest proportion in the 6-9 cm

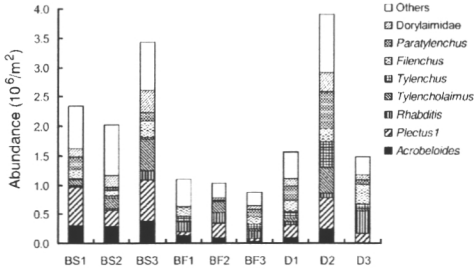


Fig. 1. Contribution of the most abundant taxa to the total numbers of identified nematodes (abundance, millions/m²) in three sites of three forest types (BS, Birch after spruce; BF, Birch after arable cropping; D, Natural deciduous). Each column is a mean of three samples (May, August, October).

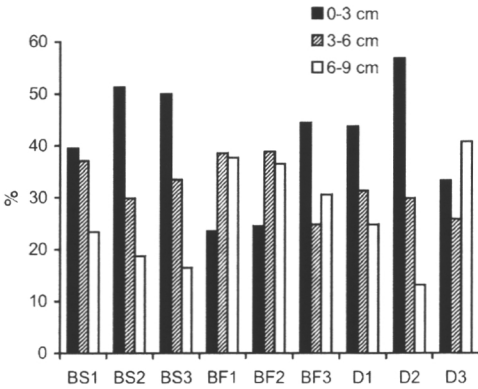


Fig. 2. Vertical distribution of nematodes (% at 0-3, 3-6 and 6-9 cm deep) in three sites of three forest types (BS, Birch after spruce; BF, Birch after arable cropping; D, Natural deciduous).

layer (Fig. 2). Low numbers in the bottom horizon were generally coupled with the highest numbers in the topmost (0-3 cm) layer.

FEEDING GROUPS

Similar to individual taxa, the densities of the nematodes of the different feeding groups were generally the lowest in BF (Table 2). The relative proportions of bacterial feeders and omnivores were higher and those of plant feeders lower in BS than in D forests. In BF there were within-treatment differences that masked potential differences from other kinds of forests (Fig. 3). Of the community indices based on proportions of different feed-

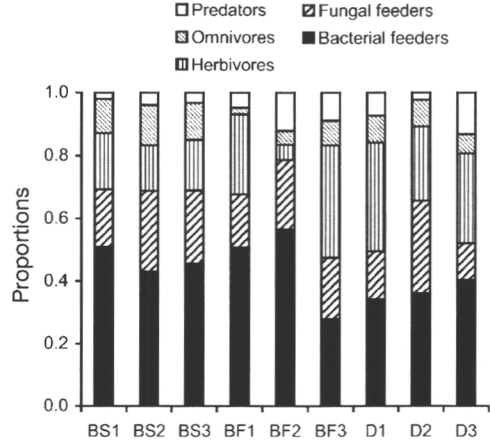


Fig. 3. Relative proportions of nematode feeding groups in three sites of three forest types (BS, Birch after spruce; BF, Birch after arable cropping; D, Natural deciduous).

ing groups, the plant-parasite index had a lower average value in BS than in BF and D. Ratio of plant parasites to predators were highly variable between replicates of the same forest type but also between main site treatments, being highest in D stands (Table 2). The Maturity index (ΣMI) and the ratio of bacterial to fungal feeders did not differ between site treatments while there were considerable within-treatment differences, especially in BS and BF sites (Table 2). Contrary to ΣMI , enrichment (*ET*) and structure (*SI*) indices revealed differences between treatments. However, faunal profiles representing the structure and enrichment conditions of the soil food web did not reveal distinct groupings of the site treatments (Fig. 5). The data points are scattered and widely overlapping in quadrat D. Channel index (*CI*) showed distinctions, with certain exceptions, between former arable soil (BF + D3) and forest soil (BS + D1, D2) (Table 2; Fig. 5).

COMMUNITY STRUCTURE

Birch after spruce sites had the highest and BF the lowest species diversity in terms of *SR*, Shannon Index and number of taxa (Table 2). From the viewpoint of community similarity (Renkonen's index), the BS and D sites showed high within-treatment similarities while the BF sites differed greatly from each other (Table 3). Birch after field showed a low similarity with BS, and also with D stands, except that BF3 had high similarity values with

Table 3. 'Percentage Similarities' (Renkonen's Index) of the nematode communities between the study sites (ln-transformed data, all samples combined). Values exceeding 75% in bold.

	BS1	BS2	BS3	BF1	BF2	BF3	D1	D2
BS2	80.3							
BS3	78.0	79.9						
BF1	57.2	60.3	64.8					
BF2	66.5	71.1	70.9	66.6				
BF3	60.9	60.4	69.8	66.2	67.6			
D1	74.0	75.1	80.5	63.2	71.9	77.9		
D2	78.2	74.7	78.3	64.7	72.2	70.1	81.8	
D3	67.2	64.8	73.9	62.9	70.7	81.8	83.8	76.2

D1 and D3. Sites D1 and D2 showed high similarities with the BS sites.

Ordination by NMS revealed clear groupings of the study sites in the space determined by three ordination axes (Fig. 4). The three BS sites can hardly be separated from each other. One of the D sites (D2) lies in the vicinity of these while the other two (D1 and D3) are located farther away, at least in one dimension. The BF sites are each in one cluster and clearly separated from each other. In some axis combinations, BF3 comes close to D3.

Several environmental variables were significantly correlated with the ordination axes (Table 4; Fig. 4). The vectors of soil moisture (*pF*) and microbial biomass (*SIR*) are roughly in the same direction (negative correlation with axis 2, *SIR* also with axis 3) and pH was strongly correlated with axis 3. The other variables indicate soil structural properties, and are roughly in the opposite direction to *pF* and *SIR*. Water holding capacity was correlated with axis 1, clay fraction with 1 and 2, aggregate content with 2 and 3 and fine mineral fraction with all three axes.

Discussion

The total numbers of nematodes in BS are comparable with those reported earlier from coniferous forests. Unfortunately, we have no data from central Finland, but total densities around 1.5 million/m² have been found in spruce (*Picea abies*) stands (Huhta & Koskenniemi, 1975) and 2 million/m² in pine (*Pinus sylvestris*) stands in southern Finland (Huhta *et al.*, 1986). Nielsen (1949) also observed higher total populations of nematodes in pine forests than in spruce forests in Denmark. These findings suggest that average abundances of nematodes are greater in birch stands established on spruce forest soil than in intact spruce forests.

The proportion of bacterial feeders in the total populations was 50% or less in our BS sites while in pine forests it was higher (Sohlenius, 1979; Huhta *et al.*, 1986). The five most abundant taxa in our data are *Plectus*, *Acrobeloides*, *Tylencholaimus*, Dorylaimidae and *Filenchus*. In the Swedish pine stand (Sohlenius, 1979), they were *Acrobeloides*, *Tylenchus*, *Plectus*, *Aphelenchoides* and *Tera-tocephalus* and, in the Finnish pine stands (Hyvönen & Huhta, 1989), *Plectus*, Cephalobidae, *Aphelenchoides*, *Tylenchus* and *Rhabditis*. Although the taxonomic composition is rather similar in these two kinds of forests, there are considerable differences in relative proportions of the common taxa. The samples of Sohlenius (1979) were taken monthly during one year, and those of Hyvönen and Huhta (1989) monthly from May to September.

The total abundance of nematodes in the BF sites (1 million per m²) was slightly more than one third of the average in BS. Most genera and all feeding groups except predators were also less abundant in BF, and the taxonomic diversity was clearly lower than in BS. The predominating genera were the same in both kinds of forests, though the relative proportions of taxa varied from site to site. Thus, the BF community could be characterised as similar to but impoverished in relation to BS. However, insufficient sampling depth probably biases this comparison, since a greater proportion of populations are expected to be below 9 cm in BF than in BS, the deeper distribution of nematodes in BF reflecting soil mixing during cultivation.

According to several studies the total numbers of nematodes in arable soils (omitting extreme values) range between two and nine million per m² (Wasilewska, 1974, 1979; Sohlenius *et al.*, 1988; Hansson *et al.*, 1990). When comparing our figures with these, correction is to be made for sample depth (generally 20 cm in the cited studies) since in cultivated soils as many as 75% of total nema-

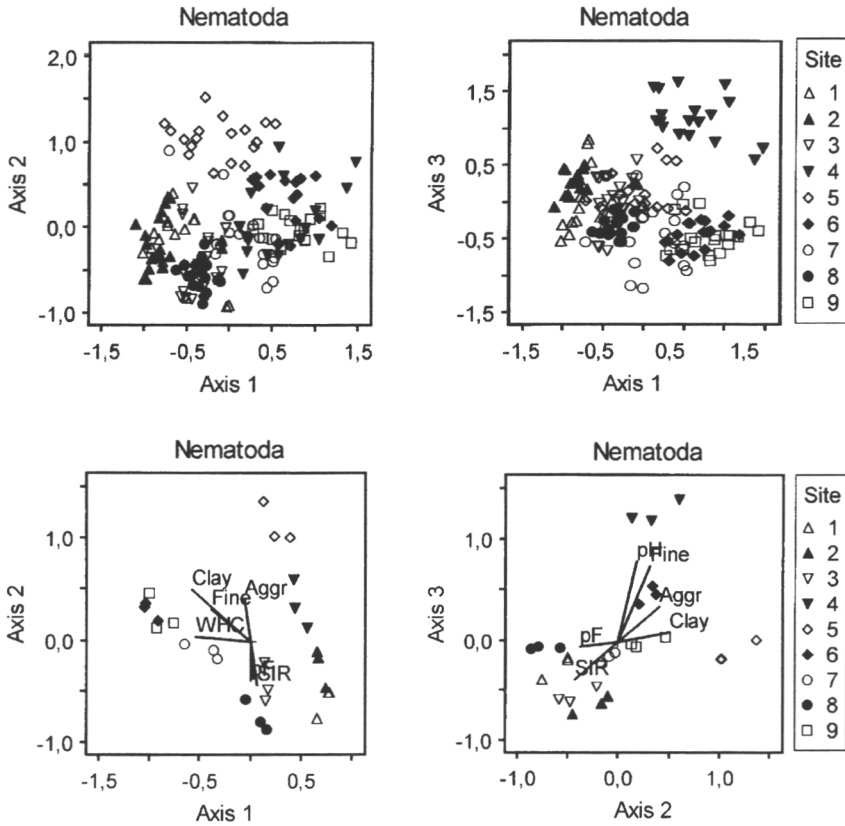


Fig. 4. Selected plot diagrams in three axis solutions of the Non-Metric Multidimensional Scaling ordinations of nematodes and environmental variables in three sites of three forest types (sites 1-3, BS, Birch after spruce; 4-6, BF, Birch after arable cropping; 7-9, D, Natural deciduous). Top: total data; Bottom: pooled data (sample averages).

todes may be found below 10 cm (Sohlenius & Sandor, 1987). Even after multiplying our average numbers by two, the nematode densities in BF remain at the lower range for soils under cultivation. The proportion of bacterial feeders was somewhat higher and the ratio of bacterial to fungal feeders lower than in arable soils studied by Wasilewska (1974) and Sohlenius *et al.* (1988). In a Swedish barley field (Sohlenius & Sandor, 1987) the most abundant taxa were Cephalobidae, *Tylenchus*, *Merlinus* (plant feeder), *Aphelenchoides*, *Acrobeloides* and *Rhabditis* (in that order). In our BF sites, *Rhabditis*, *Plectus*,

Tylencholaimus, *Filenchus*, *Paratylenchus* and *Acrobeloides* reached high densities in at least one replicate.

The great variation between replicates of the D sites makes it virtually impossible to conclude whether the nematode communities of planted birch stands have become similar to those of natural deciduous forests during the period of *ca* 30 years. The average populations of several taxa were lower in D than in BS but in D2, which had high total numbers, some (*Tylenchus*, *Paratylenchus*) were even more abundant than in any BS site. According to literature data, deciduous forests tend to

Table 4. Pearson correlations of environmental variables with the ordination axes (NMS, three-dimensional solution with sample averages). OM = organic matter; Aggr = water stable aggregates (%) > 2 mm, SIR = microbial biomass, Clay = mineral fraction <0.002 mm, Fine = mineral fraction <0.06 mm.

Axis:	1	2	3
pF	-0.064	-0.545**	-0.191
OM	-0.189	-0.16	-0.218
pH	-0.035	0.388*	0.803**
NH4 ⁺	-0.173	0.314	-0.237
NO3 ⁻	-0.172	-0.007	0.147
Aggr	-0.225	0.573**	0.528**
SIR	0.211	-0.579**	-0.548**
Clay	-0.679**	0.639**	0.283
Fine	-0.560**	0.503**	0.773**
WHC	-0.663**	0.204	0.427*

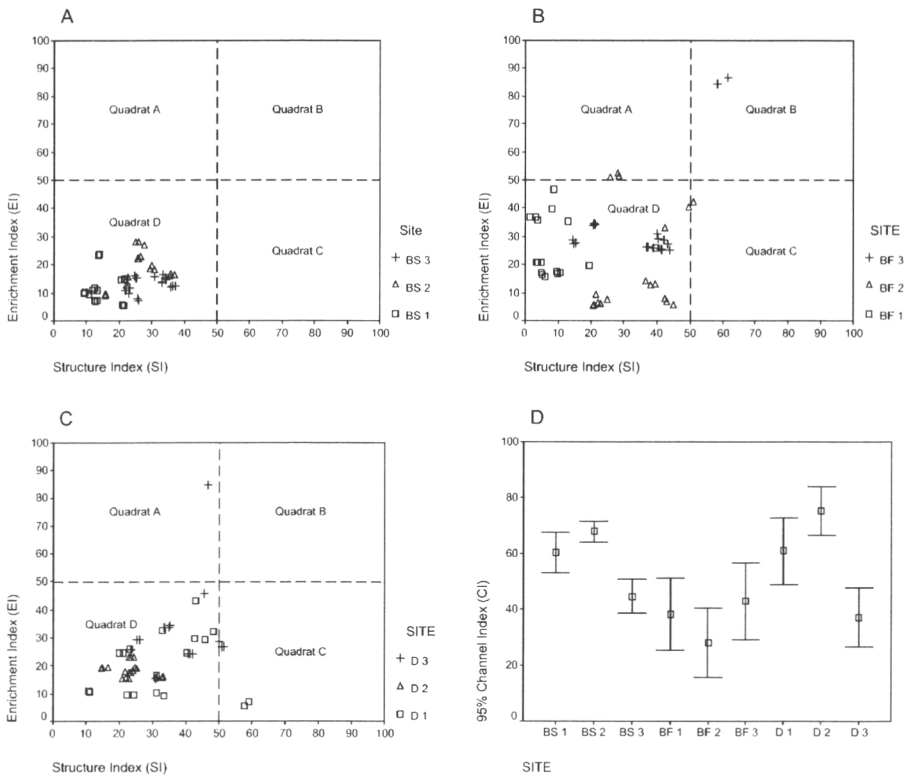


Fig. 5. Faunal profiles symbolising the structure and enrichment conditions of the soil food web in three sites of three forest types. A: BS, Birch after spruce; B: BF, Birch after arable cropping; C: D, Natural deciduous; D: Channel Index indicating the predominant decomposition pathways.

have greater nematode populations than coniferous forests (Wasilewska, 1971; Petersen & Luxton, 1982).

The Maturity Index, based on weighted mean of scores of genera or families along a 'persisters' to 'colonisers' gradient, was introduced by Bongers (1990) to describe the position of a nematode community in successional time series or to monitor its disturbance or recovery from a disturbance (de Goede, 1993). In the present study the index value did not differ between the site treatments but it differed within the treatments. The same was the case with the ratio of bacterial feeders to fungal feeders, which tends to increase after addition of easily available resources such as manures and organic amendments (Ettrema & Bongers, 1993). Respective faunal profiles along the 'richness' and 'structure' trajectory were clustered in quadrat D indicating degraded food web conditions in all study sites. This suggests that anthropogenous birch stands or their nematode communities are not more disturbed or less 'mature' than those in 'natural' deciduous forests.

The 'natural' deciduous stands in this research have in fact been influenced more or less by humans in the past. At this latitude, in the boreal coniferous forest biome, true natural deciduous forests can only be found at early phases of succession after forest fire, or after clear felling before silvicultural practices are applied. Coniferous trees later colonise the area and suppress the deciduous vegetation unless managed by man. According to an old map, site D3 was under cultivation in the 1800s, which can still be seen in the vertical distribution of nematodes. Respectively, the channel index revealed disparities, with certain exceptions, between former arable soil (including D3) and forest soil. This suggests that the predominant decomposition pathways of former arable soil might be bacterial-mediated which can be evident decades after afforestation. Site BS3 is divergent, having the lower index value, which is probably due to higher pH associated with absence of 'geophagous' earthworm species. Sites D1 and D2 have also probably been exploited as forest pastures and for selective tree felling. Differences within the BF and D sites (contrary to BS these are widely scattered in the ordination space) may be partly explained by their different utilisation in the past.

According to the NMS analysis, several environmental factors contribute to explain the observed differences in community structure. The BS sites together with D2 appear to be associated with high matrix potential and microbial biomass, but with low values of the other factors. As the pF value increases with decreasing moisture,

these soils can be considered to be 'dry' in contrast to those that are 'moist' with high water holding capacity and contents of clay and fine mineral fractions. The latter variables together seem to correlate with the communities in BF3 and D3. Low acidity (high pH) is associated with BF1.

Moisture and pH are among the most important factors that affect nematode populations (Yeates, 1981a). Depending on soil type, both positive and negative correlations between soil moisture and total populations of nematodes have been reported (Wasilewska, 1991; Schouten *et al.*, 1998) but, independently of total numbers, moisture certainly affects the species composition (Sohlenius & Wasilewska, 1984; Sohlenius, 1985). Hyvönen and Huhta (1989) reported an increase of bacterial feeding nematodes 2 years after liming or ash application (rise of pH), though this increase may be transitory (Hyvönen & Persson, 1990) and the long-term effect may be a reduction in total numbers (de Goede & Dekker, 1993).

There are also biotic relationships that probably explain part of the variation in nematode populations. The study sites differ markedly with respect to their earthworm communities: all BF sites and D3 are densely populated by the burrowing earthworms *Lumbricus terrestris* and *Aporrectodea caliginosa*. Both species are also present in smaller numbers in BS1, *L. terrestris* alone inhabits sites BS2 and D2, and both are absent in BS3 and D1 (Räty & Huhta, unpubl.). Since the first report by Yeates (1981b), there is increasing evidence of negative relationships between earthworms and nematodes (obviously earthworms consume microfauna as part of their diet by feeding on soil and detritus). In the experiments of Hyvönen *et al.* (1994), the presence of the earthworm *Dendrobaena octaedra* suppressed nematode populations. The same effect on nematodes by *L. rubellus* and *A. caliginosa* was observed in an experiment of the present authors (Räty & Huhta, in press). All the sites with large biomass of *A. caliginosa* (BF1-3 and D3) had small total numbers of nematodes. Site D2 with high abundance of nematodes was inhabited by *L. terrestris* that feeds on litter from the soil surface and thus probably interacts less with nematodes than does the geophagous *A. caliginosa*. Site D1 with no earthworms differs from all other sites by its thick organic horizon that includes the whole sample depth; thus probably other factors than earthworms explain the low nematode numbers there.

We conclude that the communities of nematodes in birch stands established after spruce are comparable with those in coniferous forests, but there are differences in rel-

ative proportions of the taxa. Compared with BS stands, the nematode communities in birch after arable cropping can be characterised as similar but impoverished, and their total densities and species diversity are low and most genera and feeding groups less abundant. The ample variation between different natural deciduous sites makes it difficult to compare the communities of planted birch stands and original forests. Community analysis suggests that anthropogenous birch stands are not more disturbed or less mature than natural deciduous forests. Environmental factors related to pH and moisture contributes to explaining the differences in community structure. The BS sites and one D site can be considered to be dry. Moisture factors, associated with high WHC and contents of clay and fine mineral fractions, characterised one BF and one D site, while high pH was associated with one BF site. In addition to physio-chemical parameters, biological interactions play a role in determining the community structure of nematodes. All sites with large biomass of the earthworm *A. caliginosa* harboured low populations of nematodes. Differences within the site replicates may be partly explained by their different utilisation in the past having presented different opportunities for colonisation by earthworms.

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Communities of Enchytraeidae (Oligochaeta) in planted birch stands as compared with natural forests in central Finland

MIKA RÄTY* and VEIKKO HUHTA¹

Finnish Forest Research Institute, Suonenjoki Research Station
FI-77600 Suonenjoki, Finland

^bCurrent address: Department of Biological and Environmental Science, P.O.Box 35,
FI-40014 Jyväskylä University, Finland

*Author for correspondence: e-mail: mika.raty@metla.fi (M. Rätty)

Abstract

The aim of the study was to compare the enchytraeid communities in anthropogenous birch stands of different origin with each other and with natural forests at the same latitude in Finland. A total of nine forest sites were investigated: three birch stands (*Betula pendula*) planted ca. 30 years prior to the study after clear-cutting of spruce stands, three birch stands established ca. 30 years earlier on arable soil (cleared from earlier coniferous forest) that had been under normal cultivation until reforestation, and three natural deciduous forests. These were sampled three times (May, August and October) in 1999, animals were extracted using the “wet funnel” method, counted and identified. Non-Metric Multidimensional Scaling was used to analyze the communities. There were clear differences between the birch stands established after spruce forest and after cultivation, and between these and natural deciduous stands, but even more between replicates of similarly managed forests. Total numbers and populations of most species were lower in “Birch after Field” than in “Birch after Spruce”. The “superdominant” species in coniferous forests, *Cognettia sphagnetorum*, was dominant in all “Birch after Spruce” sites and one “Natural Deciduous” site. *Enchytronia parva* was the only species more abundant in “Birch after Field” than in “Birch after Spruce”. A hypothesis is put forward that in addition to soil acidity, accidental transport by man explains the presence of many species on a given locality, and that competition with earthworms plays role in regulating enchytraeid abundances.

Key-words: Enchytraeidae, Birch, Forest soil, Reforestation, Dispersal

Introduction

Enchytraeids or potworms (Enchytraeidae) are one of the most important animal groups in boreal coniferous forest soils. They occur commonly in densities of tens of thousands per square meter, in biomass exceeding all other faunal groups in dry, less fertile forest types, but also in moister, more productive forests at higher latitudes (Huhta and Koskenniemi 1975; Persson et al. 1980; Huhta et al. 1986). Functionally they are regarded as key components in the decomposer communities of such forests (Huhta et al. 1998; Laakso and Setälä 1999). On the other hand, the species structure of the enchytraeid community of acid soils is very simple: a single “superdominant” species, *Cognettia sphagnetorum*, alone makes up more than 95 % of total numbers. A few other species occur sporadically (Nurminen 1967; Abrahamsen 1972a; Lundkvist 1982), while most enchytraeid species are intolerant to low pH and are only found in less acid and more productive forest sites (Abrahamsen 1972a; Didden 1993). In the latter kind of forests, earthworms also contribute essentially to the biomass of soil fauna (Huhta and Koskenniemi 1975; Abrahamsen 1972b), probably exceeding the importance of enchytraeids in promoting decomposition and mineralisation (Huhta et al. 1998).

Nordic coniferous forests have undergone many changes due to human influence. During the 20th century, the proportion of deciduous and mixed forests decreased at first after abandonment of the slash-and-burn agriculture, and then further after adopting the effectual forestry practice that tended to grow spruce or pine in monocultures (Finnish Statistical Yearbooks of Forestry). During the last two decades an opposite tendency has prevailed, and a 10 - 30 % mixture of deciduous trees (mainly silver birch) is generally recommended in practical forestry depending on site type (Metsätalouden kehittämiskeskus 2001; Valkonen et al. 2001). In addition, abandoned fields are usually reforested with birch, as a result of which young birch stands of homogeneous age structure are commonly seen. Agricultural policy in the EU countries will promote expeditious changes in the operational environment of agriculture. During forthcoming years, 25 million hectares of agricultural soil is assessed to be substituted for afforestation (Hytönen and Polet 1995). In future, expected warming of the global climate will probably further contribute to the change of boreal forests in favour of broadleaved trees (Kellomäki et al. 1996).

The aim of the present study was to compare the enchytraeid communities of anthropogenous birch stands of different origin with those of natural forests at the same latitude in Finland. This is one in a series of papers, each dealing with different animal groups (Huhta 2002; Huhta and Niemi 2003, Rätty and Huhta 2003b; Rätty and Huhta 2004). We also make an effort to discuss and explain the observed differences and similarities between the communities. Laboratory experiments for testing several hypotheses were carried out simultaneously with the field study, and the results of these has been published separately (Rätty and Huhta 2003a; Rätty, in press).

Material and methods

Site description

A total of nine forest sites were investigated. Three of these are birch (*B. pendula*) stands planted 28 to 33 years prior to the study after clear-cutting of spruce stands (“Birch after Spruce”, symbol BS). Three are birch stands planted 26 to 43 earlier on arable soil (originally cleared from spruce forests) that had been under cultivation (leys and cereals) until reforestation (“Birch after Field”, BF). Three stands were “Natural Deciduous” forests (D), though one of them (D3) has been under cultivation in the 19th century (in fact, virtually all deciduous forests at this latitude have been more or less under human influence). Birch is the dominating tree species also at the D sites, but up to ¼ of the stand density is covered by other species (Table 1). Natural coniferous forests were not included in the study, since relevant data for comparisons are available in earlier studies. The BS sites are thus characterized by lower pH and higher organic matter content than the BF sites. The D1 site had a very high organic content and low pH compared with the other D sites, D3 was in the range of the BF sites and D2 in between.

All the sites are located in central Finland, the BS and BF sites 30 to 90 km north of the city of Jyväskylä, D1 and D2 ca. 40 km south of Jyväskylä, and D3 in the town area (62°13'N 25°45'E). A more detailed description of the sites is given by McLean and Huhta (2002), and a full description will be published later (Huhta and Rätty, unpublished).

Sampling, identification and measurements

Three samplings were carried out, in May, August and October 1999. The samples, each consisting of six sample units, were taken randomly from the same representative area of ca. 30 x 30 m, independently of the total size of the similarly managed area. The samples were taken with a cylindrical steel corer (area 25 cm²), inside which plastic rings (3 cm deep) were inserted. The soil cores were cut between the rings, and the layers 0-3, 3-6 and 6-9 cm were extracted separately using the wet funnel method (O'Connor 1962).

Enchytraeids were identified to species whenever possible, but immature specimens of several genera could be identified only to genus. Identification and nomenclature are mainly based on Nielsen and Christensen (1959; 1961; 1963) and Dózsa-Farkas (acknowledgements). The data from the three layers (0 to 9 cm) were summed, except when vertical distributions were compared, and the results were transformed into numbers per square meter.

Separate soil samples were taken from each soil layer for determining several environmental variables: pH_{H₂O}, water content (overnight at 80°C), loss on ignition (4.5 h at 550°C) and mineral nitrogen (NH₄⁺ and NO₃⁻; 2-M KCl; SFS standard 3032) were measured two or three times in 1998. Content (% of weight) of water-stable aggregates (determined by Viljavuuspalvelu Ltd, Mikkeli, Finland, using wet and dry sieving method (Hillel 1982)), microbial biomass (SIR method; Anderson and Domsch,

1978; Nordgren, 1988) and particle size distribution of mineral soil (dry sieving down to 0.2 mm, smaller fractions using SYMPATEC diffraction spectrophotometer) were measured only once and on different dates. pF values (matrix potential) were calculated based on WHC and water content. Water retention was determined by using a pressure plate chamber at potentials -0.3, -1, -5, -10 and -100 kPa. Retention at -10 kPa was used to illustrate the approximate water retention characteristics at field capacity (Table 1). The environmental data were only used in ordination analyses; detailed results will be reported in another paper.

Statistical treatments

Species richness (SR) and Shannon Index of Diversity (H') were calculated for each sample unit, after which all taxa present in numbers less than 40 in the whole material were discarded from further analyses. Ln-transformation was applied to the species data before the analyses, since the log-normal distribution generally prevails in soil animal communities (Debauche 1962). The differences in population densities between the site treatments (BS, BF, D) and treatment replicates (1, 2, 3) were tested by two-way Analysis of Variance (Site, Date). The tests between site treatments (BS, BF, D) were carried out on sample averages of each site and date ($n = 3$), while each group of treatment replicates (BS1, 2 and 3, etc.) was tested on original data ($n = 6$). (There were few significant time effects or time x site interactions, and as these factors are unimportant in the present context, they are not presented.) Vertical distributions (separate data for 0-3, 3-6 and 6-9 cm layers) were tested with total numbers by three-way ANOVA (Site, Date, Layer), and a significant site/layer interaction was interpreted as a significant difference in distribution. The tests were performed using the SPSS for Windows.

Community ordinations on the identified material (all species included) were carried out with the aid of Non-Metric Multidimensional Scaling (NMS), using the PC-ORD program (version 4; MjM Software Design) (McCune and Mefford 1999). It was run in NMS Autopilot mode, using the Sørensen (Bray & Curtis) index as distance measure. The data were ln-transformed prior to the analyses. The choice of these options was based on the experience of Huhta (1979). (The name 'Sørensen index' was earlier used for presence/absence data, and the inverse of the current 'Sørensen' was known as Renkonen's index, or 'Percentage Similarity' (Renkonen 1938; Sørensen 1948)). The ordinations were applied to the whole data, but as this resulted in too many sample points in the graphs, they were also run with sample averages. As the population data of the whole sample depth (0-9 cm) were combined and because the environmental data of different depths are not additive, the physico-chemical measurements of the 0-3 cm layer were only used for the analyses, since the top layer was considered more descriptive to the study sites. However, mineral nitrogen was calculated per m^2 including the 0-6 cm depth, and particle size distribution was measured in the mineral soil below the organic horizon. 'Percentage similarities' were also calculated between all sites on pooled total data (ln-transformed).

Table 1. Soil characteristics of the study sites

Site	Soil	pH	OM	WHC	S ₀	Md	Clay	% SA	Ground vegetation % (B.A. m ² /ha) and stand age (yr)	Tree species composition
BS1 Birch after spruce Limattala, Äänekoski 62° 40' N 25° 47' E	Podzol	5.1	16	29.2	4.6	0.22	1.98	20.4	<i>Deschampsia flexuosa</i> 58,	<i>Betula pendula</i> (18),
	Mor/moder								<i>Melampyrum sylvaticum</i> 20,	<i>Juniperus communis</i> (< 1),
	Sandy till								<i>Maianthemum bifolium</i> 12	35 yr
BS2 Birch after spruce Limattala, Äänekoski 62° 41' N 25° 49' E	Podzol	4.9	18	25.8	4.4	0.36	1.94	10.2	<i>Agrostis capillaris</i> 42,	<i>Betula pendula</i> (11),
	Mor/moder								<i>Calamagrostis</i>	<i>Juniperus communis</i> (< 1),
	Sandy till								<i>arundinacea</i> 22, <i>Rubus saxatilis</i> 17	32 yr
BS3 Birch after spruce Iitsalo, Äänekoski 62° 48' N 25° 57' E	Podzol	5.4	16	26.3	6.2	0.26	2.92	17.6	<i>C. arundinacea</i> 24,	<i>Betula pendula</i> (10),
	Mor								<i>M. bifolium</i> 9	32 yr
	Sandy till								(total herbs 38)	
BF1 Birch after field Uurainen, Oikari 62° 23' N 25° 30' E	Podzol ^a	6.2	11	38.6	4.5	0.06	3.75	30.3	<i>A. capillaris</i> 28,	<i>Betula pendula</i> (12),
	Mull								<i>Silene dioica</i> 14 (total	26 yr
	Fine sand								herbs 53), mosses 23	
BF2 Birch after field Ilmolahti, Viitasaari 63° 0' N 25° 52' E	Podzol ^a	5.4	15	32.3	15.5	0.37	10.24	28.2	<i>Deschampsia caespitosa</i> 13,	<i>Betula pendula</i> (14),
	Mull								<i>Veronica chamaedrys</i> 10	42 yr
	Fine sandy till								(total herbs 50)	
BF3 Birch after field Ilmolahti, Viitasaari 62° 58' N 25° 51' E	Podzol ^a	5.6	13	35.4	13.2	0.18	12.75	26.2	<i>A. capillaris</i> 11,	<i>Betula pendula</i> (15),
	Mull								<i>Filipendula ulmaria</i> 8	33 yr
	Fine sandy till								(total herbs 55)	
D1 Deciduous forest Rutalahti, Leivonmäki 61° 57' N 25° 58' E	Brown earth ^b	4.7	62	45.2	3.5	0.07	2.1	3.0	<i>M. bifolium</i> 13,	<i>Betula pendula</i> (12), <i>Populus</i>
	Mull								<i>Viola palustris</i> 13	<i>tremula</i> (3), <i>Picea abies</i> (1),
	Fine sand								(total herbs 47), <i>Athyrium filix-femina</i> 10	<i>Alnus glutinosa</i> (1), <i>Salix</i> sp. (< 1), 65 yr ^c
D2 Deciduous forest Oittila, Korpilahti 61° 56' N 25° 44' E	Podzol	5.2	20	32.4	8.0	0.24	4.65	13.2	<i>Matteuccia struthiopteris</i> 27,	<i>Betula pendula</i> (12),
	Moder/mull								(total herbs 22),	<i>Alnus</i> sp. (4),
	Sandy till								<i>Vaccinium myrtillus</i> 13	<i>Populus tremula</i> (1), 90 yr ^c
D3 Deciduous forest Kuokkala, Jyväskylä 62° 13' N 25° 45' E	Brown earth ^b	5.6	12	46.3	12.7	0.09	10.6	34.0	<i>Oxalis acetosella</i> 26	<i>Betula pendula</i> (8),
	Mull								(total herbs 50), <i>Equisetum</i>	<i>Pinus sylvestris</i> (4),
	Fine sandy till								<i>sylvaticum</i> 13, mosses 37	75 yr ^c

Soil characters (solum, humus form, texture), pH_{H2O}, loss on ignition (OM, % of d.m.) (0-3 cm layer), water retention at 10 kPa (WHC), degree of sorting ($S_0 = \sqrt{Q_3/Q_1}$), mean particle size (mm, Md = Q2), clay content (%), < 0.002 mm), percentage of water stable aggregates (%SA), dominating plant species in the ground vegetation (percent coverage), proportional distribution of tree species (stand basal area, m²/ha) and stand age (yr) in the study sites. Site symbols as fig 1.

^aDisturbed. ^bNot permanent. ^cDominant age class.

Results

Population densities

The enchytraeid populations were highly variable between replicates of the same forest type. About half of the taxa that were tested differed significantly within BS and BF, and virtually all differed within the “Natural Deciduous” stands. It was more a rule than an exception that a species was absent from one or two of the site replicates and abundant in one or two others (Table 2). This made it hard to revealed differences between the different site treatments, but an obvious general trend was that average population densities, including total numbers, were lower in “Birch after Field” than in “Birch after Spruce”. An exception was *Enchytronia parva*, the most abundant species at BF; all other species occurred in low numbers. The most abundant species in “Birch after Spruce” was *C. sphagnetorum*, which was also superdominant in one of the natural deciduous sites (D1). On the contrary, it was rather sparse in D2 and D3, where *E. parva*, *Fridericia bisetosa*, *F. bulboides*, *Henlea nasuta* and *Enchytraeus buchholzi* reached high densities. The same species were also common but not as abundant in the “Birch after Spruce” sites 2 and 3. The highest total numbers were found in D2 (Fig. 1).

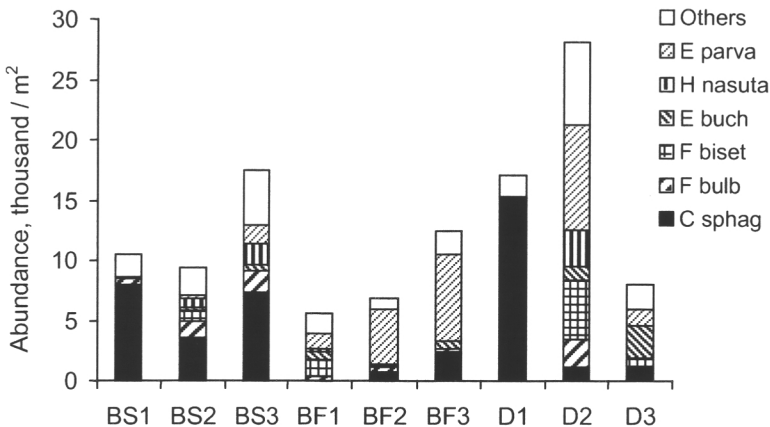


Figure 1. Contribution of the most abundant species to the total numbers of identified enchytraeids (abundance, thousand/m²) in different kinds of forests (BS = “Birch after Spruce”, BF = “Birch after Field”, D = “Natural Deciduous” forests). Each column is a mean of three samples (May, August, October).

Table 2. Numbers of common species, genera and total Enchytraeidae (averages of three samples: May, Aug., Oct.), and species richness and diversity in different study sites. Column 'p' indicates differences between site treatments; asterisks in columns '3' those between replicates (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).
BS = birch after spruce, BF = birch after field, D = deciduous forest.

Site treatment Replicate	p	BS			BF			D		
		1	2	3	1	2	3	1	2	3
<i>Mesenchytraeus pelicensis</i>	0.046*	0	111	978***	0	0	44	0	0	22
<i>Buchholzia</i> spp.	0.049*	356	578	378	0	0	422***	0	200	178
<i>Bryodrilus</i> spp.	0,409	822	44	0***	0	0	0	178	22	0*
<i>Bryodrilus ehlersi</i>	0,186	0	89	644	0	0	22	622	267	22**
<i>Cognettia sphagnetorum</i>	0.006**	7978	3511	7400	0	800	2400***	15311	1111	1044***
<i>Cognettia glandulosa</i>	0.039*	0	0	0	0	0	89	867	0	400**
<i>Fridericia</i> spp.	0,809	1556	1333	689	1133	511	844	67	1422	933***
<i>Fridericia bulbosa</i>	0.002**	356	911	311	200	0	267	0	0	0
<i>Fridericia bulboides</i>	0,152	533	1489	1667*	400	356	311	22	2267	89***
<i>Fridericia bisetosa</i>	0,219	22	778	89***	1378	156	0***	0	4933	733***
<i>Fridericia ratzeli</i>	0,193	289	44	222	622	289	133**	0	378	89**
<i>Enchytraeus buchholzi</i>	0,434	22	333	489*	578	133	578**	0	1156	2733***
<i>Enchytraeus lacteus</i>	0,202	0	67	133*	111	0	0*	0	1578	0***
<i>Enchytraeus minutus</i>	0,284	0	0	0	556	156	0***	0	333	44**
<i>Henlea perpusilla</i>	0,185	0	400	822**	22	0	0	0	1667	0***
<i>Henlea nasuta</i>	0,370	0	667	1800***	244	0	22*	0	3044	0***
<i>Henlea similis</i>	0,308	0	0	644**	0	0	44	0	1244	0***
<i>Enchytronia parva</i>	0.044*	111	311	1422***	1289	4556	7244***	0	8800	1378***
Total	0.050*	12111	11022	18711*	6844	7378	13400*	17200	29689	8978***
Species richness	0,557	3,72	5,83	6.83***	5,00	3,83	5,11	2,39	9,89	5.72***
Shannon diversity	0,979	0,77	1,42	1.47***	1,34	1,02	1.15*	0,35	1,90	1.39***

Roughly half of the total numbers of Enchytraeidae were found in the topmost soil layer (0-3 cm), the proportion in the bottom layer (6-9 cm) being ca. 15 %. The average vertical distribution did not differ between different forests (Fig. 2).

Community structure

Average species diversity did not differ between the site treatments, whereas there were significant differences between treatment replicates (Table 2). The “Natural Deciduous” forest D1 was extremely uniform with few other species than *C. sphagnetorum*, and BS1 was another ‘low diversity’ site. The most diverse site (D2) was also found within the “Natural” forests. Among “Birch after Field”, BF1 harbored a rather diverse community in relation to the low total numbers (Fig. 1).

The NMS ordination revealed distinct groupings of the different site treatments and their replicates (Fig. 3). The data points of “Birch after Spruce” were scattered and widely overlapping. Of the “Birch after Field” sites, BF3 overlapped with BS, and BS1 is most separated from these. Of the Natural Deciduous” forests, D1 was close to the area of BS1, D2 was far from it in the opposite direction, and D3 was located between these, sharing the area with BF1. From a viewpoint of ‘Percentage Similarity’, the highest similarities were found - as expected - between replicates of the same site treatment (BS2/BS3, BF2/BF3), but also between different treatments (D1/BS1, D2/BS3). The replicates of “Birch after Spruce” were most similar to each other, and those

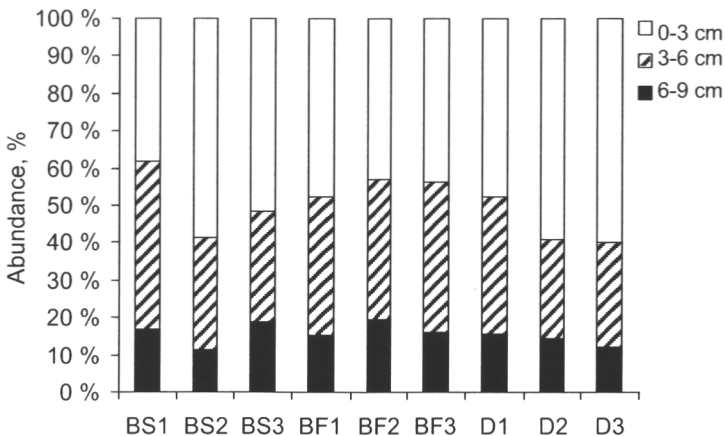
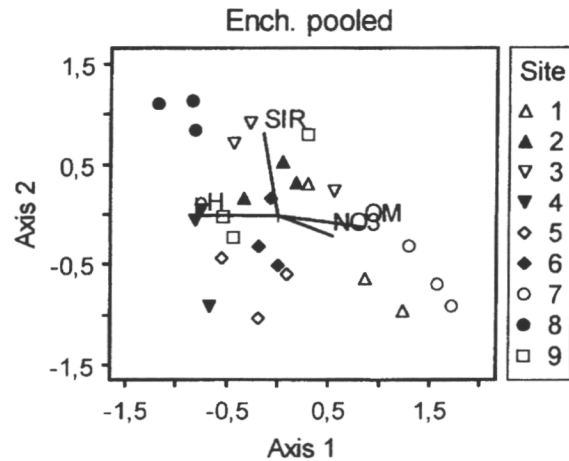
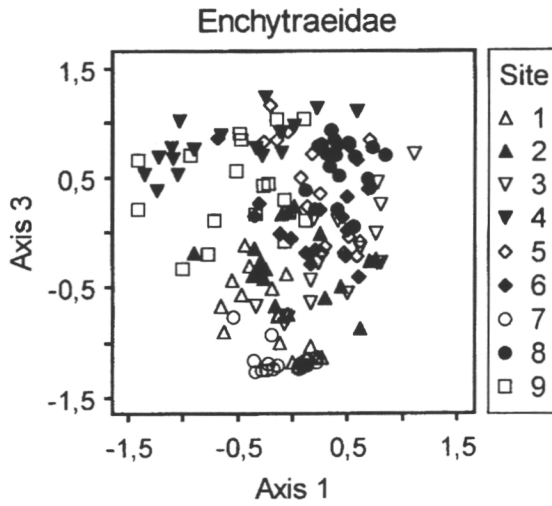
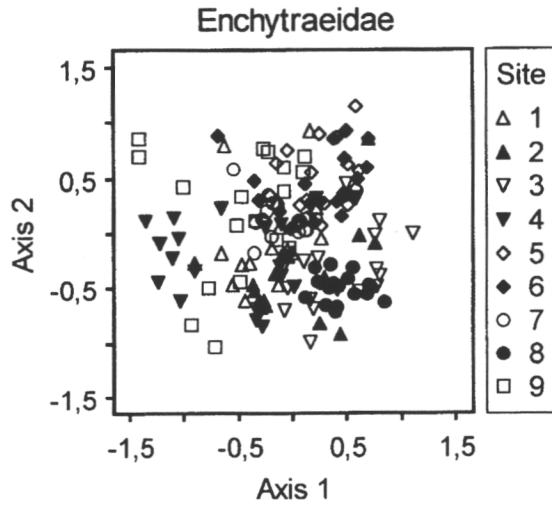


Figure 2. Vertical distribution of Enchytraeidae (%) in different soil layers (0-3 cm; 3-6 cm; 6-9 cm) in study sites (BS = “Birch after Spruce”, BF = “Birch after Field”, D = “Natural Deciduous” forests).

Figure 3.

Selected plot diagram in a three-axis solution with total data of enchytraeid communities (NMS analysis), and the same with environmental variables in a two-axis solution with pooled data (sample averages). Sites 1 to 3 = "Birch after Spruce", 4 to 6 = "Birch after Field", 7 to 9 = "Natural Deciduous" forests.



of “Natural Deciduous” stands least similar (Table 3). D1 was very dissimilar to the BF sites, but also to D2. Microbial biomass, pH, organic matter and NO₃-nitrogen were in significant positive correlation with the ordination axes (Table 3). OM correlated positively and pH negatively with axis 1 but not in the slightest with axis 2, while SIR correlated with axis 2 but not with 1.

Discussion

Despite the fact that there were considerable differences between replicates of similarly managed forests, it is evident that still 30 years after reforestation the enchytraeid communities of planted birch stands established on spruce forest soil and on cultivated soil differ markedly from each other. Total numbers were higher in “Birch after Spruce”, and the dominating species was *C. sphagnetorum*, the superdominant enchytraeid in coniferous forests (Nurminen 1967; Abrahamsen 1972a). In “Birch after Field” this species was much less abundant or absent, and *Enchytronia parva* was dominant instead. *Enchytraeus albidus*, which is a widely distributed, almost cosmopolitan species, was found only at BF sites. The species is commonly found in arable soils, compost, decaying seaweed etc. and recently also in earthworms middens in laboratory conditions (Räty and Huhta, in press). Within the BS sites, BS1 was most similar to the spruce forest community, and within BF, BF1 least similar to it (no clear dominant, *C. sphagnetorum* absent)

Within the deciduous forest sites the replicates differed drastically from each other, especially D1 having very little in common with D2 and D3. The community in D1 was nearly identical to that of spruce forests, with *C. sphagnetorum* comprising 89 % of total numbers, and even the two next abundant species *C. glandulosa* and *Bryodrilus ehlersi* are shared with coniferous forests (Nurminen, 1967). D1 and D2 were most dissimilar from each other, located as opposite extremes in NMS ordination, and with

Table 3. “Percentage similarities” of the enchytraeid communities between the study sites (ln-transformed data). The figures are based on three samples (May, Aug., Oct.). Site symbols as in Fig. 1. (Values exceeding 50 % in bold.)

	BS1	BS2	BS3	BF1	BF2	BF3	D1	D2
BS2	56,8							
BS3	44,3	70,1						
BF1	26,5	44,0	39,5					
BF2	39,3	42,6	44,8	51,1				
BF3	44,8	51,7	53,3	43,3	63,7			
D1	48,9	24,7	25,8	0,8	17,8	23,0		
D2	25,3	59,5	64,8	57,8	45,2	39,9	11,2	
D3	25,6	41,5	45,9	42,0	42,6	47,8	24,6	51,7

Table 4. Pearson correlations of environmental variables with the ordination axes (NMS, 2-axis solution, pooled data). OM = organic matter, SIR = microbial biomass, Aggr = water stable aggregates (%) > 2 mm, Clay = mineral fraction <0.002 mm, Fine = mineral fraction <0.06 mm.

Axis	1	2
pF	.087	.260
OM	.696**	-.252
pH	-.678**	.019
NH ₄ ⁺	.078	-.071
NO ₃ ⁻	.554**	-.346
Aggr	-.482**	-.147
SIR	-.290	.687**
Clay	-.320	-.134
Fine	-.397*	-.131
WHC	.017	-.123

‘Percentage Similarity’ of 0.06. Thus it is impossible to assess which of the three D sites can be considered the “natural” deciduous forest with which the anthropogenous birch stands should be compared.

It is a well-known fact that the enchytraeid community in coniferous forests, bogs and moorlands in cold and temperate climates is simple and strongly dominated (>95 %) by *C. sphagnetorum*, though the total numbers are often high (Nurminen 1967; Abrahamsen 1972a; Lundkvist 1982; Maculec 1983; Didden 1993). On the contrary, in deciduous forests and even in more fertile spruce forests the species diversity is much higher and the dominance of *C. sphagnetorum* is lower. Abrahamsen (1972a) recorded 7 to 21 species in herb and fern-dominated spruce stands in southern Norway, Kairesalo (1978) 21 and 18 species in two rich deciduous stands in southern Finland, and Axelsson et al. (1984) 10 species in a deciduous woodland in central Sweden. Graefe (1989) showed that the number of enchytraeid species was much lower under spruce than in adjoining beech stands. Nowak (1975) studied the enchytraeid communities in two successional series in Poland, from meadow or old field towards mixed coniferous forests. In medium phases dominated by birch, *C. sphagnetorum* was the most abundant species, and about half of the common species were shared with our study sites. Species diversity declined with the stand age, and many species were no more present in the coniferous phase.

According to several authors, pH is one of the most important environmental factors that influence the occurrence of enchytraeid species in a given soil. Most species are intolerant to acid environments, while *C. sphagnetorum* and a few other species are acidophilic or acid-tolerant (Standen 1980; Didden 1993). *C. sphagnetorum* has been shown to decrease after liming and ash fertilization, both treatments tending to increase

the pH value (Bååth et al. 1980; Abrahamsen 1983; Huhta 1984; Persson 1988). Soil pH associated with certain moisture and nutrient conditions may also be the triggering factor in sexual reproduction of *C. sphagnetorum*, in which parthenogenesis by fragmentation is the chief reproduction mechanism (Standen 1973; Lundkvist 1982, 1983). Standen (1980) and Nowak (1975) have observed a positive correlation between pH and number of enchytraeid species. Against this background, the high species richness in “Birch after Field” and in natural deciduous forests, and an increase of diversity and decrease of *C. sphagnetorum* in “Birch after Spruce” in relation of original spruce stands, are expected. In cultivated soils liming controls acidity, and the effect of lime on soil pH and microbial activity is long-lasting (Aarnio et al. 2003). Birch leaf litter tends to increase the soil pH, while spruce needle litter tends to lower it (Mikola 1985). pH was also one of the explaining variables in our data (NMS ordination). However, acidity can hardly explain all differences between the site replicates, particularly not in the case of site D1 that harbored a simple community similar to that of coniferous forests.

As the enchytraeid assemblages of coniferous forest soils are species-poor, lacking most species that could potentially occur in deciduous stands, dispersal ability of such species is expected to play a role in the colonization of birch plantations established in an earlier spruce forest. Unfortunately, virtually nothing is known about dispersal in Enchytraeidae. In some laboratory experiments, *C. sphagnetorum* has been observed to spread only a few centimeters per week (Sjögren et al. 1995; Salminen and Sulkava 1996). If this holds generally for enchytraeids, active dispersal over long distances by land seems unlikely. Passive transport by man is known to play a decisive role in the dispersal of earthworms (Lee 1985), and since these are similar to enchytraeids in general biology and evolutionary backgrounds, this can be assumed to be true also in enchytraeids. This means that species invasions to new localities are accidental, and thus the species assemblage at a certain site is largely determined by chance. This may explain the very different composition of the communities between the site replicates. For instance within “Birch after Spruce”, the highest number of species was found in BS3 that was the most isolated of the three replicates, surrounded by coniferous forest from all sides. Contrary to BS, the “Birch after Field” sites had a long cultural history before reforestation, and thus most potential species could be expected to have colonized the sites. Among these, the most isolated was BF2, and this also had the lowest species diversity.

Within the “Natural Deciduous” forests, the species-poor site D1 was most isolated from cultural environments, and it was also exceptional in not having earthworm populations. Thus, isolation may explain the absence of several potential species in D1. In D2 there was a low population of *Lumbricus terrestris*, and in D3 dense populations of two burrowing species, *L. terrestris* and *Aporrectodea caliginosa* (Räty and Huhta, in press). Observations indicate a negative relationship between earthworms and enchytraeids. Schaefer and Schauer mann (1990) found in German beech forests that the abundances and biomasses of Lumbricidae and Enchytraeidae were inversely related. Huhta and Vikberg (1999) have shown that the earthworm *Dendrobaena octaedra* reduces the population of *C. sphagnetorum*. Yli-Olli and Huhta (2000) concluded that while the presence of the former is determined by the soil pH, the latter is regulated by

interplay between pH, moisture and presence of *Dendrobaena octaedra*. Experiments of Rätty (in press) and Rätty & Huhta (2003) also indicate that *L. terrestris* can live and reproduce in the soil of the D1 site, and that the earthworms *L. terrestris* and *Aporrectodea caliginosa* reduce substantially the enchytraeid populations. Thus the high earthworm biomass may explain the low total density of enchytraeids in D3, while in D2, due to less intense competition, high numbers and diversity of Enchytraeidae were possible.

The NMS ordination revealed an opposite relationship between pH and organic matter in relation to the first axis. This reflects the general inverse relation between acidity and accumulation of organic matter on one hand, and decomposition rate and presence of burrowing earthworms on the other. In D1 – in the absence of earthworms – a thick layer of incompletely decomposed litter had accumulated on the soil surface, and thus the topmost soil layer was almost purely organic, while at all other sites mechanical (tillage) or biological (earthworms) activities had resulted in mixing of mineral matter with the topsoil. In D1 also the NO_3^- concentration was higher than at any other site and the soil pH was unexpectedly low, almost equal to coniferous forest soil.

Conclusions

The enchytraeid communities were highly variable within the same forest type. The highest similarities were found between replicates of the same site treatment, but also between different treatments. This hampers the comparison between different forests, but we conclude that birch stands established on spruce forest soil and on cultivated soil differ markedly from each other still 30 years after reforestation. In “Birch after Spruce” the predominant species is *C. sphagnetorum*, the “superdominant” enchytraeid in coniferous forests. In “Spruce after Field” the population densities are low, *C. sphagnetorum* is sparse or absent, and *E. parva* dominates instead. *C. sphagnetorum* was also superdominant at one of the “Natural Deciduous” sites, which was nearly identical to coniferous forests in community structure.

Soil acidity is one of the principal factors to determine the community structure of Enchytraeidae. However, pH alone can not explain all the variation between the study sites. We conclude that, as in earthworms, accidental transport by man may largely determine the presence of a species on a given locality. Isolation probably explains the absence of many enchytraeid species at one of the “Natural Deciduous” sites. On the contrary, “Birch after Field” sites have a long cultural history before reforestation, and most potential species can be expected to have colonized. Further, the presence of earthworms is known to reduce enchytraeid populations. Thus the high earthworm biomass may explain the low densities of enchytraeids in the “Birch after Field” sites, but also in one “Deciduous” site that was cultivated its earlier history.

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Earthworm communities in birch stands with different origin in central Finland

Mika Rätty*, Veikko Huhta¹

Finnish Forest Research Institute, Suonenjoki Research Station, FI-77600 Suonenjoki, Finland

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Earthworms;
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Human impact

Summary

The aim of the study was to compare earthworm communities in anthropogenous birch stands with different origin in Finland. A total of nine forest sites were investigated: three birch stands (*Betula pendula*) planted ca. 30 years prior to the study after clear-cutting of spruce stands ("Birch after Spruce", BS), three birch stands planted ca. 30 years earlier on arable soil that had been under normal cultivation until forestation ("Birch after Field", BF), and three "Natural Deciduous" forests (D). Earthworms were sampled in May and October 1999 using a combination of formaline extraction and modified wet funnels. There were conspicuous differences between replicates of similarly managed forests. Earthworms were totally lacking in one of the D sites, while another had an abundant and diverse community. Only *Dendrobaena octaedra* was present in one BS site, while the two others harboured also *Aporrectodea caliginosa* and three *Lumbricus* species. All these species were also present in the BF sites, where their total biomass (ranging from 70 to 138 g (f.w.)/m²) was 2.6 times the average in BS, and of the same magnitude as the average in natural deciduous stands. A separate experiment revealed that *L. terrestris* and *A. caliginosa*, which are not found in the surrounding coniferous forest, are able to live and reproduce in the soil of the D site where they were absent. It was concluded that earthworm species survive and reproduce in birch stands established on arable soil, where they have invaded during the long cultivation. On the other hand, their possibilities to disperse from cultural landscapes determine their presence not only in birch stands established in earlier coniferous forests, but also in "natural deciduous" forests where source populations are not present in the surroundings.

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*Corresponding author.

E-mail address: mika.ratty@metla.fi (M. Rätty).

¹Current address: Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, 40351 Jyväskylä University, Finland.

Introduction

Earthworms, together with other "macrodecomposers", are among the most important soil organisms due to their ability to promote decomposition, nutrient cycling and soil formation (Edwards and Bohlen, 1996; Lavelle and Spain, 2001). Low species number and high degree of variation in their population density and community composition between different habitats characterize the lumbricid fauna of boreal regions (Terhivuo, 1988, 1989). Due to Quaternary glaciations, endemic species are lacking in Fennoscandia. The species present are thus post-glacial immigrants that have colonized the areas northbound either spontaneously or by human activity. Population dynamics of earthworms is controlled by various factors, in which dispersal ability, habitat characteristics, interspecific interaction and human influence are the most important (Huhta, 1979; Terhivuo, 1988; Curry, 1998). The northern coniferous forest soils are typically classified as Haplic Podzols with low pH. The soil type is usually sandy till covered by a thin mor humus layer. Most burrowing earthworm species are intolerant to low pH (Edwards and Bohlen, 1996). They are thus almost lacking in acid mor soils, leaving the acid tolerant enchytraeid *Cognettia sphagnetorum* as the dominant faunal component (Persson et al., 1980; Huhta et al., 1986).

Willis et al. (1997) addressed that dispersion of deciduous tree species (e.g. silver birch *Betula pendula*) was one of the triggering mechanism by which a podzols changed to a brown-earth soil following the postglacial climate change. This succession influenced markedly the soil properties, favouring colonization of earthworms. Later, natural disturbances and human influence, e.g. wildfires and slash-and-burn agriculture in the boreal forests led to similar successional changes in tree species composition favouring development of deciduous tree species. After wildfire or burn beating, pioneer deciduous trees dominated the landscape before conifers gradually reoccupy the area. Acknowledging successional trends of boreal forests, earthworm population dynamics is obviously affected by plant succession dynamics (Bernier et al., 1993).

During the 20th century, proportion of deciduous and mixed forests has decreased gradually due to plantation forestry that aims to grow spruce and pine in monocultures. Due to selective clearing of sapling stands, deciduous tree species have been cleared at an earlier phase of succession en route to pure coniferous stands. Recently an opposite tendency has prevailed, and approximately a

10–30% mixture of deciduous trees (mainly silver birch, *B. pendula*) is recommended in practical sustainable forestry in order to conserve or amplify biodiversity in forests (Valkonen et al., 2001). Deciduous trees are also commonly used in reforestation of abandoned fields in Finland. The agricultural policy of EU will conduct a marked adjustment in the operational environment of agriculture, which will release ca. 25 million hectares of agricultural soil to forestry or recreational use (Hytönen and Polet, 1995). Increased value of deciduous trees in forestry and in landscape ecology will promote their use in reforestation. In addition, expected warming of the global climate is assessed to affect geographical vegetation zones, resulting in changes in stand composition and probably favouring broadleaved trees (Kellomäki et al., 1996).

The aim of the present study was to compare the earthworm communities of anthropogenous birch stands of different origin with those of natural deciduous forests at the same latitude. We aim to discuss and explain the observed differences between different habitats, and bring forward presumptions that in addition to soil properties, accidental transport by man and vicinity of cultural environment explains the presence of earthworms on a given locality. Concurrently with the present study, laboratory experiments for testing several hypotheses were conducted (Rätty and Huhta, 2003a; Rätty, in press). This is one in a series of papers, each dealing with different groups of soil organisms in anthropogenous birch stands in central Finland (Huhta, 2002; McLean and Huhta, 2002; Huhta and Niemi, 2003; Rätty and Huhta, 2003b).

Materials and methods

Site description

As a whole, nine forest sites were investigated. Three of the sites are birch (*B. pendula*) stands planted 28–33 years prior to the study after clear-cutting of mature spruce stands ("Birch after Spruce", symbol BS). Three sites are birch stands planted 26–43 earlier on arable soil (originally cleared spruce forests) that had been under cultivation (leys and cereals) until reforestation ("Birch after Field", BF). Three stands were "Natural Deciduous" forests (D), though one of them (D3) has been under cultivation in the 19th century (virtually all deciduous forests at this latitude have been under human influence to a greater or lesser extent). Birch stands BS and BF are

homogeneous monocultures in which selective clearing and logging have been conducted. Birch is the dominating tree species also in the D sites, but up to $\frac{1}{4}$ of the stand density is covered by other species, e.g. black alder (*Alnus glutinosa*), European alder (*Alnus incana*), willows (*Salix* spp.) and European aspen (*Populus tremula*). Natural coniferous forests were not included in the study, since relevant data for comparisons are available in earlier studies. The BS sites are characterized by lower pH and higher organic matter content than the BF sites. The D1 site has a very high organic matter content and low pH compared to the other D sites, D3 is in the range of the BF sites and D2 is between (Table 1).

All the sites are located in central Finland, the BS and BF sites 30–90 km north of the town of Jyväskylä, D1 and D2 ca. 40 km south of Jyväskylä, and D3 in the town area (62°13'N 25°44'E). Primal soil characters (solum, humus form, texture), pH_{H₂O}, loss on ignition, water holding capacity, degree of sorting, mean particle size, clay content, soil structure, dominating plant species in the ground vegetation and tree species composition are shown in Table 1. Stand age was determined by an increment borer, and stand basal area by the relascope method (angle-gauge method).

Sampling, identification and measurements

Two samplings were carried out, in May and October 1999, at the time of maximum activity and lowest variation in populations (Nordström and Rundgren, 1973). Soil samples, each consisting of six 25 × 25 cm² sample units, were taken randomly from the same representative area of ca. 30 × 30 m², independently of the total size of the similarly managed area. The samples were taken with a steel spudder, and the layers 0–5 and 5–10 cm were treated separately. Earthworms were extracted using modified wet funnels (Huhta and Koskeniemi, 1975). In addition, formaline extraction was conducted with 2.5‰ and 5‰ solutions to catch the deep burrowing species *Lumbricus terrestris*. Earthworms were stored for 2 days in moist paper to empty their gut contents, and weighed. The worms were identified to species level, except immature specimens of *Lumbricus* spp., which were identified to genus. Identification and nomenclature were based on Stöp-Bowitz (1969). The data of the two layers (0–10 cm) were summed; except for comparing vertical distribution, and the results were calculated per square meter.

Statistical treatments

Differences in population densities between the site treatments (BS, BF, D) and treatment replicates, including vertical distribution, were analyzed using the SPSS 10.0 statistical package. Ln-transformation was applied to the data before analyses, since log-normal distribution generally prevails in soil animal communities (Debauche, 1962). For testing treatment effects, two-way analysis of variance was used. The tests between site treatments were conducted by using sample means of each site and date ($n = 3$), while treatment replicates were tested on entire data ($n = 6$). Tukey's test was used for pairwise multiple comparisons. Normality of distributions was checked using the Kolmogorov–Smirnov statistic with a Lilliefors test, and homogeneity of variances using the Levene's test.

Results

Earthworm populations were highly variable between site treatments, but even more significantly between replicates of the same treatment (Table 2). The variation between sites replicates hampers to reveal the main effects, but in general the population densities were lower in BS than in BF, except for *Dendrobaena octaedra*. Similar distinct grouping was revealed in "Natural Deciduous" stands between D2 and D3, in which latter represent distant agricultural soil and former podzoled forest soil. Extreme variation was found in D stands, D3 having very high earthworm densities (average total 277.6/m²), and D1 totally lacking earthworms. Neither average abundance nor biomass differed between the sampling time (Fig. 1).

The endogeic species *Aporrectodea caliginosa* was a typical species in most study sites, and the dominant component of the community in one D site (D3) and all BF sites (Table 2). However, in terms of biomass, the anecic *Lumbricus terrestris* reached or exceeded the importance of *A. caliginosa*. Both species were lacking in sites BS3 and D1. In the BS sites, roughly 65% of all specimens belong to epigeic species, *Dendrobaena octaedra* being the most abundant and forming a single-species community in BS3. Other epigeic species, *Lumbricus rubellus*, *L. castaneus*, *Dendrodriilus rubidus* and *Octolasion tyrtaeum* were found in lower densities. *O. tyrtaeum* was found only in D2. Total proportion of epigeic lumbricids was significantly higher in BS than in BF ($p < 0.001$), where the endogeic

Table 1. Soil characters (solum, humus form, texture), pH_{H_2O} , loss of ignition (OM, % of d.m.) (0–3 cm layer), water retention at 10 kPa (WHC), degree of sorting ($S_0 = \sqrt{Q_3/Q_1}$), mean particle size (mm, Md = Q2), clay content (%), <0.002 mm), percentage of water stable aggregates (%SA), dominating plant species in the ground vegetation (percent coverage), proportional distribution of tree species (stand basal area, m^2/ha) and stand age (yr) in the study sites

Site	Soil	pH	OM	WHC	S_0	Md	Clay	% SA	Ground vegetation %	Tree species composition (B.A. m^2/ha) and stand age (yr)
BS 1	Podzol Mor/moder Sandy till	5.1	16	29.2	4.6	0.22	1.98	20.4	<i>Deschampsia flexuosa</i> 58, <i>Melampyrum sylvaticum</i> 20, <i>Maianthemum bifolium</i> 12	<i>Betula pendula</i> (18), <i>Juniperus communis</i> (< 1), 35 yr
BS 2	Podzol Mor/moder Sandy till	4.9	18	25.8	4.4	0.36	1.94	10.2	<i>Agrostis capillaris</i> 42, <i>Calamagrostis arundinacea</i> 22, <i>Rubus saxatilis</i> 17	<i>Betula pendula</i> (11), <i>Juniperus communis</i> (< 1), 32 yr
BS 3	Podzol Mor Sandy till	5.4	16	26.3	6.2	0.26	2.92	17.6	<i>C. arundinacea</i> 24, <i>M. bifolium</i> 9 (total herbs 38)	<i>Betula pendula</i> (10), 32 yr
BF 1	Podzol* Mull Fine sand	6.2	11	38.6	4.5	0.06	3.75	30.3	<i>A. capillaris</i> 28, <i>Silene dioica</i> 14 (total herbs 53), mosses 23	<i>Betula pendula</i> (12), 26 yr
BF 2	Podzol* Mull Fine sandy till	5.4	15	32.3	15.5	0.37	10.24	28.2	<i>Deschampsia caespitosa</i> 13, <i>Veronica chamaedrys</i> 10 (total herbs 50)	<i>Betula pendula</i> (14), 42 yr
BF 3	Podzol* Mull Fine sandy till	5.6	13	35.4	13.2	0.18	12.75	26.2	<i>A. capillaris</i> 11, <i>Filipendula ulmaria</i> 8 (total herbs 55)	<i>Betula pendula</i> (15), 33 yr
D 1	Brown earth** Mull Fine sand	4.7	62	45.2	3.5	0.07	2.1	3.0	<i>M. bifolium</i> 13, <i>Viola palustris</i> 13 (total herbs 47), <i>Athyrium filix-femina</i> 10	<i>Betula pendula</i> (12), <i>Populus tremula</i> (3), <i>Picea abies</i> (1), <i>Alnus glutinosa</i> (1), <i>Salix</i> sp. (< 1), 65 yr****
D 2	Podzol Moder/mull Sandy till	5.2	20	32.4	8.0	0.24	4.65	13.2	<i>Matteuccia struthiopteris</i> 27, (total herbs 22), <i>Vaccinium myrtillus</i> 13	<i>Betula pendula</i> (12), <i>Alnus</i> sp. (4), <i>Populus tremula</i> (1), 90 yr****
D 3	Brown earth** Mull Fine sandy till	5.6	12	46.3	12.7	0.09	10.6	34.0	<i>Oxalis acetosella</i> 26 (total herbs 50), <i>Equisetum sylvaticum</i> 13, mosses 37	<i>Betula pendula</i> (8), <i>Pinus sylvestris</i> (4), 75 yr****

Site symbols as Fig. 1.

*Disturbed.

**Not permanent.

****Dominant age class.

Table 2. Mean abundance (ind./m²) and biomass (f.w. g/m² in *Italic*) of common taxa (averages of two samples: May and Oct.) in different study sites

Replicate	<i>p</i>	Site treatment								
		BS			BF			D		
		1	2	3	1	2	3	1	2	3
<i>Lumbricus terrestris</i> (ind./m ²)	0.010*	15.0	8.3	—	23.3	25.3	15.7	—	14.3	45.3
f.w. g /m ²	<i>0.009**</i>	<i>27.0</i>	<i>16.1</i>	—	<i>52.4</i>	<i>39.0</i>	<i>31.2</i>	—	<i>34.1</i>	<i>93.8</i>
<i>Lumbricus rubellus</i> (ind./m ²)	0.154	17.3	—	—	8.0	10.7	10.7	—	4.0	9.3
f.w. g /m ²	<i>0.151</i>	<i>11.8</i>	—	—	<i>5.5</i>	<i>7.1</i>	<i>7.3</i>	—	<i>2.7</i>	<i>6.4</i>
<i>Lumbricus castaneus</i> (ind./m ²)	0.290	13.3	12.0	—	24.0	9.3	8.0	—	6.7	8.0
f.w. g /m ²	<i>0.260</i>	<i>3.9</i>	<i>3.5</i>	—	<i>6.9</i>	<i>2.6</i>	<i>2.3</i>	—	<i>1.9</i>	<i>2.2</i>
<i>Lumbricus</i> sp. <i>juv</i> (ind./m ²)	0.270	15.3	12.3	—	24.3	10.3	8.0	—	6.1	8.3
f.w. g /m ²	<i>0.860</i>	<i>8.9</i>	<i>6.7</i>	—	<i>14.4</i>	<i>5.5</i>	<i>4.4</i>	—	<i>3.4</i>	<i>3.4</i>
<i>Aporrectodea caliginosa</i> (ind./m ²)	<0.001***	36.0	30.7	—	126.7	100.0	50.7	—	21.3	170.7
f.w. g /m ²	<0.001***	<i>18.0</i>	<i>16.7</i>	—	<i>58.6</i>	<i>47.86</i>	<i>20.7</i>	—	<i>8.6</i>	<i>93.2</i>
<i>Dendrobaena octaedra</i> (ind./m ²)	0.009**	44.0	17.3	16.0	—	—	24.0	—	25.3	36.0
f.w. g /m ²	<i>0.036*</i>	<i>3.8</i>	<i>1.5</i>	<i>1.4</i>	—	—	<i>2.6</i>	—	<i>2.5</i>	<i>3.5</i>
<i>Dendrodrilus rubidus</i> (ind./m ²)	0.957	—	8.0	—	—	—	6.7	—	6.6	—
f.w. g /m ²	<i>0.987</i>	—	<i>1.6</i>	—	—	—	<i>1.5</i>	—	<i>1.7</i>	—
<i>Octolasion tyrtaeum</i> (ind./m ²)	0.270	—	—	—	—	—	—	—	10.6	—
f.w. g /m ²	<i>0.250</i>	—	—	—	—	—	—	—	<i>2.3</i>	—
Total ind./m ²	0.003**	140.9	88.6	16.0	206.3	155.6	123.8	—	94.9	277.6
Total f.w. g/m ²	<i>0.002**</i>	<i>73.4</i>	<i>46.1</i>	<i>1.4</i>	<i>137.8</i>	<i>102.1</i>	<i>70.0</i>	—	<i>57.2</i>	<i>202.5</i>

Column '*p*' indicates significant differences between site treatments (**p*<0.05, ***p*<0.01, ****p*<0.001). BS = "Birch after Spruce", BF = "Birch after Field", D = "Natural Deciduous" forest.

A. caliginosa was more dominant (Fig. 2). Relative proportions of different ecological groups differed significantly between the site treatments (*p*<0.001).

Approximately 80% of the epigeic and endogeic lumbricids were found in the topmost soil layer (0–5 cm). Vertical differences in lumbricids location were obvious in BS sites (*p*<0.001). However, vertical differences were not significant in BF and D stands with regard to average biomass, but significant in terms of abundance. The average vertical distribution of different ecological groups differed in some extent between forest types. Epigeic and endogeic species were distinctly concentrated in the litter layer, while in terms of biomass the endogeic *A. caliginosa* was more evenly distributed between the soil layers. In mixed and clearly more aggregated former agricultural soils (BF1-3 and D3) both endogeic and epigeic lumbricids were dispersed

more uniformly. Vertical distribution of anecics *L. terrestris* was not recorded due to different sampling method.

Due to high variation between the replicates, the species number did not differ significantly between the site treatments, whereas there were clear differences between treatment replicates (Fig. 1). BF3 was extremely uniform consisting only very sparse population of *D. octaedra*. The most diverse sites were found within the "Natural" forest (D2) and one of the former agricultural soil (BF3). In a view of the species diversity and community structure, original podzole forest soils (BS1, BS2) and one of the "Natural" forest site (D2) diverge similarity harbouring a rather diverse community in relation to the low total number. Correspondingly former arable soils (BF1, BF2) and one of the deciduous site (D3) were more similar among each other with the lower diversity and higher species density.

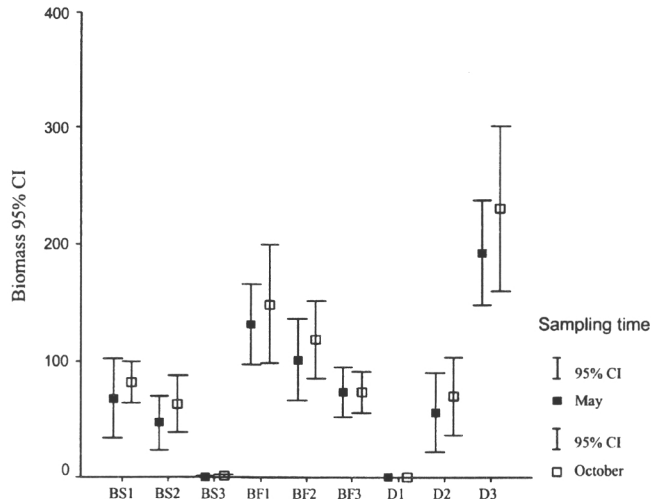


Figure 1. Mean biomass (f.w. g/m², 95% confidence interval for mean) of earthworms in study site (BS = "Birch after Spruce", BF = "Birch after Field", D = "Natural Deciduous" forests) in May and October.

Discussion

Acid coniferous forest soil is an unfavourable habitat for most lumbricid species. *Dendrobaena octaedra*, *Dendrodrilus rubidus*, *Lumbricus rubellus* and *Aporrectodea rosea* have been reported in low densities in coniferous forests in Finland; at higher latitudes only *D. octaedra* and *D. rubidus* (Terhivuo, 1988). *D. octaedra* and *D. rubidus* were also recorded in our BS sites, *D. octaedra* in all three and *D. rubidus* in BS2 only. BS3 contained only a sparse population of *D. octaedra*, while three *Lumbricus* species, *L. terrestris*, *L. rubellus*, *L. castaneus*, and the endogeic *A. caliginosa* were recorded in BS1 and BS2 in addition. This suggests that the earthworm community in former forest soil has significantly changed during the 30 years' influence of birch.

A. caliginosa together with *L. terrestris*, *L. rubellus* and *L. castaneus* were found in the BF sites. All these are common inhabitants of agricultural soils (Terhivuo, 1988). *A. caliginosa* was the dominant faunal component in all BF sites. In addition, *D. octaedra* and *D. rubidus* were present in BF3. As the community structure in BF resembles that in arable soils, it can be concluded that the composition of lumbricid community has not changed much after afforestation. Most species of arable soils also inhabit deciduous forest soils (Terhivuo, 1988). It is noteworthy that the soil matrix in terms of pH, texture and structure in our

BF sites still resembles agricultural soils. Existing source population and favourable soil properties may explain the similarity of the Lumbricid population to agricultural soils.

Broad-leaved forests generally harbour the most diverse earthworm community in the boreal latitudes (Terhivuo, 1988). However, the most drastic differences between replicates of virtually similar forests were observed among D sites. Earthworms were totally lacking in D1, D2 had a very diverse community and moderate total density, and D3 had the highest total density with *A. caliginosa* strongly dominating. Due to great variation between replicates, it is impossible to conclude whether the lumbricid communities of planted birch stands have changed towards those of D forests. In the coniferous forest (taiga) biome, broad-leaved forests typically form the initial stage of succession after forest fire or heavy storm, or in managed forests after clear felling before subsequent silvicultural practices are applied. Later in the succession, conifers colonise the area and depress the deciduous vegetation. This implies that older deciduous stands in fact are, or have been in the past, more or less under human influence. This was also obvious in our D sites. According to available maps, site D3 was under cultivation in the 1800s, which can still be seen in the soil structure and texture. Grazing by cattle and selective harvesting of conifers have probably affected the stand composition in D2, and presence of the old cultural

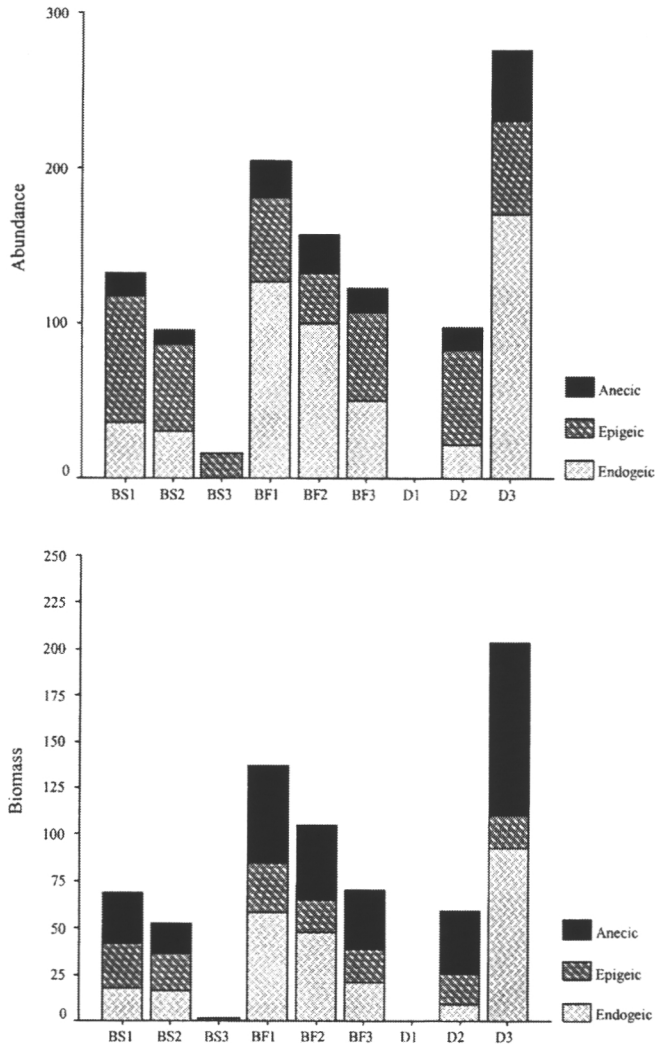


Figure 2. Mean abundance (specimens/m²) and biomass (f.w. g/m²) of earthworms divided into ecological categories in study sites (BS = "Birch after Spruce", BF = "Birch after Field", D = "Natural Deciduous" forests). Each column is a mean of two samplings (May, October).

plant Common hops (*Humulus lupulus* LINN.) in the otherwise unmanaged site D1 indicate human influence.

The most marked differences in the earthworm community structure were found between recent coniferous forest soil (BS) and former arable soil (BF and site D3). In the latter, the community was more diverse and had higher total numbers and biomass than in the BS sites. Numerous studies have revealed that the distribution of earthworms

depends on soil physico-chemical properties such as texture and structure, pH, and organic matter content and depth. Nordström and Rundgren (1974) reported a positive relationship between clay content and, e.g. *A. caliginosa* and *L. terrestris*. Baker et al. (1992) found similar positive interaction between clay content and numbers and biomass of *Aporrectodea* spp. Correspondingly, sand and gravel fractions have been shown to depress the population of *A. caliginosa* (Khalaf

El-Duweini and Ghabbour, 1965). Soil fertility is in positive correlation with clay content; thus clayey soils are preferred for cultivation. This is also seen in the present study; the former agricultural soils (BF1, BF3 and D3) have a smaller mean particle size and higher clay content than in the non-cultivated soils (Table 1). The influence of soil texture on earthworms may also be indirect, through its effect on soil moisture.

Coniferous forest soils typically have low pH, and most earthworms, endogeic and anecic species in particular, are sensitive to acidity (Edwards and Bohlen, 1996). In general, earthworms are absent in acid soils (pH < 3.5) and sparse in soils with average pH < 4.5. On the other hand, there is evidence that earthworms by their activities gradually tend to counteract soil acidity; higher pH has been registered in earthworm casts than in the bulk soil (Haimi and Huhta, 1990). Site D1 had pH of 4.7, which is suboptimal but tolerable to burrowing earthworms, and a separate experiment revealed that *L. terrestris* and *A. caliginosa* maintained their populations and even reproduced in the soil taken from the study site where they were absent (Rätty, 2004).

Quality of litter as food also plays an important role for litter-feeding species such as *L. terrestris* and *L. rubellus*. Earthworm populations are often food-limited, but litter quality rather than its quantity most often limits earthworm populations (Satchell and Lowe, 1967; Swift et al., 1979). Since the litter input in our study sites is mainly composed of high-nitrogen and low-phenolic leaf litter, it is unlikely that differences in food supply explains differences in the earthworm populations.

Within the D forests, the species-poor site D1 was most isolated from cultural environments. Isolation may explain the lack of earthworms there. Also the enchytraeid community in D1 was species-poor resembling communities in coniferous forest soils (Rätty, unpublished). According to Lee (1985), passive transport by man is an essential agent in the dispersal of earthworms. Invasion of species into new habitats is thus more or less accidental. This may explain the absence of earthworms in D1. Similarly, BS3 was the most isolated site within BS, being surrounded by coniferous forest from all sites. *D. octaedra* was the only lumbricid species present in this site.

Conclusions

The earthworm communities were highly variable both between and within different forests, and this

variation partly masked the differences between the main site treatments. The data allow a conclusion that earthworm communities in birch stands established on spruce forest soil and on arable soil differ clearly from each other still 30 years after reforestation. On the other hand, former cultivated soils seem to maintain their populations after afforestation. "Extreme" variation within "Natural Deciduous" stands prevents conclusion whether the communities in anthropogenic birch stands become similar to those of natural forests. The clearest changes in this direction were observed in original spruce forests after reforestation with birch. In addition to edaphic factors and quality of litter as food source, human influence, zoochory and land use history markedly affect the composition of earthworm communities. Lack of possibilities to disperse from surrounding cultural landscapes probably explains the absence of endogeic and anecic species in some potentially favourable sites.

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Mika Rätty · Veikko Huhta

Earthworms and pH affect communities of nematodes and enchytraeids in forest soil

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Abstract In northern boreal forests the occurrence of endogeic and anecic earthworms is determined by soil pH. Increasing evidence suggests that large detritivorous soil animals such as earthworms can influence the other components of the decomposer community. To study the effects of earthworms and pH on soil nematode and enchytraeid communities, a factorially designed experiment was conducted with *Lumbricus rubellus* and/or *Aporrectodea caliginosa*. Earthworms were added to “mesocosms” containing unlimed (pH 4.8) or limed (pH 6.1) coniferous mor humus with their natural biota of micro-organisms. In the absence of earthworms, nematodes were significantly more abundant in limed than in unlimed humus. Earthworms markedly decreased the numbers of nematodes both in unlimed and limed soils. Earthworm activities eliminated enchytraeids in unlimed soil, but liming improved the survival of some species. It was concluded that liming of soil, either alone or mediated by the earthworm populations, is likely to affect soil nematode and enchytraeid community and mineralisation.

Keywords pH · Earthworms · Nematodes · Enchytraeids · Interactions

Introduction

Earthworms, together with other “macrodecomposers”, are among the most important soil organisms due to their ability to promote decomposition and mineralisation, and

to their activities as “ecosystem engineers” (Edwards and Bohlen 1996; Lavelle and Spain 2002). However, coniferous forest soils typically have low pH, and most earthworms, the burrowing (“engineering”) species in particular, are sensitive to acidity (Edwards and Bohlen 1996). Thus in acid mor soils earthworms are lacking or only represented by the epigeic species *Dendrobaena octaedra*. This leaves the acid-tolerant enchytraeid *Cognettia sphagnetorum* more or less in the position of dominant faunal component (Persson et al. 1980; Huhta et al. 1986). There is evidence for competitive interactions between earthworms and enchytraeids: Huhta and Viberg (1999) have shown that the presence of *D. octaedra* suppresses the population of *C. sphagnetorum*. Hyvönen et al. (1994) made a similar observation of *D. octaedra*, which reduced numbers of *C. sphagnetorum* in limed soil. Enchytraeids also contribute to decomposition processes by enhancing N mineralisation (Lundkvist 1981; Abrahamson 1990), and they play some role in soil formation by mixing and channelling detritus and excreting nutrient-rich wastes (Griffiths and Bardgett 1997).

Nematodes are also typical soil inhabitants and are present in millions per square metre in all soils (Petersen and Luxton 1982). Nematode numbers have been reported to increase in response to manipulation of pH by liming (Franz 1959; Bassus 1960) but in some other studies their numbers have remained unchanged after liming (Hyvönen and Huhta 1989; Hyvönen and Persson 1990). Decreasing populations of nematodes are often associated with an increase in numbers and biomass of earthworms (Yeates 1981; Hyvönen et al. 1994). The latter authors concluded that nematodes may be accidentally or selectively ingested by earthworms (*D. octaedra*). There may also be interactions between earthworms, nematodes and pH; according to Hyvönen et al. (1994), *D. octaedra* reduced the nematode populations in limed raw humus, but not in unlimed humus.

This experiment is part of a study on soil decomposer communities in anthropogenic birch forests, as compared with natural deciduous forests at the same latitude (Huhta 2002; Huhta and Niemi 2003). In the field study plots we

M. Rätty (✉)
Suonenjoki Research Station,
Finnish Forest Research Institute, 77600 Suonenjoki, Finland
e-mail: mika.ratty@metla.fi
Tel.: +358-10-2114857
Fax: +358-10-2114801

V. Huhta
Department of Biological and Environmental Science,
University of Jyväskylä, P.O. Box 35 (Ambiotica),
40351 Jyväskylä, Finland

observed that there was a negative relationship between earthworms and most other animal groups (Räty and Huhta, unpublished). We suggest that soil pH and the possibility of earthworms colonising a given forest stand determine the composition of the lumbricid community, which further influences the rest of the soil biota through interspecific interactions. In this context, the present experiment was designed to test the following hypotheses:

1. Soil pH affects the populations and community structure of earthworms, nematodes and enchytraeids.
2. The presence of earthworms affects the populations and community structure of nematodes and enchytraeids.
3. There are interactions between soil pH, earthworms and other components of the soil community.

Materials and methods

Experimental design

The experiment (Table 1) had a randomised three-factor design. Organic topsoil containing no earthworms or earthworm cocoons was taken from a silver birch (*Betula pendula* L.) plantation, established 30 years earlier after clear-cutting a spruce stand on an *Oxalis-Maianthemum* site (Cajander 1949), located 60 km north of Jyväskylä, central Finland (62° 48' N, 25° 57' E). The soil was classified as haplic podzol and the soil type was assorted coarse sand covered by mor humus. The soil material was passed gently through a 10-mm mesh to remove roots and other coarse material. Loss of ignition of the sieved humus was 83.5%. pH_{H2O} 4.9, and exchangeable NH₄⁺ content 6.8 µg g⁻¹ dry matter.

The experiment was carried out in 14-l plastic containers. Humus (3 kg w.m.) was weighed into 40 jars. Water content was adjusted and maintained to 60% of maximum water holding capacity (determined after 2 h draining of inundated soil samples). Lime (6 g CaCO₃/kg w.m. soil) was added to half of the jars and mixed thoroughly with the humus, resulting in a pH of 6.1.

Earthworms, *Aporrectodea caliginosa* (Savigny) and *Lumbricus rubellus* (Hoffmeister), were collected from a deciduous forest. Five adult and five juvenile or subadult specimens were transferred into each jar of the single-species treatments, and three and two specimens, respectively, of each species into the combined treatment jars (average live biomass per jar: *A. caliginosa* 5.85 g, *L. rubellus* 4.89 g, both together 5.57 g). Enchytraeids were extracted from a birch forest soil and the mixed community was inoculated into all units, including the controls [total 300 specimens per jar: *Cognettia sphagnetorum* (Vejdovsky) 41%, *Henlea nasuta* (Eisen) 9%, *Fridericia* sp. Michaelsen 8%, *Enchytronia parva* n. sp. 7%, *Bryodrilus ehlersi* Ude 4%, other species 29%]. Birch leaf litter (20 g per jar) was added as food supply for the earthworms, and more litter was added when needed. All jars were covered with plastic lids with an opening for aeration. The jars were incubated in a climate chamber at 15°C, and water was added monthly to compensate for evaporation.

Sampling and analyses

The experiment was started on 10 December 1999 and continued for 32 weeks. The nematode community was analysed at week 24 by taking subsamples of 2 g (f.m.) from each replicate. Nematodes were extracted using wet funnels, killed in hot water and stored in 70% water/29% alcohol/1% glycerol for enumeration. Feeding

Table 1 Experimental design (* adults + juveniles or subadults)

Species	Symbol	Number of specimens transferred	
		Unlimed	Limed
No earthworms	0	0	0
<i>Aporrectodea caliginosa</i>	C	5+5*	5+5*
<i>Lumbricus rubellus</i>	R	5+5*	5+5*
<i>A. caliginosa</i>	CR	3+2*	3+2*
+ <i>L. rubellus</i>		3+2*	3+2*

groups were determined according to Yeates et al. (1993), and allocation to c-p groups followed Bongers (1990).

Enchytraeids were sampled at week 32 from 0–6 cm in each jar, using a cylindrical corer with an aperture of 25 cm². Undisturbed samples were extracted using the wet funnel technique of O'Connor (1962). Extracts were stored at 5°C for up to 2 days, identified, measured, and their maturity status recorded. Species were identified according to Nielsen and Christensen (1959, 1961, 1963) and Dóza-Farkas (see Acknowledgements), Abrahamsen's (1973a, 1973b) equations of body volume and density were used to calculate the biomass of different species. Because the immature individuals of the genera *Fridericia* could not be identified, the genera was treated as one unit and assigned to Abrahamsen's class D.

Carbon dioxide evolution was measured repeatedly in the course of the experiment. At measurement the jars were aerated, and the aeration holes were then closed with rubber septa. Air samples were taken through the septa with a syringe, and the concentration of CO₂ was measured with an infrared universal carbon analyser (Unicarbo EQ 92) before and after 2-h incubation at 15°C. Microbial biomass was estimated at week 24 using the SIR (Substrate Induced Respiration) method (Anderson and Domsch 1978). Maximum respiration was achieved with glucose addition of 20 mg ml⁻¹ soil water (80% WHC).

Earthworms were collected by hand-sorting, stored for 2 days in moist paper to empty their guts, and weighed; pH_{H2O} was measured at the end of the incubation period.

Statistical treatments

The results were analysed using the SPSS 10.0 statistical package. For testing the treatment effects, two-way analysis of variance was used with the factor "pH" at two levels (lime and no-lime) and the factor "earthworms" at four levels (*L. rubellus* + *A. caliginosa*, *A. caliginosa*, *L. rubellus*, and control). The NPK test was used for paired comparisons. Normality of distributions was checked using the Kolmogorov-Smirnov test and homogeneity of variances using the Levene's test. The nematode data was *ln*-transformed prior to the analyses. The following indices and ratios of the nematode fauna were calculated for each sample as described by Yeates (1984, 1994, 1997) and Pielou (1975): species richness (SR), Shannon-Weaver Diversity Index (H'), Simpson's index of dominance (λ), ratio of bacterial-feeding to fungal + bacterial feeding nematodes (B/(B + F)), and maturity Index (Σ MI). To examine the structure of the nematode communities, Non-Metric Multidimensional Scaling (NMS; MjM software design PC-ORD 4.0) was used (McCune and Mefford 1999).

Table 2 Mean abundance (ind./g d.m. soil) of different taxa, feeding categories and various community indices of nematodes (CR both earthworms, C *Aporrectodea caliginosa*, R *Lumbricus*

Taxon	Unlimed				Limed				(P < 0.05) Difference between unlimed (U) and limed (L)
	CR	C	R	0	CR	C	R	0	
Total	10.7	12.7	11.4	35.2	37.2a	33.7a	34.9a	67.1b	U < L
Bacterial feeders	8.0	8.6	7.5	20.3	26.5a	24.3a	23.8a	51.8b	U < L
<i>Acrobeloides</i>	2.9	3.4	2.9	5.6	9.5a	8.3a	8.2a	15.2b	U < L
<i>Cervidellus</i>	0.3	0	0.1	1.0	0.3a	1.4a	0.5a	3.3b	U < L
<i>Prismatolaimus</i>	0	0.2	0.3	1.4	0.6a	0.4a	0.6a	1.3b	
<i>Plectus</i>	1.3	1.6	1.4	2.6	5.2a	3.3a	3.7a	8.1b	U < L
<i>Wilsonema</i>	0.1	0.2	0	2.2	1.0a	0.5a	0.5a	6.3b	U < L
<i>Teraocephalus</i>	0.8	0.5	0.5	1.3	2.4	2.1	2.8	3.2	U < L
<i>Euteratocephalus</i>	0.3	0	0	0.2	0.4	0.6	0	0.3	U < L
<i>Rhabditis</i>	1.7	2.6	2.0	4.2	6.4ab	6.1ab	5.1a	9.0b	
<i>Bunonema</i>	0	0	0	0.3	0a	0a	0a	0b	U < L
<i>Monhystera</i>	0	0.1	0.1	0.3	0.2a	0.4a	0.5a	1.2b	U < L
<i>Alaimus</i>	0.3	0.1	0.1	0.8	0.5	0.4	0.4	0.7	
<i>Metateratocephalus</i>	0.4	0.2	0.2	0.9	0.4a	1.0a	1.3a	2.2b	U < L
Fungal/root feeders	2.7	3.2	3.4	13.4	8.3a	6.1a	8.1a	10.6b	U < L
<i>Tylenchus</i>	0.8	1.0	0.9	2.4	3.3ab	1.5a	2.5ab	2.5b	U < L
<i>Ditylenchus</i>	0.5	0.5	0.5	2.2	1.1a	0.3a	0.5a	1.5b	
<i>Aphelenchoides</i>	0.1	0.3	0.3	2.9	2.3a	1.9a	2.3a	3.0b	U < L
<i>Tylencholaimus</i>	0.3	0.2	0.3	0.8	1.5	1.0	1.6	0.7	U < L
<i>Malenchus</i>	0.6	1.1	0.7	2.9	0.1a	1.0a	0.7a	1.9b	
<i>Paratylenchus</i>	0.3	0.1	0.7	2.3	0.3a	0.4a	0.4a	0.9b	
Omnivores	0	0.3	0	0.2	0.8a	1.6ab	1.0ab	2.1b	U < L
Unclassified	0	0.3	0.5	1.1	0.7ab	0.3a	1.1ab	1.3b	
No. of taxa	9.40	9.20	9.40	15.80	11.80a	12.40a	12.60a	15.20b	U < L
Species richness SR	1.21	1.16	1.21	1.83	1.32a	1.41a	1.44a	1.62b	
Shannon diversity H'	1.97	1.88	2.00	2.53	2.10a	2.11a	2.20a	2.40b	
Shannon equitability J	0.88	0.85	0.88	0.92	0.84	0.84	0.87	0.87	
Simpson diversity λ	0.17	0.19	0.17	0.13	0.17a	0.17a	0.14a	0.12b	
Ratio bf/bf' + ff'	0.81	0.81	0.77	0.70	0.76	0.85	0.79	0.88	U < L
Maturity index ΣMI	2.00	1.75	1.87	1.91	2.10	2.02	2.10	2.02	U < L

rubellus, 0 no earthworms). Significant differences ($P < 0.05$) between CR, C, R and 0 within unlimed and limed are labelled with a different letter

Results

Earthworm population

Numbers and biomass of earthworms (both species) decreased during the incubation; at the end the total numbers ranged from 4 to 11 per jar in each treatment, except the controls. *L. rubellus* was able to reproduce during the experiment, since juveniles were found in spite of decreasing biomass. *A. caliginosa* reproduced only in the presence of *L. rubellus*. When the latter species was absent, the biomass of *A. caliginosa* was higher but no juveniles were found.

Nematode populations and community structure

The mean numbers of nematodes were relatively low in all treatments when compared to those in raw humus soils in natural conditions. In this investigation, 18 nematode genera were recorded. The mean abundances of the most common taxa are given in Table 2. Bacterial feeders dominated, with *Acrobeloides* being the most abundant. Numbers of root/fungal feeders and omnivores were low, and no predators were found in any treatment (Fig. 1)

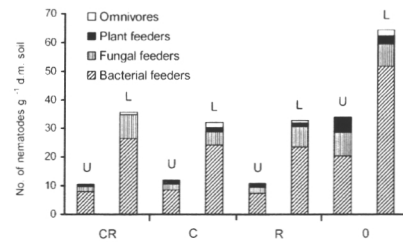


Fig. 1 Mean numbers of nematodes (individuals g⁻¹ dry matter soil), and proportions of different feeding groups (CR both earthworms, C *A. caliginosa*, R *L. rubellus*, 0 no earthworms, U unlimed, L limed)

pH and earthworms had treatment-specific effects on the community of nematodes. The presence of earthworms reduced the total abundance of nematodes and decreased the species richness of the nematode community, independently of pH (Table 2). Differences in total nematode numbers were mainly caused by changes in a few taxa, *Acrobeloides*, *Cervidellus*, *Prismatolaimus*, *Plectus*, *Rhabditis* and *Wilsonema*, whereas the genera

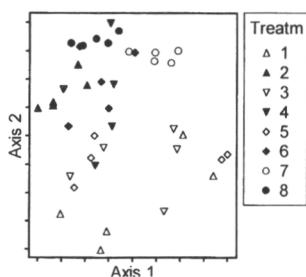


Fig. 2 Plot diagram of nematode communities in the NMS ordination (selected two axes in a three-axis solution). Treatments: *Open shapes* no lime; *closed* limed; 1, 2 both earthworms; 3, 4 *A. caliginosa*; 5, 6 *L. rubellus*; 7, 8 no earthworms

Teratocephalus, *Euteratocephalus*, *Alaimus* and *Tylencholaimus* did not respond to the presence of earthworms.

Total numbers of nematodes were about two to three times greater at higher pH than at lower pH. Omnivores were found almost exclusively in limed soil. However, pH had no significant effect on various diversity indices except that the number of taxa was higher in limed soil. Ratio of bacterivorous to fungivorous nematodes was markedly higher in manipulated pH (Table 2), but only in the absence of earthworms. The nematode maturity index (ΣMI) was significantly lower in unlimed soil and in the presence of *A. caliginosa* or *L. rubellus* (separately). This change was mainly due to the decreased proportion of bacterivorous taxa at low pH, assigned to c-p group 2, and the increase in proportion of omnivorous nematodes at higher pH (c-p group 4). No differences were found when both earthworms were present, nor in the limed treatments.

NMS-ordination clearly separates the nematode communities of limed humus from those of unlimed: all sample points representing limed treatments are located in the upper left quarter of a representative two-axis space (Fig. 2), while those of unmanipulated humus are distributed over the rest of the area. The points representing humus without earthworms form a relatively compact group at the top of the diagram, limed and unlimed close to each other, while those showing the communities of nematodes together with earthworms are widely scattered.

Enchytraeid populations and community structure

In all treatments the total numbers of enchytraeids were clearly lower than in original forest humus (cf. Huhta et al. 1986), and the presence of earthworms further decreased their densities. In general, only 8 of the 18 species were able to maintain their populations during the incubation (Table 3, Fig. 3). In unlimed soil, no enchytraeids were found in the presence of earthworms. When earthworms were absent, *Cognettia sphagnetorum* and

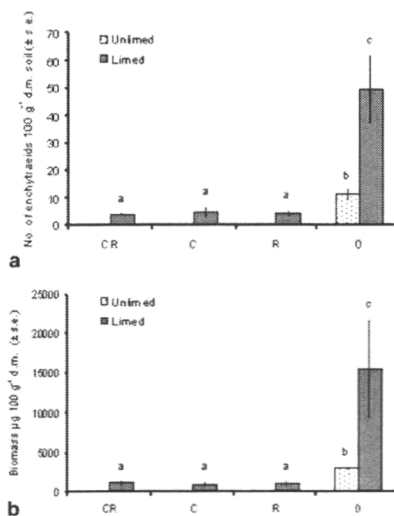


Fig. 3 Mean numbers (ind. 100 g^{-1} d.m. soil \pm SE) and biomass ($\mu\text{g } 100\text{ g}^{-1}$ d.m. soil \pm SE) of enchytraeids (CR both earthworms, C *A. caliginosa*, R *L. rubellus*, 0 no earthworms). Significant differences ($P < 0.05$) between CR, C, R and 0 within unlimed and limed are indicated with a different letter

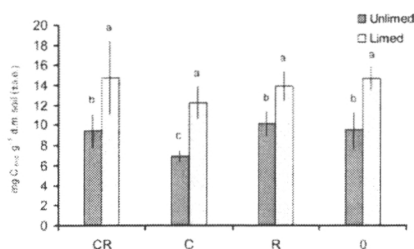


Fig. 4 Estimated microbial biomass C ($\text{mg } C_{\text{mic}}\text{ g}^{-1}$ d.m. soil \pm SE) in untreated and limed humus with different faunal composition (CR both earthworms, C *A. caliginosa*, R *L. rubellus*, 0 no earthworms). Significant differences ($P < 0.05$) between CR, C, R and 0 within unlimed and limed are indicated with a different letter

Bryodrillus ehlersi were found in small numbers. In limed soil some species (*E. buchholzia*, *H. nasuta*, *C. sphagnetorum* and *E. parva*) were able to reproduce and maintain populations even in the presence of earthworms. *E. parva*, *E. buchholzia*, *Friderizia* spp. and *C. sphagnetorum* were the dominant species in limed soil.

Soil microbes and community respiration

Liming increased the response of the microbial biomass (SIR: ANOVA: $f = 0.283$, $p < 0.001$; Fig. 4). Earthworms

Table 3 Mean abundance (ind./100 g d.m.) of enchytraeids in different treatments (CR both earthworms, *C. Aprrectodea caliginosa*, *R. Lumbricus rubellus*, 0 no earthworms). Significant

differences ($P < 0.05$) between CR, C, R and 0 within unlimed and limed are labelled with a different letter

Taxon	Unlimed				Limed				$P < 0.05$ difference between unlimed and limed
	CR	C	R	0	CR	C	R	0	
Total	-	-	-	11.0	4.1a	4.6a	4.3a	49.5b	U < L
<i>Bryodrilus ehlersi</i>	-	-	-	0.87	-a	-a	-a	0.7b	
<i>Mesenchytraeus pelicensis</i>	-	-	-	-	0.4	-	-	0.2	U < L
<i>Enchytraeus buchholzi</i>	-	-	-	-	1.1	1.3	1.3	3.6	U < L
<i>Enchytraeus lacteus</i>	-	-	-	-	0.2	-	0.8	2.7	U < L
<i>Henlea</i> sp.	-	-	-	-	-a	-a	-a	0.9b	U < L
<i>Henlea perpusilla</i>	-	-	-	-	-a	-a	-a	155b	
<i>Henlea nasuta</i>	-	-	-	-	0.9a	1.1a	1.6a	14.7b	U < L
<i>Fridericia</i> sp.	-	-	-	-	-	-	-	0.60	
<i>Fridericia bulboides</i>	-	-	-	-	-a	0.2a	-a	1.4b	U < L
<i>Fridericia razelli</i>	-	-	-	-	0.2a	0.2a	0.2a	1.7b	U < L
<i>Cognettia sphagnetorum</i>	-	-	-	9.9	-a	-a	-a	2.3b	U < L
<i>Enchytronia parva</i>	-	-	-	-	1.4a	0.7a	0.5a	4.9b	U < L
No. of taxa				2.00	2.00a	2.20a	2.20a	6.80b	U < L
Species richness SR				0.44	0.66a	0.69a	0.61a	1.50b	U < L
Shannon diversity H'				0.38	0.59a	0.60a	0.56a	1.40b	U < L
Simpson diversity λ				0.78	0.60a	0.63a	0.67a	0.35b	U < L

generally had no significant effect on microbial biomass, though it was markedly lower when *A. caliginosa* was present in unlimed soil. Basal respiration was measured monthly throughout the experiment. No significant treatment effects were found in long-term CO₂ evolution, but average respiration was somewhat lower in the control without earthworms.

Discussion

Replacement of softwood trees by birch or a mixture of deciduous trees in a coniferous stand is associated with marked changes in the soil (Chapman et al. 1988; Nordén 1994; Willis et al. 1997; Priha 1999). It was shown by Huhta (1979) that a simple application of birch litter is enough to cause a distinct change in the earthworm populations even without manipulation of pH. The present experiment demonstrates that existing populations of lumbricids will further affect the composition and biomass of the nematode and enchytraeid communities. These two factors, pH and earthworms, affect the soil biota both directly and in interaction with each other.

Effects of pH

Soil pH is one of the principal physicochemical parameters that control the distribution and activity of many soil animals, and also affect animal/microbial interactions (Richards 1987; Killham 1994). In general, earthworms are absent in very acid soils (pH < 3.5) and are sparse in soils with pH below 4.5 (Curry 1998). While there are considerable differences among earthworm species in their pH preferences, *L. rubellus* and *A. caliginosa* are found in nearly all kind of soils from neutral moulds down

to pH 4 (Stöp-Bowitz 1969). Although *A. caliginosa* rarely occurs in coniferous forests, it is commonly found together with *L. rubellus* in various habitats. In our experiment the numbers and biomass of earthworms decreased during incubation. However, despite the soil pH decreasing slightly in all treatments (including the control), the upper and lower limits of pH fell well within the range of both species. Therefore it is unlikely that the decrease of earthworms was caused by soil acidity. However, no decline was observed when both species were present. While interspecific competition generally plays a major role in earthworm communities, co-existence seems to be advantageous to these two species, probably due to their different feeding habits (Curry 1998).

Liming substantially increased the nematode numbers, and also affected species composition of the assemblage. Much of this increase was due to bacterial-feeding species. Consequently, a change in the ratio of bacterial-feeding to fungal-feeding nematodes was recorded. This suggests a shift in the microbial community in favour of bacteria. Estimated total microbial biomass (SIR) was also higher in limed than in unlimed humus.

pH also significantly affected the community of enchytraeids. These were more abundant in limed than in unlimed soil; *C. sphagnetorum* and *B. ehlersi* were the only species in the unlimed treatment with no earthworms, and in the presence of earthworms enchytraeids were totally lacking. The results are in line with earlier records that only a few enchytraeid species are tolerant to low pH (Standen 1980; Huhta 1984; Graefe 1989; Didden 1993).

Effects of earthworms

Reduced numbers of nematodes were associated with the presence of earthworms. Decrease of nematodes under the influence of earthworms has also been reported by Yeates (1981). This might indicate competition for resources (microbes as food) between nematodes and earthworms. Elliott et al. (1980) demonstrated that earthworms can compete for food with bacterial-feeding nematodes. However, Hyvönen et al. (1994) found no reduction of bacteria in the presence of earthworms, in fact a slight increase was observed. In our experiment, total microbial biomass (SIR) decreased only in the presence of *A. caliginosa* (alone) in unlimed soil, thus giving no explanation to the decrease of nematodes. Some workers have reported dead nematodes in the digestive systems of lumbricids (Munt'yan et al. 1969; Dash et al. 1980). This indicates that, by feeding on their substrate, earthworms may accidentally ingest nematodes, but Dash et al. (1980) have suggested that such feeding may also be selective. Thus the decline of nematodes in the presence of earthworms is more likely to be due to predation by earthworms than to food competition (Cole et al. 2000).

The presence or absence of earthworms appeared to be a fundamental factor in determining the biomass and composition of the enchytraeid community. In unlimed soil, no enchytraeids were found in the presence of earthworms. *Cognettia sphagnetorum* has been reported to be sensitive to competition with the earthworm *Dendrobaena octaedra* (Huhta and Viberg 1999). Hyvönen et al. (1994) reported that *D. octaedra* did not affect the biomass of *C. sphagnetorum* in unlimed humus, whereas in limed soil it caused a considerable decrease of enchytraeids. *D. octaedra* also lost weight throughout the experiment, indicating reduced feeding activity. The enchytraeid *C. sphagnetorum* is considered to be a keystone species in the humus layer of ferric podzols, in terms of its biomass and function in the soil processes (Laakso and Setälä 1998; Huhta and Viberg 1999). In dry, acid pine forests it almost entirely replaces the functionally similar earthworms that have the key position in less acid and more productive forests (Persson et al. 1980; Huhta et al. 1986).

Conclusions

The results seem to support the three hypotheses suggested in the introduction. (1) Rise of soil pH after liming increases bacterial feeding nematodes, numbers and biomass of enchytraeids, and total microbial biomass (SIR). A change in the community structure of enchytraeids takes place and the effect of pH depends on species. (2) The presence of earthworms decreases the populations of nematodes and enchytraeids, and changes the nematode community structure. (3) There are interactions between components of the soil biota, and between soil biota and pH: *A. caliginosa* reproduced only in the presence of *L. rubellus*, and the earthworms

maintained their biomass only when both species were present. The ratio of bacterivorous to fungivorous nematodes was higher in limed soil only in the absence of earthworms. Microbial biomass decreased when *A. caliginosa* was present in unlimed soil.

Thus we conclude that a change in pH combined with presence or absence of earthworms may exert significant influences on other soil biota, and further on the vital ecosystem processes.

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V

Growth of *Lumbricus terrestris* and *Aporrectodea caliginosa* in an acid forest soil, and their effects on enchytraeid populations and soil properties

MIKA RÄTY

Finnish Forest Research Institute, Suonenjoki Research Station
FI-77600 Suonenjoki, Finland; mika.raty@metla.fi
Tel. +358 10 211 4857, fax: +358 10 211 4801

Summary

A laboratory experiment was carried out to test the hypothesis that the earthworms *Lumbricus terrestris* and *Aporrectodea caliginosa* are able to maintain their populations and reproduce in the acid forest soil of a deciduous forest where no lumbricids were found in the field. The experiment was conducted in 45-l containers in which layers of mineral subsoil, humus and organic topsoil collected from the site were established. Both species survived and at least *L. terrestris* reproduced during the 60 weeks' incubation. Burrows and middens of *L. terrestris* were recorded and quantities of litter consumed were estimated. The presence of lumbricids increased the organic matter concentration of humus, reduced the acidity of the topsoil and humus layers, and suppressed the population of the enchytraeid *Cognettia sphagnetorum*. A dense population of *Enchytraeus albidus* was found in *L. terrestris* middens. I concluded that edaphic factors do not explain the absence of earthworms, but isolation from cultural landscapes and lack of opportunity to colonize the site from the surroundings are the decisive factors.

Keywords: Earthworms; *Lumbricus terrestris*; *Aporrectodea caliginosa*; Colonization; Enchytraeidae; *Enchytraeus albidus*

Introduction

Earthworms are the most important group of soil fauna in temperate deciduous forests (Edwards and Bohlen, 1996). Also in boreal regions earthworms may be represented by several species and a considerable biomass in fertile forest types (Terhivuo, 1988), including moist, less acid coniferous forests in the south (Abrahamsen, 1972; Huhta and Koskenniemi, 1975). By contrast, in dry and acid forest soils and at higher latitudes earthworms are lacking or represented by a sparse population of the acid-tolerant *Dendrobaena octaedra*, leaving the enchytraeid *Cognettia sphagnetorum* as the dominating component of the soil fauna (Huhta, et al. 1986).

Endemic lumbricids are lacking in Fennoscandia due to the Pleistocene glaciation. Thus the present species are post-glacial immigrants, and casual transport by man obvi-

ously plays a decisive role in their dispersal (Lee, 1985). *Lumbricus terrestris* and *Aporrectodea caliginosa* are among the most common and widespread species that regularly occur in most cultivated soils. They are also commonly found in forest habitats in association with epigeic lumbricids such as *D. octaedra*, *Lumbricus rubellus* and *Dendrodrilus rubidus* (Terhivuo, 1988; Rätty and Huhta, 2004).

Interspecific competition presumably prevails in earthworm communities, but co-existence may well be possible for species with different feeding habits (Curry, 1998). Concerning burrowing species, the mesohumic endogeic species *A. caliginosa* forms a network of horizontal burrows and ingests large quantities of low quality soil, processing it through its efficient digestive system. By contrast, the anecic *L. terrestris* forms permanent vertical burrows and feeds on high quality litter collected from the soil surface (Doube and Brown, 1998). Due to the ecological disparity of these species their habitat requirements only partially overlap, which may enable their coexistence. However, Terhivuo (1989) addressed that rather few species co-occur particularly in high frequencies and that negative associations may prevail in fertile soils, whereas in extreme biotopes associations, either positive or negative, are insignificant.

Earthworms exert marked influences on several soil physico-chemical properties (Lee, 1985; Haimi and Huhta, 1990; Haimi and Boucelham, 1991; Edwards and Bohlen, 1996; Lavelle and Spain, 2001). Transformation of mor or moder humus into mull has been associated with the activity of an earthworm populations (Bernier and Ponge, 1994; Parkinson and McLean, 1998). Earthworms also have a considerable effect on populations of other soil fauna (Parkinson and McLean, 1998; Huhta and Viberg, 1999; Maraun and Scheu, 2000; Rätty and Huhta, 2003a).

The reason for the present experiment originates from a recent observation that earthworms were totally lacking in a fertile deciduous forest, where the presence of a diverse community could be expected (Rätty and Huhta, 2004). Absence of earthworms obviously explained the presence of a thick, unmixed and non-aggregated organic horizon of mull type. The soil pH at the site (4.5 – 4.7) was lower than in deciduous forests with earthworms, but yet in the range of the common burrowing species (Satchell and Lowe, 1967; Curry, 1998). The aim of the experiment was to test the hypothesis that *L. terrestris* and *A. caliginosa* are able to maintain populations in the soil of the forest stand in question. I also measured how earthworms affect soil acidity, organic matter distribution and populations of Enchytraeidae. The experiment is part of a study on soil decomposer communities in anthropogenic birch forests in central Finland (Huhta, 2002; McLean and Huhta, 2002; Huhta and Niemi, 2003; Rätty and Huhta, 2003a; Rätty and Huhta, 2003b; Rätty and Huhta, 2004).

Materials and methods

Soil materials for the experiment were taken from a deciduous forest where no earthworms were detected in a preceding study (Rätty and Huhta, 2004). The soil type at the site was fine sand covered by a thick (30-40 cm), layered organic horizon of mull humus type. Loss on ignition of the humus was 37%, pH (H₂O) 4.5, exchangeable NH₄⁺ content 27 ¼g g⁻¹ dry matter and content (% of weight) of water stable aggregates 3.0. Detailed description of the site is given by Rätty and Huhta (2003b).

Table 1. Mean number and biomass (in brackets) of earthworms and enchytraeids (data from middens not included), and mean biomass per specimens of earthworms (g f.w. / individual) at the beginning (week 1) and the end of the experiment. NE = control without earthworms. Significant differences between sampling dates are indicated with an asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Earthworms	week 1		week 60		NE (week 60)
	No. and g f.w./ tub	g f.w./ individual	No. and g f.w./ tub	g f.w./ individual	
<i>L. terrestris</i> (mature)	2.0 (4.94)	2.48	2.2 (8.62)	3.56	
<i>L. terrestris</i> (juv.)	1.0 (0.77)	0.76	1.3 (1.29)	0.91	
<i>L. terrestris</i> (total)	3.0 (5.71)	1.90	3.2 (9.91)	2.61	
<i>A. caliginosa</i> (mature)	5.0 (3.97)	0.79	1.1** (1.11**)	0.79	
<i>A. caliginosa</i> (juv.)	5.0 (2.00)	0.39	4.8 (1.82)	0.41	
<i>A. caliginosa</i> (total)	10.0 (5.97)	0.59	5.8 (2.93)	0.56	
Earthworms (total)	13.0 (11.68)		9.0 (12.86)		
Enchytraeids	No. and mg 100 g ⁻¹ soil (d.m.)		No. and mg 100 g ⁻¹ soil (d.m.)		No. and mg 100 g ⁻¹ soil (d.m.)
<i>C. sphagnetorum</i>	69.1 (20.80)		7.9** (2.38**)		61.7 (18.64)
<i>C. glandulosa</i>	3.8 (1.15)		- **		- **
<i>B. ehlersi</i>	3.6 (1.34)		3.2 (1.14)		20.3* (5.66*)
<i>Fridericia</i> spp.	0.5 (0.08)		1.8 (0.82)		1.9 (0.81)
Enchytraeids (total)	77.0 (23.62)		12.9** (4.34**)		83.9 (25.1)

The experiment was carried out in nine 45-l plastic tubs. Each soil layer (mineral subsoil, humus and incompletely decomposed topsoil) was collected separately, and a total of 20 kg (f.m.) of soil material was spread layer by layer in each container. The resulting soil columns were 50 cm thick with a surface area of 800 cm². Water content was adjusted to 60% of maximum water holding capacity of humus and water was added monthly to compensate for evaporation. Earthworms, *Aporrectodea caliginosa* and *Lumbricus terrestris*, were collected from the field and kept 48 h in moist paper to empty their guts for weight determination. In order to avoid confusion between juvenile *Lumbricus* spp., *L. terrestris* was collected from a site where *L. rubellus* and *L. castaneus* were known to be absent. Three adult or juvenile specimens of *L. terrestris*, and ten adult or juvenile specimens of *A. caliginosa* (average biomass 5.71 g and 5.97 g f.m., respectively) were transferred into each of six tubs; the remaining three were left as controls. The endemic enchytraeid community in the soil was determined; it consisted of *Cognettia sphagnetorum* (89%), while other species (*Bryodrilus ehlersi*, *Cognettia glandulosa* and *Fridericia* spp.) occurred in low numbers (Fig. 2, Table 1). Mixed, moistened litter of birch and alder (80/20 by weight) was spread on the soil surface (20 g per tub) as food for the earthworms, and more litter was added later when needed. The containers were covered with plastic lids with an opening for aeration, and incubated in a climate chamber at 15°C, which is the optimum temperature for development of *L. terrestris* (Daniel et al., 1996).

The experiment was started on 15th September 2000, and the incubation continued for 60 weeks. After 12 weeks the temperature was decreased stepwise down to 5°C for three months to simulate winter conditions. Soil samples for physico-chemical analyses, each consisting of two sample units from each container, were taken from each soil layer using a cylindrical corer (area 10 cm²). Additional samples were taken from the *L. terrestris* middens, when such were present. Enchytraeids were sampled correspondingly, two units of 25 cm² being taken from the topsoil layer (0-5 cm depth) and additional samples from the middens. Enchytraeids were extracted using the wet funnel technique (O'Connor, 1962), and identified. Litter consumption was monitored during the incubation, and remaining litter was weighed at the end. At the termination of the experiment, earthworms were collected from the soil by hand-sorting, stored for 48 hours in moist paper, and weighed.

The results were analyzed using the SPSS 11.0 statistical package. Differences in numbers and biomass of lumbricids were analyzed using the non-parametric Mann-Whitney and Kruskal-Wallis tests. One-Way ANOVA with the Tukey's test for pairwise multiple comparisons was used to test the treatment effects on pH and organic matter concentration. Normality of distributions was checked using the Kolmogorov-Smirnov statistic with a Lilliefors test, and homogeneity of variances using the Levene's test.

Results

L. terrestris became well established in the containers; litter was consumed and middens were created (1-3 per tub). Numbers of *L. terrestris* remained unchanged after the 60 weeks' incubation (Table 1). The mean biomass (both adults and immatures) increased during the experiment, but statistically the difference was masked by an extreme variation among replicates: *L. terrestris* was totally absent in one unit (it possibly died or escaped in an early phase). The mean weight of the (remaining) mature specimens increased slightly but not significantly due to high variation among the replicates (Table 1). Numbers and biomass of mature *A. caliginosa* decreased significantly during the incubation, while those of immatures remained unchanged (Table 1). The average individual weight of *A. caliginosa* (both adults and immatures) did not change during the experiment.

Litter breakdown was distinct when lumbricids were present. During the incubation, on average 91.6 g (d.m.) of litter was consumed in each tub with earthworms (low consumption in the replicate where *L. terrestris* disappeared). At the end, the initially homogeneous and non-aggregated mull had developed a crumb structure in the topsoil, particularly in the middens. Cocoons of *L. terrestris* were frequently found in the soil matrix close to the burrows (not quantitatively determined).

The presence of earthworms drastically depressed the enchytraeid numbers, roughly to one fifth compared to the initial density (Table 1, Fig. 1). Most of the decline was due to *Cognettia sphagnetorum*, whereas *Bryodrilus ehlersi* and *Fridericia* spp. were able to maintain their populations through the incubation period. In the absence of earthworms, numbers and biomass of enchytraeids remained unchanged, and the community structure resembled the initial composition, except that *Cognettia glandulosa* was absent at the end (Table 1, Fig. 1). *Enchytraeus albidus* was found only in *L. terrestris* middens, where it comprised a dense (64.8 specimens and 6.3 mg 100 g⁻¹

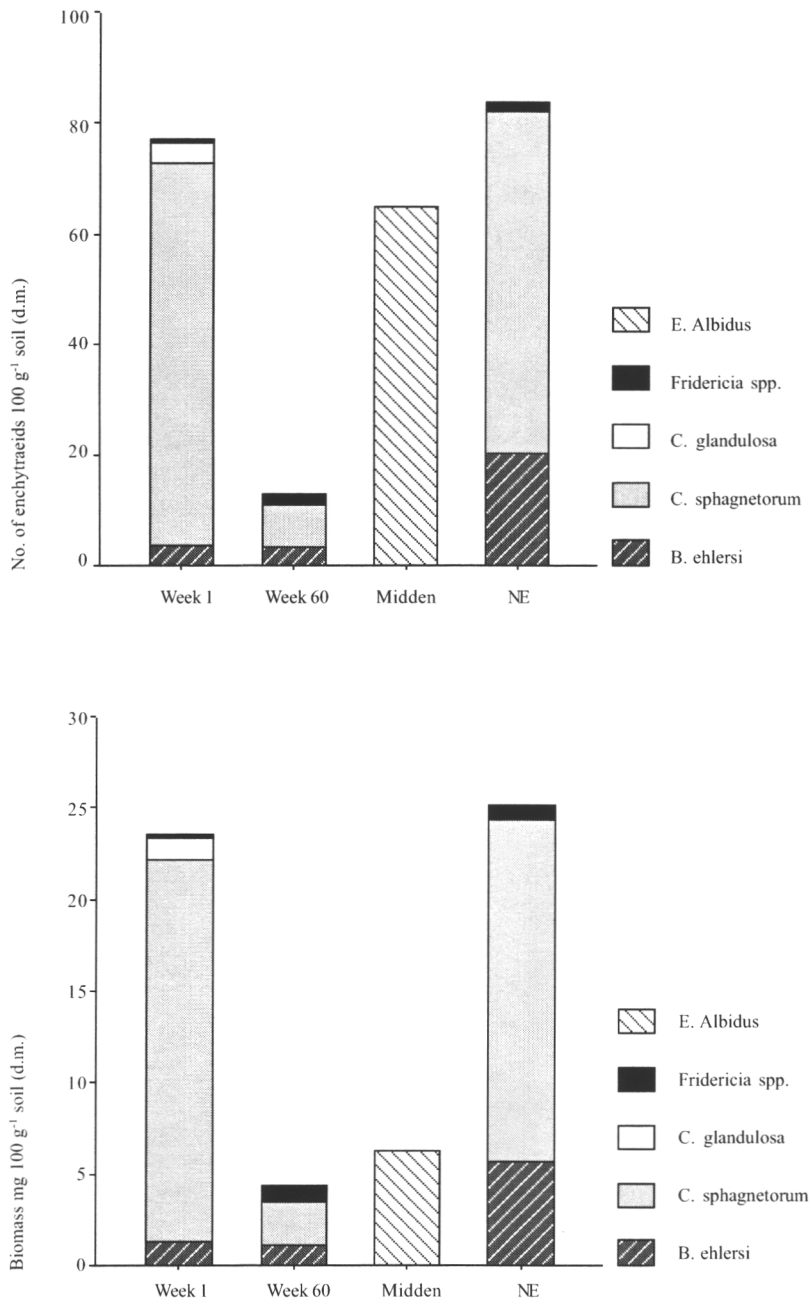


Fig. 1. Abundance (specimens 100 g⁻¹ soil d.m.) and biomass (mg 100 g⁻¹ soil d.m.) of the enchytraeids at the beginning (week 1) and the end (week 60, soil and middens separately) of the experiment. NE = control without earthworms.

d.m. of soil) one-species community (Fig. 1). *E. albidus* was not native in the soil that was used for the experiment.

In the control containers without earthworms, the pH remained unchanged during the incubation in all soil layers. The presence of earthworms increased the pH significantly in topsoil and humus (Fig. 2). pH was also elevated in the *L. terrestris* middens. Organic matter content increased in the humus layer when earthworms were present. In the middens the OM content was lower than in the bulk topsoil (Fig. 2).

Discussion

The present experiment verified hypothesis that *L. terrestris* and *A. caliginosa* are able to survive and maintain their populations in the acid mull soil where earthworms were absent in the field. *A. caliginosa* is a eurytopic species inhabiting a variety of habitats, frequently in coexistence with *L. terrestris*. Both species are commonly found in rich mull soils, deciduous forests, riparian alder stands, meadows etc. (Stöp-Bowitz, 1969; Terhivuo, 1988; Rätty and Huhta, 2004). They are normally absent in acid coniferous forest soils, but on the other hand, complete absence of lumbricids is exceptional in deciduous forests of the southern boreal region. Our recent finding of this kind suggests that besides soil characteristics and litter quality, previous land use history and human influence may markedly affect the composition of earthworm communities (Rätty and Huhta, 2004). Passive transport by man is a notable agent in the dispersal of earthworms (Lee, 1985). Consequently, invasion of species into new habitats and the ultimate composition of the community are partially determined by the cultural history of the site. Certainly, edaphic factors are also crucial, and soil pH is generally regarded as the most important of them. Most earthworm species are absent from acid soils (pH < 3.5) and sparse in semi-acid soils (pH < 4.5) (Curry, 1998). The present experiment reveals that *L. terrestris* and *A. caliginosa* can survive and even reproduce in the soil taken from the site (pH 4.5-4.7); thus acidity cannot explain the absence of earthworms. One reason could be periodical flooding; waterlogged and anaerobic soils may be noxious particularly for deep-burrowing species (Curry, 1998). However, in spite of its littoral situation the ground water table at the site was sufficiently low for *L. terrestris*. It should also be noted that earthworms were absent from a cultivated field in the vicinity of the study site. These facts together suggest that burrowing earthworms were absent because they have never colonized the site.

After 60 weeks' incubation the organic matter concentration in the humus layer was increased by the activity of earthworms. This indicates that mixing of the organic topsoil with deeper soil layers was in progress. Correspondingly, the organic matter in *L. terrestris* middens was lower than in the bulk topsoil, which reflects to the presence of mineral matter in the casts. The result also indicates that *A. caliginosa* had not penetrated the mineral subsoil, which would result in increase of organic matter content in subsoil.

In accordance with earlier findings (Haimi and Huhta, 1990), the presence of earthworms increased the pH value in the topsoil and humus layers. This observation indicates that earthworms were not absent at the field site because of acidity, but rather the pH was low due to the absence of earthworms. Increased pH may be associated with

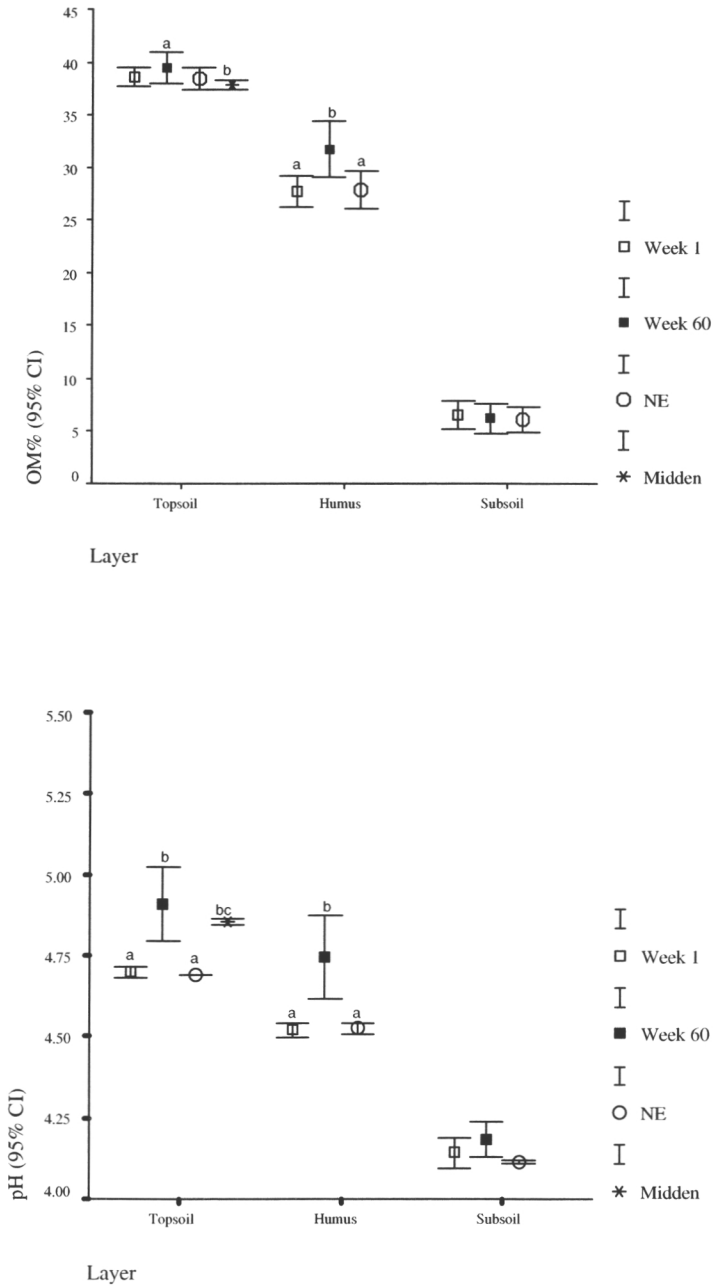


Fig. 2. Organic matter concentration (OM%) and pH in topsoil, humus and subsoil at the beginning (week 1) and the end (week 60, topsoil and middens separately) of the experiment. NE = control without earthworms. Error bars display confidence interval of 95%. Significant differences ($p < 0.05$) between treatments in each layer are indicated with a different letter.

increased content of organic matter with a higher pH than the mineral soil, and possibly direct alkalization due to cutaneous mucus excreted by earthworms (Haimi and Huhta, 1990; Schrader, 1994; Tiunov and Scheu, 1999).

It was demonstrated by the experiment that presence of earthworms drastically decreased the abundance and biomass of Enchytraeidae. Most of the decline was due to a single species *C. sphagnetorum*, which is considered as a keystone species in coniferous forest soils in terms of its biomass and function in soil processes (Laakso and Setälä 1998). In less acid and more productive forests it is replaced by functionally similar earthworms (Huhta et al., 1998). Antagonistic influence of earthworms on enchytraeids has also been observed in earlier studies: Huhta and Viberg (1999) reported that the epigeic species *D. octaedra* depressed the population of *C. sphagnetorum*. Rätty and Huhta (2003a) showed that *A. caliginosa* and *Lumbricus rubellus* greatly reduced enchytraeid populations.

In the *L. terrestris* middens, a dense population of the enchytraeid *E. albidus* was found. The species was absent in the bulk soil, thus it was probably accidentally introduced into the soil together with earthworms. *E. albidus* is a widely distributed cosmopolitan species, which is commonly found in composts and related accumulations of organic waste, but also in arable soils (Nielsen and Christensen, 1959). The species probably benefits from the rich cutaneous excretions of earthworms, and became therefore established in the middens. *L. terrestris* casts and middens may be inhabited by several soil animal taxa, and they also differ from the surrounding soil in their microbial populations (Maraun et al., 1999; Tiunov and Scheu, 2000a; Tiunov and Scheu, 2000b).

Mean biomass and abundance of *L. terrestris* (123.9 g m⁻², 40.0 specimens m⁻²) at the end of the incubation was comparable to that found in complex earthworm assemblages in deciduous forest soil, where the population density of *A. caliginosa* was also extremely high (170 specimens m⁻²) (Rätty and Huhta, 2004). Due to ecological disparities of the species with different ecological character, their habitat requirements may only partially overlap enabling their coexistence. However, Terhivuo (1989) found rather few associations among the species in extreme biotypes, while in more fertile soils negative associations may had been more consequential. Thus it may be possible that the observed population density of *L. terrestris* suppressed the abundance of mature *A. caliginosa*.

In conclusion, the experiment revealed that *L. terrestris* and *A. caliginosa* can maintain their populations, and *L. terrestris* at least was able to reproduce in the soil taken from a deciduous forest where no field populations were present. This indicates that edaphic factors do not explain the absence of earthworms, but isolation from cultural landscape and lack of possibilities to colonize the site from the surroundings is the decisive factor. When experimentally introduced, the lumbricids started the process of mixing soil materials, increased the pH value and suppressed the population of the enchytraeid *C. sphagnetorum*.

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