Soil Animal Communities of Planted Birch Stands in Central Finland

Veikko Huhta and Mika Räty

Huhta, V. & Räty, M. 2005. Soil animal communities of planted birch stands in central Finland. Silva Fennica 39(1): 5–19.

The aim of this study was to compare soil animal communities in planted birch (*Betula pendula*) stands of different origin with each other and with natural forests. Six 30-year-old birch stands were investigated, three planted after clear-cutting of spruce stands, and three planted on cultivated soil. The faunal communities were markedly different in plantations established on spruce forest soil and on arable soil. "Birch after Spruce" communities were relatively similar to those of coniferous forests, though the population densities were generally lower. "Birch after Field" communities were sparse and could be characterised as "impoverished forest communities", except in Lumbricidae and Enchytraeidae that have affinities with deciduous forests and cultural landscapes. Soil conditions are not sufficient to explain the differences between the forests. Colonisation and transport by man may determine the presence of certain species, especially earthworms. These in turn affect soil properties, and compete with or otherwise have negative effects on other soil fauna. Thus the community differences between different forests are an outcome of several factors: soil characteristics, site history, colonisation ability and interspecific interactions.

Keywords birch, forest management, plantations, soil fauna

Authors' addresses *Huhta*: Department of Biological and Environmental Science, University of Jyväskylä, P.O.Box 35, 40014 Jyväskylä University, Finland; *Räty*: Ojalanlenkki 4, 80140 Joensuu, Finland
E-mail v.huhta@pp.inet.fi

Received 16 June 2004 **Revised** 24 August 2004 **Accepted** 24 August 2004

1 Introduction

Nordic coniferous forests have undergone many changes under the human influence. The old slash-and-burn agriculture that after clear-cutting and some years of cultivation left the ground open for natural succession favoured development of deciduous stands, mainly composed of the birch species (*Betula pendula* and *B. pubescens*), but also other species such as *Alnus incana*, *Populus tremula* and *Sorbus aucuparia*. If left undisturbed, communities are gradually replaced by the two climax tree species, the conifers Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). In the 20th century, the slash-and-burn practice was abandoned, and the more modern forestry approach tended to grow spruce or pine in monocultures, saplings of deciduous trees being destroyed mechanically or by using herbicides. This strongly reduced the proportion of deciduous or mixed stands in the total forest area. During the last two decades an opposite tendency has prevailed: a mixture of deciduous trees, silver birch (*B. pendula*) being the most favoured, is recommended in practical forestry. In addition, abandoned fields are most usually reforested by silver birch, as a result of which young birch stands of homogeneous age structure are now commonly seen (Finnish Forest Research Institute 1992). In the future, expected warming of the global climate will probably further contribute to the change of boreal forests in favour of broad-leaved trees (Kellomäki et al. 1996).

Facing these trends, it is important to know more about biological changes in forest soils accompanying the alterations in stand composition. Will the community structure in coniferous forest soil after replanting with birch resemble that of a natural deciduous forest? To what extent does the decomposer community of a birch stand established on cultivated land change towards a forest soil community, or does it rather retain the character of arable soil? What are the mechanisms that regulate these changes?

The forest floor at boreal and temperate latitudes harbours an abundant and diverse soil faunal community, but there are also marked differences between different kinds of forests. In coniferous forest soils with low pH, microarthropods and enchytraeids predominate, while in less acid deciduous forests "macrodecomposers" such as diplopods, isopods and earthworms contribute essentially to the total biomass (Macfadyen 1963, Petersen and Luxton 1982). Related differences are even found within deciduous forests on different soil types (Schaefer and Schauermann 1990). The soil fauna of Nordic coniferous forests is relatively well known; several studies have been published, together covering all major animal groups. On the other hand, quantitative assays in deciduous forests are scarce and casual, almost restricted to a single paper (Axelsson et al. 1984). The microarthropod fauna of a beech forest in Denmark was thoroughly studied by Luxton (1981a,b,c,d,e) and Petersen (1980).

The present paper summarizes the results of a recent study, the aim of which was to compare the decomposer communities of anthropogenic birch stands of different origin with each other, and with those of natural forests and arable soils at the same latitude. Detailed results on each main group of organisms have been or will be published elsewhere (Huhta 2002, McLean and Huhta 2002, Huhta and Niemi 2003, Räty and Huhta 2003a, 2004a, b, Huhta et al. 2005). As the community structure is thoroughly described in these papers, the present report tends only to summarize the species-level data, and mainly concentrates on soil properties and vegetation, faunal biomasses and general conclusions.

2 Material and Methods

2.1 Site Description

Six planted birch (*Betula pendula*) stands were investigated. Three of these were planted 28 to 33 years prior to the study after clear-cutting of spruce stands ("Birch after Spruce", symbol BS), and three were planted 26 to 43 years earlier on arable soil ("Birch after Field", BF). The soil type of the BS sites is ferric podsol. The fields on the BF sites were established on earlier coniferous (spruce) forest soil and cultivated for decades or even centuries before reforestation. All the sites are located in central Finland, 30 to 90 km north of the town of Jyväskylä (62°24'–63°00'N, 25°30–50'E). The stand characteristics are as follows:

Site code	Stand age (years)	Height (m)	Density (trunks/ha)
BS1	33	16	1300
BS2	28	13	1100
BS3	33	13	1000
BF1	26	10	1800
BF2	43	19	700
BF3	33	15	1000

Three "natural" deciduous stands were also studied, but these differed so much from each other that comparison with the planted stands was hardly possible. Therefore, the results of the reference sites are presented in another paper (Huhta et al. 2005), and only briefly referred to in the present context.

2.2 Vegetation and Soil Analyses

The ground vegetation was analysed in July 1998 by estimating the coverages of vascular plant species from ten random 1 m^2 plots at each study site.

The following soil variables were determined from three samples (n = 6) taken in 1998 (May, August and October), separately for the 0–3 and 3–6 cm soil depths:

- pH_{H2O} in soil-water suspension (5:25 m/m).
- Dry matter and water contents, drying overnight at 80°C.
- Organic matter content as loss on ignition (4.5 h at 550°C).
- Mineral nitrogen (NH_4^+ and NO_3^-) was extracted in 2-M KCl and measured according to SFS standard 3032. The results were calculated as mg N/m^2 in the whole depth of 0–6 cm.
- Microbial biomass and basal respiration were determined using the substrate induced respiration (SIR) method (Anderson and Domsch 1978, Nordgren 1988). The results were calculated as mg C/g dry mass and mg C/cm^3.

The following variables were determined only once and on different dates:

- Soil texture: particle size distribution of mineral soil was determined by dry sieving down to size class 0.2 mm, and smaller fractions using SYMPATEC diffraction spectrophotometer.
- Water retention was determined using a pressure plate chamber at potentials –0.3, –1, –5, –10 and –100 kPa. Retention at –5 kPa was used as water holding capacity (WHC). Matrix potential (pF) was calculated on the basis of WHC and water content measured at each sampling (topmost 5 cm of soil excluding litter).
- Soil structure: content (% of weight) of water-stable aggregates was determined by Viljavuuspalvelu Oy, Mikkeli (SFS-EN-ISO 9002).

2.3 Faunal Analyses

Soil faunal samples were taken in May, August and October 1998 for macroarthropods, August and October 1998 for microarthropods, May, Aug. and Oct. 1999 for nematodes and enchytraeids, and May and Oct. 1999 for lumbricids. The samples, each consisting of six sample units, were taken separately for each animal group, and randomly from a representative area of ca. 30 × 30 m independently of the total size of the similarly managed area. The macroarthropod and lumbricid samples were 25 × 25 cm blocks of topsoil, depth 0–5 cm for arthropods and 0–10 cm (two 5-cm layers separately) for earthworms. Other samples were taken with cylindrical steel corers (area 10 or 25 cm^2), and the layers 0–3 and 3–6 cm, and also 6–9 cm for nematodes and enchytraeids, were treated separately.

Macroarthropods were extracted using large Tullgren funnels (Huhta 1972), microarthropods using a modified high gradient apparatus (Macfadyen 1961), enchytraeids by wet funnels with O'Connor's (1962) heating regime, nematodes from ca. 1.5 cm^3 subsamples with the wet funnel technique of Sohlenius (1979), and earthworms using the wet extraction technique of Huhta and Koskenniemi (1975). In addition, formaline extraction (Daniel et al. 1992) was separately applied for the earthworm *Lumbricus terrestris* (three 0.5 m^2 plots per sample).

All major animal groups were identified to species level whenever possible (genera level for nematodes). The data from all soil layers were summed and the results were transformed into numbers per square metre.

2.4 Estimation of Biomasses

Collembola were counted in size classes at intervals of 0.1 mm (up to 1.2 mm) or 0.2 mm, and their biomasses were estimated by species using the regression formulae of Tanaka (1970) and Petersen (1975). For species not found in these, regressions for species of similar body shape were used. The weights for adult Oribatida were mainly taken from Luxton (1975), and for missing species interpolated from species of similar size and shape. Average individual weights for Prostigmata, Astigmata and juvenile Oribatida were taken from Huhta et al. (1986a). Weights for Mesostigmata were obtained from the data of Huhta et al. (1979, 1986a,b), or using the regression formula of Persson and Lohm (1977). Abrahamsen's (1973) equations of body volume and density were used to calculate the biomass of

Enchytraeidae. Earthworms were weighed fresh after keeping 48 h on moist paper to empty their guts, and transformed to dry weights by assuming a dry mass content of 16%. Total biomasses of Nematoda were estimated on the basis of average individual weight taken from Huhta et al. (1986a). The biomass determinations for macroarthropods follow Huhta (2002).

2.5 Statistical Analyses

Differences between the site types (BS, BF) were tested by two-way analysis of variance (Site type, Date) on sample averages of each site and date. Because of low number of replicates ($n = 3$), the level of $p < 0.1$ was also considered to indicate significance. Differences between site replicates (BS1,2,3 and BF1,2,3) were separately tested by ANOVA (Site, Date; $n = 6$). For DM, OM, pH and SIR the two soil depths were tested separately. As there were few significant time effects or Site × Date interactions, and these are not important in the present context, only the main effects are presented. The biomass data were *ln*-transformed prior to the analyses. Biomasses were tested only at group level; the tests at species level have been conducted on numbers of individuals and presented in other papers (see Introduction).

Community ordination was carried out on microarthropods and enchytraeids using Non-Metric Multidimensional Scaling (NMS). It was done using the PC-ORD programme (version 4; MjM Software Design) in NMS Autopilot mode, with the Sørensen (Bray and Curtis) index as distance measure. For microarthropods, species present only as one specimen in the whole material were discarded. The data were *ln*-transformed prior to the analyses. The measured soil variables were included in the ordinations; for pH, OM and SIR only the data of 0–3 cm were used, which was considered more descriptive to the study sites.

3 Results

3.1 Vegetation

The plant communities differed considerably between the birch stands established on forest soil and on arable soil (Table 1). The grasses *Deschampsia flexuosa*, *Calamagrostis arundinacea* and *Agrostis capillaris* were characteristic to the "Birch after Spruce" sites, followed by some common forest herbs such as *Melampyrum sylvaticum* and *M. pratense*, *Rubus saxatilis*, *Maianthemum bifolium* and *Trientalis europaea*. Dwarf-shrubs that dominate in coniferous forests were found only sporadically. *A. capillaris* was also abundant in one "Birch after Field" site, but all other predominant plants in BF were herbs of cultural origin: *Silene dioica*, *Fragaria vesca*, *Geum rivale*, *Filipendula ulmaria*, *Veronica chamaedrys* etc.

3.2 Soil Characteristics

Organic matter and water contents in the deeper soil layer (3–6 cm) were higher in "Birch after Field" than in "Birch after Spruce" ($F = 4.51$, $p = 0.055$, and $F = 60.3$, $p < 0.001$, respectively), indicating a more even vertical distribution of soil organic fraction in BF (Fig. 1). pH was also higher in "Birch after Field" ($F = 12.6$, $p = 0.004$ and $F = 18.05$, $p = 0.001$ for top and bottom layers, respectively). Clay content and fine fraction of mineral soil were clearly higher in the "Birch after Field" sites ($F = 6.03$, $p = 0.070$, and $F = 17.33$, $p = 0.014$, respectively), reflecting the fact that clay and silt soils have been preferably taken for cultivation, in comparison with coarse soils. WHC was higher ($F = 5.47$, $p = 0.079$) and average pF lower in BF ($F = 3.35$, $p = 0.092$), which indicates a better water availability. Contents of mineral nitrogen varied considerably between replicates, but the average NO_3^- concentration was higher in BF ($F = 3.68$, $p = 0.08$). Content of water stable aggregates, indicating earthworm activity, was also much higher in the BF sites. Total microbial biomass (SIR) per dry mass of soil (0–3 cm layer) was about 50% higher in "Birch after Spruce" ($F = 23.03$, $p < 0.001$), probably due to high fungal biomass (McLean and Huhta

Table 1. Field-layer vegetation of the study sites in July 1998 (coverage %; species exceeding cover of 0.5% at any site are included).

	Treatment					
	”Birch after Spruce”			”Birch after Field”		
	Replicate					
	1	2	3	1	2	3
Equisetum sylvaticum				+		0.5
Dryopteris carthusiana	0.8		+	+	+	+
Silene dioica				13.6		
Ranunculus acris			+	2.8	0.1	2.4
Ranunculus repens			+	5	1.4	0.5
Rubus saxatilis	6.4	16.7	4.5	1.3		+
Rubus idaeus	+			+	1.8	1.6
Fragaria vesca		0.1	0.2	+	17.7	4.2
Potentilla erecta	0.1	0.1			+	1.1
Geum rivale					6.7	16.5
Filipendula ulmaria				3.3	6.1	8.4
Alchemilla spp.				+	+	0.9
Vicia sylvatica			+	2	0.1	0.1
Lathyrus pratensis			0.6	0.5		0.2
Oxalis acetosella	7.3		0.2			
Geranium sylvaticum			7	0.7	2.6	+
Hypericum maculatum			+	3.2	+	+
Epilobium angustifolium		0.2		2.1	0.7	6
Epilobium montanum				2.5	+	0.1
Angelica sylvestris		3.8	0.5			+
Pyrola minor				1	+	+
Pyrola media		+		4.8		
Vaccinum myrtillus	0.7	+	0.5			
Trientalis europaea	5.8	7.8	0.6			0.1
Veronica officinalis	0.5			+	0.4	+
Veronica chamaedrys	1.3		0.8	1.9	8.9	4.2
Melampyrum sylvaticum	20.3	7.1			4.9	2.5
Melampyrum pratense			12.1			
Galium uliginosum	1.2		0.1	+		+
Linnaea borealis		1.3	1.2			
Prunella vulgaris				1.2		
Solidago virgaurea	+	9.2	+	+	0.1	0.5
Cirsium helenioides						6.9
Cirsium arvense				0.6		
Taraxacum spp.				6	0.3	+
Maianthemum bifolium	11.9	4.2	8.7		+	
Luzula pilosa	0.9	1.1	0.7		0.1	+
Agrostis capillaris	6.7	42	1.1	28.4	0.1	11
Poa pratensis	1.6	+	0.6	0.3	+	0.3
Melica nutans		0.3	0.3		+	
Deschampsia flexuosa	57.5	+	1.6			
Deschampsia cespitosa	+	+	0.1	+	12.7	7.8
Calamagrostis arundinacea	1.5	22	24.1		+	4.5
Alopecurus pratensis				1		2.9
Bushes:						
Picea abies		1		0.2	+	0.1
Alnus incana	+	+				0.3
Prunus padus	0.6				+	+
Sorbus aucuparia	0.9	+	+		+	+
Acer platanoides					4.4	
Number of species	32	37	43	49	50	55
Field layer. total cover	127.3	117.6	67.2	106.1	70.7	85.4
Mosses	1.1	0.3	0.3	22.7	1.6	1.4
Litter	36	50	82	53	40	53.5

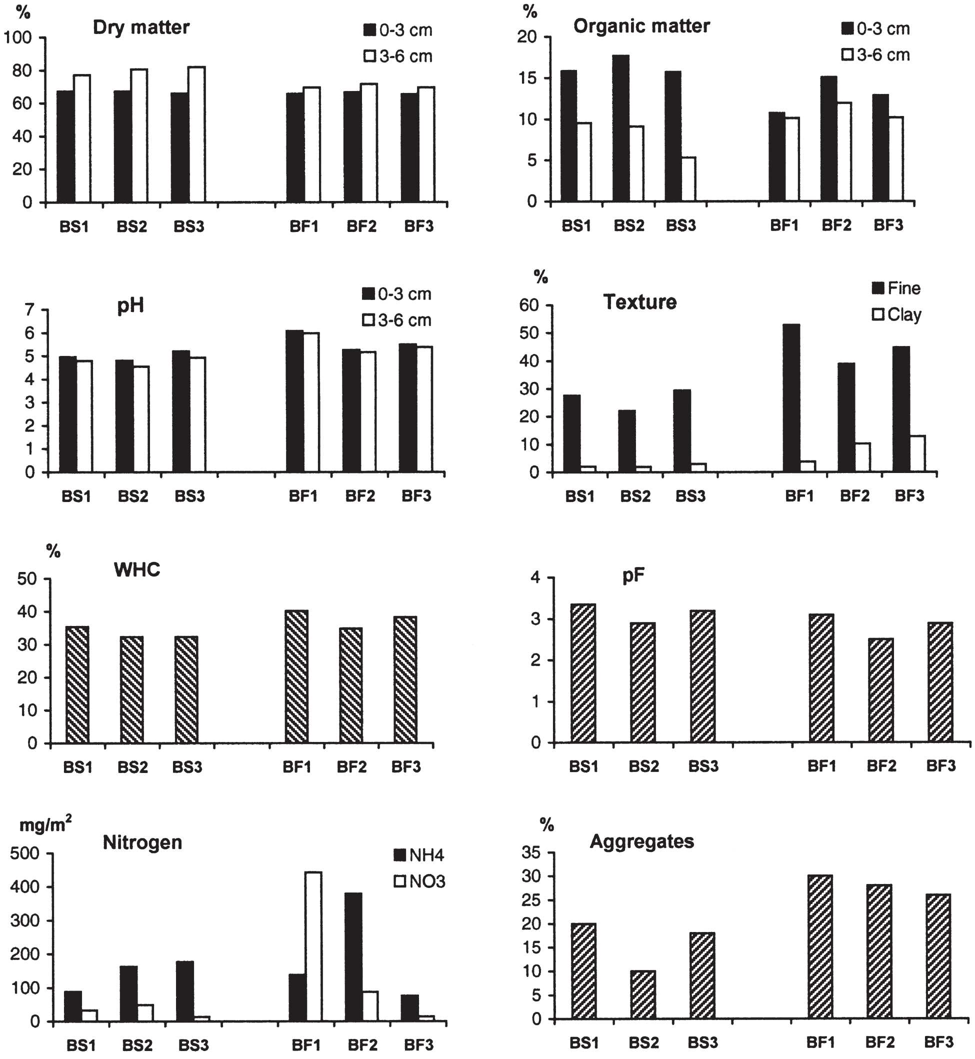

Fig. 1. Soil characteristics of the study sites. BS = “Birch after Spruce”, BF = “Birch after Field”.

2002), and basal respiration was also higher (0–3 cm; F = 7.87, p = 0.016) (Table 2). However, when calculated per soil volume, the differences were less obvious (SIR: F = 4.78, p = 0.049; BAS: F = 0.119, p = 0.976), and basal respiration in the 3–6 cm depth was even higher in BF (F = 5.61, p = 0.036). The site replicates differed significantly from each other, in BF concerning all soil variables except dry matter (p < 0.001 in most cases), and in BS concerning pH, particle size, SIR and basal respiration.

3.3 Macroarthropoda

The macroarthropod communities and biomasses were relatively similar at all study sites. When significant differences in biomasses between “Birch after Spruce” and “Birch after Field” were observed, they were higher in BS (Coleoptera and Diptera larvae, Homoptera and Chilopoda; Huhta 2002). The coleopteran community did not differ much between different kinds of birch stands, while there were more differences in Araneida. The spider communities were fairly similar to

Table 2. Microbial biomass (SIR) and basal respiration (BAS).

		Site					
		BS			BF		
		Replicate					
		1	2	3	1	2	3
SIR, mg C/g d.m.	0–3 cm	2.95	3.30	4.20	1.47	2.08	2.07
	3–6 cm	1.53	0.96	1.11	1.00	1.35	1.36
SIR, mg C/cm^3	0–3 cm	1.59	2.05	2.11	1.17	1.50	1.53
	3–6 cm	1.20	0.78	1.06	0.87	1.10	1.13
BAS, mg C/g d.m.	0–3 cm	0.07	0.09	0.17	0.03	0.06	0.06
	3–6 cm	0.03	0.02	0.03	0.02	0.05	0.04
BAS, mg C/cm^3	0–3 cm	0.03	0.05	0.08	0.02	0.04	0.04
	3–6 cm	0.02	0.02	0.03	0.02	0.04	0.04

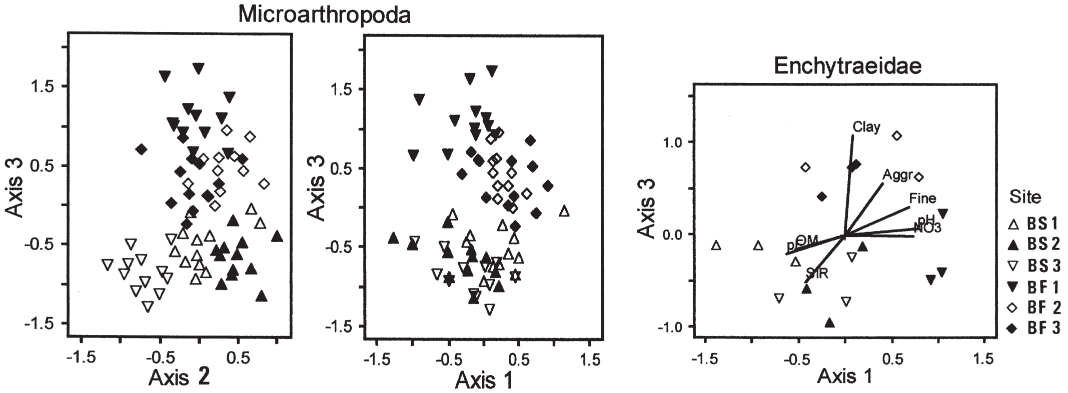

Fig. 2. Plot diagrams of microarthropods (separate samples) and enchytraeids (pooled samples) based on NMS analyses (3-axis solutions). Environmental variables shown with Enchytraeidae. Non-informative axis combinations are omitted.

those of coniferous forests, while in Coleoptera some of the most abundant species are rare in spruce forests. All dominant species in the study sites are common members of the forest floor fauna, and differ from those of open terrain. The populations in ”Birch after Field” were generally low, and the communities could be characterised as impoverished forest communities. There were considerable differences between replicates of the same kind of forests, especially in Araneida. (Biomass data for macroarthropods were given by Huhta (2002), and are not repeated here.)

3.4 Microarthropoda

There were significant differences between birch stands established after spruce forest and after cultivation, and between these and natural deciduous forests (Huhta and Niemi 2003, Huhta and Ojala, unpublished). The communities of ”Birch after Spruce” were rather similar to those of natural spruce forests, but the population densities were lower. The populations in ”Birch after Field” were low, especially in Oribatida, and in all cases when significant differences were found, they were in favour of BS. Total biomass of Collembola and Oribatida differed significantly between BS and BF. All the dominating species in the study sites are common members of the forest soil fauna. In terms of biomass, the most dominant species were *Isotoma* spp. among Collembola, *Lysigamasus vagabundus* and *Veigaia nemorensis* in Mesostigmata, and *Nothrus silvestris*, *Ceratozetes gracilis* and *Hemileius initialis* in Oribatida (Table 3).

NMS ordination reveals a distinct grouping of the microarthropod communities (Monte Carlo permutation: $p < 0.032$) (Fig. 2). The BS sites

Table 3. Biomasses (mg d.m./m^2) of the most dominant species in biomass, and totals of each main group (ANOVA main effects shown on the row 'total').

Site	BS				BF	
Replicate	1	2	3	2	2	3
Collembola						
Neanura muscorum	1.7	0.2	6.6	0.0	4.5	0.2
Onychiurus armatus	0.4	0.2	19.7	5.2	0.9	5.5
Folsomia quadrioculata	6.3	8.7	0.0	0.2	2.8	1.9
Isotomiella minor	19.1	6.7	16.0	0.8	8.3	10.0
Isotoma notabilis	19.1	6.7	16.0	0.8	8.3	10.0
Isotoma divergens	17.0	5.1	40.6	0.0	1.7	11.9
Isotoma viridis/anglicana	20.8	3.3	3.7	0.0	0.0	0.0
Tomocerus flavescens	0.2	5.0	9.0	6.7	0.9	11.7
Total (F = 13.61, p = 0.006**)	105.0	54.8	126.6	27.0	35.4	60.6
Mesostigmata						
Alliphis siculus	0.0	0.0	0.0	6.8	0.0	0.0
Hypoaspis aculeifer	4.3	6.1	4.7	0.0	0.8	0.0
Parazercon radiatus	1.9	5.0	4.4	0.0	0.0	2.7
Pergamasus brevicornis	19.9	3.0	4.9	0.0	3.0	12.7
Lysigamasus vagabundus	29.7	19.5	45.6	9.2	33.1	18.8
Vulgarogamasus kraepelini	4.5	0.0	6.9	4.0	8.4	11.5
Veigaia kochi	0.0	3.0	6.0	9.0	15.0	6.0
Veigaia nemorensis	25.4	11.8	13.3	3.8	18.3	20.0
Trachytes aegrota	1.5	1.1	4.8	0.6	1.4	5.6
Dinychus perforatus	2.9	3.8	11.1	0.0	5.7	0.0
Total (F = 1.06, p = 0.234)	107.2	64.5	132.1	59.0	97.0	104.3
Oribatida						
Atopochthonius artiodactylus	1.3	1.1	6.9	0.2	0.1	0.1
Phthiracarus globosus	9.6	8.4	0.0	0.0	20.4	19.2
Phthiracarus longulus	9.1	0.8	5.0	0.0	2.5	10.8
Steganacarus carinatus	0.0	9.9	12.4	0.0	0.0	0.0
Nothrus silvestris	116.1	10.8	68.4	0.9	0.0	8.1
Oppiella nova	22.0	7.1	13.3	11.7	9.8	12.8
Conchogneta traegardhi	0.5	7.9	16.5	0.0	0.0	0.0
Hemileius initialis	33.0	10.2	18.3	0.6	12.3	37.2
Ceratozetes gracilis	26.4	61.2	27.2	0.0	0.0	0.4
Parachipteria willmanni	13.2	0.0	0.0	0.0	0.0	0.0
Oribatida adults	265.4	155.6	270.3	15.3	69.9	100.7
Oribatida total (F = 11.09, p = 0.010**)	352.7	192.8	314.2	18.6	73.1	119.2
Prostigmata	1.8	1.5	1.8	0.6	0.9	1.2
Astigmata	0.5	0.2	0.6	0.1	0.3	0.5
Total microarthropods	567	314	575	105	207	286
Total macroarthropods	381	413	615	271	348	306
Enchytraeidae						
Mesenchytraeus pelicensis	0.0	17.1	135.4	0.0	0.0	11.8
Bryodrilus ehlersi	0.0	4.4	194.6	0.0	0.0	0.0
Cognettia sphagnetorum	205.0	92.3	184.4	0.0	22.6	69.3
Fridericia bulboides	26.0	61.4	70.7	16.1	7.8	13.6
Fridericia bisetosa	2.9	90.8	11.7	139.6	18.0	11.7
Fridericia ratzeli	435.3	24.4	253.6	633.9	247.5	164.5
Fridericia spp.	45.9	25.1	28.5	32.9	18.4	22.1
Henlea nasuta	0.0	32.2	120.4	7.3	0.0	0.4
Henlea similis	0.0	0.0	81.4	0.0	0.0	1.1
Total (F = 2.28, p = 0.133)	768.8	409.9	1240.9	881.9	349.2	376.6
Lumbricidae (g/m^2)	12.25	9.17	0.25	24.62	18.56	12.97
Grand total (g/m^2)	13.97	10.31	2.68	25.88	19.47	13.94

Table 4. Pearson´s correlations of environmental variables with the ordination axes (NMS ordination) in communities of Microarthropoda (sample units separate) and Enchytraeidae (pooled samples). OM = organic matter %, SIR = microbial biomass, Aggr. = water-stable aggregates > 2 mm (%), Clay = mineral fraction < 0.002 mm, Fine = mineral fraction < 0.06 mm. Significances: * $p < 0.05$, ** $p < 0.01$.

	Microarthropoda			Axis	Enchytraeidae		
	1	2	3		1	2	3
pF	0.073	–0.157	–0.457**		–0.645**	0.23	–0.370
OM	–0.106	0.170	–0.820**		–0.592**	–0.253	–0.323
pH	0.074	–0.180	0.755**		0.718**	0.184	0.221
NH_4^+	0.233*	0.074	0.014		0.276	–0.159	0.370
NO_3^-	–0.165	0.032	0.662**		0.698**	0.382	–0.096
Aggr	0.281	–0.102	0.814**		0.514*	0.165	0.613**
SIR	–0.198	–0.457**	–0.843**		–0.529*	–0.382	–0.583**
Clay	0.428**	0.066	0.456**		0.226	–0.142	0.851**
Fine	0.127	–0.109	0.870**		0.676**	0.193	0.450
WHC	0.166	0.002	0.812**		0.482*	0.358	0.359

are clearly separated in the ordination space both from each other and from the BF sites. Among BF, site BF1 is located most remote from the BS sites, while BF2 and BF3 overlap and lay between BF1 and BS. All the environmental factors except NH_4 are significantly correlated with the ordination axes, most distinctly with axis 3, with which pH, NO_3, WHC, clay, fine fraction and aggregate content are in positive, and organic matter, SIR and pF in negative correlation (Table 4).

3.5 Enchytraeidae

Similarly to microarthropods, the enchytraeid communities also showed marked differences between the birch stands established on forest soil and on arable soil, but even more between replicates of similarly managed forests (Räty and Huhta 2004b). Total numbers and populations of most species were lower in “Birch after Field” than in “Birch after Spruce”. *Cognettia sphagnetorum*, the “superdominant” enchytraeid in coniferous forests, was the second dominant in the BS sites. *Fridericia ratzeli* had the highest biomass in both site types, and strongly dominated the enchytraeid biomass in BF (Table 3). In the NMS ordination the enchytraeid communities of the BS and BF sites are located in opposite directions from the origo, though different samples are rather scattered and partly overlapping (Monte Carlo permutation: $p < 0.020$). As in microarthropods, site BF1 is distinctly separated from the other BF sites and BS (Fig. 2). Correlations between the axes and environmental factors are in agreement with those for microarthropods (Table 4).

3.6 Lumbricidae

Two of the ”Birch after Spruce” sites harboured a community of *Dendrobaena octaedra*, *Aporrectodea caliginosa* and two or three species of *Lumbricus*, while *D. octaedra* alone was present in BS3. All these species were present in the three “Birch after Field” sites, where their total biomass, ranging from 14 to 26 g (d.m.) m^{-2}, was 2.6 times the average in “Birch after Spruce”. (Species-level data for lumbricids, including biomass, are given by Räty and Huhta 2004a.)

3.7 Nematoda

Total numbers, diversity, and densities of most taxa and feeding groups were lower in “Birch after Field” than in “Birch after Spruce”. The “BS” sites were relatively similar in community structure to natural deciduous forests, but the “BF” sites were dissimilar with both (Räty and Huhta 2003a).

3.8 Total Biomass

The average total biomass of all major soil animal groups except Lumbricidae was higher in “Birch after Spruce” than in “Birch after Field”. However, the earthworm biomass showed an opposite trend, being lowest (virtually zero) in BS3 where the summed biomass of other groups was highest, and much higher in BF than in BS (Fig. 3). As the biomass of earthworms was several times higher than that of all remaining groups together, “Birch after Field” harboured, on the average, ca. 2.5 times more soil animal biomass than did “Birch after Spruce” (Table 3).

4 Discussion

4.1 Community Structure in Different Forests

It became obvious that even 30 years after reforestation the soil animal communities of planted birch stands established on spruce forest soil and on cultivated soil differ markedly from each other. Generally, the communities of “Birch after Spruce” are relatively similar to those of original spruce forests, though the population densities are usually lower. Concerning most faunal groups, the “Birch after Field” communities are poorer in densities, biomass and diversity, but they mainly share the same dominant species. They can thus be characterized as “impoverished” forest communities, having little in common with those of arable soils under cultivation. However, the animal groups also differ from each other in the degree of “community specialisation”: Coleoptera and Collembola have relatively similar communities in different forests, Araneida, Mesostigmata and Nematoda deviate more, and in Oribatida, Enchytraeidae and Lumbricidae the differences between study sites are conspicuous. Earthworms are the only group to have a considerably higher biomass in “Birch after Field” than in “Birch after Spruce”, and they largely determine the total faunal biomass.

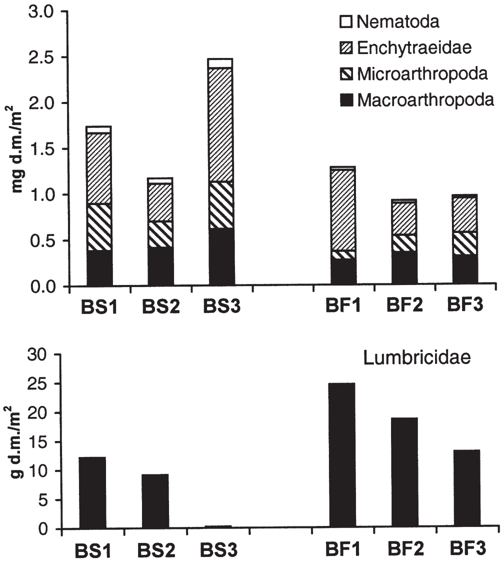

Fig. 3. Soil faunal biomasses (dry matter /m^2) on the study sites; means of 2 or 3 samples (please note the different scales).

4.2 Resource Quality and Soil Structure

Coniferous forest soil and litter are optimal habitats for such animals as microarthropods and enchytraeids. Most of the species are microbidetritivores, either fungal feeders or consumers of dead organic matter with fungal growth inside (Petersen 1971, Luxton 1972, Springett and Latter 1977, Latter and Howson 1978, Siepel and de Ruiter-Dijkman 1993). The amount and quality of organic matter are considered an important determinant for the fungal-based soil food web (Swift et al. 1979). The average plant community differs between the different study sites: grasses dominate in “Birch after Spruce”, herbs in “Birch after Field” and dwarf-shrubs in coniferous forests. As litter derived from different plants differs in quality, this might result in differences in the litter-feeding fauna. An experiment was carried out by Ojala and Huhta (unpublished), in which the preference of Collembola and Oribatida for different litter substrates was tested. No species showed preferences for birch litter over spruce or over grasses and herbs; thus the presence of birch did not explain their abundances in the study sites. Most species that were equally common in BS and BF, preferred either grass, herb or fern litter, or two of these. This is in accordance with Maraun and Scheu (2000), who concluded that the forest type or litter quality is of minor importance for the density and community structure of oribatids.

The study sites also differ in the physical structure of the topsoil. In "Birch after Spruce" there is a loose microstructure among litter and bases of grass tussocks, whereas in BF there is a scanty litter layer with more distantly-spaced bases of herbs. Physical structure of the soil surface is probably an important factor to explain the community structure of spiders. Small web-building species (Linyphiidae spp.) that form the majority of the spider community of forest floor (Huhta 1971) require small spaces for anchorage of their webs. This probably explains the greater numbers and diversity of spiders in ”Birch after Spruce” stands than in ”Birch after Field”. For euedaphic animals such as enchytraeids the physical structure is less important.

4.3 Soil Acidity

pH is generally regarded as one of the most important environmental factors for soil fauna. Many species are intolerant to acid environments, but several oribatids, the enchytraeid *Cognettia sphagnetorum* and the earthworm *Dendrobaena octaedra* reach the highest densities in raw humus soils with low pH (Standen and Latter 1977, Hågvar and Abrahamsen 1980, Standen 1980, Koskenniemi and Huhta 1986, Didden 1993). The species diversity of Oribatida is highest in acid soils, while most enchytraeids are acid-sensitive; Standen (1980) and Nowak (2001) have observed a positive correlation between pH and the number of enchytraeid species. As the "Birch after Field" sites have higher soil pH than the "Birch after Spruce" sites, the species richness of enchytraeids is expected to be higher, and that of oribatids lower in BF than in BS. This is supported by our observations in oribatids, but not in enchytraeids. Increase of enchytraeid diversity and decrease of oribatid diversity in "Birch after Spruce" in relation of original spruce forest can also be expected, which agrees with the observations. pH also contributes to explain the differences in community structure of nematodes.

The higher soil pH in "Birch after Field" originates from the time of cultivation, since arable soils are routinely neutralized by liming, the effect of which is very long-lasting (Aarnio et al. 2003). In "Birch after Spruce" an increase of pH in comparison with original spruce forest is expected due to deciduous litter (Mikola 1985).

However, pH alone can not explain all the variation between the study sites. Soil pH may in fact be less important than previously believed, since moder soil of pH 5.5 may harbour an abundant oribatid community with similar species structure as acid raw humus soils (Maraun and Scheu 2000). Hågvar (1990) also has shown that some "acidophilic" oribatids actually reproduce better in more neutral soil in the absence of competition by other microarthropods.

4.4 Dispersal

Long-lasting cultivation is expected to decimate the populations of forest soil arthropods. Ability to colonise vacant environments is thus a factor that may influence the possibilities of forest species to invade the BF sites after reforestation. For flying insects such as most Coleoptera this is hardly a problem. Spiders are also good colonisers due to their capability for aeronautic dispersal. Epigeic spiders, beetles and large predatory mites have good dispersal ability by land. Many nematodes and mesostigmatid and astigmatid mites have capacity for phoretic dispersal (Nicholas 1983, Karg 1989, 1993). In contrast, dispersal ability of small wingless soil animals may be poor.

Regrettably, virtually nothing is known about dispersal in Enchytraeidae, Oribatida and edaphic Collembola. *Onychiurus armatus* (Collembola) and *Cognettia sphagnetorum* (Enchytraeidae) have been observed to spread only a few centimeters per week in the laboratory (Sjögren et al. 1995, Sjögren 1997, Salminen and Sulkava 1996). In connection with the present study, a dispersal experiment was carried out by Ojala and Huhta (2001), which indicates that most microarthropod species have potential capacity for land colonisation over the distance of 30 m (from forest edge to the sampling sites) in the time of 30 years that had elapsed after reforestation. Even the species with the slowest rate of dispersal (*Medioppia* *subpectinata*, Oribatida) had viable populations in all the BF sites.

Passive transport by man is known to play a decisive role in the dispersal of earthworms (Lee 1985). Species invasions to new localities are thus accidental, and the species assemblage at a certain site is largely determined by chance. The same is probably true in Enchytraeidae, which are similar to earthworms in general biology. Contrary to BS, the "Birch after Field" sites have a long cultural history before reforestation, and most potential species could be expected to have colonized the sites. All potential earthworm species as well as diverse enchytraeid communities were in fact present in the BF sites, while the earthworm community in the most isolated BS site (BS3) solely consisted of the ubiquitous species *Dendrobaena octaedra*. However, the latter site harboured a diverse community of Enchytraeidae.

4.5 Interspecific Interactions

There was an overall inverse relationship between the abundance of earthworms and other animal groups. Earthworms had a high average biomass in the "Birch after Field" sites where microarthropods, enchytraeids and nematodes were less abundant, and with the exception of enchytraeids also their communities were less diverse. Among the "Birch after Spruce" sites, earthworms were virtually lacking in BS3, where all other groups showed the highest biomass.

There is both correlative and experimental evidence that earthworms can suppress populations of other soil animals. Schaefer and Schauermann (1990) found in German beech forests that the abundances and biomasses of Lumbricidae and Enchytraeidae were inversely related. Huhta and Viberg (1999) have shown that the earthworm *Dendrobaena octaedra* reduces the population of *Cognettia sphagnetorum*. A negative relationship between earthworms and nematodes has been observed by Yeates (1981). Hyvönen et al. (1994) showed that the presence of the earthworm *Dendrobaena octaedra* suppresses the populations of nematodes, and suggested that earthworms consume microfauna as part of their diet. In connection with the present study, Räty and Huhta (2003b) carried out an experiment where the earthworms *Lumbricus terrestris* and *Aporrectodea caliginosa* reduced substantially the enchytraeid and nematode populations.

Physical structure of the topsoil is related to the abundance of burrowing earthworms that mix the soil layers and consume the litter layer which, during its decomposition, provides nutrition for litter-feeding fauna and fungal-based soil food web. Thus earthworms probably affect negatively the populations of several soil animals, e.g. spiders and microarthropods, by disturbing their microhabitats and reducing their resources. Maraun and Scheu (2000) also concluded that disturbance and reduction of habitable space by earthworms is a major determinant of the community structure of Oribatida.

5 Conclusions

The community structure of soil fauna is markedly different in birch stands established on earlier spruce forest soil and on arable soil. The communities in "Birch after Spruce" are relatively similar to those of coniferous forests, though the population densities are generally lower. The communities of "Birch after Field" are generally sparse and could be characterised as "impoverished forest communities", except Lumbricidae and Enchytraeidae that have affinities with deciduous forests and cultural landscapes.

The soil characteristics in birch stands established on earlier forest and cultivated soils differ from each other to such an extent that this can be expected to influence the decomposer communities for several decades after reforestation. Some of these characteristics (clay and fine mineral matter) reflect the original soil properties, some others (pH and soil stratification) result from agricultural practices, and some are secondary properties resulting from the former (organic matter, water holding capacity, nitrification).

However, the prevailing soil conditions are not enough to explain all observed differences in soil fauna. At least for earthworms, probably also for enchytraeids and many other edaphic animals, colonisation abilities and accidental transport by man may determine the presence or absence of certain species at a site. The long cultivation history of the "Birch after Field" sites "guarantees" the presence of the common burrowing earthworms, while isolation from cultural landscape may prevent colonisation in "Birch after Spruce". On the other hand, the biomass of earthworms also depends on soil acidity, and simply due to low pH may remain lower in BS than in BF.

Earthworms, further, have marked impacts on several soil properties due to their burrowing activity and feeding on litter. They also directly or indirectly compete with or otherwise have a negative effect on other soil faunal components. Thus the observed structure of the soil communities and the differences between "Birch after Spruce" and "Birch after Field" are an outcome of a complex and interacting set of factors: soil characteristics, site history, dispersal and interspecific interactions.

Acknowledgements

We wish to express our gratitude to our co-workers in the project, Jari Haimi, Mary Ann McLean and Riikka Ojala, as well as Mustapha Boucelham, Leena Kontiola and Marja Kurkela for technical assistance. Vegetation analyses were carried out by Piippa Wäli-Blomqvist, and soil texture analyses by Erkki Järvinen. Oribatid mites were identified by Ritva Penttinen, collembolans by Sanna Hänninen, and beetles by Petri Ahlroth, Jaakko Mattila and Teemu Rintala. Taxonomic supervision was offered by Klara Docza-Farkas (Enchytraeidae), Jari Haimi (Collembola) and Heikki Setälä (Nematoda). Our best thanks are due to all of them. The research was supported by the Academy of Finland.

References

Aarnio,T., Räty, M. & Martikainen, P.J. 2003. Long-term availability of nutrients in forest soil derived from fast- and slow-release fertilizers. Plant and Soil 252: 227–239.

Abrahamsen, G. 1973. Studies on body-volume, body-surface area, density and live weight of Enchytraeidae (Oligochaeta). Pedobiologia 13: 6–15.

Anderson, J.P.E. & Domsch, K.H. 1978. A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biology and Biochemistry 10: 215–221.

Axelsson, B., Lohm, U. & Persson, T. 1984. Enchytraeids, lumbricids and soil arthropods in a northern deciduous woodland. Holarctic Ecology 7: 91–103.

Daniel, O., Jager, P., Cuendet, G. & Bieri, M. 1992. Sampling of Lumbricus terrestris (Oligochaeta, Lumbricidae). Pedobiologia 36: 213–220.

Didden, W.A.M. 1993. Ecology of terrestrial Enchytraeidae. Pedobiologia 37: 2–29.

Finnish Forest Research Institute 1992. Yearbook of forest statistics 1990–1991. Folia Forestalia 790. 281 p.

Hågvar, S. 1990. Reactions to soil acidification in microarthropods: Is competition a key factor? Biology and Fertility of Soils 9: 178–181.

— & Abrahamsen, G. 1980. Colonisation by Enchytraeidae, Collembola and Acari in sterile soil samples with adjusted pH levels. Oikos 34: 245–258.

Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Annales Zoologici Fennici 8: 483–542.

— 1972. Efficiency of different dry funnel techniques in extracting Arthropoda from raw humus forest soil. Annales Zoologici Fennici 9: 42–48.

— 2002. Soil macroarthropod communities in planted birch stands in comparison with natural forests in central Finland. Applied Soil Ecology 20: 199–209.

— & Koskenniemi, A. 1975. Numbers, biomass and community respiration of soil invertebrates in spruce forests at two latitudes in Finland. Annales Zoologici Fennici 12: 164–182.

— & Niemi, R. 2003. Communities of soil mites (Acarina) in planted birch stands as compared with natural forests in central Finland. Canadian Journal of Forest Research 33: 171–180.

— & Viberg, K. 1999. Competitive interactions between the earthworm Dendrobaena octaedra and the enchytraeid Cognettia sphagnetorum. Pedobiologia 43: 886–890.

— , Ikonen, E.K. & Vilkamaa, P. 1979. Succession of invertebrate populations in artificial soil made of sewage sludge and crushed bark. Annales Zoologici Fennici 16: 223–270.

— , Hyvönen, R., Kaasalainen, P., Koskenniemi, A., Muona, J., Mäkelä, I., Sulander, M. & Vilkamaa, P. 1986a. Soil fauna of Finnish coniferous forests. Annales Zoologici Fennici 23: 345–360.

— , Hyvönen, R., Koskenniemi, A., Vilkamaa, P., Kaasalainen, P. & Sulander, M. 1986b. Response of soil fauna to fertilization and manipulation of pH in coniferous forest soil. Acta Forestalia Fennica 195. 30 p.

— , Räty, M., Ahlroth, P., Hänninen, S.-M., Mattila, J., Penttinen, R. & Rintala, T. 2005. Soil fauna of deciduous forests as compared with spruce forests in central Finland. Memoranda Soc. Fauna et Flora Fennica 81.

Hyvönen, R., Andersson, S., Clarholm, M. & Persson, T. 1994. Effects of lumbricids and enchytraeids on nematodes in limed and unlimed coniferous mor humus. Biology and Fertility of Soils 17: 201–205.

Karg, W. 1989. Acari (Acarina), Milben. Unterordnung Parasitiformes (Anactinochaeta), Uropodina Kramer, Schildkrötenmilben. Die Tierwelt Deutschlands 67. 203 p.

— 1993. Acari (Acarina), Milben. Parasitiformes (Anactinochaeta). Cohors Gamasina Leach. – Raubmilben (2nd Ed.). Die Tierwelt Deutschlands 59. 523 p.

Kellomäki, S., Väisänen, H. & Strandman, H. 1996. Response of the boreal forest ecosystem to climatic change and its silvicultural implications: modelling. In: The Finnish Research Programme on Climatic Change, Final Report. Publications of the Academy of Finland 4/96: 252–253.

Koskenniemi, A. & Huhta, V. 1986. Effects of fertilization and manipulation of pH on mite (Acari) populations of coniferous forest soil. Revue d'Ecologie et du Biologie du Sol 23: 271–286.

Latter, P.M. & Howson, G. 1978. Studies on the microfauna of blanket bog with particular reference to Enchytraeidae. II. Growth and survival of Cognettia sphagnetorum on various substrates. Journal of Animal Ecology 47: 425–448.

Lee, K.E. 1985. Earthworms, their ecology and relationships with soils and land use. Academic Press, Sudney 411 p. ISBN 0-12-440860-5.

Luxton, M. 1972. Studies on the oribatid mites of a Danish beech wood soil I. Nutritional biology. Pedobiologia 12: 434–463.

— 1975. Studies on the oribatid mites of a Danish beech wood soil II. Biomass, calorimetry, and respirometry. Pedobiologia 15: 161–200.

— 1981a. Studies on the oribatid mites of a Danish beech wood soil III. Introduction to the field populations. Pedobiologia 21: 295–305.

— 1981b. Studies on the oribatid mites of a Danish beech wood soil V. Vertical distribution. Pedobiologia 21: 359–380.

— 1981c. Studies on the oribatid mites of a Danish beech wood soil VI. Seasonal population changes. Pedobiologia 21: 381–403.

— 1981d. Studies on the astigmatid mites of a Danish beech wood soil. Pedobiologia 22: 29–38.

— 1981e. Studies on the prostigmatid mites of a Danish beech wood soil. Pedobiologia 22: 277–303.

Macfadyen, A. 1961. Improved funnel-type extractors for soil arthropods. Journal of Animal Ecology 30: 171–184.

— 1963. The contribution of the fauna to the total soil metabolism. In: Doeksen, J. & van der Drift, J. (Eds.). Soil organisms. North Holland, Amsterdam. p. 3–17.

Maraun, M. & Scheu, S. 2000. The structure of oribatid mite communities (Acari, Oribatida): patterns, mechanisms and implications for future research. Ecography 23: 374–383.

McLean, M.A. & Huhta, V. 2002. Microfungal community structure in anthropogenic birch stands in central Finland. Biology and Fertility of Soils 35: 1–12.

Mikola, P. 1985. The effect of tree species on the biological properties of forest soil. National Swedish Environmental Board, Report 3017. 27 p.

Nicholas, W.L. 1983. The biology of free-living nematodes. 2 ed. Clarendon Press, Oxford. 251 p. ISBN 0-19-857587-4.

Nordgren, A. 1988. Apparatus for the continuous, long-term monitoring of soil respiration rate in a large number of samples. Soil Biology and Biochemistry 20: 955–957.

Nowak, E. 2001. Enchytraeid communities in successional habitats (from meadow to forest). Pedobiologia 45: 497–508.

O'Connor, F. B. 1962. The extraction of Enchytraeidae from soil. I: Progress in soil zoology. London. p. 279–285.

Ojala, R. & Huhta, V. 2001. Dispersal of microarthropods in forest soil. Pedobiologia 41: 443–450.

Persson, T. & Lohm, U. 1977. Energetical significance of the annelids and arthropods in a Swedish grassland soil. Ecological Bulletin (Stockholm) 23: 3–211.

Petersen, H. 1971. Collembolernes ernaeringsbiologi og dennes ökologiske betydning. Entomologiske Meddelelser 39: 97–118.

— 1975. Estimation of dry weight, fresh weight, and calorific content of various Collembolan species. Pedobiologia 15: 222–243.

— 1980. Population dynamic and metabolic characterization of Collembola species in a beech forest ecosystem. Proc. VII Int. Coll. Soil Zool., Syracuse, USA. EPA publications 1979: 806–833.

— & Luxton, M. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39: 287–388.

Räty, M. & Huhta,V. 2003a. Nematode communities in anthropogenous birch stands in central Finland. Nematology 5: 629–639.

— & Huhta,V. 2003b. Earthworms and pH affect communities of nematodes and enchytraeids in forest soil. Biology and Fertility of Soils 38: 52–58.

— & Huhta, V. 2004a. Earthworm communities in birch stands with different origin in central Finland. Pedobiologia 48: 52–58.

— & Huhta,V. 2004b. Communities of Enchytraeidae (Oligochaeta) in planted birch stands as compared with natural forests in central Finland. Biology and Fertility of Soils 40: 413–420.

Salminen, J. & Sulkava, P. 1996. Distribution of soil animals in patchily contaminated soil. Soil Biology and Biochemistry 28: 1349–1355.

Schaefer, M. & Schauermann, J. 1990. The soil fauna of beech forests: a comparison between a mull and a moder soil. Pedobiologia 34: 299–314.

Siepel, H. & de Ruiter-Dijkman, E.M. 1993. Feeding guilds of oribatid mites based on their carbohydrase activities. Soil Biology and Biochemistry 25: 1491–1498.

Sjögren, M. 1997. Dispersal rates of Collembola in metal polluted soils. Pedobiologia 41: 506–513.

— , Augustsson, A. & Rundgren, S. 1995. Dispersal and fragmentation of the enchytraeid Cognettia sphagnetorum in metal polluted soil. Pedobiologia 39: 207–218.

Sohlenius, B. 1979. A carbon budget for nematodes, rotifers and tardigrades in a Swedish coniferous forest soil. Holarctic Ecology 2: 30–40.

Springett, J.A. & Latter, P.M. 1977. Studies on the microfauna of blanket bog with particular reference to Enchytraeidae. I. Field and laboratory tests of micro-organisms as food. Journal of Animal Ecology 46: 959–974.

Standen, V. 1980. Factors affecting the distribution of Enchytraeidae (Oligochaeta) in associations at peat and mineral sites in northern England. Bulletin of Ecology 11: 599–608.

— & Latter, P.M. 1977. Distribution of a population of Cognettia sphagnetorum (Enchytraeidae) in relation to microhabitats in a blanket bog. Journal of Animal Ecology 46: 213–229.

Swift, M.J., Heal, O.W. & Anderson, J.M. 1979. Decomposition in terrestrial ecosystems. Blackwell Scientific Publications, Studies in Ecology 5. 372 p. ISBN 0-520 04001-5.

Tanaka, M. 1970. Ecological studies on communities of soil Collembola in Mt. Sobo, southeast Japan. Japanese Journal of Ecology 20: 102–110.

Yeates, G.W. 1981. Nematode populations in relation to soil environmental factors: a review. Pedobiologia 22: 312–338.

Total of 64 references