

Distribution of soil saprophagous macrofauna along a zonal gradient in the Biebrza River floodplain (Poland)

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Abstract. The soil saprophagous macrofauna consisting of Lumbricidae, Oniscidea and Diplopoda in the Biebrza River floodplain was studied in natural ecological zones determined by seasonal flooding and fluctuations in river-induced groundwater levels. Five habitats along a zonal gradient were sampled: reeds, tall-sedge, mineral hillock, moss-sedge and swamp alder wood. General ecological parameters: abundance, species richness, alpha-diversity, evenness, beta-diversity and similarity, were measured for all the assemblages of each of the groups studied and the whole group of macrosaprophages. The assemblage in the swamp alder wood was the most diverse and best developed in terms of dominance structure and may be a refuge for soil macrofauna. The most specific and poor in species was the assemblage recorded for the mineral hillock, which is isolated from that in the surrounding habitats that are subjected to flooding.

Key words. Soil zoology, ecology, wetlands, river floodplain, soil fauna, diversity, Lumbricidae, Oniscidea, Diplopoda, Biebrza, Poland.

INTRODUCTION

Spatial aspect of species diversity is one of the most important problems in ecology. Areas with natural environmental gradients, such as river floodplains, provide suitable field sites for such research. Only a few unmodified, pristine floodplains are left in Europe and North America (Junk & Welcomme 1990, Jankowski & Świerkosz 1995, Dohle et al. 1999), and floodplains that are ecological zoned by river flooding and have diverse, natural peatland sites, are unique. The Biebrza River valley (NE Poland) is the last European river valley that still has extensive wetland areas and fairly undisturbed hydrological conditions. The Biebrza wetlands are considered to be one of the most important wetland areas in Europe due to the high diversity of peatland sites (Platteeuw & Pieterse 2005). The peat in this ice-marginal valley records the history of the development of the vegetation in this area. The most natural and valuable sites are located at the boundary between the Central European geobotanical unit and the boreal zone of Eastern Europe. The hydrogenic sites occupy 60% of the whole area of the Biebrza River valley (Liwski et al. 1984) and the peatlands 78.8%. Regular ecological zoning of the habitats is typical for this area. The best preserved and most valuable areas of the Biebrza valley are protected and included into the Biebrza National Park.

The aim of this study was to increase the knowledge of the distribution of soil saprophagous macrofauna along a transect extending from the river bank to the valley margin and to characterise

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the assemblages in the habitats that make up the mosaic landscape within this unique floodplain system.

MATERIAL AND METHODS

Study area

The Biebrza River valley is located in the north-east of Poland. It is over 120 km long and varies in width from 1.5 to 40 km, and most of it is in the protected Biebrza National Park (between latitude 52° 21' and 53° 41' N and longitude 22° 28' and 23° 32' E). Based on hydrological, geo-morphological and hydrogeological features the Biebrza valley is divided into Upper, Middle and Lower Basins (Żurek, 1984). The Lower Basin is less paludal than the Middle and Upper Basins, and peat-deposits are common there. The study was carried out in the Lower Basin, where the transverse zones determined by seasonal river flooding are best developed. Five sites differing in plant community and type of soil or its nutrient status (from nutrient rich to poor fens) were investigated: reed association *Phragmitetalia* subjected to intensive flooding (T1); tall-sedge association (*Caricetum elatae*) subjected to long-term and shallow flooding (T2); drier mineral hillocks on sandy soils (T3); moss-sedge association (*Caricetum diandrae*) subjected to sporadic flooding (T4); swamp alder forest (*Carici-elongate-Alnetum*) permanently wet, enriched by underground and deluvial water, but never flooded by river water (T5).

Sampling

Soil macrofauna was sampled in October 2000, 2001 and 2002. Three soil samples, each of an area of 1/16 m² and 10 cm deep, were taken at each site on each date. Soil animals were extracted by heat using a modified Kempson apparatus. The specimens of Lumbricidae, Oniscidea and Diplopoda extracted using this apparatus were identified to species.

Statistical analysis

Mann-Whitney-U-test with post-hoc pair-wise comparison was used for comparing the population density and species richness of assemblages. Species accumulation curves were drawn to assess the efficiency of the collection method (based on samples) and to compare the number of species recorded (based on individuals) (Gotelli & Colwell 2001, Colwell et al. 2004). Expected number of species was also estimated by non-parametric indices Chao 2 and Jackknife 1 (Magurran 2004). The structural changes in assemblages along the zonal gradient was evaluated by SHE analysis as relations between species (S), Shannon diversity (H) and evenness (E) expressed as values of their natural logarithm (Hayek & Buzas 1997, Magurran 2004). The comparison of beta-diversity was calculated according to Whittaker's measure (Whittaker 1960). The calculations were done using PAST 2.07 and Statistica 7.1 programme packages.

RESULTS

Density

A total of 995 earthworms (Lumbricidae), terrestrial isopods (Oniscidea) and millipedes (Diplopoda) were collected. The average density of soil saprophagous macrofauna varied from 151 ind. m⁻² on the mineral hillock (T3) to 604 ind. m⁻² at the tall-sedge site (T2) (Fig. 1), where millipedes were the most abundant and dominant (Fig. 2). The most balanced ratio of the abundances of these three groups was recorded in the swamp alder forest (T5).

Statistical comparison of the abundances (Fig. 3) showed significant differences within the assemblages of Lumbricidae, Diplopoda and in all three groups of soil macrofauna evaluated together. In each of the groups, the assemblages at the mineral hillock (T3) and tall-sedge site (T2) differed significantly in terms of abundance (Fig. 3).

Species richness

Eight species of earthworms (Lumbricidae), three species of terrestrial isopods (Oniscidea) and 10 species of millipedes (Diplopoda) were recorded in this study (Table 1). The rarefaction curves based on the samples of Lumbricidae and Diplopoda taxa indicate that collecting more samples is unlikely to reveal more species (Fig. 4). The sample-based rarefaction curves for all macrofauna material (3 groups altogether) for each of the study sites indicate that the most likely underestimated habitats are sites T1, T2 and T4, which are regularly flooded, whereas the best estimate is that for the mineral hillock (T3) for which statistically all the species occurring there are identified (Fig. 5).

Table 1. List of species of earthworms (Lumbricidae), terrestrial isopods (Oniscidea) and millipedes (Diplopoda) recorded in different habitats in the Biebrza River floodplain. For abbreviations see Fig. 1

	T1	T2	T3	T4	T5
Lumbricidae					
<i>Aporrectodea caliginosa</i> (Savigny, 18256)		+			
<i>Aporrectodea rosea</i> (Savigny, 1826)					+
<i>Dendrobaena octaedra</i> (Savigny, 1826)	+	+	+	+	+
<i>Dendrodrilus rubidus</i> (Savigny, 1826)	+	+			
<i>Eiseniella tetraedra</i> (Savigny, 1826)	+	+			+
<i>Lumbricus rubellus</i> Hoffmeister, 1833	+	+	+		+
<i>Octolasion lacteum</i> (Oerley, 1885)					+
<i>Octolasion tyrtaeum</i> Savigny, 1826	+				
Oniscidea					
<i>Ligidium hypnorum</i> (Cuvier, 1792)				+	+
<i>Trachelipus rathkii</i> (Brandt, 1833)	+	+	+	+	+
<i>Trichoniscus pusillus</i> Brandt, 1833	+			+	+
Diplopoda					
<i>Craspedosoma rawlinsi</i> Leach, 1814				+	+
<i>Cylindroiulus latestriatus</i> (Curtis, 1845)	+	+	+		
<i>Glomeris tetrasticha</i> Brandt, 1833					+
<i>Leptoiulus cibdellus</i> (Chamberlin, 1921)	+	+			
<i>Leptoiulus</i> cf. <i>proximus</i> (Němec, 1896)					+
<i>Mastigophorophyllon saxonicum</i> Verhoeff, 1916					+
<i>Megaphyllum sjaelandicum</i> (Meinert, 1868)	+	+	+		
<i>Polydesmus complanatus</i> (Linnaeus, 1761)	+	+		+	+
<i>Rossiulus vilnensis</i> (Jawlowski, 1925)		+		+	+
<i>Xestoiulus laeticollis</i> (Porath, 1889)			+	+	+

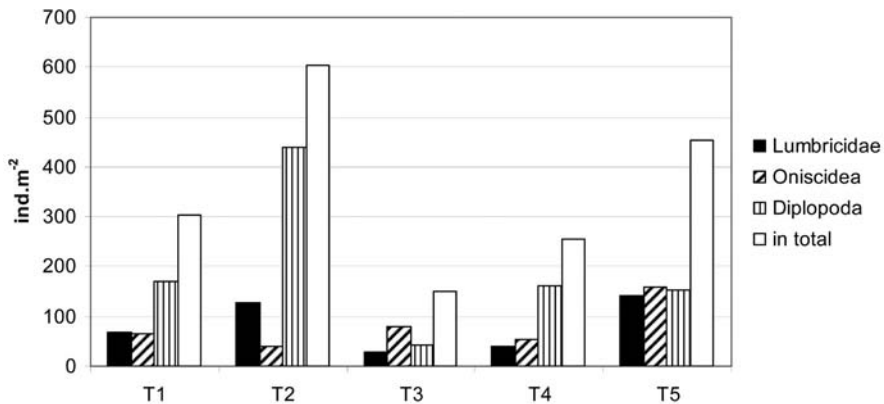


Fig. 1. Population density of soil saprophagous macrofauna at the study sites in the Biebrza River valley. Abbreviations: T1 – reed association, T2 – tall-sedge association, T3 – mineral hillock, T4 – moss-sedge association, T5 – swamp alder forest.

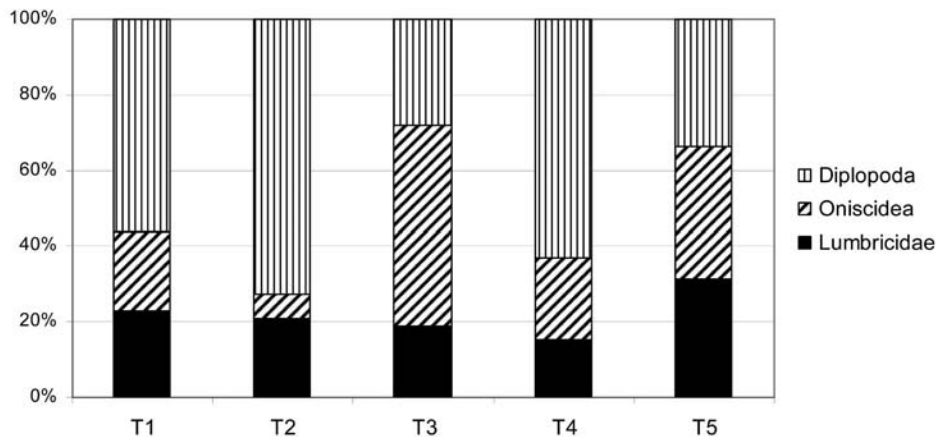


Fig. 2. Representation (% of total population density) of individual soil saprophagous macrofauna groups at the study sites in the Biebrza River valley. For abbreviations see Fig. 1.

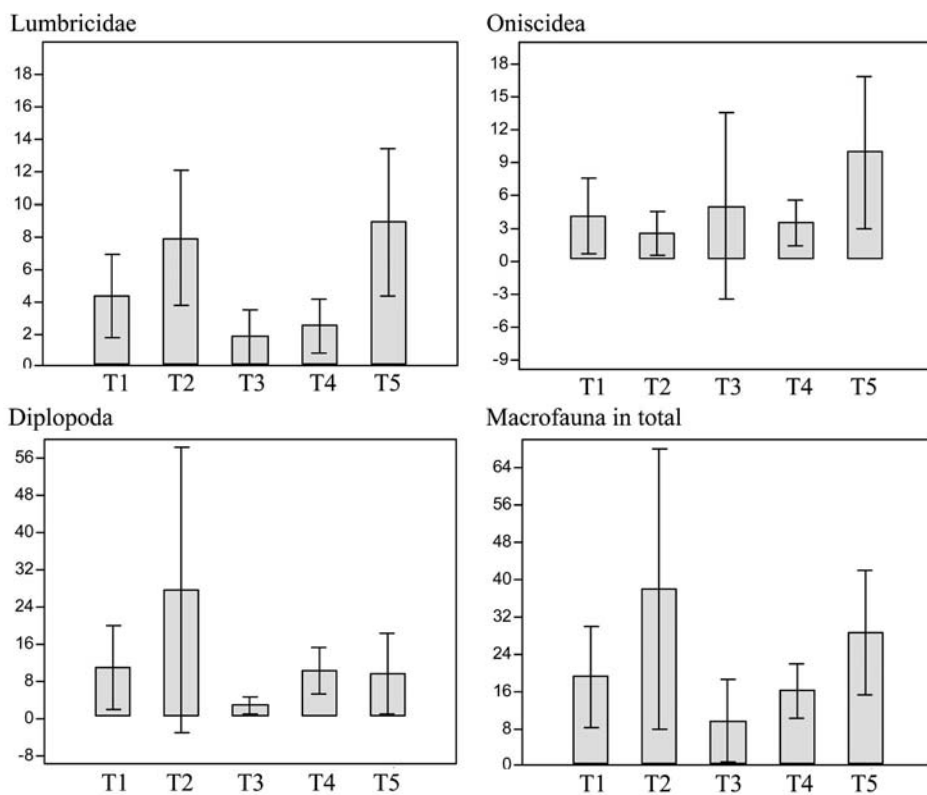


Fig. 3. Abundance (mean number of individuals in a sample of 1/16 m² ± SD) of soil saprophagous macrofauna and the results of Mann-Whitney test (significant values in bold, p<0.05). For abbreviations see Fig. 1.

Table 2. Comparison of species richness using nonparametric estimators. For abbreviations see Fig. 1

		S recorded	Chao 2	Chao2 SD	Jackknife1	Jackknife1 SD
Macrofauna	T1 (9 samples)	11	13.67	4.04	13.67	1.33
	T2 (9 samples)	11	11.00	0.11	11.89	0.89
	T3 (9 samples)	6	6.00	0.42	6.00	0.00
	T4 (9 samples)	9	9.89	1.65	11.67	1.33
	T5 (9 samples)	15	15.15	0.50	16.78	1.18
	T1–T5 (45 samples)	21	21.98	1.78	23.93	1.65
Lumbricidae	T1–T5 (45 samples)	8	8.00	0.24	8.98	0.98
Oniscidea	T1–T5 (45 samples)	3	3.00	0.00	3.00	0.00
Diplopoda	T1–T5 (45 samples)	10	10.49	1.27	11.96	1.37

The comparison of the mean number of species at the five study sites indicates that the macrofauna studied is richest in the swamp alder forest (T5) (Fig. 6). The assemblages in the swamp alder forest (T5) and tall-sedge (T2) differ significantly from the other assemblages, except that in the reeds (T1). The assemblages in reeds differ significantly only from the poorest assemblage on the mineral hillock (T3). The comparison, based on rarefaction curves of total numbers of individuals, indicate a sequence from the least rich site, mineral hillock (T3) through moss-sedge (T4), tall sedge (T2) and reeds (T1) to the most rich site, swamp alder forest T5 (Fig. 7). Non-parametric estimators Chao 2 and Jackknife 1 give the same sequence of assemblage richness. In addition, they indicate that all species living on the mineral hillock were recorded and it is unlikely that many more species will be recorded at the other study sites, at most 2 more species at the reed site is predicted by both estimators (Table 2). The most underestimated of the three taxa is the Diplopoda.

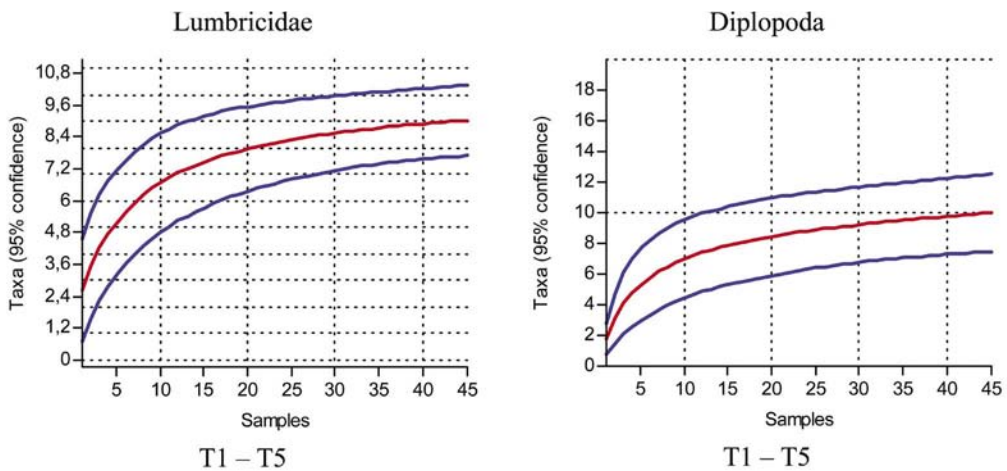


Fig. 4. The rarefaction curves (mean \pm 95% confidence intervals) for Lumbricidae and Diplopoda based on samples from the five study sites. For abbreviations see Fig. 1.

Table 3. The values of Whittaker index calculated for the assemblages of soil saprophagous macrofauna recorded at the study sites. For abbreviations see Fig. 1

	T2	T3	T4	T5
T1	0.91	1.47	1.10	0.62
T2		1.47	1.10	0.62
T3			1.80	1.00
T4				0.75

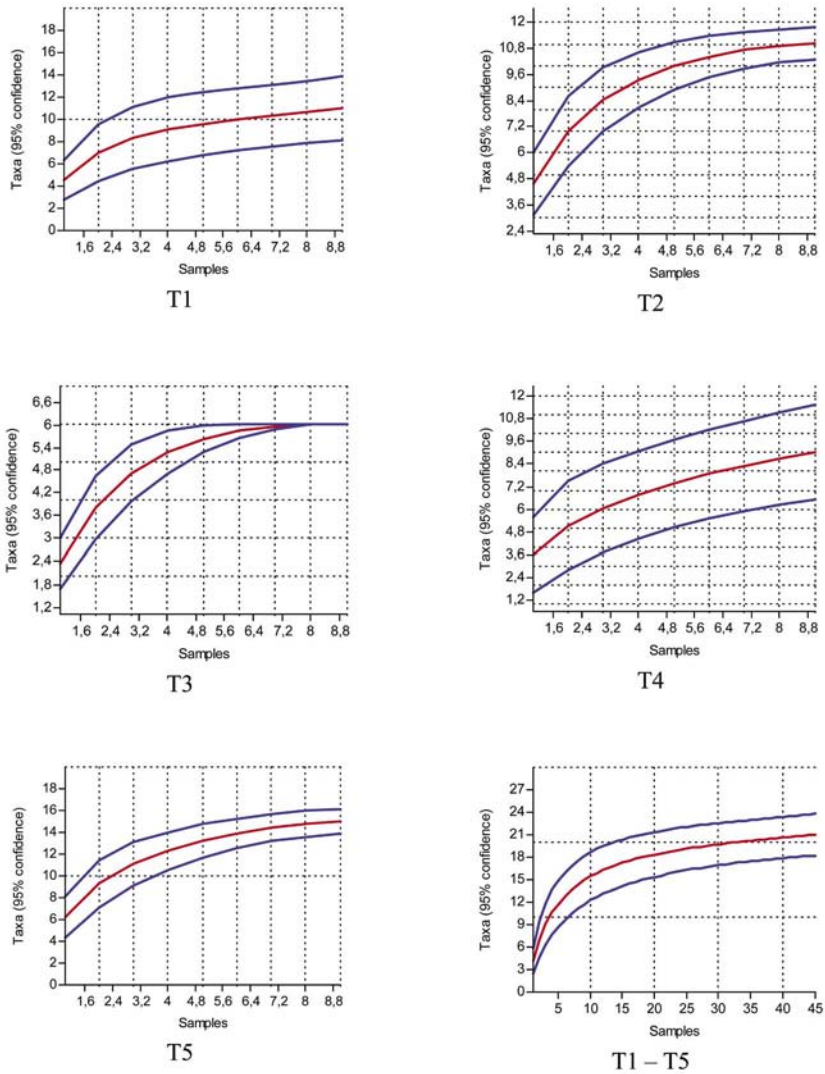


Fig. 5. The rarefaction curves (mean \pm 95% confidence intervals) for soil saprophagous macrofauna based on samples from particular and all study sites. For abbreviations see Fig. 1.

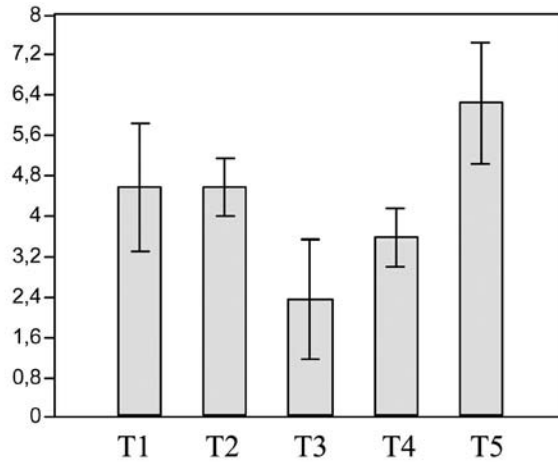


Fig. 6. Species richness of soil saprophagous macrofauna (mean \pm SD), with results of Mann-Whitney test (significant values in bold, $p < 0.05$). The mean values are shown by a bar with marked standard error. For abbreviations see Fig. 1.

Alpha-Diversity

The results of SHE analysis indicate that the differences in the assemblages of Lumbricidae in the different habitats are relatively small: with the richness and diversity curves increasing slightly and the evenness curve decreasing to the lowest value for swamp alder wood (Fig. 8). The Oniscidea assemblages are rather stable from reed to mineral hillock (T1–T3), then the richness remains at the same level but the diversity curve increase as a result of domination smoothing. The main direction of change in the Diplopoda assemblages is similar to that recorded for Lumbricidae, but

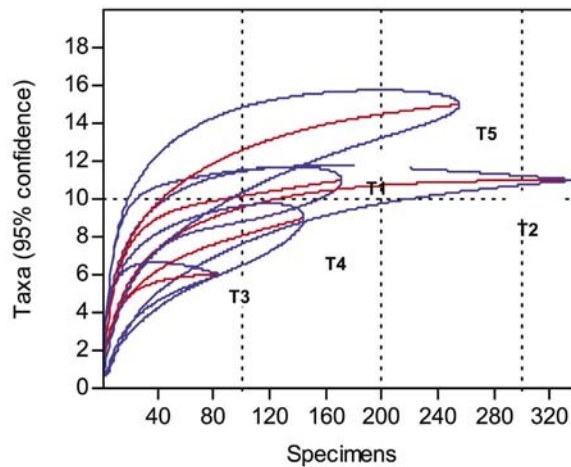


Fig. 7. Comparison of species richness of the five assemblages of macrofauna studied using individual-based rarefaction curves. For abbreviations see Fig. 1.

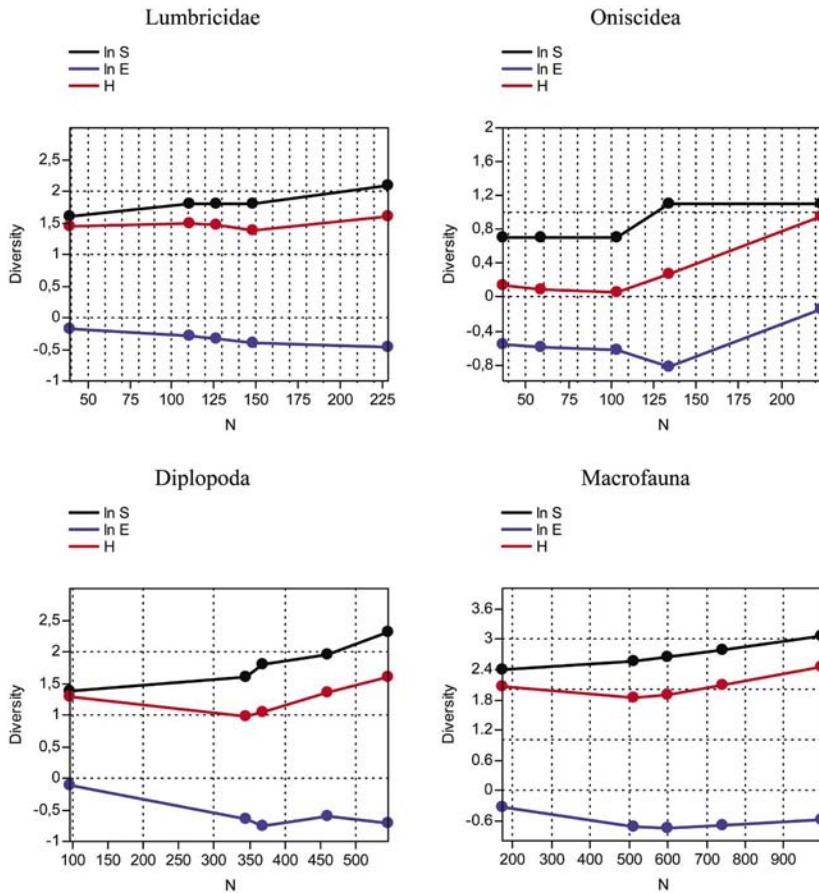


Fig. 8. Cumulative SHE profiles: logarithmic species abundance ($\ln S$), Shannon index (H) and logarithmic evenness ($\ln E = H - \ln S$) for individual groups and soil saprophagous macrofauna.

in the changes occurring T1–T2, the diversity and evenness curves decline more steeply. Generally, the assemblages of the soil saprophagous invertebrates studied are similar to those recorded for earthworms and millipedes. Their richness and diversity in the swamp alder forest (T5) are close to the maximum and evenness to the minimum values recorded.

Beta-diversity

The values of the Whittaker index for the assemblages of the soil saprophagous macrofauna studied were higher for the mineral hillock (T3) than the other sites (Table 3). This indicates that the assemblages on the mineral hillock are relatively isolated and their fauna is the most specific of the assemblages evaluated.

Similarity

The cluster analysis of the density data indicates that the assemblage of saprophagous macrofauna at the tall-sedge site (T2) differs most from all the other assemblages (Fig. 8).

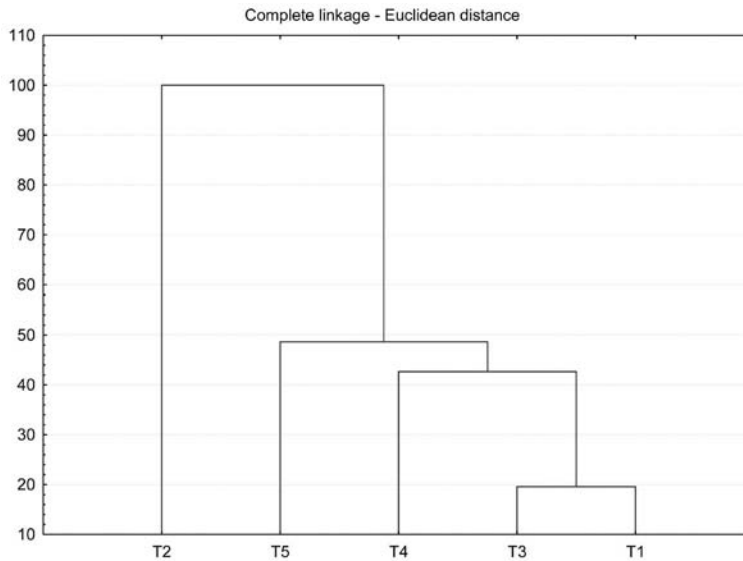


Fig. 9. Cluster analysis (complete linkage with Euclidean distance) of the diversity of soil saprophagous macrofauna at the sites studied. For abbreviations see Fig. 1.

DISCUSSION

The variation in soil macrofauna assemblages observed across the studied environmental transect indicates the important changes in their organization. The differences in the tested attributes between the assemblages from mineral hillock and others sites showed that drought, not inundation, is a factor of prime importance. It contributes significantly to the organization of the soil macrofauna in river floodplain. There were significant differences among the sites sampled in the Biebrza River valley in the population density of earthworms, diplopods and total soil macrofauna. In each of these groups, the density recorded on the mineral hillock (T3) was significantly lower than at the tall-sedge site (T2). The sandy soil, frequent dry periods and limited food supply, i.e. unsuitable conditions for soil fauna, may be the main reasons for the low density recorded on the mineral hillock. On the other hand, the high density of r-selected species in the tall-sedge habitat, which is subjected to long periods of flooding, may reflect their ability to survive flooding (Adis & Junk 2002).

All soil macrofauna species recorded in this study are classified as ubiquitous. This accords with Adis & Junk (2002) in that unlike tropical river floodplain systems, terrestrial invertebrates in lowland river floodplains of Central Europe are mostly eurytopic species that inhabit surrounding uplands and are able to cope with short periods of flooding. Rarefaction curves indicate that the method of sampling used in this study recorded almost all the species belonging to Lumbricidae, Oniscidea and Diplopoda present in the different habitats. Reed and moss-sedge sites seem to be the most underestimated habitats.

The richest assemblages of soil macrofauna were recorded in the swamp alder wood, which accords with the results of other comparative studies (e.g. Tajovský 1998, 1999, Dohle et al. 1999, Ivask et al. 2007, Pižl 1999, Plum 2005) that indicate that woodlands on lowland flood-

plains are more species-rich than those on floodplain grasslands. The SHE analysis indicates that the assemblages recorded there had the highest species richness and species diversity values and the lowest evenness values. This indicates that the dominance structures of the assemblages are highly developed, with the assemblages including both species with high and relatively low densities. Hence, swamp alder wood appears to be a refuge for the soil fauna of neighbouring wetland habitats.

Most of the above studies also indicate that number of species is usually highest in the drier areas and declines with increasing flood stress. For example, in the Lower Oder Valley, only two of the 13 diplopods recorded in the adjacent high ground were found in floodplain habitats inundated for several weeks, and none in sites flooded for up to five months (Zerm 1999). In this study, however, the evaluation of species richness by individual-based rarefaction and non-parametric estimators indicate the following sequence of assemblages: mineral hillock (T3) < moss-sedge (T4) < tall-sedge (T2) < reed (T1) < alder wood (T5).

The immigration strategy is one of the most important pre-adaptation of the terrestrial arthropods to survive in the inundated habitats (Rothenbücher, Schaefer 2006). The low changes observed in the species turnover (beta-diversity) between the outermost points of studied transect (reed and swamp alder wood) can indicate the presence of the immigration strategy of soil macrofauna species in river floodplain. However the values of the beta-diversity index indicate that the soil macrofauna assemblages on the mineral hillock differed most from all the other assemblages. Contrary to the above results, the cluster analysis showed that the assemblage of soil macrofauna in the tall-sedge habitat differed most from that in all the other habitats studied. However, it should be noted, that the Whittaker index is based on presence/absence data and suggests dissimilarity in species composition of assemblages while the cluster analysis based on the complete structure of assemblages indicates more the difference in dominance structure.

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