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Enchytraeid fauna (*Oligochaeta, Enchytraeidae*) in the Białowieża Primeval Forest

Abstract: Enchytraeid communities were studied at 15 sites in different types of forest within the Białowieża Primeval Forest. Thirty-six species were identified. Analysis of species composition similarity revealed the presence of 2 dissimilar groups of communities, associated with broad-leaved forests and coniferous forests respectively. Within each group, the highest similarity was observed between communities from ash-alder carrs and Scots pine forests while communities inhabiting the soil in the bog birch forest and the linden-oak-hornbeam forest were the least similar. The abundance of enchytraeids was not limited by high soil acidity or moisture.

Key words: Enchytraeidae, species composition, habitat preference, Białowieża Primeval Forest

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INTRODUCTION

The Białowieża Primeval Forest (Puszcza Białowieska), occupying an area of 1500 km^2 in Poland and Belarus, is the best preserved natural forest refugium in the European lowlands, with over 11.000 species of animals recorded to date (GUTOWSKI, JAROSZEWICZ 2001). The forests of this area are dense and considerably diversified. A variety of types of open-area and forest habitats differing with respect to fertility and moisture can be found there, promoting considerable faunal richness.

This diversification has created a great diversity of conditions for the development of soil fauna, including Enchytraeidae, the majority of species of which are amphibiontic.The earliest mention of enchytraeid fauna in the Białowieża Primeval Forest can be found in a paper by MOSZYŃSKI (1928), while the next report was only published in the 1990's (PILIPIUK 1993, 1995). Preliminary information on the occurrence of enchytraeids in several types of forest habitats is contained in (PILIPIUK 1998). However, to date no papers have dealt with communities of *Enchytraeidae* in the different types of forests in the Białowieża Primeval Forest.

The aim of this paper was to compare *Enchytraeidae* communities inhabiting the soil in forest habitats with a view to identifying communities typical of individual forest types and specifying the habitat preferences of individual species of *Enchytraeidae*.

Analyses were concerned with the relationship between the species composition and structure of enchytraeid communities on the one hand and the type of plant association, habitat moisture and fertility, and soil acidity and type on the other. The similarity of species composition and of communities was assessed and explained with regard to these factors. In order to determine the habitat preferences of individual species, their frequency and density at the study sites was analysed.

STUDY AREA

The samples were taken from 15 sites, which were situated in seven types of forest ecosystems were studied: the swamp alder forest, the bog pine forest, the bog birch forest, the ash-alder carr, the linden-oak-hornbeam forest, the mixed coniferous forest and the Scots pine forest (Table I). A scale of fertility and moisture for the forests under study is given after MATUSZKIEWICZ 1981 and SZUJECKI 2001. It accounts for soil type and soil acidity.

Table I. Characteristic of study area.

No.	Stand	Description	Soil type	pH	Fertility	Moisture
1	A	swamp alder forest Ribeso nigri-Alnetum, div. 514, Hajnówka forest inspectorate	peat	6.0	eutro-phic	swamp
2	V	bog-pine forest *Vaccinio uliginosi-Pinetum*, div. 572, Michnówka reserve, Hajnówka forest inspectorate	peat-gley	4.4	oligo-trophic	swamp
3	B	bog birch forest *Thelypterido-Betuletum pubescentis*, div. 661, Hajnówka forest inspectorate	peat-gley	5.7	mesot-rophic	swamp
4	C1	ash-alder carr *Fraxino-Alnetum*, div. 315, Białowieża National Park	peat-mucky	6.1	eutro-phic	wet
5	C2	ash-alder carr *Fraxino-Alnetum*, div. 599, Hajnówka forest inspectorate	gley	5.9	eutro-phic	wet
6	C3	ash-alder carr *Fraxino-Alnetum*, div. 600, Hajnówka forest inspectorate	mucky black earth	6.7	eutro-phic	wet
7	O1	linden-oak-hornbeam forest *Tilio-Carpinetum*, div. 633, Hajnówka forest inspectorate	leached brown	5.1	eutro-phic	moist
8	O2	linden-oak-hornbeam forest *Tilio-Carpinetum*, div. 334, Dębowy Grąd reserve, Hajnówka forest inspectorate	gleyed lessive	5.5	eutro-phic	moist
9	O3	linden-oak-hornbeam forest *Tilio-Carpinetum*, div. 399, Białowieża National Park	brown	6.9	eutro-phic	moist
10	O4	linden-oak-hornbeam forest *Tilio-Carpinetum*, div. 399, Białowieża National Park	lessive	6.9	eutro-phic	moist
11	M1	mixed coniferous forest *Calamagrosti arundinaceae-Piceetum*, div. 699, Hajnówka forest inspectorate	leached brown	4.9	meso-trophic	moist
12	M2	mixed coniferous forest *Calamagrosti arundinaceae-Piceetum*, div. 288/318, Białowieża National Park	podzolized rusty	3.8	oligo-trophic	slightly moist
13	P1	Scots pine forest *Peucedano-Pinetum*, div. 538, Hajnówka forest inspectorate	podzolic	4.4	oligo-trophic	slightly moist
14	P2	Scots pine forest *Peucedano-Pinetum*, div. 667, Hajnówka forest inspectorate	podzolic	4.4	oligo-trophic	slightly moist
15	P3	Scots pine forest *Peucedano-Pinetum*, div. 668, Hajnówka forest inspectorate	rusty	4.2	oligo-trophic	slightly moist

MATERIAL AND METHODS

Fieldwork was carried out in the years 1986-2001 with individual sites studied for a maximum of two years. Two series of samples were obtained each year, in spring (April–June) and autumn (September–October). There were 40 samples taken at each site, which were 20 cm^2 in area and 16 cm deep. The enchytraeids were extracted using a modified O'Connor method and identified while still alive. A total of 16,117 individuals were collected.

Principal Components Analysis was applied to asses habitat preferences of the species using $y' = \ln(a_y+c)$ where a=1, c=1 transformation of species data (CANOCO programme).

The following indices were used to describe the soil communities of *Enchytraeidae*: species richness (Margalef 1957), Shannon-Wiener's index of general species diversity (SHANNON, WEAVER 1949) and Morisita's index of similarity modified by HORN (1966), The basis for grouping was the method described by MOUNFORD (1962).

RESULTS

Species composition

A total of 36 species were recorded in all communities of *Enchytraeidae* in the Białowieża Primeval Forest (Table II). Communities from broad-leaved forests were richer in species, with 27 species found in the linden-oak-hornbeam forest, 24 in the bog birch forest, 21 in the ash-alder carr and 19 in the swamp alder forest, than those inhabiting coniferous forests (8 species in the mixed coniferous forest, 6 in the Scots pine forest and 3 in the bog pine forest. The number of species recorded from a site varied from 3 in the bog pine forest (V) and the mixed coniferous forest site within the Białowieża National Park (stand M2) to 24 in the bog birch forest (B). All of the species found in the Białowie ża Primeval Forest in this study had been previously recorded from broad-leaved forests, with 26 occurring only in this type of forest and 10 reported from both broad-leaved and coniferous forests. No species was limited to coniferous forests. *Cognettia sphagnetorum* was the only species found in all types of forests under study. A total of 9 and 1 species were found to occur in all types of broad-leaved and coniferous forest respectively. Two species (*Stercutus niveus* and *Fridericia bulbosa*) were found only in the linden-oak-hornbeam forest, and four (*Cernosvitoviella goodlui, Cernosvitoviella palustris, Marionina riparia* and *Hemifridericia parva.*) only in the swamp alder forest.

The index of species richness was highest in the bog birch forest *Enchytraeidae* community (3.11) and the linden-oak-hornbeam forest community from stand O3 (2.84). It was higher than 2.0 in the linden-oak-hornbeam forest community from stand O4 and in the ash-alder forest. Lower species richness (above 1.0) characterized communities from the other linden-oak-hornbeam forest sites and from the swamp alder forest. Communities from the scots pine forest, bog pine forest and mixed coniferous forest stand within the Białowie ża National Park (M2) had very low species richness (< 1.0) (Table II).

Table II. Species composition and dominance index of enchytareid communities at the study area.

Species	Sites														
	O1	O2	O3	O4	B	C1	C2	C3	A	M1	M2	P1	P2	P3	V
Stercutus niveus MICH.	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mesenchytraeus armatus (LEV.)	0.00	0.00	0.14	0.00	1.85	0.67	0.44	0.50	0.75	0.00	0.00	0.00	0.00	0.00	0.00
M. pelicensis ISSEL.	2.21	1.48	0.00	0.03	0.00	0.00	0.00	0.00	1.19	13.50	0.00	0.40	0.00	0.00	0.00
Cernosvitoviella atrata (BRET.)	0.00	0.00	0.00	0.00	0.60	0.13	0.00	0.17	0.79	0.00	0.00	0.00	0.00	0.00	0.056
C. goohui HEALY	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00
C. palustris HEALY	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Buchholzia appendiculata (BUCHH.)	0.00	0.00	4.07	3.85	1.64	0.27	0.88	0.25	0.00	0.00	0.05	0.00	0.00	0.00	0.00
B. fallax MICH.	0.88	0.00	0.14	8.59	4.91	0.40	0.44	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bryodrilus ehlersi UDE.	0.00	0.00	0.00	0.00	0.17	0.27	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.44	0.00
Cognettia glandulosa (MICH.)	0.00	0.00	0.00	0.00	9.87	0.00	0.00	0.00	4.14	0.00	0.00	0.20	0.06	0.44	0.056
C. sphagnetorum (VEJD.)	**64.70**	**74.80**	1.76	**9.31**	4.96	**27.60**	**16.2**	**54.80**	**82.20**	**74.90**	**99.50**	**98.70**	**99.66**	**99.07**	**99.89**
Marionina argentea (MICH.)	0.00	1.14	0.41	0.52	6.08	0.00	0.00	0.00	3.31	0.10	0.00	0.00	0.00	0.00	0.00
M. riparia BRET.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Enchytraeus albidus HENLE	0.00	0.00	0.14	0.06	0.34	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00
E. buchholzi VEJD.	0.33	0.46	2.30	0.38	1.34	0.00	0.15	0.00	0.04	0.00	0.00	0.30	0.14	0.00	0.00
Fridericia bisetosa (LEV.)	0.55	1.83	**25.20**	2.95	3.62	0.81	2.78	0.42	0.18	0.00	0.10	0.00	0.00	0.00	0.00
F. bulboides NIEL.&CHRIST.	0.22	0.23	1.08	0.03	1.47	0.81	0.73	1.00	1.01	0.00	0.00	0.00	0.00	0.00	0.00
F. bulbosa (ROSA)	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F. connata BRET.	0.00	0.00	3.35	0.00	0.00	0.13	0.15	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F. galba (HOFFM.)	0.00	0.00	0.00	0.06	0.13	2.69	0.29	1.75	0.04	0.00	0.00	0.00	0.00	0.00	0.00
F. gracilis BULOW	0.00	0.00	0.00	0.09	0.13	0.13	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F. leydigi (VEJD.)	0.00	0.00	0.00	0.03	0.04	0.00	0.58	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F. maculata ISSEL	0.00	0.11	0.00	0.06	0.00	0.00	1.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F. paroniana ISSEL	0.00	0.00	0.54	0.00	0.17	0.00	0.29	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F. perrieri (VEJD.)	0.00	0.00	0.00	0.98	0.60	0.81	1.17	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F. ratzeli EISEN	3.32	0.23	0.81	0.61	0.17	1.08	0.00	0.25	0.04	0.10	0.00	0.00	0.00	0.00	0.00
F. tubulosa DÓZSA-FARKAS	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Enchytronia parva NIEL.& CHRIST.	0.00	0.00	0.41	9.25	0.26	0.00	0.15	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Henlea heleotropha STEPH.	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00
H. nasuta EISEN	0.11	0.00	10.40	1.59	1.72	3.09	4.68	7.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00
H. perpusilla FRIEND	0.22	0.68	0.00	0.52	**21.1**	12.50	13.50	5.58	2.95	0.00	0.00	0.00	0.00	0.00	0.00
H. similis NIEL.& CHRIST.	0.00	0.00	0.00	0.00	3.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
H. ventriculosa D'UDEK.	1.55	0.00	0.54	1.01	5.39	1.88	0.88	0.33	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Hemifridericia parva NIEL.&CHRIST	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Achaeta bohemica (VEJD.)	0.33	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00	0.00	0.00	0.00
A. eiseni VEJD.	0.00	1.14	0.41	0.23	0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.40	0.14	0.05	0.00
Mesenchytraeus sp.	12.60	0.91	0.00	1.59	0.69	2.42	0.29	5.83	0.66	5.27	0.05	0.00	0.00	0.00	0.00
Cernosvitoviella sp.	0.00	0.00	0.00	0.00	0.04	0.94	0.88	0.17	0.13	0.00	0.00	0.00	0.00	0.00	0.00
Buchholzia sp.	0.00	0.00	0.51	0.64	0.30	0.67	1.75	1.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Marionina sp.	1.88	2.85	1.49	0.43	0.00	9.27	14.90	3.50	0.00	0.10	0.00	0.00	0.00	0.00	0.00
Enchytraeus sp.	1.44	0.34	3.12	1.79	3.10	3.36	1.61	0.50	0.53	0.00	0.00	0.00	0.00	0.00	0.00
Fridericia sp.	8.19	8.22	40.70	52.10	25.80	27.8	35.10	12.8	1.54	2.90	0.26	0.00	0.00	0.00	0.00
Henlea sp.	0.00	0.00	0.40	0.03	0.30	1.34	0.88	0.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Achaeta sp.	1.47	4.90	1.90	3.15	0.02	0.94	0.00	0.08	0.00	1.87	0.05	0.00	0.00	0.00	0.00
	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Number of species	11	11	18	21	24	16	17	19	19	6	3	5	4	4	3
density indiv./m2	22600	21900	11510	24700	29000	9300	8500	15000	14175	24175	31950	20830	17830	22110	22375
Index of species richness	1. 34	1. 33	**2. 84**	2. 58	**3. 11**	2. 27	2. 45	2. 54	1. 29	0. 87	0. 53	0. 54	0. 42	0. 41	0. 27
index of diversity	2. 18	1. 59	**2. 91**	2. 66	**3. 01**	**3. 08**	**2. 98**	2. 48	1. 06	1. 30	0. 06	0. 18	0. 04	0. 09	0. 01

The frequency and average abundance at each site were calculated for each species to aid in determining their habitat preferences with regard to the type of plant association, type of soil, moisture and acidity.

Habitat preferences of species of *Enchytraeidae* in the forests of the Białowieża Primeval Forest

PCA diagram contain 28 species, which occur on more than one site and 15 sites. (Fig. 1). PCA – ordination diagram point out, that the direction of the arrow indicates the direction in which the abundance of the corresponding species increases most, and the length of arrow equals the rate of change in that direction.

Of all the species studied, the following were most abundant in the swamp and wet deciduos forest: *M. armatus, C. atrata,M. argentea, F. galba, F. leydigi, H. heleotropha* and *H. perpusilla*. There were few species which prefer the more fertile linden-oak-hornbeam forest (O3, O4) and bog birch forest: *B. appendiculata, B. fallax, E. albidus, E. buchholzi, F. bisetosa, F. bulboides,, F. gracilis, F. paroniana, F. perrieri, E. parva, H. nasuta* and *H. ventriculosa.*

Three species were most abundant in mixed coniferous forest (M1) and less fertile linden-oak-hornbeam forest (O1, O2) on leached brown soil and gleyed lessive soil: *M. pelicensis, A. bohemica* and *A. eiseni*. In the Scots pine forest , mixed coniferous forest and the bog pine forest on soil pH 3.8–4.9, the most abundant species was *C. sphagnetorum*. This species is the mainstay of all enchytraeid communities inhabiting coniferous forests. It was similarly frequent, but less abundant, in the linden-oak-hornbeam forest and the swamp alder forest.

Occurrence of *Enchytraeidae* at different soil pH values

The range of soil pH values at the study sites was 3.8–6.9. The lowest number of species (3) were found in the soil with the lowest pH 3.8. As pH increased, the number of species also rose (The correlation coefficient $r = 0.89$ is significant at $p < 0.05$). The correlation between soil pH and mean density of enchytraeid communities was significant too ($r = -0.52$). As pH decline, mean density rose.

The highest number of species (24) was found in at pH 5.7. At pH above this value (5.9–6.9), the number of species was a little lower, ranging from 16 to 20 at one site on average (Fig. 2). *C. sphagnetorum* was the only species which was abundant and occurred frequently at low pH (3.8–4.9). Other species occurring most frequently and abundantly at pH 4.9, apart from *C. sphagnetorum*, were *M. pelicensis* and *A. bohemica* Of 11 species found in soils with a pH of 5.1, it was *F. ratzeli* which found the most favourable conditions, while *A. eiseni* benefited the most from a pH of 5.5. Twelve out of 24 species found in a soil with a pH of 5.7 had optimum conditions there. At the higher pH 5.9 – 6.7 two species were the most abundant. Soils with a pH of 6.9. provided an optimum habitat in terms of density for 6 out of 26 species registered there (Fig. 2).

The above findings show that optimum pH varies with the species and individual pH ranges have differing widths. The largest number of species (12) found the most favourable conditions at a pH of 5.7.

Of 36 species found at the study sites in the Białowieża Primeval Forest, the lowest number of species (3) were found in the mixed coniferous forest at pH 3.8 and in the bog pine

forest at pH 4.4. The largest number of species (24) were found in the soil of the bog birch forest. In moist soils, soil pH has a negative (limiting) influence on species, as can be observed in the bog pine forest. Thus, the least favorable conditions can be observed in acid (pH<5.0) and slightly moist sites, and the most favorable – in wet, swamp and less acidic (pH>5.0) soils. The former category includes Scots pine and mixed coniferous sites, while soils of the other category are associated with ash-alder carrs, swamp alder forests and bog birch forests. The linden-oak-hornbeam stands under study differed in terms of soil acidity, with pH ranging from 5.1 to 6.9. Still, these forests were less moist compared to other broad-leaved forest types. In the linden-oak-hornbeam forest growing on fertile brown soil and lessive soil, the number of enchytraeid species was high, ranging from 18 to 21.

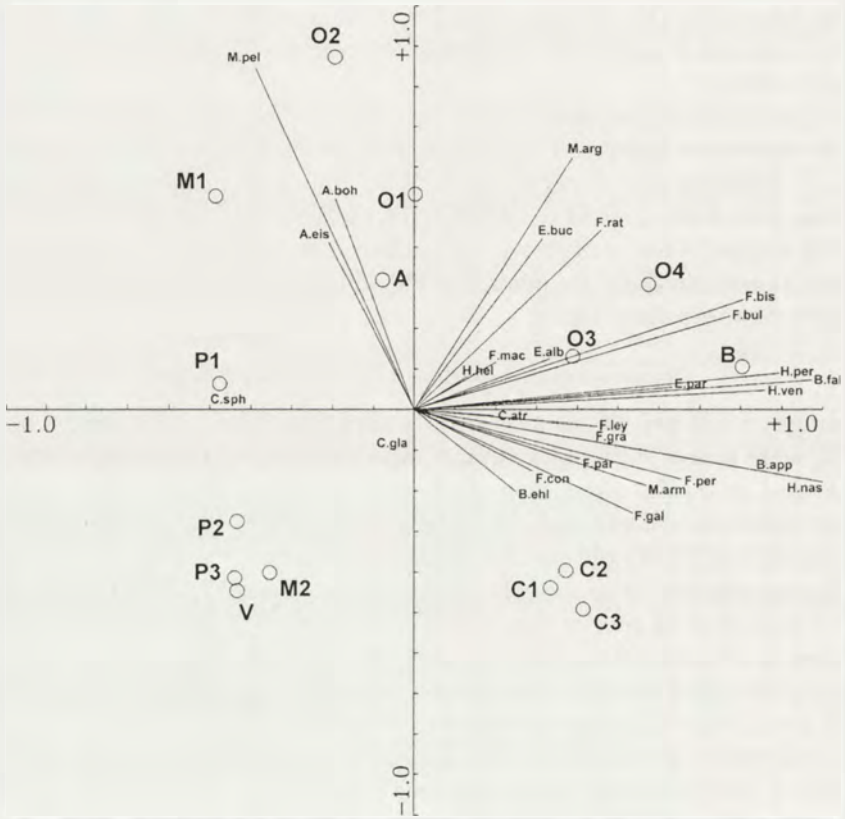

Fig. 1. PCA –ordination diagram. Biplot of species and sites. Species are represented by arrows, sites by circles. Eigenvalues of first and second axes are 0.494 and 0.136 respectively. Abbreviations: A. boh - A. bohemica, A. eis - A. eiseni, B. app - B. appendiculata, B. fal. - B. fallax, B. ehl - B. ehlersi, C. atr - C. atrata, C. gla - C. glandulosa, C. sph - C. sphagnetorum, E. alb - E. albidus, E. buc - E. buchholzi, E. par - E. parva, F. bis - F. bisetosa, F. bul - F. bulboides, F. con - F. connata, F. gal - F. galba, F. gra - F. gracilis, F. ley - F. leydigi, F. mac - F. maculata, F. par - F. paroniana, F. per - F. perrieri, F. rat - F. ratzeli, H. hel - H. heleotropha, H. nas - H. nasuta, H. per - H. perpusilla, H. ven - H. ventirculosa, M. arg - M. argentea, M. arm - M. armatus, M. pel - M. pelicensis. Abbreviations of species names: three first letter was used according Table II - eg. A. boh - *A.. bohemica* etc.

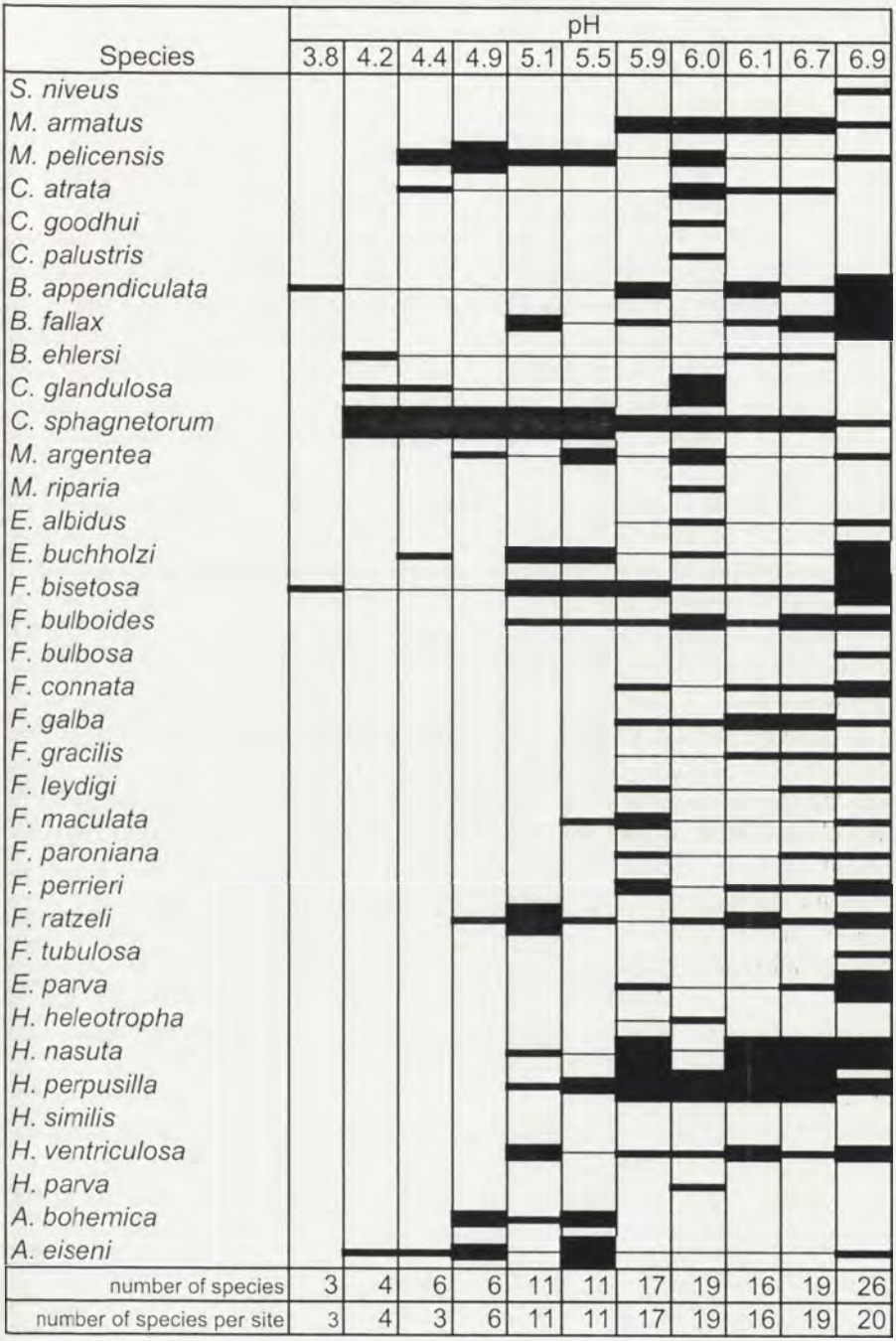

Fig. 2. Species density in relation to soil pH.

Enchytraeidae communities in different types of forest

Linden-oak-hornbeam forests. Linden-oak-hornbeam forests support a great variety of habitat types, so that the communities of *Enchytraeidae* compared in this study inhabited various types of soil differing in fertility and acidity. This was reflected in the species composition and dominance structures of these communities. There were a total of 27 species of *Enchytraeidae* found in the soil of 4 sites in linden-oak-hornbeam forests and the number of species per site ranged from 11 to 21. The largest number of species were found at sites located within the Białowieża National Park. The average density of *Enchytraeidae* at site O3 (11,500 indiv./m^2) was twice lower than at the other sites in this type of forest (Table 2). Linden-oak-hornbeam forests are more fertile in the Białowieża National Park and the soil is less acidic there. The community inhabiting brown soil, where *F. bisetosa* is the dominant (25%), stands out most considerably from the others in the linden-oak-hornbeam forests. Other abundant species in this community include *H. nasuta* and *B. appendiculata* and sexually immature individuals of the genus *Fridericia* (41%). In the community inhabiting lessive soil in a linden-oak-hornbeam forest, young individuals of the genus *Fridericia* are the most abundant (52%). This community is also characterized by a low contribution of *C. sphagnetorum* (9%) with similar shares of *E. parva* and *B. fallax*. More pronounced dominance of *C. sphagnetorum* (65%) is seen in the community from linden-oak-hornbeam site O1. Other abundant species in that community include *F. ratzeli* and *M. pelicensis* and juvenile forms of the genera *Mesenchytraeus* and *Fridericia* The highest share of *C. sphagnetorum* (75%) was found in the community from site O2. Other important species in that community are *F. bisetosa, M. pelicensis, A. eiseni, M. argentea* and sexually immature individuals of the genera *Fridericia* and *Achaeta* Thus, individuals of the genus *Fridericia* have the largest share in terms of abundance in *Enchytraeidae* communities of linden-oak-hornbeam sites within the Białowieża National Park, while *C. sphagnetorum* is dominant at more acidic linden-oak-hornbeam sites on leached brown soil or gleyed lessive soil. The values of Margalef's index of species richness vary from 1.33 to 2.84. Shannon-Wiener's index of species diversity ranges from 1.59 to 2.91. Both indices reach their maximum values in the community from the linden-oak-hornbeam forest growing on brown soil. Linden-oak-hornbeam forest sites within the Białowieża National Park may thus be used as reference in studies of the fauna of linden-oak-hornbeam forests.

Ash-alder carrs. Twenty-one species of *Enchytraeidae* were identified in ash-alder carrs in the Białowieżą Primeval Forest, with 16–19 species found per site. Mean densities of *Enchytraeidae* at two ash-alder sites were low: 8,550 and 9,300 indiv./m^2 respectively, while at the third one, which grew on black earth soil and was the driest, this value was much higher, reaching 15,000 indiv./m^2 (Tab. 1). A characteristic feature of ash-alder carr *Enchytraeidae* communities developing in different types of soil is the dominance of *C. sphagnetorum*, from 16% to 55%. Other species of considerable abundance are two species of the genus *Henlea: H. perpusilla* and *H. nasuta* and young individuals of the genus *Fridericia*, the latter being dominant at site C2, and having a share equal to that of the dominant species *C. sphagnetorum* at site C1. The values of Margalef's index of species richness for ash-alder carr *Enchytraeidae* communities

ranged from 2.27 to 2.54. A comparison of these communities shows that while the highest species richness was observed at the site with the soil with the highest pH, it is considerable moisture of the soil that has the greatest effect on the development of communities. Shannon-Wiener's index of general diversity reached maximum values in communities from ash-alder carr sites within the Białowieża National Park, where it was 3.08, and from site C2, where it had a similar value (2.98). It was lower (2.48) in the community from the third ash-alder site investigated.

Mixed coniferous forests. Eight species of *Enchytraeidae* were found in communities inhabiting mixed coniferous forest sites. The highest average density across all communities studied in the Białowieża Primeval Forest was determined for the community from mixed coniferous forest site M2 within the Białowieża National Park (31,950 indiv./m^2). The other community inhabiting a mixed coniferous forest site (M1) had a density of 24,175 indiv./m^2, which is also a high value. These communities are characterized by a marked dominance of *C. sphagnetorum*. *M. pelicensis* was quite abundant in communities from mixed coniferous forests growing on leached brown soil and the community from a mixed coniferous forest site on very acidic podzolized rusty soil was composed almost entirely of *C. sphagnetorum* (99%). The index of species richness ranged from 0.53 to 0.87.

The index of diversity was very low for the community from the site in the Białowieża National Park (0.06), while for the other site it was 1.3.

Pine forests. Six species of *Enchytraeidae* were found in communities from Scots pine forests, with 4–5 species occurring at individual sites. Average density ranged from 17,830 to 22,110 indiv./m^2.

The species-poor communities from scots pine forests are characterized by very marked dominance of *C. sphagnetorum*. *M. pelicensis* had a small share in these communities. The index of species richness was low, ranging from 0.41 to 0.54. The index of diversity was also low (0.04–0.18).

Swamp alder forest. The enchytraeid community inhabiting the swamp alder forest site consisted of 19 species, with an average density of 14,175 indiv./m^2. *C. sphagnetorum* was the dominant species, but *M. armatus*, *C. glandulosa* and *H. perpusilla* were also quite abundant. The index of species richness was lower there than in other communities inhabiting broad-leaved forests (1.29). The index of diversity was also lower than at other broad-leaved forest sites (1.06). Despite a relatively high number of species, the diversity statistic for this community was low, which shows that the soil of a swamp alder forest produces worse conditions for *Enchytraeidae* than the soil in ash-alder carrs and linden-oak-hornbeam forests.

Bog birch forest. The highest number of species per site (24) was recorded at the bog birch site. Average density was also high, at 29,000 indiv./m^2. The dominant species was *H. perpusilla* (21%); other abundant species were *B. fallax*, *M. argentea* and *H. ventriculosa* However, it was individuals of the genus *Fridericia* that had the greatest share in the community (26%). The species richness index for this community was very high (3.11). The species diversity index was also very high, at 3.01. Thus, the bog birch forest creates good conditions for enchytraeids, as can be seen from the finding of a large number of species, high density and diversity.

Bog pine forest. The *Enchytraeidae* community from the bog pine forest was the poorest in species and was characterised by a marked dominance of *C. sphagnetorum*. *C. atrata* and *C. glandulosa* complete the list of species found at the site. Average density was quite high, at 22,375 indiv./m^2. The species richness index and the species diversity index reached their lowest values for all communities studied in the Białowieża Primeval Forest, at 0.27 and 0.01 respectively.

Species composition similarity

Analysis of similarity of species composition of *Enchytraeidae* communities based on Sørensen's index showed that they can be divided into two dissimilar groups, corresponding to broad-leaved and coniferous forests (Fig. 3). Within each subgroup. the highest similarity (at 0.89) was determined for two sites each in ash-alder carrs and scots pine forests. In the "broad-leaved forest" group, a high degree of similarity of species composition was seen between all communities from ash-alder carrs (0.82) and the bog birch forest (0.77). Linden-oak-hornbeam communities were less similar. These can also be divided into two groups, with the similarity index for sites O1 and O2 equalling 0.73 and for sites O3 and O4 (both within the Białowieża National Park) 0.68. The former group of linden-oak-hornbeam sites is similar to the swamp alder site (0.53), and the latter is similar to the group comprising ash-alder carrs and the bog-birch forest at 0.65. Thus, *Enchytraeidae* communities of broad-leaved forests form two independent groups. One includes linden-oak-hornbeam sites O1 and O2 and the swamp alder site, and the other consists of ash-alder carrs, the bog birch site and two linden-oak-hornbeam sites within the Białowieża National Park. A summary index of species composition similarity for all broad-leaved sites was 0.43. In the coniferous forest site group, the greatest similarity was seen between scots pine forests, at 0.71, with the bog pine forest being much less similar, at 0.55. Communities from mixed coniferous forest sites are not similar to one another or to communities from the other coniferous forest sites (0.39 and 0.29 respectively). The index of similarity for all sites investigated was 0.21. The differences in species composition similarity or the finding of no common species reflect the considerable diversification of the communities and indicate their dependence on the type of habitat. There is a distinct correlation between ash-alder carrs and the bog birch forest, which are moist, not acidic and fertile, on the one hand, and the acidic, oligotrophic and rather dry scots pine forests on the other. Communities from linden-oak-hornbeam sites are much more diversified in this respect and divide into two groups associated with different soil pH values. Thus, one group is formed by communities from sites O1 and O2, with pH values of 5.1 and 5.5 respectively, while communities from linden-oak-hornbeam sites of pH 6.9. form a separate group on the diagram of species composition similarity. A similarity index of 0.65 characterizes a large group of broad-leaved forest sites with a pH range of 5.9–6.9. The swamp alder site (pH 6.0), is an exception here as it is similar (0.53) to the linden-oak-hornbeam sites with pH 5.1–5.5. Among communities from coniferous forest sites, an index of 0.53 characterizes scots pine forests and the bog pine forest with pH 4.2-4.4. Communities from mixed coniferous forest sites of both pH 3.8 and a higher pH of 4.9 are not similar.

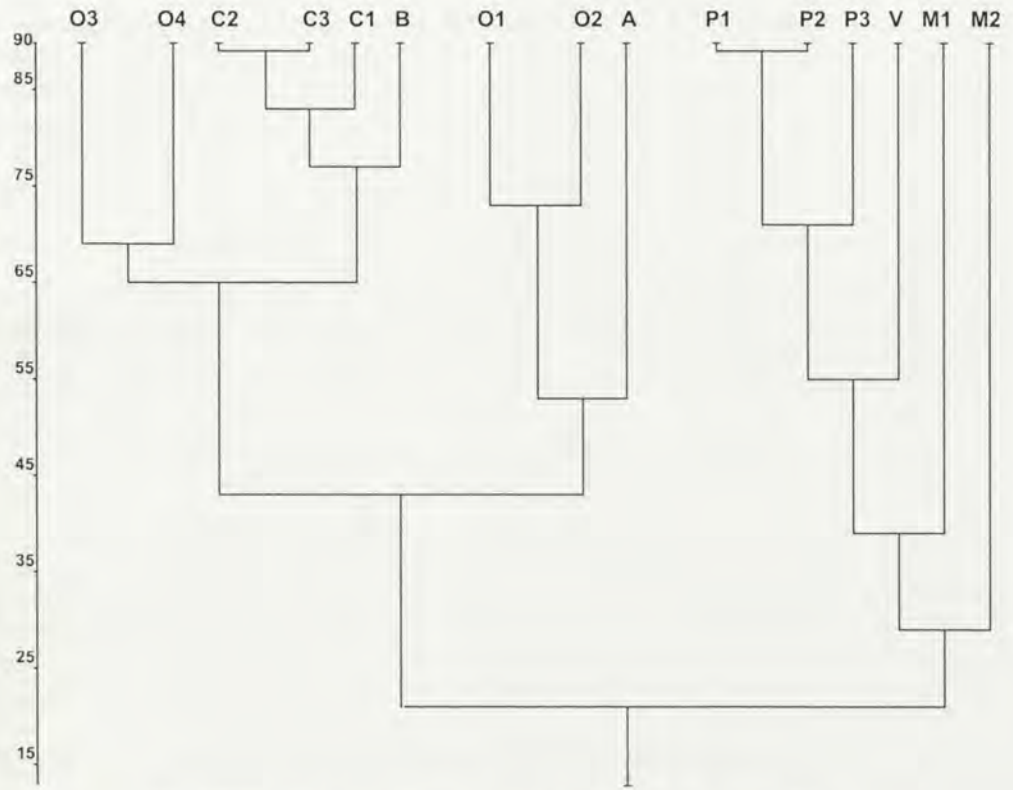

Fig. 3. Similarity of species composition at the study sites (Sørensen index).

The diagrams of similarity of species composition and structures of dominance of *Enchytraeidae* communities are different

Similarity of the structures of dominance of *Enchytraeidae* communities

Analysis of similarity of dominance structures of *Enchytraeidae* based on Morisita's index revealed the presence of a few groups (Fig. 4). The highest index (0.99) of similarity was obtained for the communities from Scots pine forests, the bog pine forest and the mixed coniferous forest (site M2) and the communities from the swamp alder forest and the linden-oak hornbeam forest. The community from mixed coniferous site M1 was very similar to those from the swamp alder forest and the linden-oak-hornbeam forest (site O2), at 0.98. The index was also high for the communities from two ash-alder sites (C1 and C2), at 0.94. The same degree of similarity of dominance structures was obtained for the communities from the swamp alder forest, linden-oak-hornbeam site O2, mixed coniferous sites, scots pine forest sites and the bog pine forest. These habitats are quite diversified in terms of soil acidity, moisture and fertility. A slightly lower degree of similarity (0.93) was seen between two sites: linden-oak-hornbeam site O1 and ash-alder carr site C3. These two communities were quite similar (0.88) to the communities from the 8 sites listed above (swamp alder forest, linden-

oak-hornbeam O2, mixed coniferous forests, Scots pine forests, bog pine forest). A separate group was formed by two linden-oak-hornbeam sites: O3 and O4, with similarity at 0.93. The ash-alder carr sites C1 and C2 are most similar to the bog birch site (0.76), and this entire group is most similar to the two linden-oak-hornbeam sites from within the Białowieża National Park (O3, O4), at 0.71.

There is little similarity between this group of communities and the one discussed earlier (0.26).

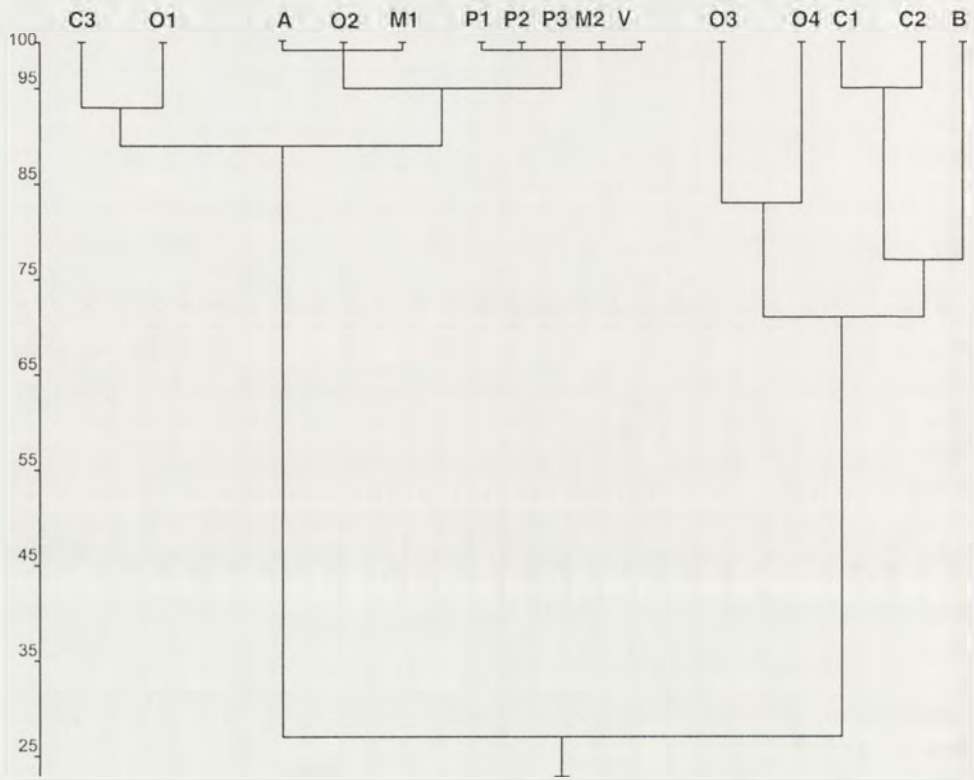

Fig. 4. Similarity of dominance structure of enchytraeid communities at the study sites (Morisita index).

The diagram of dominance structure is considerably influenced by the dominant species *C. sphagnetorum*. An index of 0.99 was obtained for the communities from the scots pine forest sites, mixed coniferous forest site M2 and the bog pine forest site, where *C. sphagnetorum* made up 97–99% of the community. Another group on the diagram was formed by the swamp alder site, linden-oak-hornbeam site O2 and mixed coniferous site M1 (an index of 0.98), where the share of *C. sphagnetorum* ranged from 75% to 82%. A third group consisted of the communities from linden-oak-hornbeam site O1 and ash-alder carr site C3, with the share of *C. sphagnetorum* ranging from 55% to 65%, and similarity of dominance structures at 0.93. The communities

from ash-alder sites C1 and C2 have lower shares of *C. sphagnetorum* (16–28%) and a similarity index of 0.94. This group also includes the community from the bog birch forest (index value 0.76), where another species, *H. perpusilla*, is the dominant. Also in the last group, consisting of the linden-oak-hornbeam sites from the Białowieża National Park, with a similarity index of 0.83, *C. sphagnetorum* has a share of only 9.3% at one site and *F. bisetosa* is the dominant species at the other one.

Species diversity

The highest index of general diversity was obtained for the communities from the ash-alder carr site C1 in the Białowieża National Park (3.08) and the bog birch site (3.01). Slightly lower values were recorded at the C2 ash-alder site (2.98) and the linden-oak-hornbeam site (O3) on brown soil (2.91) (Table 2). Communities with a diversity index of 2.18–2.66 inhabited the linden-oak-hornbeam site on lessive soil (O4), ash-alder carr site C3 and linden-oak-hornbeam site O1. The next group, with the index ranging from 1.06 to 1.39, consisted of the communities from the swamp alder forest, mixed coniferous site M1 and linden-oak-hornbeam site O2. For scots pine forests, bog pine forest and mixed coniferous site M2, the index was below zero. The greatest diversities of enchytraeid communities were in the soils of the bog birch forest and the linden-oak-hornbeam forest. Thus, the bog birch forest is the most important refugium of *Enchytraeidae*, with the largest number of species, the most abundant community and the greatest diversity of all the sites studied. Thus, it can be stated that of all forest habitats in the Białowieża Primeval Forest, the bog birch forest offers the best conditions for enchytraeids.

DISCUSSION

The species recorded at the study sites represent 40% of *Enchytraeidae* species reported from Poland and 60% of the fauna of Polish lowland forests. Thus, the Białowieża Primeval Forest is a significant refugium for this group of animals. Species occurring in only one habitat type are not characteristic only of that habitat type, even though they are undoubtedly rare species. For example, *S. niveus* and *F. bulbosa* were found only at linden-oak-hornbeam sites. *S. niveus* has not been recorded in Poland from any other site. Still, it has been reported from broad-leaved forests and meadows in other areas, so it can hardly be regarded as characteristic of the linden-oak-hornbeam forest. *F. bulbosa* is also found in the swamp alder forest, in meadows and fields of sedge. The following four species were only found in the swamp alder forest: *C. goodhui*, *C. palustris*, *M. riparia* and *H. parva*. *C. palustris* and *C. goodhui* occur in marshy and peat soils. *M. riparia* occurs in water and wet habitats. *H. parva* is also known from peatlands and peat meadows as, according to KASPRZAK (1986), from very diverse forest and open-area habitats.

Comparison of forest with different nutrient levels accounted for differences in the number of sites. Still, it should be pointed out that only two sites were classified as mesotrophic. The numbers of enchytraeids at these sites were significantly higher

compared to oligotrophic sites. A high similarity of species composition and structure of the communities from ash-alder carrs (PILIPIUK 2001) and scots pine forests (PILIPIUK 1993) prompted a comparison of communities from different types of forest.

The study carried out in the Białowieża Primeval Forest was the most comprehensive, including 7 types of forest. Another area where enchytraeids were studied in different types of forest is the Kampinos Forest. Studies in that area involved ash-alder carrs, linden-oak-hornbeam forest, mixed coniferous forest and Scots pine forest (MAKULEC 1983) and the swamp alder forest, linden-oak-hornbeam forest and mixed coniferous forest (PILIPIUK 1997) Other studies concentrated on specific forest types: the linden-oak-hornbeam forest (KASPRZAK 1975), the swamp alder forest (KASPRZAK 1977) and Scots pine forests and ash-alder carrs (see above). A comparison of the findings of the present study with data from other regions of Poland indicates that communities from ash-alder carrs are the most similar to one another in terms of species composition of all communities from broad-leaved forest sites. This may be due to the fact that ash-alder carrs, being an azonal vegetation type, show little diversification, but also important is the considerable mobility of enchytraeids along water courses. Communities from Scots pine forests also have similar species composition, which is because these forests, growing on oligotrophic acidic soils, create similar conditions for this group of animals. The factors which have the greatest influence on the development of an *Enchytraeidae* population in a forest environment include edaphic conditions, i.e. the quality of food supplied as leaf fall and the associated microflora, which has an effect on the species composition.

Another important abiotic factors are soil acidity and moisture. Healy (1980), Healy & Bolger (1984), Didden (1993) mentioned pH as one of the most important environmental factors for the distribution of enchytraeid species. These findings were corroborated in more controlled experiments by Hågvar & Abrahamsen (1980) on colonisation of sterile soil samples with adjusted pH values. This factor has a negative effect on species composition, but does not affect density, which is high in acidic soils. Soil acidity appears to be more important than moisture as communities of *Enchytraeidae* in the relatively dry soils of Scots pine forests and the bog pine forest are very similar. Theoretically, with increasing moisture, the number of species should also increase. Still, in the acidic soil of the bog pine forest, the number of species is very low. Similarly, few species were found in linden-oak-hornbeam forests with lower pH.

The best conditions for the development of multi-species and abundant communities are afforded by the bog birch forest with a good nutrient base, adequate moisture and not very acidic soils. Since data were available only on individual communities from the bog birch forest, swamp alder forest and bog pine forest, it is difficult to determine whether these communities are typical of those types of forest. Thus, our efforts concentrated on determining the extent of dissimilarity between these communities and those occurring in other types of forest. Determination of communities characteristic of specific types of forest would require studying *Enchytraeidae* communities in different types of forest in Poland. The findings could then be used as a reference for monitoring or valuation purposes.

CONCLUSIONS

The community inhabiting the soil of the bog birch forest is the richest in species and very abundant. The diversity index of Shannon and Wiener also reaches a high value for this community. This is due to the fertility, moisture and acidity of the soil.

High soil acidity is the factor which has the most marked negative effect on the number of species, irrespective of moisture. The number of species increase when pH rose, at pH higher than 5.5 number of species is twice as numerous.

Neither high acidity nor very high moisture, nor excessive drying of the soil have a limiting effect on the abundance of *Enchytraeidae*, which shows that the animals perform their functions even in such soils.

The most similar communities in terms of species composition inhabited ash-alder carrs and Scots pine forest sites. Communities from linden-oak-hornbeam sites are very diversified and fall into two groups. The species composition of communities from broad-leaved forests is not similar to that of communities from various types of coniferous forest.

The highest similarity of dominance structures was seen between the communities from coniferous forests on soil with pH 3.8–4.4 and communities from the mixed coniferous forest, the swamp alder forest and one linden-oak-hornbeam site.

The communities of *Enchytraeidae* inhabiting ash-alder carrs and Scots pine forests can be regarded as characteristic of these types of forest. This is not possible in the case of the linden-oak-hornbeam forest due to the considerable habitat diversification, with a lot depending on the type of soil and pH.

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STRESZCZENIE

[Tytuł: Fauna wazonkowców (*Oligochaeta, Enchytraeidae*) w lasach Puszczy Białowieskiej]

Badano zależność składu gatunkowego i struktury zgrupowań wazonkowców od typu zbiorowiska roślinnego, wilgotności i żyzności siedliska, jego kwasowości oraz typu gleby. Oceniano podobieństwo składu gatunkowego i podobieństwo zgrupowań biorąc pod uwagę te czynniki. W celu określenia preferencji środowiskowych poszczególnych gatunków analizowano ich frekwencję i zagęszczenie na badanych stanowiskach.

Skład gatunkowy zgrupowań wazonkowców lasów Puszczy Białowieskiej obejmuje 36 gatunków. Wszystkie stwierdzone gatunki notowano w lasach liściastych, z czego 26 występowało wyłącznie w tego typu lasach a 10 zarówno w lasach liściastych jak i w borach. *C. sphagnetorum* był jedynym gatunkiem, który występował we wszystkich badanych typach lasów.

Czynnikiem najbardziej ograniczającym liczbę występujących gatunków jest wysoka kwasowość gleby niezależnie od wilgotności. Najmniej gatunków (3) stwierdzono w glebie o najniższym pH 3,8. W miarę wzrostu wartości pH liczba stwierdzonych gatunków rosła. Najwyższą liczbę gatunków (31) stwierdzono przy pH 6,0. Powyżej tej

wartości pH od 6,1 do 6,9 liczba gatunków jest nieco niższa i wynosi od 24 do 26. Optimum pH gleby dla poszczególnych gatunków ma różne wartości a jego zakres różną szerokość. Najwięcej gatunków – 8 znalazło optimum bytowania przy zakresie pH 5,7–6,0.

Najniższe średnie zagęszczenie (8550 osob./m² i 9300 osob./m²). stwierdzono na dwóch stanowiskach w łęgach. Najwyższe zagęszczenie stwierdzono w borze mieszanym (M2) przy najniższym pH 3,8 – (31950 osob./m²) oraz w brzezinie bagiennej (29 tys. osob./m²). W skrajnie różnych pod względem wilgotności a podobnych pod względem kwasowości borze świeżym i borze bagiennym zagęszczenie wazonkowców jest bardzo podobne.

Analiza podobieństwa składu gatunkowego zgrupowań wazonkowców przeprowadzona w oparciu o wskaźnik Sørensena wykazała, że dzielą się one na dwie niepodobne do siebie grupy – lasów liściastych i borów. Wewnątrz każdej z grup najwyższe podobieństwo (wartość wskaźnika 0,89) wykazują zgrupowania z łęgów i z borów świeżych.

Najbardziej różnorodne zgrupowania wazonkowców zasiedlają gleby brzeziny i grądu. Brzezina bagienna jest środowiskiem leśnym stwarzającym najlepsze warunki dla rozwoju zgrupowań wazonkowców. Składa się na to żyzność gleby, wilgotność i kwasowość. Zasiedlające glebę tego typu lasu zgrupowania wazonkowców są najbogatsze w gatunki i bardzo liczebne. Charakteryzują się też wysoką różnorodnością.

Ani wysoka kwasowość ani skrajne wartości wilgotności gleby nie są czynnikami ograniczającymi liczebność wazonkowców. W glebach kwaśnych, mokrych i o niskiej wilgotności występują zgrupowania wazonkowców o dużym zagęszczeniu . Wazonkowce są grupą zwierząt glebowych, które mogą pełnić swoją rolę saprofagów w glebach oligotroficznych, w których liczebność dżdżownic jest bardzo niska. Tworzą zgrupowania charakterystyczne dla niektórych typów lasów, takich jak łęgi czy bory sosnowe. Większość zgrupowań wazonkowców zasiedlających gleby różnych typów lasów jest odmienna.