Ann. Zool. Fennici 26:1–23. 1989

The Lumbricidae (Oligochaeta) of southern Finland: species assemblages, numbers, biomass and respiration

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Terhivuo, J. 1989: The Lumbricidae (Oligochaeta) of southern Finland: species assemblages, numbers, biomass and respiration. — Ann. Zool. Fennici 26:1–23.

Coniferous forests, shore alder thickets, deciduous forests, shores and meadows were sampled in three regions in S Finland (60°N) to survey the earthworm assemblages and their structural and energetic characteristics in relation to environmental and regional variables.

Coniferous forests and shores are extreme habitats for earthworms: five species were found in both, and regional means ranged between 32–115 ind./m^2 and 4–11 g/m^2 (wt. of preserved worms) in coniferous forests and similarly between 46–150 ind./m^2 and 6–10 g/m^2 on shores. Epigeic species, particularly *D. octaedra*, comprised 89–97% of the total numbers and 62–93% of the earthworm biomass in these biotopes. Meadows and deciduous forests both hosted eleven species. Meadows had 338–464 ind./m^2 and 47–164 g/m^2 and deciduous forests had 167–265 ind./m^2 and 65–131 g/m^2. The characteristic species comprised deep-burrowers, viz., *A. caliginosa*, *A. rosea* and *L. terrestris* and the epigeic *D. octaedra* and *L. rubellus*. *L. terrestris* totalled 38–51% of the earthworm biomass. Shore alder thickets represented an intermediate biotope; the ranges were 56–219 ind./m^2 and 16–70 g/m^2. *D. octaedra*, *L. rubellus* and *O. tyrtaeum* dominated there.

The assemblages also differed in their energetics: the estimated mean oxygen consumption ranged from 699 in coniferous forests to 5127 mm^3 O_2/h/m^2 in meadows. The mean rate was, however, about twice as high in coniferous forests as in meadows (97 vs. 52 mm^3 O_2/h/g of wet wt. of worms).

In all biotopes the number of species declined eastwards, and, particularly in rich soils, the numbers and biomasses of epigeic species increased while those of deep-burrowers declined. Southern Finnish earthworm assemblages resemble those of S Sweden but differ from those in central and northern Finland, where the numbers of species and individuals are much lower.

Several environmental factors of forests and open biotopes correlated with the number of species and individuals according to the generally increasing fertility of the biotopes in them, but no key factor common to all the different biotopes was found. The species have unequal habitat requirements: epigeic species preferred coniferous forests and/or shores, whereas anesic and endogeic species preferred deciduous forests and/or meadows. In extreme biotopes hardly any significant associations, either positive or negative, between the species were found. In fertile soils negative interactions between some species may occur, but the many positive associations found between the numbers of individuals of several species and of ecological groups of species may be due to the general improving impact of earthworms upon the soil which can facilitate the habitat occupancy of additional species. Most structural differences in earthworm assemblages are, however, attributed to dissimilar habitat requirements of the species.

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1. Introduction

There have been several comprehensive faunistic studies on the Lumbricidae in Finland (e.g. Karppinen & Nurminen 1964, Terhivuo 1988a; for Åland, see Backlund 1945, Haeggström & Terhivuo 1979) but detailed qualitative and quantitative data on the structure and function of earthworm assemblages in

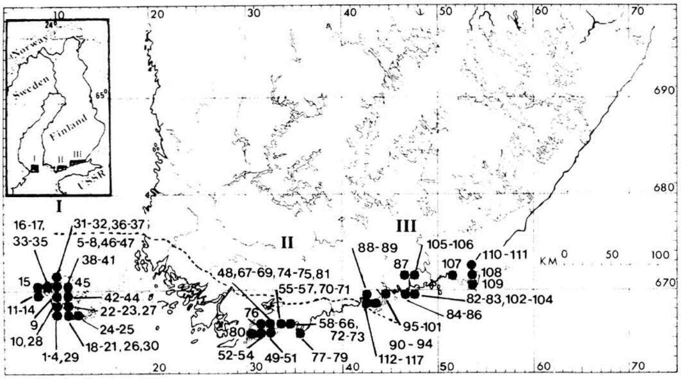

Fig. 1. The three study regions (I–III) and the sample localities (1–117) in S Finland according to the 10×10 km squares of the national unifrom grid (27°E) system (Heikinheimo & Raatikainen 1971). The broken line indicates the boundary between the hemiboreal and south boreal vegetation zones of Ahti et al. (1968). The insert shows the location of the study regions in Finland.

different biotopes are meagre. Many of the earlier surveys focus on coniferous forests that are widely spread but poor in earthworms (Siivonen 1941, Karppinen 1958, Nurminen 1967). Huhta et al. (1967), Huhta & Koskenniemi (1975), Koponen & Ojala (1975) and Huhta (1976) estimated the densities, biomasses and annual community respiration of soil invertebrates, including the earthworms of coniferous and some more luxurious forests in S and N Finland. Törmälä (1986) monitored the biomass and numbers of earthworms in central Finnish fields left lying fallow. Terhivuo & Valovirta (1978) recorded the species composition of earthworm assemblages in nine kinds of biotopes in different parts of Finland. The latter study did not indicate, however, quantitative aspects of the assemblages, which is the purpose of this study. I aimed to obtain quantitative and qualitative data on earthworm assemblages and to survey them in relation to environmental and regional variables. To maximize variability I sampled many localities once instead of continuously monitoring just a few of them. The samples originate from three regions in S Finland (about lat. 60°N) and they were taken during three autumns, i.e. at the season when earthworm numbers should be high.

In S Finland the earthworm fauna is more diverse than elsewhere in the country and changes continuously, due in particular to the increasing rate of anthropochory of species and human impact upon the environment (Terhivuo 1988a).

2. Material and methods

2.1. Sampling times, localities and biotopes

I sampled the main island of the Åland archipelago in SW Finland (I), W Uusimaa (II) and E Uusimaa & Kymi (III) in September 1977, September–October 1979 and September–November 1984, respectively (Fig. 1). The 117 sampling localities are indicated as 10×10 km squares of the national uniform grid (27°E) system (see Heikinheimo & Raatikainen 1971). They are numbered according to the sampling sequence. Each locality was visited only once. Two of the regions (I–II) are situated in the hemiboreal and one (III) in the south boreal vegetation zones. Though located at the edge of these zones they represent a west-east vegetational gradient and also a corresponding climatic gradient (e.g. Abrahamsen et al. 1977).

The biotopes comprise coniferous forests, shore alder thickets, rich deciduous forests, shores and meadows. The last two are called open biotopes, whereas the others are forests. For the numbers of localities of the biotopes see Table 1.

Most of the coniferous forests belong to the moist heath *Myrtillus* type of forests with *Vaccinium myrtillus* as the dominating dwarf schrub (Fig. 2). A few are slightly luxurious, with some deciduous trees and bushes mixed. Shore alder thickets form belt like woods on the uppermost parts of shore plains. *Alnus incana* and/or *A. glutinosa* are the dominant tree species (Fig. 3). Deciduous forests comprise rich stands characterized by broad-leaved trees and bushes (Fig. 4). For instance, *Corylus avellana*, *Betula* spp. and *Populus tremula* dominated stands are included. Shores are alluvial shore plains by the Baltic Sea. They are occasionally submerged due to the changing level of the brackish water (salinity about 0.05% or less) of the Baltic. Some are open sites, whereas in others dense growths of *Phragmites* occur on the shore line (Fig. 5). Meadows comprise fields not cultivated in one or more years prior to sampling (Fig. 6).

I visually estimated the coverage of the plant species at each sample site. The mean regional coverages of the vegetation layers are indicated in Table 1. The percentages of the species of trees and bushes are pooled but coniferous and deciduous species are considered separately.

The following soil qualities were simultaneously measured: (a) pH at depths of 1–3 cm and 5–10 cm (regions I and II); the samples for this were mixed with distilled water in the proportion of about 1:1 by volume prior to measuring pH, (b) the thickness of the organic soil at each site, (c) the quality of the parent material was observed and soil moisture content was estimated as either wet, moist, rather moist, rather dry or dry. Table 1 summarizes these data. I chose each sample plot ran-

Table 1. Percent mean coverages of the vegetation layers, soil properties and numbers of samples in the five biotopes surveyed in the three regions. I = Main Åland, II = W Uusimaa and III = E Uusimaa & Kymi (see Fig. 1), S = silt, C = clay and M = sand, gravel and big stones (= endmoraines of the Quaternary Ice Age).

Vegetation layer, soil property	Coniferous forests				Shore alder thickets				Deciduous forests				Shores				Meadows			
	I	II	III	$\bar{x}$	I	II	III	$\bar{x}$	I	II	III	$\bar{x}$	I	II	III	$\bar{x}$	I	II	III	$\bar{x}$
Coniferous trees & bushes	57	50	55	54	3	11	14	8	11	11	17	12	–	–	1	<1	–	2	1	1
Deciduous trees & bushes	10	16	18	14	110	94	86	99	104	115	91	105	–	–	–	–	2	7	8	6
Dwarf shrubs	39	60	62	52	–	–	–	–	1	–	–	<1	–	–	–	–	–	–	–	–
Grasses & herbs	18	26	25	22	70	72	60	68	73	57	64	66	80	82	88	83	100	100	99	100
Mosses	91	81	72	83	2	11	28	12	30	25	27	28	50	8	35	30	16	13	3	9
Organic layer (cm)	14	11	11	12	10	8	13	10	18	23	16	19	5	7	8	7	20	17	18	18
No. of localities	9	7	6	22	8	5	5	18	15	10	7	32	7	7	4	18	8	5	14	27
pH (1–3 cm)	4.4	5.0	–	4.7	6.8	5.2	–	6.5	6.5	5.5	–	6.0	6.9	5.6	–	6.3	5.8	5.9	–	5.9
pH (5–10 cm)	4.3	4.6	–	4.5	6.8	5.2	–	6.5	6.0	5.2	–	5.6	6.7	5.6	–	6.2	5.7	5.7	–	5.7
pH (total range)	3.3–5.6				4.3–7.7				4.4–7.7				4.5–7.6				4.4–7.1			
Soil moisture	rather dry to rather moist				moist to wet				rather moist to rather dry				wet to moist				moist to rather dry			
Soil profile	podsolic				transitional				grey-brown podsolic				layered				mixed			
Organic soil	peat				mull-like or mull				mull-like				hay & grass turf				mull			
Parent material	S,M				S,C,M				S,C,M				C,S,M				C,S			

domly within an area where the vegetation seemed to be typical of the biotope. Special microhabitats, such as stumps, under stones, etc., were not sampled.

2.2. Sampling procedure

The total sample catch was 2764 earthworms. I used a combination of formalin application and hand-sorting methods as decribed in Terhivuo (1982). This involves the application of 10 litres of 0.5% formalin to a sample plot measuring 25×50 cm. The sample plot was demarcated with an iron frame to avoid the solution being absorbed outside it. The earthworms expelled were immediately preserved in 70% ethanol. After about 5 minutes the organic soil within the frame was removed and hand-sorted on a plastic sheet. Each sample was dug down to the mineral soil level or, when clay was the parent material, to a depth of about 50 cm.

I also hand-sorted a parallel set of samples in regions I and II as explained in Terhivuo (1982). Because hand-sorting proved to be inferior in efficiency to the combined method in extracting earthworms, particularly *L. terrestris*, in fertile soils, I thus now use the data obtained by the combined method, if not otherwise stated. For further information on the relative efficiency of the methods, see Terhivuo (1982).

2.3. Identification, nomenclature and ecological groups of species

All the individuals were determined to species level. Those without a clitellum were considered to be immatures. Most of these are juveniles but some large individuals without a clitellum were evidently senile adults. The identification of juveniles is mostly based on the information given in Stöp-Bowitz (1969), but immatures of *O. cyaneum* and *A. chlorotica* with characteristic colouration when alive were secured separately in the field. The nomenclature follows Sims & Gerard (1985). The different forms or subspecies of the *Dendrodrilus rubidus* and *Aporrectodea caliginosa* complexes are not considered. For the species recorded see Fig. 9.

Based on ecological, morphological, physiological and behavioural characters Bouché (1972) divided French lumbricids into three groups: *epigeic* species are small, mobile, mesophagous, have a high rate of respiration, lack diapause and live among litter or in the upper soil layers. *Anesic* species are moderate to large in size, macrophagous, capable of rapid retreat through burrows leading deeper into soil, and diapause is common and often obligatory among them. They live deep in the soil but forage among litter. *Endogeic* species are small to moderate, microphagous, sluggish and confined to deeper soil layers.

Fig. 2. Coniferous forest (*Myrtillus* type moist heath forest) in W Uusimaa (loc. 64, Siuntio, September 1987). *Picea abies* and *Pinus silvestris* dominate in the tree layer and *Vaccinium myrtillus* abounds in the field layer. The dense carpet of mosses includes Pleurozi*um*, *Dicranum* and *Hylocomium* species.

Fig. 3. Shore alder thickets are *Alnus* dominated woods lining the uppermost parts of shore plains. *Filipendula ulmaria* is the dominant herb at this site. (W Uusimaa, loc. 62, Siuntio, September 1987).

Fig. 4. Rich decidous forest with *Betula*, *Salix*, *Alnus* and *Picea* species in E Uusimaa (loc. 71, Inkoo, September 1987). The dense layer of grasses and herbs includes *Aegopodium*, *Equisetum*, *Poa*, *Elytrigia* and *Dryopteris* species.

Fig. 5. Seashore plain in W Uusimaa (loc. 61, Inkoo, September 1987). A growth of *Phragmites communis* isolates the shore plain belt from open water, and a shore alder thicket borders the uppermost part of it. In the field layer there are e.g. *Festuca*, *Poa*, *Carex*, *Potentilla*, *Plantago* and *Cicuta* species.

Fig. 6. Meadows are old fields left lying fallow for one or more years. Grasses and herbs are abundant and here comprise *Dactylis, Anthriscus, Artemisia, Elytrigia, Phleum, Achillea* and *Fragaria* species. (W Uusimaa, loc. 75, Inkoo, September 1987).

Deep-burrowers, i.e. anesic and endogeic species, make permanent burrows that respectively run vertically or horizontally, whereas epigeic species lack these. According to Satchell (1980) deep-burrowers and surface-living species represent two divergent evolutionary lineages that may have arisen through '*K*' and '*r*' selections, respectively. According to Bouché's (1972) definitions, the epigeic species in my material comprise *E. tetraedra, D. octaedra, D. rubidus, L. castaneus* and *L. rubellus. L. terrestris* and *A. longa* belong to anesic and *A. chlorotica, A. caliginosa, A. rosea, O. tyrtaeum* and *O. cyaneum* to endogeic species. Regarding vertical distribution, *L. rubellus* living in permanent, shallow U-formed burrows close to the soil surface may be also considered an intermediate species (e.g. Edwards & Lofty 1972, Nordström & Rundgren 1973, Persson & Lohm 1977, Perel 1979). Most of the epigeic species mentioned above are parthenogenetic, whereas deep-burrowers comprise both parthenogenetic and amphigonic species (Muldal 1952, Omodeo 1952, Casellato 1987).

2.4. Counting and weighing

Digging up soil material unavoidably fragmented some of the earthworms. For counting numbers the intact worms were first grouped into immatures or matures. The fragments indisputably forming complete worms were counted as such and all the other fragments were regarded as separate individuals and added to the count.

The worms were weighed 1–3 months after sampling. Prior to weighing they were kept on paper towels for about 2 minutes to dry similarly. The intact adults and immatures were weighed according to the species in separate groups with electronic scales (Mettler) and the same applied to the fragments. The biomass estimates thus refer to the wet weight of the preserved worms.

2.5. Population parameters computed

I calculated the following indices to characterize earthworm assemblages:

1) Relative frequency denotes the percentage of the samples where the species (or any representative of the same ecological species group, see section 2.3.) was present.

2) Dominance is the percentage of the individuals of the species (or the individuals of the same species group) in relation to all the individuals of a biotope.

3) Numbers and biomass are given as values adjusted to m^2.

4) Expected species richness in a sample of *n* earthworms is estimated according to the following rarefaction formula:

$$E(S_n) = \sum_{i=1}^{S} \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right]$$

where S is the number of species expected in a random sample of n individuals, N equals the total number of individuals and N_i is the number of individuals of the ith species. Rarefaction curves predict the number of species as a function of sample size, i.e. the diversity of species can be compared between the biotopes despite the unequal total numbers of individuals sampled (see e.g. Sanders 1968, Simberloff 1978, 1979, Haila 1983).

5) I made an ordination of the mean numbers of individuals of the different species in the three regions by means of the DCA (detrended correspondence analysis). For the principles see Gauch (1982).

6) The co-occurrence of species in samples is measured according to Jaccard's (1908) formula;

$$r_J = \frac{A}{A + B + C}$$

where A = the number of samples where species A and species B are present, B = the number of samples with A present but B absent and C = the number of samples with A absent and B present. According to Janson & Vegelius (1981) this index fulfills the mathematical requirements set for an efficient measure of ecological association.

7) Based on differences in burrowing habits of earthworm species, Nordström & Rundgren (1973) introduced an index for vertical aggregation of earthworms at a site. The formula is:

$$I_V = \frac{A + 1.5\,B + 2\,C}{A + B + C}$$

where A = number of individuals of surface-living (= epigeic), B = number of individuals of intermediate (= *L. rubellus*) and C = number of the individuals of deep-burrowing (= anesic and endogeic) species.

8) The index for horizontal distribution of earthworms denotes the variance/mean ratio of earthworm numbers in samples. The departure of the ratio from unity, i.e. from the Poisson distribution, is tested by calculating $(n-1)s^2/\bar{x}$ which is an approximation to the χ^2 value with $n-1$ degrees of freedom (Jackson 1968, Wratten & Fry 1980). When the sample size >30

Table 2. The relative frequency (F, %) of the species and the groups of ecologically dissimilar species of earthworms in samples (25×50 cm), dominance of individuals (D, %) and biomass (B, %) in coniferous forests of the three study regions.

	Main Åland			W Uusimaa			E Uusimaa & Kymi			All regions		
Species	F	D	B	F	D	B	F	D	B	F	D	B
Epigeic species	78	76	60	100	94	66	100	92	52	91	89	62
D. octaedra	78	58	34	100	94	66	100	92	52	91	84	52
D. rubidus	11	4	3	–	–	–	–	–	–	5	1	1
L. rubellus	44	13	24	–	–	–	–	–	–	18	4	9
Anesic species												
L. terrestris	–	–	–	14	6	34	17	8	48	9	5	23
Endogeic species	11	24	40	–	–	–	–	–	–	4	6	16
A. caliginosa	11	20	38	–	–	–	–	–	–	4	5	15
A. rosea	11	4	2	–	–	–	–	–	–	4	1	<1
Samples		9			7			6			22	
with lumbricids (%)		78			100			100			90	
Total numbers												
Species: observed		5			2			2			6	
Species: expected[1]		4.4 ± 0.7			1.7 ± 0.4			2.0 ± 0.1			3.3 ± 1.0	
Individuals (total)		45			101			24			170	
in samples (mean ± *SD*)		5.0 ± 5.5			14.4 ± 7.1			4.0 ± 3.3			7.7 ± 7.1	
Biomass (g) (total)		8.3			9.9			3.3			21.5	
in samples (mean ± *SD*)		0.9 ± 1.3			1.4 ± 1.6			0.5 ± 0.8			1.1 ± 1.3	

[1] = mean ± *SD* for a standardized sample of 20 individuals based on rarefaction curves calculated for each region.

then $d = \sqrt{2\chi^2} - \sqrt{(2\nu-1)}$ is calculated (ν = the degree of freedom). An agreement with a Poisson series occurs if $d<1.96$, and if $d>1.96$ with a negative sign, a binomial distribution pattern is accepted. When $d>1.96$ with a positive sign, an aggregated horizontal distribution occurs.

9) Based on the principles that the more an organism loses energy the more it has to consume food, and that most of the energy uptake of an organism is lost through respiration, I used respiration as an index for the energetics and function of the assemblage, because the numbers and biomass of earthworms may not necessarily adequately characterize these aspects.

For instance, equal numbers of earthworms at any two sites may involve differences in energetics and function if their biomasses are unequal, and biomass does not indicate the number of individuals sharing it. In order to estimate energetics it is noteworthy that the rate of respiration per weight unit is a species-specific character and correlates negatively with body weight (Byzova 1965). The rate of respiration also depends on the ambient temperature (see e.g. Persson & Lohm 1977).

I applied the oxygen consumption rates indicated in Byzova (1965) and discussed by Kasprzak (1983a–c). The total oxygen consumption equals the sum of the oxygen comsumptions of the individuals of different species in each sample.

I divided the biomass of every species by the corresponding number of individuals in each sample to obtain the mean weights for the species. Oxygen uptake was estimated according to the species-specific respiration equation for each species and the result was multiplied by the number of individuals. The oxygen consumptions of the species in the sample were summed and multiplied by eight to gain the total oxygen uptake *per* m^2.

Based on the ln transformed data I calculated linear regressions between the biomasses of the earthworms in samples and the corresponding rates of respiration for each biotope. I adjusted the data to the temperature of +10°C according to the principles explained in detail by Persson & Lohm (1977, pp. 35–38 and 47–48). Thus, the variation in the species and in the numbers of individuals in the samples are taken into account in the calculations. Due to an absence of data on the oxygen consumption rates I applied to *D. rubidus* the equation for *D. octaedra*, to *A. chlorotica* that for *A. rosea* and to *A. longa* and *O. cyaneum* that for *L. terrestris*. The biomasses of these "substituted" species comprise 5.5% of the total earthworm biomass, so that the corresponding bias is not excessively high.

Estimating respiration rates for outdoor populations is subject to several sources of error, as discussed by, e.g., Laverack (1963) and Kasprzak (1983a–c). In the present context the estimated rates are used only as indices, and not as absolute values, because no changes in the temperature of the soil or fluctuations in numbers of earthworms were monitored.

Section 3.2.3., based on Tables 2–6, shows that in all the biotopes and regions there was $s^2 > \bar{x}$ for the earthworm numbers in samples. I accordingly applied non-parametric statistical tests for these data sets. The abbreviations for statistical significances are given in the legend to Table 7.

Table 3. The relative frequency (F, %) of the species and the groups of ecologically dissimilar species of earthworms in samples (25×50 cm), dominance of individuals (D, %) and biomass (B, %) in shore alder thickets of the three study regions.

	Main Åland			W Uusimaa			E Uusimaa & Kymi			All regions		
Species	F	D	B	F	D	B	F	D	B	F	D	B
Epigeic species	100	39	15	100	75	64	100	89	83	100	61	33
E. tetraedra	25	3	<1	–	–	–	–	–	–	11	1	<1
D. octaedra	75	13	2	60	41	14	80	43	12	78	30	6
D. rubidus	25	2	<1	40	14	4	20	3	<1	28	6	<1
L. rubellus	100	22	12	40	20	46	40	43	72	67	24	26
Anesic species												
L. terrestris	62	29	67	–	–	–	–	–	–	28	13	45
Endogeic species	62	32	18	60	25	36	40	12	17	56	26	22
A. caliginosa	25	19	10	–	–	–	20	9	10	17	9	8
A. rosea	12	1	<1	–	–	–	–	–	–	6	<1	<1
O. tyrtaeum	62	12	7	60	25	36	20	3	6	50	17	14
Samples		8			5			5			18	
with lumbricids (%)		100			100			100			100	
Total numbers												
Species: observed		8			5			5			8	
Species: expected[1]		6.2 ± 0.8			4.0 ± 0.1			4.7 ± 0.5			6.2 ± 0.7	
Individuals (total)		135			137			35			307	
in samples (mean ± *SD*)		16.9 ± 11.6			27.4 ± 23.7			7.0 ± 5.1			17.1 ± 16.0	
Biomass (g) (total)		70.1			24.8			9.9			104.7	
in samples (mean ± *SD*)		8.8 ± 9.4			5.0 ± 6.3			2.0 ± 2.1			5.8 ± 7.4	

[1] = mean ± *SD* for a standardized sample of 30 individuals based on the rarefaction curves calculated for each region.

3. Results

3.1. Earthworm assemblages and their regional variation

3.1.1. Coniferous forests

Table 2 summarizes the data of the earthworm assemblages in coniferous forests and warrants regional comparisons. I conclude: 1) Six species recorded in the total of 170 individuals show that coniferous forests are poor in earthworm species. 2) The number of species is higher in Main Åland than on the Finnish mainland, as shown by their absolute and their expected numbers. 3) *D. octaedra* is the only permanent member of the assemblage in all the regions. 4) *D. octaedra* comprises the majority of the numbers and about half of the biomass. 5) Anesic and endogeic species are only occasionally present in samples but due to their large size they comprise about 40% of the total biomass. 6) The three regions are heterogeneous in respect of the numbers of earthworms in samples (Kruskal-Wallis test, $H^* = 9.048^*$, $df = 2$). In W Uusimaa the mean number of individuals exeeds those of the other regions. 7) Regarding earthworm biomass in samples, the three regions are homogeneous ($H^* = 2.390$, ns, $df = 2$). 8) The relative frequencies and corresponding dominances of the species in the three regions correlate positively (Spearman's rank correlation, $r_s = 0.833^{**}$, $n = 9$).

3.1.2. Shore alder thickets

Eight earthworm species occurred in shore alder thickets (Table 3). I conclude: 1) The number of species is higher in Main Åland than in the other regions. 2) Epigeic species are present in all the samples, and, endogeic species are more frequently recorded than anesic species. 3) The three regions are

Table 4. The relative frequency (F, %) of the species and the groups of ecologically dissimilar species of earthworms in samples (25×50 cm), dominance of individuals (D, %) and biomass (B, %) in deciduous forests of the three study regions.

	Main Åland			W Uusimaa			E Uusimaa & Kymi			All regions		
Species	F	D	B	F	D	B	F	D	B	F	D	B
Epigeic species	100	25	12	100	58	24	100	51	30	100	41	17
D. octaedra	67	6	1	100	33	6	86	23	4	81	18	2
D. rubidus	7	2	1	40	9	5	–	–	–	16	4	1
L. castaneus	13	2	1	40	6	1	14	2	<1	22	4	1
L. rubellus	80	15	10	60	10	12	57	26	26	69	15	13
Anesic species	73	21	60	50	7	34	29	6	40	56	13	51
L. terrestris	73	20	58	50	7	34	29	6	40	56	13	50
A. longa	7	1	2	–	–	–	–	–	–	3	<1	<1
Endogeic species	93	54	28	67	35	42	43	44	31	72	45	32
A. chlorotica	13	3	1	–	–	–	–	–	–	6	1	1
A. caliginosa	80	31	21	40	22	19	43	38	30	59	29	22
A. rosea	27	18	4	40	5	2	14	6	1	28	11	3
O. cyaneum	–	–	–	20	7	19	–	–	–	6	–	4
O. tyrtaeum	33	2	2	10	1	2	–	–	–	19	1	2
Samples		15			10			7			32	
with lumbricids (%)		100			100			100			100	
Total numbers												
Species: observed		10			9			6			11	
Species: expected[1]		9.4 ± 0.7			8.7 ± 0.5			6.0 ± 0.2			9.8 ± 0.8	
Individuals (total)		431			331			146			908	
in samples (mean ± *SD*)		28.7 ± 25.7			33.1 ± 18.2			20.9 ± 12.2			28.4 ± 21.0	
Biomass (g) (total)		246.5			84.0			56.5			387.0	
in samples (mean ± *SD*)		16.4 ± 10.8			8.4 ± 9.5			8.1 ± 10.0			12.1 ± 10.7	

[1] = mean ± *SD* for a standardized sample of 100 individuals according to the rarefaction curves counted for each area.

homogeneous in numbers of individuals (Kruskal-Wallis test, $H^* = 3.909$, ns, $df = 2$) and biomass ($H^* = 3.376$, ns, $df = 2$). 4) In Main Åland the different ecological groups of species contribute rather equally to the numbers but in the other regions epigeic species dominate in this respect: the ratio between individuals of epigeic and deep-burrowing species varies greatly between the regions ($\chi^2 = 49.584^{***}$, $df = 2$). 5) Relative frequencies and corresponding dominances of the species are statistically significantly correlated in the three regions ($r_s = 0.689^{**}$, n = 17). 6) Deep-burrowers, viz., anesic and endogeic species comprise about 2/3 of the total earthworm biomass. 7) *D. octaedra*, *L. rubellus* and *O. tyrtaeum* are the characteristic species of the assemblage. 8) *D. rubidus* was found in all the regions but its abundance and biomass are low. In Main Åland *L. terrestris* is a permanent member of the assemblage but it is not so on the Finnish mainland.

3.1.3. Deciduous forests

Earthworms prefer this habitat: eleven species were found in the catch of 908 individuals (Table 4). I conclude: 1) The number of species again decreases eastwards. 2) Epigeic species are present in all the samples but their dominance is higher on the Finnish mainland, whereas both anesic and endogeic species decrease eastwards in these respects ($\chi^2 = 100.554^{***}$, $df = 4$). 3) The samples from the three regions have equal numbers of individuals (Kruskal-Wallis test, $H^* = 2.518$, ns, $df = 2$) but slightly different biomasses ($H^* = 7.239^*$, $df = 2$). 4) Relative frequencies and the corresponding dominances of the species are significantly correlated in the three regions ($r_s = 0.793^{***}$, $n = 25$). 5) *A. caliginosa*, *L. terrestris* and *A. rosea*, representing deep-burrowers and *D. octaedra* and *L. rubellus*, being an epigeic species, comprise the characteristic species of the

Table 5. The relative frequency (F, %) of the species and the groups of ecologically dissimilar species of earthworms in samples (25×50 cm), dominance of individuals (D, %) and biomass (B, %) in shores of the three study regions.

	Main Åland			W Uusimaa			E Uusimaa & Kymi			All regions		
Species	F	D	B	F	D	B	F	D	B	F	D	B
Epigeic species	100	98	92	57	100	100	100	95	86	78	97	93
E. tetraedra	71	30	9	29	28	14	25	1	<1	44	16	8
D. octaedra	71	35	20	43	44	23	75	17	18	61	29	20
D. rubidus	29	10	4	29	14	12	75	71	42	39	40	16
L. rubellus	29	22	59	14	14	52	50	5	25	17	12	48
Endogeic species												
O. tyrtaeum	14	2	8	–	–	–	50	5	14	17	3	7
Samples		7			7			4			18	
with lumbricids (%)		100			57			100			83	
Total numbers												
Species: observed		5			4			5			5	
Species: expected[1]		4.7 ± 0.4			4.0 ± 0.0			4.2 ± 0.7			4.6 ± 0.5	
Individuals (total)		40			43			75			158	
in samples (mean ± *SD*)		5.7 ± 4.0			6.1 ± 8.6			18.8 ± 13.0			8.8 ± 9.6	
Biomass (g) (total)		8.9			5.8			5.3			20.0	
in samples (mean ± *SD*)		1.3 ± 1.3			0.8 ± 1.7			1.3 ± 1.1			1.1 ± 1.4	

[1] = mean ± *SD* for a standardized sample of 30 individuals according to the rarefaction curves for each region.

biotope. 6) *L. castaneus*, *O. tyrtaeum* and *D. rubidus* were fairly often present in samples but their total numbers and biomass remain <5%. The other species were found in only one of the regions.

3.1.4. Shores

Shores are extreme habitats for earthworms: five species were recorded in the catch of 158 individuals (Table 5). I conclude: 1) The number of species slightly decreases eastwards. 2) The number of species, individuals and biomass are low. 3) The three regions are homogeneous as regards the numbers (Kruskal-Wallis test, $H^* = 3.423$, ns, $df = 2$) and biomass ($H^* = 2.147$, ns, $df = 2$) of earthworms in samples. 4) Relative frequences and corresponding dominances of the species are significantly correlated in all the regions ($r_s = 0.580^*$, $n = 14$). 5) Epigeic species, particularly *D. octaedra* and *D. rubidus* contribute most to the numbers, but *L. rubellus* due to its large size makes up about half of the biomass. 5) Epigeic species, namely *D. octaedra*, *D. rubidus*, *L. rubellus* and *E. tetraedra* are the characteristic species of shores in S Finland.

3.1.5. Meadows

The 1221 earthworms from meadows belong to eleven species (Table 6). I conclude: 1) The number of species declines eastwards. 2) Both epigeic and deep-burrowers were present in most samples. 3) The three regions were homogenous as regards numbers (Kruskal-Wallis test, $H^* = 0.603$, ns, $df = 2$) but slightly heterogeneous in respect of the biomass of earthworms ($H^* = 8.800^*$, $df = 2$) in the samples. 4) Relative frequences and the corresponding dominances of the species were correlated in the three regions ($r_s = 0.779^{***}$, $n = 27$). 5) Deep-burrowers contributed most to numbers and biomass, and the numbers of individuals of the three species groups are unequal in the regions ($\chi^2 = 145.665^{***}$, $df = 4$). 7) *A. rosea*, *A. caliginosa*, *D. octaedra* and *L. rubellus* exceed in numbers the other species, but *L. terrestris*, together with *A. caliginosa*, comprises >50% of the total biomass. 8) *O. tyrtaeum*, *D. rubidus* and *L. castaneus*, were recorded in all the regions but their densities were low. The other species were found only in one of the regions.

Table 6. The relative frequency (F, %) of the species and the groups of ecologically dissimilar species in samples (25×50 cm), dominance of individuals (D, %) and biomass (B, %) in meadows of the three study regions.

	Main Åland			W Uusimaa			E Uusimaa & Kymi			All regions		
Species	F	D	B	F	D	B	F	D	B	F	D	B
Epigeic species	75	25	11	100	38	21	100	44	37	93	37	20
E. tetraedra	12	1	<1	–	–	–	–	–	–	4	<1	<1
D. octaedra	62	9	1	80	21	4	100	19	6	85	16	3
D. rubidus	12	<1	<1	20	3	1	57	8	2	37	5	1
L. castaneus	12	2	<1	20	7	2	14	3	2	15	4	1
L. rubellus	62	13	9	75	7	14	51	14	27	67	12	15
Anesic species												
L. terrestris	88	21	59	75	4	30	7	1	3	41	7	38
Endogeic species	88	54	30	80	57	49	86	55	60	85	55	42
A. chlorotica	12	6	2	–	–	–	–	–	–	4	2	1
A. caliginosa	75	29	18	75	6	7	57	27	38	63	22	21
A. rosea	50	17	9	75	47	28	43	19	12	48	25	13
O. cyaneum	–	–	–	20	3	13	–	–	–	4	1	2
O. tyrtaeum	38	2	1	20	2	2	50	10	10	41	6	4
Samples		8			5			14			27	
with lumbricids (%)		100			100			100			100	
Total numbers												
Species: observed		10			9			8			11	
Species: expected[1]		9.5 ± 0.6			9.0 ± 0.1			7.9 ± 0.3			10.2 ± 0.7	
Individuals (total)		338			290			593			1221	
in samples (mean ± *SD*)		42.3 ± 26.9			58.0 ± 36.2			42.4 ± 26.1			45.2 ± 27.9	
Biomass (g) (total)		163.9			54.0			82.9			300.8	
in samples (mean ± *SD*)		20.5 ± 13.3			10.8 ± 9.9			5.9 ± 3.7			11.1 ± 10.5	

[1] = mean ± *SD* for a standardized sample of 200 individuals based on the rarefaction curves calculated for each region.

3.2 Differences between earthworm assemblages of the five biotopes

3.2.1. Diversity and co-occurrence of species

Fig. 7 shows the number of earthworm species as a function of sample size in the five biotopes. In a sample of 100 individuals from deciduous forests or meadows about twice the number of species in coniferous forests or shores can be expected. For shore alder thickets the corresponding ratio is about 1.5. To compare species co-occurrences in the different biotopes I applied the Jaccard (1908) index to the presence-absence data of the species in the samples. To avoid spuriously high index values due to co-occurrences in few samples I excluded the species recorded in <5 samples from the biotope surveyed at a time. Only the co-occurrences of *A. caliginosa* and *L. terrestris* in deciduous forests, *L. rubellus* and *D. octaedra* in meadows and *D. octaedra* and *D. rubidus* in shores had the index value ≥0.6 (Fig. 8). Many of the species pairs, however, were found in two or more biotopes with frequencies ≥40%: *D. octaedra* with *L. rubellus*, *D. rubidus*, *A. caliginosa* and *O. tyrtaeum*; *L. rubellus* with *L. terrestris*, *A. caliginosa* and *O. tyrtaeum*; *D. rubidus* with *O. tyrtaeum*; and *A. caliginosa* with *L. terrestris*. The co-occurrences thus refer to species of the same, and also to those belonging to ecologically dissimilar groups of species. A further approach to survey associations between the individuals of the species will be made in section 3.3.1.

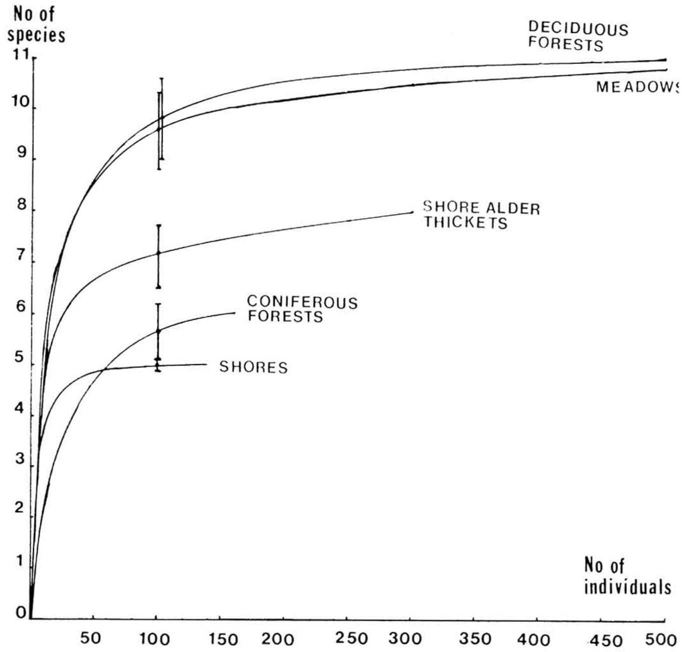

Fig. 7. Expected number of species in pooled samples as a function of sample size in the five biotopes. Vertical bars indicate standard deviation (*SD*). For the method see section 2.5.

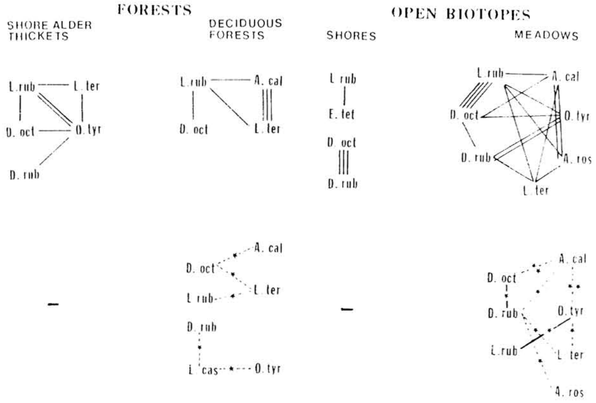

Fig. 8. Associations between earthworm species. All possible pairwise comparisons ($n \geq 5$) were made. — Upper row. Co-occurrence of species in samples (25×50 cm) according to Jaccard's (1908) index. Symbols: one line denotes index values 0.40–0.49, two lines 0.50–0.59, three lines 0.60–0.69 and four lines >0.70. — Lower row. Statistically significant ($P<0.01$) positive (unbroken line) and negative (broken line) correlations between the numbers of individuals of the species in the samples. For statistical symbols see Table 7 and for further discussion see the text.

3.2.2. Numbers, biomass and respiration

The five biotopes had significantly dissimilar numbers of individuals in pooled samples (Kruskal-Wallis test, $H^* = 52.891^{***}$, $df = 4$). The mean densities of individuals, counted over the corresponding regional means, were in the order of coniferous forests (62 ind./m^2), shore alder thickets (137 ind./m^2), deciduous forests (221 ind./m^2), shores (82 ind./m^2) and meadows 381 ind./m^2), thus equalling the proportions of 1:2:4:1:6. The corresponding figures for these biomasses are 7.2, 42.1, 87.7, 9.1 and 99.2 g/m^2, their ratio being 1:6:12:1:14 (Fig. 9A).

Table 7 shows that the estimated O_2 uptake of the mean biomass of earthworms equals 1:4:6:1:7 in the order of coniferous forests, shore alder thickets, deciduous forests, shores and meadows. It is noteworthy that the mean rate of O_2 uptake in extreme biotopes is about twice as high as in fertile soils, but the higher total earthworm biomass in the latter biotopes

Table 7. Linear regressions for the estimation of the oxygen consumption of the mean biomasses of earthworms in the five biotopes. The means are counted over corresponding regional means. The equations are adjusted to +10°C by applying $Q_{10} = 2$ (see e.g. Persson & Lohm 1977) and they are calculated based on the earthworm biomasses in samples and on the species specific oxygen consumtion rates indicated by Byzova (1965). For further explanation see the text. B = wet weight of preserved worms (g/m²), R = oxygen consumption (O_2 mm³/m²/h), Total = O_2 uptake (mm³O_2/m²/h) for the corresponding mean biomass, Rate = total O_2 uptake / mean biomass. Statistical significances: o = $0.10 \geq P > 0.05$, * = $0.05 \geq P > 0.01$, ** = $0.01 \geq P > 0.001$, *** = $0.001 \geq P$, ns = not significant.

Biotope	Linear regression	*r*	Mean biomass (g/m²)	Estimated O_2 uptake Total	Rate
Coniferous forests	$\ln R = 0.794 \ln B + 4.982$	0.969***	7.2	699	97
Shore alder thickets	$\ln R = 0.772 \ln B + 4.929$	0.974***	42.1	2481	59
Deciduous forests	$\ln R = 0.675 \ln B + 5.397$	0.955***	87.7	4523	52
Shores	$\ln R = 0.862 \ln B + 4.788$	0.954***	9.1	806	89
Meadows	$\ln R = 0.749 \ln B + 5.099$	0.965***	99.2	5127	52

Table 8. Earthworm samples grouped according to their indexes of vertical distribution (from 1 to 2, cf. Nordström & Rundgren 1973) and estimated horizontal aggregation in the five biotopes. For statistical significances see Table 7.

Biotope	Vertical distribution				Horizontal distribution			
	1.00–1.33	1.34–1.67	1.68–2.00	mean ± *SD*	s^2	mean	χ^2	*df*
Coniferous forests	19	1	–	1.08 ± 0.18	50.88	7.73	138.22***	19
Shore alder thickets	9	4	5	1.40 ± 0.34	255.10	17.06	254.21***	17
Deciduous forests	7	9	16	1.58 ± 0.34	442.43	28.38	483.27***	31
Shores	12	2	1	1.14 ± 0.27	91.36	8.78	176.90***	14
Meadows	7	6	14	1.60 ± 0.31	776.12	45.22	483.27***	26

accounts for most of the differences in total O_2 consumptions.

Fig. 9A shows the contributions of the three groups of species to total numbers, biomass and estimated respiration of the assemblages in the five biotopes and the three regions. Both in forests and in open biotopes the role of anesic and endogeic species increases according to the fertility gradient that the biotopes in them represent. Fig. 9B, based on samples pooled according to the biotope, indicates that in extreme biotopes, namely coniferous forests and shores, there are three species, *D. octaedra*, *D. rubidus* and *L. rubellus*, that comprise about 2/3 of numbers, biomass and total respiration of the assemblages, whereas in more fertile forests and meadows five species (*L. terrestris*, *A. caliginosa*, *L. rubellus*, *A. rosea* and *D. octaedra*) are needed to equal that proportion. In fertile biotopes *D. octaedra* contributes more to the total respiration of the assemblages than could be expected on the basis of its biomass. This is due to its high rate of respiration (Byzova 1965).

3.2.3. Vertical and horizontal distributions

Because burrowing activity is a species-specific character of the lumbricids (e.g. Edwards & Lofty 1972), the vertical distribution of individuals in an assemblage can be associated and roughly estimated according to the species and the numbers of their individuals at any site. For the empirical evidence see e.g. (Nordström & Rundgren 1973, Rundgren 1975, Persson & Lohm 1977, Perel 1979). The index introduced by Nordström & Rundgren (1973) varies from 1.0 (only litter-dwellers present) to 2.0 (only deep-burrowers present).

Table 8 shows that meadows resemble deciduous forests, where most of the individuals and biomass occur in deeper soil layers in contrast to shores and coniferous forests, where they are confined to the upper soil layers. In shore alder thickets earthworms tend to be rather uniformly distributed vertically. Earthworms show highly significant horizontal aggregations in the five biotopes (Table 8).

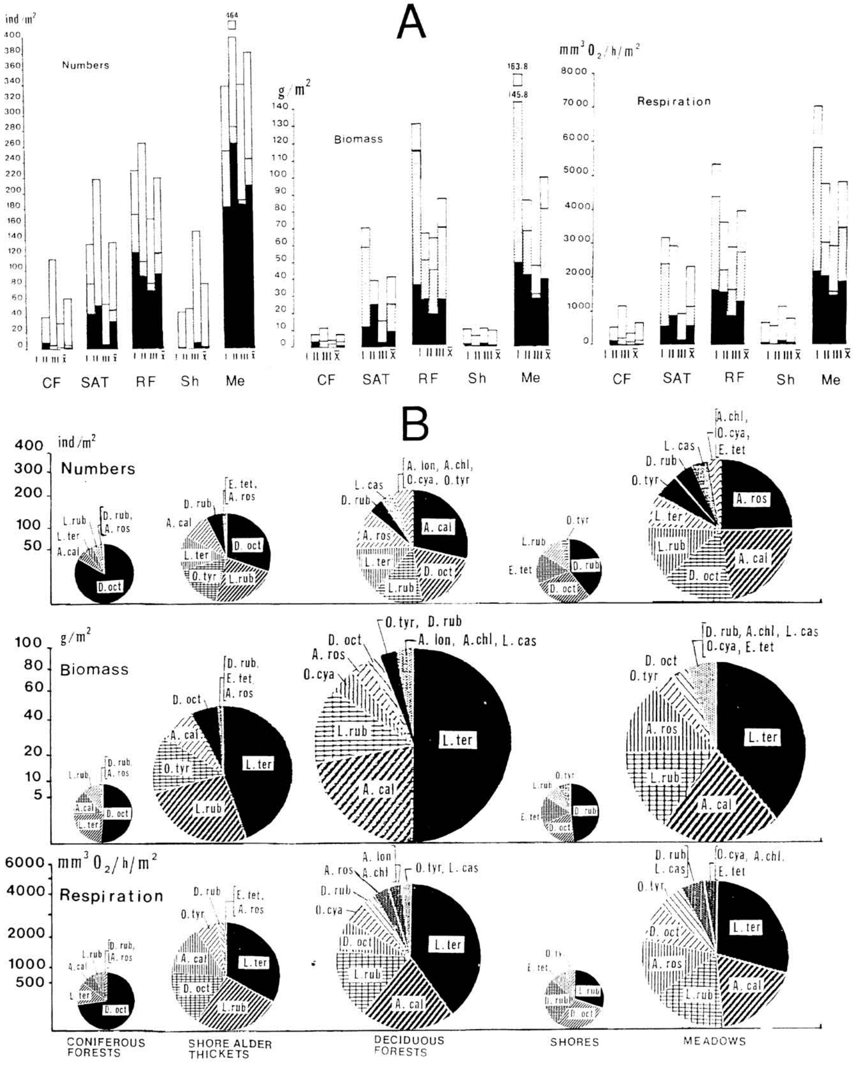

Fig. 9. A. Numbers, biomass and estimated total respiration for ecologically dissimilar groups of earthworms in the five biotopes. The black parts of the columns denote endogeic, the hatched parts anecic, and the white parts epigeic, species. I = Main Åland, II = W Uusimaa, III = E Uusimaa & Kymi (see Fig. 1), x̄ = the mean counted over the corresponding regional means. Symbols: CF = coniferous forest, SAT = shore alder thickets, RF = rich deciduous forests, Sh = shores and Me = meadows. — B. The contributions of the different species to total numbers, biomass and respiration of the assemblages in the five biotopes. The pie diagrams are based on pooled samples. The species are abbreviated as follows: A. chl = *Allolobophora chlorotica*, A. cal = *Aporrectodea caliginosa*, A. lon = *Aporrectodea longa*, A. ros = *Aporrectodea rosea*, D. oct = *Dendrobaena octaedra*, D. rub = *Dendrodrilus rubidus*; E. tet = *E. tetraedra*, L cas = *Lumbricus castaneus*, L. rub = *Lumbricus rubellus*, L. ter = *Lumbricus terrestris*, O. cya = *Octolasion cyaneum* and O. tyr = *Octolasion tyrtaeum*.

Table 9. Percent proportion of the Lumbricidae adults in pooled samples of the five biotopes. Total numbers of individuals are given in brackets. Only species with ≥15 individuals are considered in each biotope. For statistical significances see Table 7.

Species	Coniferous forests	Shore alder thickets	Deciduous forests	Shores	Meadows	χ^2	*df*
A. chlorotica	–	–	–	–	38 (21)	–	–
A. caliginosa	–	10 (29)	27 (262)	–	33 (272)	7.0*	2
A. rosea	–	–	26 (103)	–	29 (305)	ns	1
D. octaedra	29 (143)	32 (93)	20 (165)	59 (46)	23 (202)	38.7***	4
D. rubidus	–	17 (18)	63 (41)	53 (63)	46 (57)	22.1**	3
L. castaneus	–	–	30 (33)	–	43 (47)	ns	1
L. rubellus	–	31 (72)	31 (135)	68 (19)	23 (148)	17.0***	3
L. terrestris	–	15 (39)	28 (117)	–	21 (89)	ns	2
O. tyrtaeum	–	24 (51)	–	–	12 (69)	3.0°	1
O. cyaneum	–	–	25 (24)	–	–	–	–
Total	28 (179)	25 (307)	30 (908)	65 (158)	28(1221)	95.2***	4

Table 10. Percentages of *D. octaedra* adults in samples from the five biotopes in the three study regions. Total numbers of individuals are given in brackets.

Biotope	Study region and sample year Åland 1977	W Uusimaa 1979	E Uusimaa & Kymi 1984	Total	χ^2	*df*
Coniferous forests	54 (26)	20 (95)	41 (22)	29 (143)	12.9**	2
Shore alder thickets	33 (18)	30 (56)	33 (15)	31 (89)	ns	2
Deciduous forests	33 (24)	18 (108)	18 (33)	20 (165)	ns	2
Shores	86 (14)	42 (19)	54 (13)	59 (46)	6.5*	2
Meadows	40 (30)	16 (61)	22 (111)	23 (202)	6.6*	2
Total	46 (112)	22 (339)	26 (194)	–	90.0***	2

3.2.4. Reproductive status of earthworm assemblages

Age distribution influences the rates of natality and mortality of an animal population. The percentages of mature worms of the different species represent at least the potential reproductive capacity of the assemblage. Excluding shores, there are approximately 25–30% of adults in each biotope (Table 9). The corresponding proportions deviate significantly between the three regions (and consequently between the years) (coniferous forests: χ^2 = 9.885**, shore alder thickets: χ^2 = 4.685°, rich deciduous forests: χ^2 = 8.100*, meadows: χ^2 = 22.131***, *df* = 2 in all tests). Shores were, however, homogeneous in this respect (χ^2 = 0.865, ns, *df* = 2). The proportions of mature worms in many but not all the species also varied among biotopes (Table 9). Even regional (and annual) differences within a species, such as *D. octaedra*, occur (Table 10).

3.3. Factors affecting earthworm assemblages

3.3.1. Associations between the species

Fig. 8 shows that rather few species co-occurred in high frequencies in samples from the five biotopes. To survey possible interactions between the species I applied Spearman's rank correlation analysis to the numbers of individuals of the species with at least 5 records from the biotope under study at the time. According to Fig. 8 positive interactions between single species do not play any central role in the structure of the assemblage. More numerous negative associations were, however, observed, but only in fertile soils. Of these associations only that between *D. octaedra* and *A. caliginosa* referred to both fertile biotopes. Whether interspecific competition actually plays a role in earthworm assemblages remains to be seen, but, if so, it is plausibly confined to fertile soils.

Table 11. Spearman's rank correlation between numbers of individuals for the groups of species and for the species in samples from different biotopes. All possible pairwise comparisons ($n \geq 5$) were made but only those with either positive (+) or negative (–) significances ($P<0.05$) are indicated. Epig. = epigeic, Anes. = anesic species and Endog. = endogeic species, ... = comparison not adequate. For the statistical significances see Table 7, for further discussion see the text.

Species group	Shores	Shore alder thickets			Deciduous forests			Meadows	
Species	Epig.	Epig.	Anes.	Endog.	Epig.	Anes.	Endog.	Epig.	Anes.
Epigeic spec.	...	...	ns	ns	...	ns	ns	...	ns
D. octaedra	ns^{1}	ns^{1}	ns	ns	ns^{1}	ns**	ns	ns^{1}	ns
D. rubidus	+*^{1}	+*^{1}	ns	+*	ns^{1}	+**	ns	ns^{1}	ns
L. rubellus	ns^{1}	ns^{1}	ns	+**	ns^{1}	ns	+*	ns^{1}	ns
L. castaneus	ns^{1}	ns^{1}	ns	ns	ns^{1}	+**	+**	ns^{1}	ns
Anesic spec.	ns	ns	...	ns	+*	...	ns	ns	...
L. terrestris	ns	ns	...	ns	+*	...	ns	ns	...
Endogeic spec.	ns	ns	ns	...	ns	+*	...	ns	ns
A. rosea	ns	ns	ns	ns^{1}	ns	+*	+*^{1}	ns	+*
A. caliginosa	ns	ns	ns	ns^{1}	ns	+**	ns^{1}	ns*	+*
O. tyrtaeum	ns	ns	+*	+*^{1}	ns	ns	ns^{1}	+*	ns

^{1} = comparison made between the numbers of individuals of the species and that of all the other species of the same species group.

Table 12. Environmental factors correlated with the number of earthworm species (S) and with the numbers of individuals (I) in different biotopes and in the two groups of biotopes (Spearman's rank correlation). All possible comparisons were made but only those with either positive (+) or negative (–) statistical significance of $P< 0.05$, are indicated. See also the text.

Environmental parameter	Coniferous forests S	Coniferous forests I	Shore alder thickets S	Deciduous forests I	All forests S	All forests I	All open biotopes S	All open biotopes I
Coniferous trees & bushes	+***	ns	ns	ns	–***	–***	ns	ns
Deciduous trees & bushes	ns	+*	ns	ns	+***	+***	ns	ns
Dwarf shrubs	ns	ns	ns	ns	–***	–***	ns	ns
Grasses & herbs	ns	ns	+*	ns	+***	+***	+***	+***
Mosses	ns	ns	ns	ns	–***	–**	ns	ns
Thickness of organic soil	ns	ns	ns	+**	+***	+**	+**	+***
Localities	22	22	18	32	72	72	45	45
pH 1–3 cm	ns	+***	ns	ns	+***	+***	ns	ns
pH 5–10cm	ns	+*	ns	ns	+**	+**	ns	ns
pH samples	16	16	13	25	54	54	27	27

Corresponding pairwise comparisons were also made between the numbers of individuals of the species and of ecological groups of species. Table 11 indicates merely those comparisons exhibiting statistical significance, either positive or negative. Here most significances are positive. This will be discussed further in section 4.5.

3.3.2. *Environmental factors*

I made two approaches to relate environmental factors to the numbers of species and individuals in samples from the five biotopes. Firstly, the vegetation coverages and the soil properties were correlated with these parameters in each sample.

According to Table 12 in forests and in open biotopes many of the environmental factors correlate with the numbers of the species and the individuals according to the fertility gradient that the different biotopes in them represent. A corresponding analysis undertaken separately within the biotopes indicates, however, that rather few "scattered" statistical significances can be found. I think that it is the joint impact of the environmental factors, rather than any

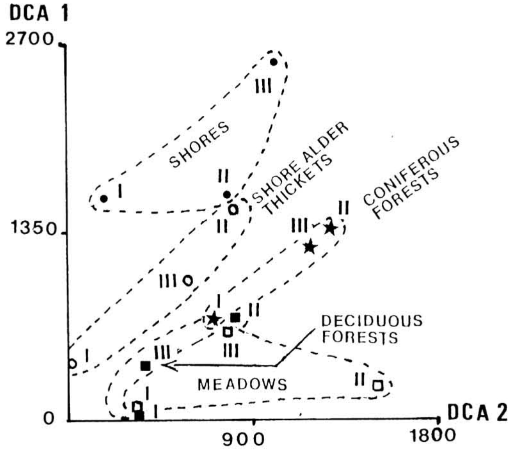

Fig. 10. The location of the mean earthworm numbers for the five biotopes of the three study regions in the DCA (detrended correspondence analysis) ordination. The eigenvalues are 0.38 for the first (DCA 1) and 0.13 for the second (DCA 2) axis, respectively. — I = Åland, II = W Uusimaa and III = E Uusimaa & Kymi (see Fig. 1).

paramount role of one or some key factors, that influences the assemblage.

Secondly, I applied the detrended correlation analysis (DCA) to the mean numbers of individuals of the species in the five biotopes and regions. To gain a wider data base for shores and coniferous forests with few species and individuals I pooled the corresponding samples by the hand-sorting and combined sample methods. Terhivuo (1982) showed that the two methods are of equal efficiency in the two biotopes. Based on non-transformed and unweighed data the biotopes are separated as oblique layers by the two DCA axes. The 1st DCA axis separates shores from the other biotopes. On the other hand, it leaves meadows and deciduous forests on the lower parts of that axis, indicating that factors other than merely the moisture content of the soil are also involved. The 2nd DCA axis seems to denote regional differences since Main Åland has the lowest value of all the biotopes. Fig. 10 also points out that no single environmental key factor gradient can separate the assemblages.

3.3.3. Habitat requirements of the species

Every earthworm responds to extrinsic factors according to its physiological and behavioural qualifications and to its genetical make-up. These factors probably underlie the habitat occupancy of the species. This is hard to define without laboratory experiments, but some clues may be gained by inspecting the relative efficiency of the species in occupying the different biotopes. I approached this as follows: in each species its highest mean relative frequency, counted over the corresponding means of the regions, and also its highest mean density of individuals (also counted over corresponding regional means) were indexed as 100%. The lower values of the other biotopes were indexed as corresponding percentages of these. Using these values the relative habitat occupancy of different species can be compared irrespective of the absolute values, which may vary considerably between the species.

In Fig. 11 the species are categorized according to the number of biotopes in which they were found. Eurytopic species (upper row) were recorded in all the biotopes, but the summits of their "biotope preference profiles" are, however, unequal. Possible negative interactions (Fig. 8) may influence their numbers in rich soils but they hardly explain all the differences, particularly those observed in extreme biotopes and shore alder thickets.

A. caliginosa, *L. terrestris* and *A. rosea* have rather similar habitat requirements, but *O. tyrtaeum* differs in having its optimum in shore alder thickets. Rare species are stenotopic (Fig. 11, lowest row) and accordingly have strict habitat requirements enabling most of them to live only in fertile soils, where a great number of other species also occur. *E. tetraedra*, being a shore species, is an exception in this respect. It is noteworthy that *D. octaedra*, *D. rubidus* and *L. rubellus* dominating in extreme biotopes are actually eurytopic and also abound in fertile soils, whereas the anesic and endogeic species (*A. caliginosa*, *L. terrestris* and *A. rosea*) that dominate in fertile soils are less eurytopic and often absent in extreme biotopes.

4. Discussion

4.1. Estimating earthworm numbers and biomass

Zicsi (1962), Satchell (1969, 1971) and Axelsson et al. (1971) pointed out that in hand-sorted samples small earthworms are more often overlooked than large ones. Heat extraction overcomes this difficulty (Abrahamsen 1972, Huhta & Koskenniemi 1975) but since it is based on digging up the sample plot, its efficiency in soils with fast moving individuals of *L. terrestris* may be not so high. According to Raw (1959), formalin application repels higher earthworm

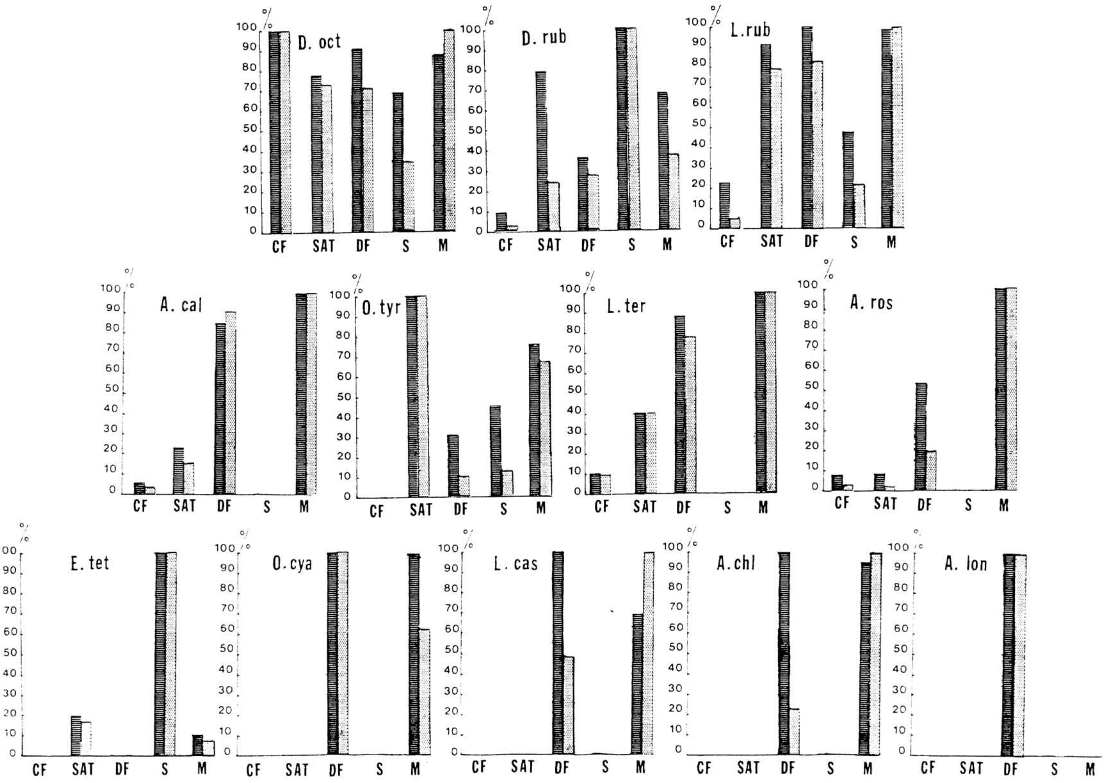

Fig. 11. The habitat preferences of the species as measured by the relative proportions of the different biotopes from the total habitat spectra of the species in S Finland. In each species the highest relative frequency, i.e. presence in samples (dark bars) and the highest mean density of individuals (stippled bars) are indexed as 100% and the other biotopes are indexed in relation to these. — CF = coniferous forests, SAT = shore alder thickets, DF = deciduous forests, S = shores and M = meadows. The abbreviations for the species are given in the legend to Fig. 9.

numbers and biomass, especially individuals of *L. terrestris* in rich soils, than the hand-sorting method. This also applies to corresponding fertile Finnish soils (Terhivuo 1982). For the comparative purposes of the present study I have preferred to use only one method, instead of many methods with efficiencies hard to assess for different types of soils.

Because all the samples were inspected by the author the relative efficiency of the extraction of worms probably varies less than expected when undertaken by more sorters. I have undoubtedly missed some earthworms in samples, and the estimates accordingly represent the minimum number of the lumbricids at a site.

Satchell (1971) showed that individuals of *L. terrestris* preserved in 4% formalin lose about 18% of their fresh weight. Corresponding rates for other species are unknown. The gut content of earthworms also affects the biomass; in small individuals (0.5 g) of *L. terrestris* it was about 26% of the fresh weight but in larger ones (7 g) about 41% (Satchell 1971). According to Persson & Lohm (1977) the gut content comprises 1.2–30.1% of the dry weight of *A. rosea*. It seems that species-specific and size-specific corrections should be made to gain definite biomass estimates but the data available are too meagre for that. I made no corrections to the raw data, which also warrants comparison with most of the corresponding studies elsewhere.

4.2. Estimating earthworm respiration

"Analysis of the functional properties of ecological systems requires consideration of a number of parameters related to energy flow. Respiration is important among these because it is a measure of that part of the food intake which is converted to heat and hence represents energy lost from the system" (Phillipson & Bolton 1976).

As Table 7 shows, most of the differences in the total oxygen uptake of the assemblages in the five biotopes are due to variation in the total biomass of lumbricids. The mean rates range between 52–97 mm^3 O_2/g/h, implying that the species composing the assemblage also influence the total amount of respiration.

The biomass estimates are affected by the worms not found in samples and by the weight the worms lost during preservation. Another inevitable weakness in estimating earthworm respiration is the dependence on the accuracy of the data indicated in the literature. Byzova (1965) demonstrated that litter-dwelling species have higher oxygen consumption rates per unit weight than deep-burrowers. Phillipson & Bolton (1976) studied two litter-dwelling (*L. castaneus* and *D. rubidus*) and two deep-burrowing (*A. rosea* and *O. cyaneum*) species and also pointed out the corresponding difference in respiration rates of the two groups of species.

The respiratory equations by Byzova (1965) indicate a size-specific respiration rate for the species but Phillipson & Bolton (1976) were unable to demonstrate this. They accordingly attribute the difference to the varying burrowing activity of the species. I used the mean weight of the individuals to even out size-specific differences, at least to some degree.

Phillipson & Bolton (1976) calculated respiration rates from the CO_2 output of the worms and their values are somewhat higher than those for the same species reported by Byzova (1965). For the comparative purposes of the present study I used only one data set to estimate the respiration rates. A great number of references dealing with community respiration of earthworms are based on the changes in numbers of individuals and in daily temperatures at different seasons of the year, considerations which were not included in this study.

4.3. Geographical variation of earthworm assemblages

Table 13 shows that earthworm numbers, biomass and number of species vary much both within and between the five biotopes in different countries. Apart from shores, the earthworm assemblages of S Finland resemble those in corresponding biotopes in more southern regions. The number of species, however, decreases northwards in Finland. Differences exist between sample methods, sample sizes and the numbers of localities surveyed by different authors. This explains why the range of the estimates rather than their absolute values are valid for comparison purposes.

Nordström & Rundgren (1973) described four types of Lumbricidae assemblages in S Sweden:

1) The *Dendrobaena octaedra* association is typical to coniferous plantations. It is poor in species (<6) and low in individuals (<50 ind./m^2) and biomass (<25 g/m^2). Litter-dwelling species, (*D. octaedra* and *D. rubidus*) characterize the assemblage. The dominance of *D. octaedra* is 60–98%. Table 2 and Fig. 9. show that the earthworm assemblage of coniferous forests in S Finland is much like that in S Sweden. This also refers to the role of *D. octaedra*. The numbers of *D. rubidus* may be underestimated in my study because no specific microhabitats such as stumps, the rotting trunks of trees, etc., were sampled (cf. Terhivuo & Valovirta 1978).

2) The *D. octaedra – Lumbricus rubellus* association is typical to alder and alder-beech woods, and also to abandoned grasslands and tall herb meadows in S Sweden (Nordström & Rundgren 1973). Both litter-dwellers and deep-burrowers are represented by a moderate number of species (5–8 in most sites), with biomass and numbers ranging between 10–50 g/m^2 and 25–100 ind./m^2. *L. rubellus* constitutes 40–60% of the total earthworm numbers. Shore alder thickets in S Finland (Table 3, Fig. 9) host assemblages that are much like these in terms of numbers, biomass and species composition; *D. octaedra* and *L. rubellus* comprise about 50% of numbers, but *O. tyrtaeum* is among the characteristic species of the assemblage.

Shore soils (Table 5, Fig. 9) show affinities to both the south Swedish *D. octaedra* association and to the *D. octaedra – L. rubellus* associations since the numbers of individuals, species and biomass are low and epigeic species, particularly *D. octaedra*, dominate there. Aside from *D. octaedra*, also *D. rubidus*, *E. tetraedra* and *L. rubellus* belong to the permanent members of the assemblage. The rarefaction curve (Fig. 7) and the DCA analysis (Fig. 10) separate shores from the other biotopes; this may accordingly be called the *D. octaedra – D. rubidus – E. tetraedra – L. rubellus* association.

3) The *Aporrectodea rosea – A. caliginosa – Lumbricus terrestris* association is typical of south

Table 13. Numbers of individuals, species and biomass recorded in the five biotopes in W and N parts of Europe.

Biotope Country	Numbers[1] ind./m^2	Biomass[1] g/m^2	No of species[2]	Data source
Coniferous forests:				
Germany	<1–22	<1–10	3	Graff 1954, Balzer 1956
Denmark & S Sweden	<1–105	<1–10	5	Bornebusch 1930, Julin 1948, Nordström & Rundgren 1973
Estonia (USSR)	<1–111	–	5	Perel 1964
S Finland	<1–117	<1–11	6	Siivonen 1941, Karppinen 1958, Huhta et al. 1967, Huhta & Koskenniemi, 1975, the present survey
C and N Finland	<1–5	<1	2,1	Huhta et al. 1967, Huhta & Koskenniemi 1975, Koponen & Ojala 1975, Niemelä 1978, Terhivuo & Valovirta 1978
Alder woods:				
Germany	8–123	3–56	6	Baltzer 1956
S Sweden	58–61	21	12	Nordström & Rundgren 1973
S Finland	48–219	16–70	8	Karppinen 1958, the present survey
Deciduous forests:				
Germany & England	30–356	16–141	15	Dreifax 1931, Graff 1954, Balzer 1956, Satchell 1967
Denmark & S Sweden	38–200	122–358	12	Bornebusch 1930, Lindquist 1938, Julin 1948, Nordström & Rundgren 1973
S Finland	52–346	65–131	11	Karppinen 1958, the present survey
C and N Finland	–	–	5,2	Terhivuo & Valovirta 1978
Shores:				
Iceland	0.5	4.0	5	Bengtson et al. 1975
S Finland	46–150	6–10	5	the present survey
C and N Finland	–	–	4,1	Terhivuo & Valovirta 1978
Meadows:				
Germany & Br.Isles	6–484	3–120	16	Dreidax 1931, Balzer 1956, Evans & Guild 1947, Guild 1951, 1952, Reynoldson 1955, Svendsen 1957
Poland	223–591	15–117	10	Nowak 1975
S Sweden	29–148	7–70	10	Nordström & Rundgren 1973
S Finland	300–464	47–164	11	Törmälä 1986, the present survey
C and N Finland	–	–	6,1	Terhivuo & Valovirta 1978

[1] = the range of the means indicated in the different data sources, [2] = all the species in the data sources counted.

Swedish deciduous woods and pastures (Nordström & Rundgren 1973). It is rich in species (7–11), dominated by deep-burrowers, and the densities of individuals (>50 ind./m^2) and biomass (>100 g/m^2) are high. The three characteristic species, namely *A. rosea*, *A. caliginosa* and *L. terrestris*, comprise >50% of individuals. The data for deciduous forests (Table 4, Fig. 9) and for meadows (Table 6, Fig. 9) correspond to this association, but in addition to the species mentioned *D. octaedra* and *D. rubellus* are among the permanent members of the assemblages.

4) The *A. caliginosa* – *A. longa* association, typical of *Corynephorous* heaths in S Sweden, is not represented in Finland.

4.4. Regionality of earthworm assemblages in S Finland

According to Table 13 the number of species declines northwards in Finland. Tables 2–6 show that the number of species also declines eastwards in all the biotopes. In extreme biotopes (coniferous forests and shores) the species not found now in all the study regions comprise *D. rubidus*, *L. rubellus*, *L. terrestris*, *A. caliginosa*, *A. rosea* and *O. tyrtaeum*. Their presence in samples from extreme biotopes is perhaps associated with the presence of their populations in the nearby, more fertile soils. The role of source populations can be observed in samples taken along environmental gradients such as those surveyed by Julin (1949) extending from shores to forests lying in more elevated parts of the landscape. The west-east declining vegetation gradient (Fig. 1), especially the eastwardly increasing abundance of the spruce (*Picea abies*) (Atlas of Finland 1976) and the eastwardly increasing continentality of the climate (Abrahamsen et al. 1977), may have influenced the regional differences in numbers of species observed in my study.

Besides extreme biotopes these reasons may also underlie the regional differences observed in shore alder thickets (Table 3, Fig. 9), but in deciduous forests and meadows (Tables 4, 6 and Fig. 9) additional factors are involved, e.g. *A. longa*, *A. chlorotica* and *O. cyaneum* have southwestern ranges in Finland and they spread mainly anthropochorously (Terhivuo 1988a). This shows the role of the distributional history of the species upon the structure of the assemblages as well.

The proportions of the adults (Tables 9 and 10) may have been influenced by the weather of the preceding winter (e.g. depth of frost and snow-cover) and summer, but this is hard to assess.

4.5. Associations between the species

According to Fig. 8 and Table 11 some interactions between the species and species groups may occur in fertile soils, but not in more extreme biotopes. Most negative associations refer to species that belong to different ecological groups of species. There could be some competition particularly between the young individuals of deep-burrowing species and the litter-dwellers because the former often live closer to the soil surface than their adults, but the present data are insufficient to demonstrate this conclusively. Perhaps juveniles of some deep-burrowers tap food resources, e.g. fallen leaves, decaying grasses and herbs consumed by litter-dwellers. On the other hand, the numerous positive correlations between the species and species groups may be due to the favourable impact of earthworms in general upon the soils. For instance, an increase in pH, improved aeration and other soil qualities may be due to the action of earthworm species with no strict habitat requirements. The soil may thus gradually become more acceptable to e.g. stenotopic species.

Because environmental factors and the numbers of species and individuals present also vary according to sample plots within a biotope the role of species interactions cannot be definitively judged based on the field data. Contributing experiments under controlled laboratory conditions are needed for that.

4.6. Environmental variability and earthworm occurrences

Earthworms are exposed to a multitude of environmental factors such as the quality and quantity of food, pH, moisture, temperature, carbon dioxide concentration, oxygen tension, amount of organic matter and type of soil (e. g. Julin 1949, Laverack 1963, Satchell 1967, Edwards & Lofty 1972). Nordström & Rundgren (1974) suggested that pH, vegetation and food resources are the main determinants of the structure of south Swedish earthworm associations. According to Table 12 the number of species and individuals increased along the fertility gradient in forests and in open biotopes, but within the biotopes relatively few factors correlated with these. Fig. 9B shows that different factor combinations may permit the formation of rather similar earthworm assemblages, such as in coniferous forests and shores or in deciduous forests and meadows. Accordingly, the joint impact of the factors rather than the determining role of any single key factor is important in this respect.

Inspection of Tables 2–6 shows that most of the species recorded in extreme biotopes were also present in shore alder thickets and in more fertile soils. Their unequal relative "habitat occupancy profiles" (Fig. 11) and differences in burrowing and feeding habits indicate their ecological versatility. If interactions between the species or groups of species play no central role in the habitat occupancy of the species, perhaps the physiological, behavioural and genetical make-ups underlie the differences observed between them in this respect.

According to Satchell (1955) a uniformly distributed earthworm population that reproduces more rapidly than the offspring disperse will be aggregated by individuals from overlapping family groups. Occasional events and/or differences in microhabitat and microclimate may also facilitate this: some sites may be more exposed to sunshine, stay longer submerged during e.g. floods or snow melting, be thinly covered by snow in winter, or there may be edaphic differences etc., that need not be observable as e.g. differences in the vegetation of the sample sites. There may also be a negative impact upon earthworms by some plants, as in the case of clubmosses (*Lycopodium*) (Bertsch & O'Leary 1976). Since in extreme biotopes where parthenogenetic litter-dwellers dominated the individuals were as highly aggregated as those in fertile soils dominated by deep-burrowers, reproductive behaviour leading to a higher mating frequency in amphigonic species cannot be the ultimate reason for aggregation. As for pedogenesis, i.e. soil formation, the aggregation of earthworms shows that their impact is not uniform even in the same biotope. Differences in vertical distributions (Table 8) imply that, depending on the biotope, earthworm activity is unequally directed at different soil layers.

4.7. The role of *Dendrobaena octaedra* in Finnish earthworm assemblages

Tables 2–6 and Fig. 9 show that in S Finland *D. octaedra* plays a key role in the structure and function of the earthworm assemblages in all the biotopes studied. In central and northern parts of the country this is even more pronounced because most other earthworm species are absent or rare and their habitat spectrum narrows there, a phenomenon which was not observed in *D. octaedra* (Terhivuo & Valovirta 1978, Terhivuo 1988a). The ecological success of the species depends on many characteristics: it is parthenogenetic, eurytopic and it can efficiently utilize different food resources which may facilitate the establishment and maintainance of new populations. It possesses great power for passive dispersal without human agency (Terhivuo 1988a) and it can withstand substantial annual variation in environmental factors. It lives permanently in upper parts of the soil and also winters there (Huhta et al. 1967, Rundgren 1975). It also exhibits wide morphological (Terhivuo 1988b) and genetic (Terhivuo & Saura 1990, Hongell & Terhivuo 1989) variation in eastern Fennoscandia.

Acknowledgements. I wish to express my gratitude to Olli Järvinen and Kari Vepsäläinen, as well as to an unknown referee, for constructive criticism and advice. I am also indebted to Yrjö Haila, Jari Kouki and Rauno Yrjölä for their help in computerizing some parts of the data. Leigh Plester checked the English of the manuscript and Reino Tyynelä photographed the figures.

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Received 10.IV.1988, revised 16.XII.1988
Printed 23.VI.1989