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ORIGINAL PAPER

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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; Abrahamsen 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

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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 NH_4^+ 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 $CaCO_3$/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%, *Bryodrillus 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 groups were determined according to Yeates et al. (1993), and allocation to c-p groups followed Bongers (1990).

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

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

Enchytraeids were sampled at week 32 from 0–6 cm in each jar, using a cylindrical corer with an aperture of 25 cm^2. 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 Dózsa-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 CO_2 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 Kolgomorov-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 (ΣMI). 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 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 (*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
Acrobeloides	2.9	3.4	2.9	5.6	9.5a	8.3a	8.2a	15.2b	U < L
Cervidellus	0.3	0	0.1	1.0	0.3a	1.4a	0.5a	3.3b	U < L
Prismatolaimus	0	0.2	0.3	1.4	0.6a	0.4a	0.6a	1.3b	
Plectus	1.3	1.6	1.4	2.6	5.2a	3.3a	3.7a	8.1b	U < L
Wilsonema	0.1	0.2	0	2.2	1.0a	0.5a	0.5a	6.3b	U < L
Teratocephalus	0.8	0.5	0.5	1.3	2.4	2.1	2.8	3.2	U < L
Euteratocephalus	0.3	0	0	0.2	0.4	0.6	0	0.3	U < L
Rhabditis	1.7	2.6	2.0	4.2	6.4ab	6.1ab	5.1a	9.0b	
Bunonema	0	0	0	0.3	0a	0a	0a	0b	U < L
Monhystera	0	0.1	0.1	0.3	0.2a	0.4a	0.5a	1.2b	U < L
Alaimus	0.3	0.1	0.1	0.8	0.5	0.4	0.4	0.7	
Metateratocephalus	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
Tylenchus	0.8	1.0	0.9	2.4	3.3ab	1.5a	2.5ab	2.5b	U < L
Ditylenchus	0.5	0.5	0.5	2.2	1.1a	0.3a	0.5a	1.5b	
Aphelenchoides	0.1	0.3	0.3	2.9	2.3a	1.9a	2.3a	3.0b	U < L
Tylencholaimus	0.3	0.2	0.3	0.8	1.5	1.0	1.6	0.7	U < L
Malenchus	0.6	1.1	0.7	2.9	0.1a	1.0a	0.7a	1.9b	
Paratylenchus	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

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)

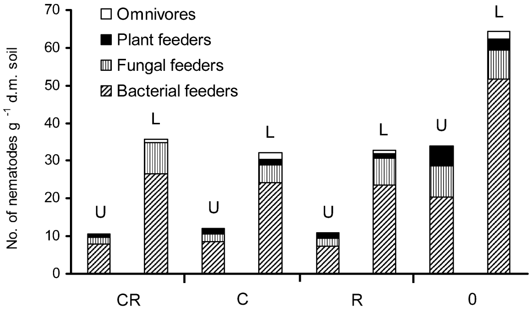

Fig. 1 Mean numbers of nematodes (individuals g^{-1} dry matter soil), and proportions of different feeding groups (*CR* both earthworms, *C A. caliginosa*, *R L. rubellus*, *0* no earthworms, *U* unlimed, *L* limed)

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

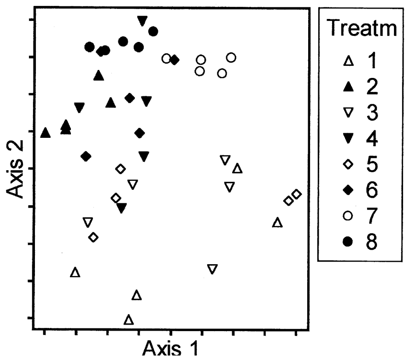

Fig. 2 Plot diagram of nematode communities in the NMS ordination (selected two axes in a three-axis solution). Treatments: *Open shapes* no lime; *closed* limed; *1, 2* both earthworms; *3, 4 A. caliginosa*; *5, 6 L. rubellus*; *7, 8* no earthworms

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

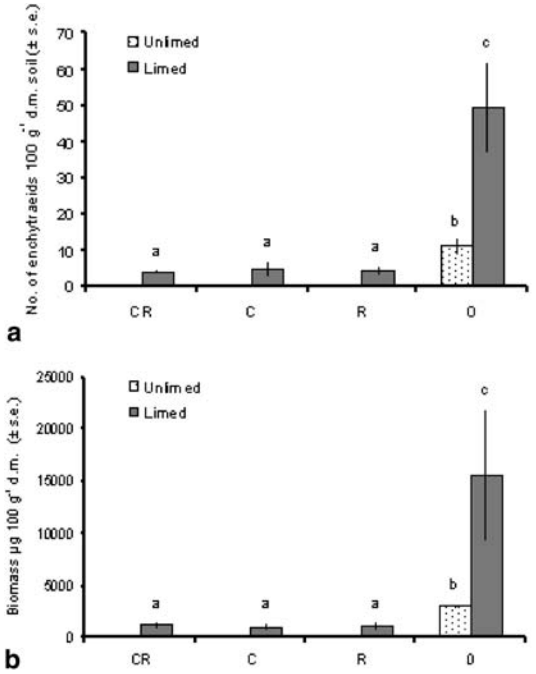

Fig. 3 Mean numbers (ind. 100 g^{-1} d.m soil ± SE) and biomass (μg 100 g^{-1} d.m soil ± SE) of enchytraeids (*CR* both earthworms, *C A. caliginosa*, *R L. rubellus*, *0* no earthworms). Significant differences (P <0.05) between CR, C, R and 0 within unlimed and limed are indicated with *a different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

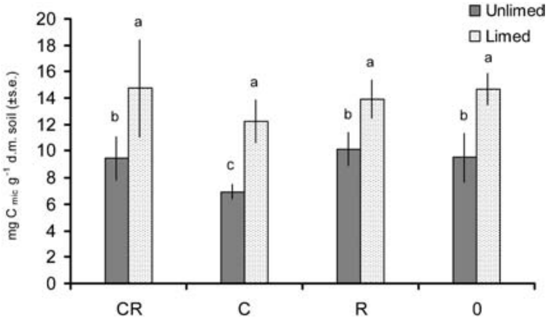

Fig. 4 Estimated microbial biomass C (mg C_{mic} g^{-1} d.m. soil ± SE) in untreated and limed humus with different faunal composition (*CR* both earthworms, *C A. caliginosa*, *R L. rubellus*, *0* no earthworms). Significant differences (P <0.05) between CR, C, R and 0 within unlimed and limed are indicated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

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 Aporrectodea 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
Bryodrillus ehlersi	–	–	–	0.87	–a	–a	–a	0.7b	
Mesenchytraeus pelicensis	–	–	–	–	0.4	–	–	0.2	U < L
Enchytraeus buchholzi	–	–	–	–	1.1	1.3	1.3	3.6	U < L
Enchytraeus lacteus	–	–	–	–	0.2	–	0.8	2.7	U < L
Henlea sp.	–	–	–	–	–a	–a	–a	0.9b	U < L
Henlea perpusilla	–	–	–	–	–a	–a	–a	155b	
Henlea nasuta	–	–	–	–	0.9a	1.1a	1.6a	14.7b	U < L
Fridericia sp.	–	–	–	–	–	–	–	0.60	
Fridericia bulboides	–	–	–	–	–a	0.2a	–a	1.4b	U < L
Fridericia razelli	–	–	–	–	0.2a	0.2a	0.2a	1.7b	U < L
Cognettia sphagnetorum	–	–	–	9.9	–a	–a	–a	2.3b	U < L
Enchytronia parva	–	–	–		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 CO_2 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, coexistence 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 seems 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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