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PROGRESS IN STUDIES ON MYRIAPODA AND ONYCHOPHORA

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Centipede (Chilopoda) communities of some forest habitats of Puszcza Białowieska in Poland

Abstract: Species composition and structure of Chilopoda communities were studied in five natural forest habitats of Puszcza Białowieska, eastern Poland: fresh pine forest, pine-spruce mixed forest, linden-oak-hornbeam forest, ash-alder flood plain forest, and bog-alder forest. Species number ranged from 7 to 9 and was the highest in the linden-oak-hornbeam forest. The centipede communities were very similar in species composition. The abundance of centipedes increased along the fertility gradient (pine forest → linden-oak-hornbeam forest). The edaphic component of each community was dominated by *Lithobius curtipes*, while *Lithobius mutabilis* was the dominant species in the epigeic component, with the exception of the bog-alder forest where the community was also dominated by *L. curtipes*. In this type of forest, community structure was the least similar to those of the other communities, particularly with respect to the epigeic component. Centipede communities in habitats characterised by extreme moisture conditions (fresh pine forest, ash-alder flood plain forest and bog-alder forest) showed either the highest or the lowest homogeneity of dominance structure.

Key words: Chilopoda, Puszcza Białowieska, forest type, diversity, community structure

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INTRODUCTION

Puszcza Białowieska is a unique complex of natural primeval lowland forests of the boreo-nemoral zone, where the primary phytosociological and ecological differentiation corresponds to the habitat variety specific for denudation plains of the eastern part of the postglacial North European Lowland (FALIŃSKI 1994).

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Owing to this, a comprehensive analysis of centipede communities in different forest habitats provides an opportunity to learn more both about the fauna of the region and the factors governing the population and biotic structure characteristic of a given community (WYTWER 1999).

STUDY AREA

Centipedes were collected in forests representing the five basic units of vegetation landscape, described by KWIATKOWSKI (1994) as forest biogeocenoses of Puszcza Białowieska, on the basis of a classification of forest associations by SOKOŁOWSKI (1980), namely:

1. Fresh pine forest (*Vaccinio vitis-idaeae-Pinetum)* – a thinned coniferous forest with pine as dominant and admixtures of spruce and birch; ground cover is composed chiefly of mosses and undershrubs. There is lack of species typical of moist habitats while xerothermal species are numerous. This type of forest is found on plains of aeolian accumulation; ground water is present at medium depths (2–5 m).
2. Pine-spruce mixed forest (*Calamagrostio arundinaceae-Piceetum*) – typical of ablation moraine plains, with spruce as dominant and a high contribution of pine, and an admixture of birch, sporadically, of oak and hornbeam; a lush ground flora is composed of species characteristic of spruce forests and, generally, of forest habitats, reflecting a relatively eutrophic biocenosis; ground water table lies deep, at 5–15 m;
3. Linden oak-hornbeam forest (*Tilio-Carpinetum typicum*) – multi-species and multi-layer forest stands found on ground moraine flat plains, composed of hornbeam, maple, small-leaved linden, oak and spruce; fertile-habitat species abound in the ground flora; ground water table beyond the soil profile.
4. Ash-alder flood plain forest (*Circaeo-Alnetum*) – a swampy alder forest growing along streams on ground moraine plains, with a considerable contribution of ash and a small admixture of either spruce or hornbeam and linden; it has a poorly developed understory and a well developed herb layer with numerous bog-associated species and a tufted, mosaic structure; ground water table reaches the soil profile but periods of stagnation and flooding are not long.
5. Bog-alder forest (*Carici elongatae-Alnetum*) – a marshy alder forest of mosaic and tussock structured ground vegetation; spruce and birch are constant elements and, together with scrub layer species, form and occupy bog tussocks; prolonged periods of ground water stagnation; the ground flora of tussocks is composed of species characteristic of meso- and oligotrophic habitats, while the waterlogged areas are occupied by marshy vegetation, with a high proportion of tall perennials; plants typical of water habitats are found locally in hollows in the ground.

The first three forest types represent lithogenic habitats and have been grouped in the order of increasing fertility from an oligotrophic fresh pine forest via a mesotrophic pine-spruce mixed forest to an eutrophic linden-oak-hornbeam forest. In contrast, forest associations 4 and 5 are hydrogenic habitats; the ash-alder flood plain

forest resembles the linden-oak-hornbeam forest in terms of fertility while the bog-alder forest provides a mesotrophic environment.

Sampling was only carried out in mature natural stands, i.e. approximately 100-year old in the pine forest and linden-oak-hornbeam forest, and at least 60-year old in both alder forests.

METHODS OF SAMPLING AND FAUNISTIC ANALYSES

Two methods were used for quantitatively sampling the Chilopoda:

1. litter sifting wherever it was found practicable, i.e. in both types of coniferous forest and the linden-oak-hornbeam forest; in both types of inundated alder forest, where the upper soil layer, litter and ground cover were difficult to separate, soil samples were taken to a depth of about 15 cm; sample size was the same for both (10 x 0.1 m²); the specimens were then collected by hand.
2. Barber's pitfall trapping, used from April to October; 10 open traps filled with a 10% glycol solution with some detergent were set up in each forest section.

Data on the periods and methods of quantitative sampling at individual sites are presented in Table I.

Table I. Study sites and methods of sampling of Chilopoda.

	Habitat	Sites (forest section)	Soil sampling/litter sifting		Pitfall trapping	
			Time of study	Number of samples**	Time of study	Frequency of trap empting
1	Fresh pine forest (*Peucedano-Pinetum*)	**538, 667, 668**	1986–1987	24	1986–1987	2 weeks
2	Pine spruce mixed forest (*Calamagrostio arundinaceae-Piceetum*)	288/318, 521, **699**	1994–1995	8	1995	4 weeks
3	Linden oak-hornbeam forest (*Tilio-Carpinetum typicum*)	334, 399, **633**	1994–1995	8	1995	4 weeks
4	Ash-alder flood plain forest (*Circaeo-Alnetum*)	**315, 599, 600**	1991	7	1991	2 weeks
5	Bog-alder forest (*Carici elongatae-Alnetum*) – bog tussocks	**514/539**	1997, 2000	2	1997	4 weeks

Sections marked in bold were sampled also by pitfall trapping
*A sample means 10 x 0.1 m²

The material obtained from siftings and from soil samples was regarded as representative of the edaphic component of communities, whereas those collected by means of pitfall trapping and reflecting the intensity of centipede penetration into the surface layer of the forest soil served as representive of the epigeic component.

Qualitative sampling, i.e. looking for centipedes specifically in dead wood, mould, stumps etc., was carried out several times during the season.

The analyses of the Chilopoda communities used standard indices employed in faunistic studies and soil zoology (MAGURRAN 1988, GÓRNY & GRÜM 1993):

- index of density = number of individuals per m² of soil sample or sifting;
- trapability index = number of individuals caught by 10 Barber's pitfall traps over 14 days;
- the Marczewski-Steinhaus index of similarity in species composition:

$$I_{MS} = \frac{S_c}{S_x + S_y - S_c}$$

where S_x and S_y represent the number of species in habitats X and Y, respectively, and S_c is the number of species common to both habitats;

- index of dominance:

$$x_i = \frac{n_i}{N} 100\%$$

where n_i represents the density (trapability) of a given species, N represents the density (trapability) of the community;

- Morisita's index of similarity of dominance structures, modified by HORN (1966)

$$M = \frac{2\sum_{i=1}^{S} x_i y_i}{\sum_{i=1}^{S} x_i^2 + \sum_{i=1}^{S} y_i^2}$$

where x_i and y_i are dominance structure indices of i-th species in habitats X and Y, repectively, and S is the total number of species;

- Shannon's index of species diversity:

$$H' = \sum_{i=1}^{S} \frac{n_i}{N} \log_2 \frac{n_i}{N}$$

with the same symbols as above;

- Pielou's index of eveness:

$$J' = \frac{H'}{H_{\max}}$$

where $H_{max} = log_2 S^*$ and is equal to potential diversity at the maximum possible number of species S^* in a community;

ABUNDANCE

The Chilopoda communities studied showed variation in abundance relative to the habitat (Fig. 1). As the lithogenic habitats increased in fertility, both density and trapability rose. The density, estimated from soil samples, was found to range from 3.25 ind./m² in the pine forest to 19.75 ind./m² in the linden-oak-hornbeam forest. The trapability, estimated by pitfall trapping, was revealed as ranging from 0.75 to 2.33 ind./10 traps x 14 days. In the inundated, though fertile, ash-alder flood plain forest, the values of both indices were lower, with the trapability index reaching its minimum

there (0.20 ind./10 traps x 14 days). Conversely, tussocks in the bog alder forest showed the highest density of centipedes (39.50 ind./m^2) and, also, a very low trapability index (0.69 ind./10 traps x 14 days). Depressions in this type of forest were either excluded from sampling on account of being inundated or they were too swampy to yield any centipedes.

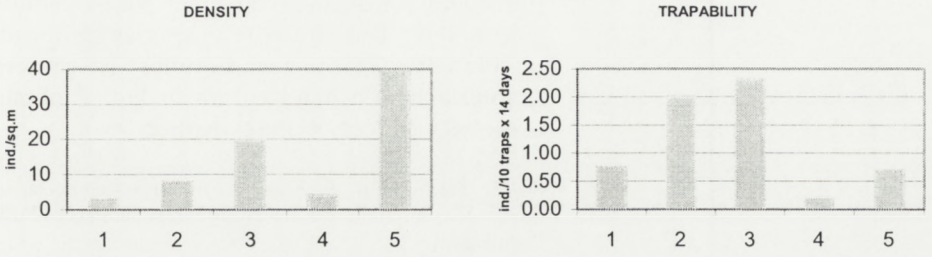


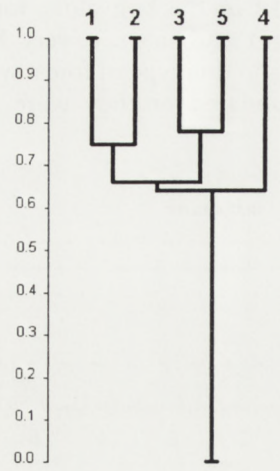
Fig. 1. Values of the abundance indices (density and trapability) in different forest habitats of Puszcza Bialowieska.

SPECIES COMPOSITION

A total of 10 species of Chilopoda were identified in the study habitats (Table II). All study habitats were characterized by relatively similar species richness estimates. Interestingly, different habitats of similarly high fertility were show to contain both the highest (9 – linden-oak-hornbeam forest) and the lowest (6 – ash-alder flood plain forest) number of species. Four (sub)species were common to all study habitats: *Lithobius forficatus*, *L. tenebrosus fennoscandius*, *L. lapidicola*, and *L. curtipes*.

Table II. Occurrence of Chilopoda species in five different habitats of the Białowieża Forest.

No	Species	Habitat				
		1	2	3	4	5
1	*Geophilus proximus* C. L. KOCH, 1847			+	+	+
2	*Pachymerium ferrugineum* (C. L. KOCH, 1847)	+				
3	*Lithobius erythrocephalus* C. L. KOCH, 1847	+	+	+		+
4	*Lithobius forficatus* (LINNAEUS, 1758)	+	+	+	+	+
5	*Lithobius lapidicola* MEINERT, 1872	+	+	+	+	+
6	*Lithobius mutabilis* L. KOCH, 1862	+	+	+	+	
7	*Lithobius pelidnus* HAASE, 1880	+	+	+		+
8	*Lithobius tenebrosus fennoscandius* LOHMANDER, 1948	+	+	+	+	+
9	*Lithobius curtipes* C. L. KOCH, 1847	+	+	+	+	+
10	*Lithobius crassipes* L. KOCH, 1862			+		
	Total	8	7	9	6	7



All the communities of centipedes included in this study were characterized by relatively high similarities in species composition, with values of the Marczewski-Steinhaus index ranging from 0.56 for the fresh pine forest and ash-alder forest centipede communities to 0.78 for the linden-oak-hornbeam forest and bog alder forest centipede associations. The similarity in species composition of the five study communities is presented graphically by a dendrogram in Fig. 2, obtained using MOUNTFORD's (1962) method.

Fig. 2. Dendrogram of similarities in species composition of centipede communities in the study forest habitats of Puszcza Białowieska.

DOMINANCE STRUCTURE

The edaphic component of all Chilopoda communities studied in the different habitats of Puszcza Białowieska (estimated from soil samples or by sifting) was dominated by *Lithobius curtipes*, whose estimated percentage contribution ranged from nearly 45% in the bog alder forest to more than 90% in the mixed pine-spruce forest and the ash-alder flood plain forest (Table III). The epigeic component (estimated by Barber's pitfall trapping) was dominated by *Lithobius mutabilis*, with the exception of the bog alder forest where *L. curtipes* was the dominant species in both community components. In this community, *Geophilus proximus* was subdominant, this holding true for both components. It was also subdominant in the ash-alder forest, yet only in the epigeic component, but it was totally absent from the coniferous forest habitats.

Table III. Percentage contribution of individual species of Chilopoda in the material collected from the different habitats in Puszcza Białowieska, estimated from sifting/soil samples (ss) or Barber's pitfall traps (pt); + refers to species collected using other techniques.

No	Species	Habitat									
		1		2		3		4		5	
		ss	Pt	Ss	pt	ss	pt	ss	Pt	ss	pt
1	*Geophilus proximus*					**3.8**	+	**7.1**	+	**43.0**	28.8
2	*Pachymerium ferrugineum*)	**2.6**	+								
3	*Lithobius erythrocephalus*	+	+			+	+			+	+
4	*L. forficatus*	+	8.0	+	+	+	+	+	+	**8.9**	+
5	*L. lapidicola*	**5.1**	4.3	+	6.5	+	+	+	+	**1.3**	+
6	*L. mutabilis*	**10.3**	73.0	**6.3**	74.7	**17.1**	75.1	+	43.2		
7	*L. pelidnus*	**12.8**	1.6	**1.6**	10.3	**0.6**	4.0			**1.3**	+
8	*L. tenebrosus fennoscandius*	+	6.6	+	+	+	+	+	14.2	+	+
-	*Lithobius (L.)* sp.	**5.1**	4.7		8.6					**1.3**	
9	*L. curtipes*	**64.1**	1.8	**92.1**	+	**78.5**	21.0	**92.9**	42.6	**44.3**	71.2
10	*L. crassipes*					+	+				

The structure of dominance of the centipede communities in the five study habitats appears relatively similar when the material obtained from sifting or soil samples is analysed, i.e. in the edaphic component. For this component, the lowest values of Morisita's index of similarity of pairs of communities were 0.66–0.69. When the individual communities are clustered using Mountford's method, the bog alder forest centipede community stands out as the least similar to the others, being segregated only at a similarity value of 0.69 (Fig. 3A).

The structure of dominance of the centipede communities showed a greater diversity when material obtained by pitfall trapping was compared. The values of Morisita's index for pairs of communities ranged widely, from 0.01 to 0.98. A graph showing the similarity for the epigeic component of Chilopoda communities reveals that the highest similarity of dominance structure can be seen between communities from lithogenic habitats (fresh pine forest, pine-spruce mixed forest and linden-oak-hornbeam forest), the index values being at least 0.96 (Fig. 3B). The ash-alder forest communities displayed a similarity index of 0.74 as regards these three communities, while the bog alder forest Chilopoda communities were the least similar to all others, at 0.26.

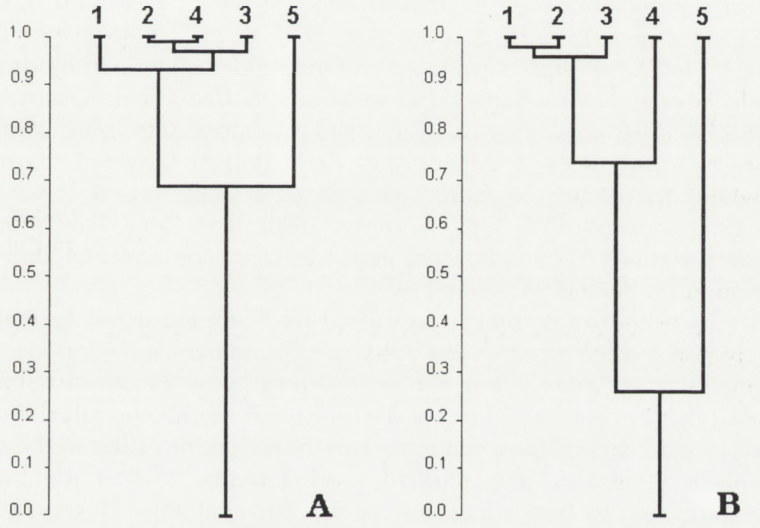


Fig. 3. Dendrograms of dominance structure similarity for the two components of Chilopoda communities: **A** – edaphic, **B** – epigeic.

SPECIES DIVERSITY

The linden-oak-hornbeam forest habitat supported the highest number of species of centipedes recorded and, consequently, the highest maximum diversity (H_{max}) of the Chilopoda community (Tab. IV). However, this did not entail a high actual diversity (H') or eveness (J) of the dominance distribution in either of the community components. The highest values of these two indices for the edaphic component were

obtained for both habitats characterized by extreme moisture conditions, i.e. the fresh pine forest and the bog alder forest. The epigeic component of the communities is subject to more complex relations. Here the values of the index of eveness, more suitable for comparisons, were the highest in the ash-alder flood plain forest, followed by the fresh pine forest, indicating most even (=flat) dominance structures.

Table IV. Comparison of various diversity parameters for Chilopoda communities in the five different habitats of Puszcza Białowieska.

	Habitat	1	2	3	4	5
	H_{max}	3.00	2.58	3.17	2.58	2.81
Edaphic part of the community	H′	1.48	0.46	0.89	0.37	1.35
	J	**0.49**	0.18	0.28	0.14	**0.48**
Epigeic part of the community	H′	1.28	0.91	0.97	1.45	0.87
	J	**0.43**	0.35	0.31	**0.56**	0.31

DISCUSSION

The study habitats of Puszcza Białowieska are not as abundant in centipedes as Central European beech forests (ALBERT 1982, FRÜND 1987, LEŚNIEWSKA 2000), where studies have yielded several dozen to several hundred centipede individuals per sq. m and usually a dozen or so species. Nonetheless, the linden-oak-hornbeam forests of Puszcza Białowieska are quite rich in centipedes (almost 20 ind./m²) compared to the same type of forest in the Wielkopolska (Great Polish) Lowland or the Mazovian region, where the same collecting techniques normally reveal lower community densities (KACZMAREK 1977, 1989, WYTWER 1990). The same holds for Chilopoda communities of pine forests in Puszcza Białowieska, as compared to their counterparts in other regions of Poland (WYTWER 1992).

The results of the study, which comprised five different forest habitats located in the same region, can be taken to show that the abundance of Chilopoda depends not only on moisture conditions, but also on soil fertility of the forest habitat. For it is unlikely that the thin *mull*-type litter of the linden-oak-hornbeam forest would provide better moisture conditions for Chilopoda than the thicker *mor* litter in the mixed forest. In each of the forest habitats studied, during periods when the litter is drier, centipedes are able to find adequately moist microhabitats. However, community abundance increases markedly along with rising fertility in lithogenic habitats: from the pine forest to the mixed pine-spruce forest to the linden-oak-hornbeam forest. Thus, it appears that a higher abundance may simply be due to the presence of a better nutritive base in a more fertile habitat, for example one with a more abundant mesofauna.

On the other hand, the abundance of centipedes in habitats where the soil is inundated by ground water and is subject to periodic floods, appears to be independent on soil fertility. In the ash-alder flood plain forest, where flood water can cover the entire area, even though the flooding is but short in duration, the abundance of Chilopoda is dramatically lower. Centipedes are also virtually absent from the swampy hollows of the bog alder forest, where water is usually present during most of the year, while in the

tussocks of the alder forest, usually situated above water level during flooding, Chilopoda are twice as abundant as on the ground surface in the linden-oak-hornbeam forest, a habitat supporting the highest number of Chilopoda species.

The above changes in abundance are also associated with reshaping the dominance structure of the Chilopoda communities, less so with change in species composition. In the study communities representing lithogenic forest habitats of Puszcza Białowieska, the lithobiomorphs *Lithobius curtipes* and *L. mutabilis* were absolute dominants. The latter species is typically epigeic, hence the most frequently captured by pitfall trapping. It is much less abundant, however, in the ash-alder flood plain forest and is absent from the bog alder forest, where Chilopoda are only found on small-sized tussocks separated from one another by stagnant water. *L. curtipes* remains abundant in this habitat, but equally abundant is the edaphic *Geophilus proximus*, a co-dominant in the bog alder forest community. This explains why, despite a high density of Chilopoda in the bog alder forest, not many centipedes were caught in pitfall traps.

The structural changes in the communities as revealed by diversity indices do not lend themselves to an unequivocal interpretation. The most even (flat) pattern of dominance structure observed in this study in communities from habitats characterised by extreme moisture conditions can be taken as a sign of intensified competition between species or may indicate a community well adapted to changing habitat conditions. However, while the even structure of dominance was observed for both edaphic (J=0.49) and epigeic (J=0.43) components in the fresh pine forest community of Chilopoda, in the ash-alder flood plain forest this was only seen in the epigeic component (J=0.56) while in the bog alder forest this was seen in the edaphic component of the Chilopoda community (J=0.48). The edaphic component of the ash-alder forest Chilopoda community and the epigeic component of the bog alder forest community have the same dominant species, *L. curtipes*, a widespread form (ZALESSKAJA 1978) which is among the few centipedes known to inhabit inundated areas (ZULKA 1992, ZERM 1997).

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