



## Mites (Oribatida and Mesostigmata) and vegetation as complementary bioindicators in peatlands



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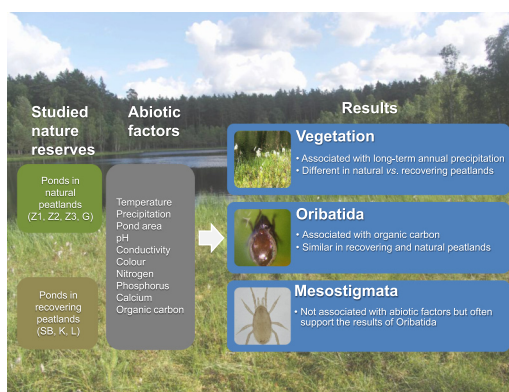
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### HIGHLIGHTS

- Ponds (dystrophic or not) were sampled in natural vs disturbed peatlands in Poland.
- Vegetation communities were significantly associated with long-term precipitation.
- Oribatida were associated with organic carbon in water, Mesostigmata with no factor.
- Vegetation differed between natural and disturbed peatlands, but not mites.
- Vegetation and mites are indicators of complimentary aspects of peatland condition.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Vegetation is widely used in the assessment of the quality of peatlands, while the invertebrate fauna of peatlands is relatively poorly studied. We compared the bioindicator values of vegetation with two arthropod groups widespread in peatlands, saprophagous Oribatida (Acariformes) and predatory Mesostigmata (Parasitiformes) mites. Samples were collected from ecotones at the edges of peatland ponds in Poland, including four in near-natural condition (i.e., peatlands unaffected by human activity) and three in previously disturbed but now recovering peatlands. A set of abiotic parameters was measured at each site: pond area, mean annual temperature, annual precipitation, and water parameters (pH, conductivity, colour, total nitrogen, phosphorus, calcium, and organic carbon). Overall, 63,635 specimens of Oribatida and 448 of Mesostigmata were recovered in the sampling. Species richness of Oribatida (56 species) was higher than that of flora (46) and Mesostigmata (15). Vegetation was significantly associated with annual precipitation in the years 1998–2007 which accounted for 29.1 % of the variation in vegetation communities. Oribatida variability was significantly associated with the content of organic carbon in water accounting for 32.4 % of variation. In contrast, variation in the Mesostigmata was not significantly associated with any of the abiotic parameters. Vegetation at ponds in previously disturbed and now recovering peatlands had higher bush cover than at near-

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natural ponds and the pond in the cutaway peat had lowest moss cover and the highest number of associate species (i.e., species with wide tolerance not characteristic of the certain community). Mite communities did not differ consistently between near-natural and recovering peatlands. *Sphagnum divinum* Flatberg et Hassel was recorded from Poland for the first time.

## 1. Introduction

Peatlands cover 4.23 million sq. km of the Earth's surface (i.e., approximately 3 % of the land area) and are found in almost every country, being especially abundant in cold and wet regions (Xu et al., 2018). In Poland they cover ca. 4.9 % of the country and are located mainly in the north (Tanneberger et al., 2017).

Peatlands provide many important ecosystem services, including carbon sequestration and storage, water regulation, and biodiversity conservation (Joosten et al., 2017). They are special and extreme habitats, nutrient-poor, acidic and water-saturated and they host highly specialized and unique flora and fauna, markedly contributing to biodiversity. The species diversity of peatlands is generally considered low (Rydin and Jeglum, 2013), but some groups, such as *Sphagnum* mosses (Laine et al., 2018) or oribatid mites (Mumladze et al., 2013) flourish there.

Peatlands are threatened by different human activities, in particular mining for peat, conversion to agricultural use, drainage (e.g., for forestry), improper forest management (e.g., plantation of tree species with high water requirements), pollution from nearby areas, but also by global warming (Dise, 2009). Therefore, it is important to monitor peat condition using multi-taxa bioindicators which reflect different aspects of the peatland's condition (Lehmitz et al., 2020).

Peatland vegetation is well known and is commonly used in the assessment of the condition of peats (e.g., Parish et al., 2008; Schumann and Joosten, 2008; González et al., 2013; Andersen et al., 2017; Monsalve et al., 2021). Assessment using vegetation is relatively quick and easy, and, although currently it allows only a general analysis, it can in some cases be applied using modern methods of remote sensing (e.g., McPartland et al., 2019). *Sphagnum* mosses are particularly valuable indicators of peatland conditions. For example, a list of *Sphagnum* species is good indicators of pH, Ca concentration, shading and water level (Rydin and Jeglum, 2013). However, vegetation is not sensitive enough to detect short-term changes in the water regime of peatlands (Lehmitz et al., 2020). *Sphagnum* mosses can withstand droughts for some time (Daniels and Eddy, 1990) and show a delayed reaction to changes in water regime. Also, it takes some time for the growth of shrubs and trees to react to changes in drainage (Talbot et al., 2010). In contrast, the invertebrate fauna is very sensitive to changes in their microhabitat and can indicate peatland degradation (Lehmitz, 2014; Seniczak et al., 2016). However, the identification of numerous and diverse invertebrates, e.g., Oribatida and Mesostigmata groups involves more complicated sampling and is very time-consuming.

Oribatida and Mesostigmata are small arachnids (on average ca. 0.3–0.8 mm in length), commonly called 'mites', although they belong to two separate superorders: Acariformes and Parasitiformes, respectively. They are primarily terrestrial animals, but some are adapted to wet habitats or even open water and can be found abundantly in peatlands (Schatz and Behan-Pelletier, 2008; Gerecke et al., 2009; Walter and Proctor, 2013). Oribatida are mostly saprophagous and can reach densities of 300,000 ind. m<sup>-2</sup> (Seniczak, 2011) and are the dominant and most diverse group of arthropods in peatlands (Rydin and Jeglum, 2013). They move very slowly horizontally, only few centimeters a day (Åström and Bengtsson, 2011; Lehmitz et al., 2012; Lehmitz and Maraun, 2016) what makes them particularly suitable bioindicators of their microhabitat conditions. Mesostigmata are mostly predators, and they are important regulators of abundances of

small invertebrates (e.g., Nematoda, Oribatida, Collembola) in peatlands (Walter and Proctor, 2013).

The invertebrate fauna of peatlands, including Oribatida and Mesostigmata, is poorly studied compared to vegetation. Oribatida are good predictors of moisture – the key factor affecting their communities in peatlands (Donaldson, 1996; Kuriki, 1998; Seniczak, 2011; Minor et al., 2019; Lehmitz et al., 2020). Less is known about Mesostigmata in peatlands, but for example in Ireland, where there are extensive peatlands, and the Mesostigmata fauna has been comparatively well studied, one quarter of mesostigmatid species known to occur nationally are found in peatlands (Wisdom et al., 2011; Bolger et al., 2018).

Given that the importance of Oribatida as bioindicators of water conditions in peatlands is already known (Markkula, 1981, 1982; Seniczak et al., 2016; Minor et al., 2019; Lehmitz et al., 2020), in this study we concentrated on a water-soaked peatland microhabitat – the shores of ponds. This ecotone (contact zone between floating mat and open water) is particularly valuable from an ecological point of view because it is known to host specific species of algae, crustaceans, rotifers (Hutorowicz, 2004), Oribatida (e.g., Seniczak et al., 2019) and Mesostigmata (e.g., Kaczmarek et al., 2008). As a rule, this ecotone is also much richer in plant species comparing to adjacent zones (Waldon, 2011).

Dystrophic lakes and ponds are important components of the landscapes in northern regions with a cool and humid climate, and are protected in the European Union (Anonymous, 2013). In Poland they occur mainly in the northern and western parts of the country. They are usually situated in forested areas, in the neighborhood of peatlands, and are surrounded by *Sphagnum* mats of different sizes; extending up to several hundred meters in places (Wilk-Woźniak et al., 2012; Drzymulska et al., 2013). Together with their unique flora and fauna, they constitute very interesting areas which warrant study and conservation. In the course of succession, these habitats disappear slowly, becoming overgrown by forest, but the natural processes are usually very slow. However, due to climate change, in North-eastern Poland, winter warming, short snow cover and predominance of dry springs (Drzymulska et al., 2013), and intensified negative human influences the successional processes may be accelerated (Pawlaczyk et al., 2005), so these habitats need special attention and protection. One of the main threats for dystrophic lakes and ponds is lowering of the water level and drying of the *Sphagnum* mat, which leads to changes in enrichment with humic and mineral substances and the most frequently to fast, most likely permanent changes in the water chemistry (Herbichowa, 2004): higher pH, higher calcium concentration, and lower organic carbon concentration (Drzymulska et al., 2013).

The aim of this paper is to characterize and compare Oribatida and Mesostigmata mites and plant communities in peatlands under different peatland conditions, varying from near natural conditions, where they are comparatively unaffected by human activities, to severely impacted. We also aim to compare the bioindicator values of the groups studied.

Considering previous studies in peatlands (Kaczmarek et al., 2008; Seniczak, 2011; Seniczak et al., 2016; Lehmitz et al., 2020) we hypothesized that (i) Oribatida, Mesostigmata, and vegetation would respond in different ways to the environmental factors in peatland ponds thus being complimentary bioindicators, (ii) ponds in near-natural peatlands would host abundant oribatid fauna highly dominated by specialists and few Mesostigmata represented by aquatic species, and (iii) disturbed peatlands would have more diverse oribatid and mesostigmatid fauna comparing to natural peatlands, dominated by species with wider ecological tolerance.



## 2. Material and methods

### 2.1. Study sites

Study sites were located in peatland nature reserves in Warmia and Masuria province in North-eastern Poland (Fig. 1). Samples were collected from the edges of seven ponds: Zakręt 1 (Z1), Zakręt 2 (Z2), Zakręt 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L). They differed in their climatic conditions, size, water parameters, floristic composition and degree of human influence (Table 1). According to the documentation about the reserves, peatlands Z1, Z2, Z3 and G were in a near-natural state (i.e., unaffected by human activity). Peatlands K and L were drained at the end of nineteenth century using drainage ditches but since 1958 have been legally protected and ditches became naturally silted and overgrown (pers. comm. from forest division Jamy, 2022). The peatland SB had been destroyed by peat exploitation, and since 1993 has been protected (Nowicka, 2014). On the last sampling site, the samples were collected from the edge of a pond in cutaway peat. Drainage has rapidly reduced the sizes of ponds K and L; the area of K has been reduced by 0.26 ha over 30 years (Czerwiński and Jankowski, 1991), and L has nearly disappeared in the course of succession (Fig. 1). Świńskie Bagno, although it is a natural reserve, is still threatened by nearby agriculture (e.g., chemicals) and synanthropes (Wróbel and Kuczora, 1998). The detail characteristics of the ponds are presented in Table 1.

### 2.2. Water analyses

For the water analyses, 3 l of water were taken from each pond in autumn 2007. Water was analyzed in the authorized Laboratory of Environmental Protection (Naftobazy Baza Paliw No. 2) in Nowa Wieś Wielka. The analyses followed the standard protocols of analytical manual and

they included: pH, conductivity, colour, total nitrogen, total phosphorus, calcium, and total organic carbon. The test for pH was carried out with pH meter according to the standard protocol (PN-90/C-045400/01) and electrical conductivity was measured using an electrical conductivity meter (PN-EN 27888:1999). The determination of water colour was done by visual comparison method, using platinum-cobalt scale (PN-EN ISO 7887:2002). Total phosphorus content was measured with spectrophotometric method with ammonium molybdate (PN-EN ISO 6878:2006), total nitrogen was measured using oxidative digestion with peroxodisulfate (PN-EN ISO 11905-1:2001), calcium was measured with EDTA titration method (PN-ISO 6059:1999) and the total organic carbon (TOC) was measured by infrared (IR) spectroscopy (PN-EN 1484:1999). All measurements were carried out at 20 °C, the measured parameters are given in Table 1.

### 2.3. Vegetation analyses

A list of plant species was prepared for the shore of each pond, each on the area of 25 m<sup>2</sup> (5 m × 5 m). Vascular plant cover, moss cover and bush cover were determined. The abundance of species at each site was assessed using an extended scale of Braun-Blanquet (1964), modified by Barkman et al. (1964). For the statistical analyses the Braun-Blanquet scale was transformed to 9-level scale according to van der Maarel (1979). The names of species of vascular plants follow Mirek et al. (2002), while those of mosses follow Ochyra et al. (2003) and Hassel et al. (2018).

### 2.4. Mite analyses

Samples were collected from *Sphagnum* mosses from the edges of the ponds in the autumn 2007. Ten samples, each 100 cm<sup>2</sup> in area and 5 cm in depth, were collected from each pond at distances of ca 1 m from one another. The arthropods were extracted using Tullgren funnels for 14 days

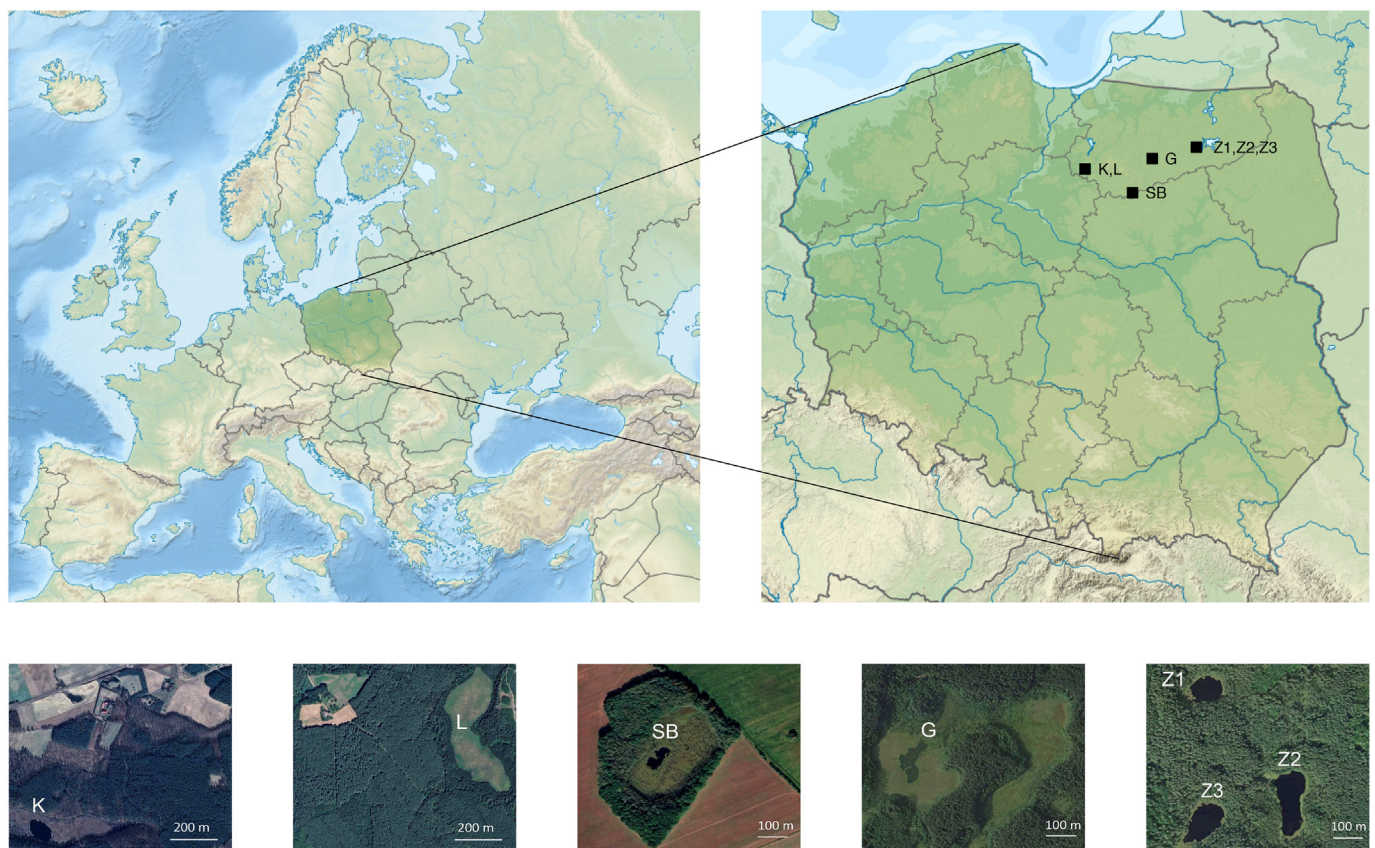


Fig. 1. Locations of ponds studied in North-eastern Poland: Zakręt 1 (Z1), Zakręt 2 (Z2), Zakręt 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L) (modified from <https://commons.wikimedia.org> and <https://www.google.com/maps>).

**Table 1**

Characteristics of ponds in peatlands in North-eastern Poland: Zakrę 1 (Z1), Zakrę 2 (Z2), Zakrę 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L); abbreviations refer to characteristics presented in RDA analyses.

Characteristics	Abbreviation	Z1	Z2	Z3	G	SB	K	L
Locality		Zakrę	Zakrę	Zakrę	Galwica	Świńskie Bagno	Kociołek	Łabędź
Coordinates		53.688, 21.410	53.685, 21.415	53.684, 21.411	53.496, 20.830	53.224, 20.379	53.492, 19.408	53.497, 19.434
Height above sea level (m)		155	134	138	126	178	97	92
Area of the reserve (ha)		105.9	105.9	105.9	94.6	15.9	7.2	18.7
Date of establishing the reserve		30.04.1957	30.04.1957	30.04.1957	04.02.1958	31.12.1993	04.02.1958	04.02.1958
Area of the pond (ha)	PondArea	0.70	1.66	1.13	0.60	0.50	0.90	0.01
Human disturbance		No	No	No	No	Peat exploitation	Drainage ditches	Drainage ditches
Climate								
Mean long-term annual temperature (°C) <sup>a</sup>		6.8	6.8	6.8	6.7	6.8	7.3	7.3
Long-term annual precipitation (mm) <sup>a</sup>		600.0	600.0	600.0	580.0	500.0	625.0	625.0
Mean annual temperature in 1998–2007 (°C) <sup>a</sup>		8.0	8.0	8.0	7.6	8.2	8.1	8.1
Annual precipitation, in 1998–2007 (mm) <sup>a</sup>	AnnPrec	671.9	671.9	671.9	616.7	562.5	598.5	598.5
Mean annual temperature in 2007 (°C) <sup>a</sup>		8.6	8.6	8.6	8.2	8.8	8.6	8.6
Annual precipitation in 2007 (mm) <sup>a</sup>		698.7	698.7	698.7	593.2	561.0	664.1	664.1
Physicochemical parameters of water								
pH	pH	4.6	4.6	6.2	6.7	4.6	6.8	4.6
Conductivity (µS/cm)		21	28	11	93	35	13	37
Colour (mgPt/dm <sup>3</sup> )		80	90	40	40	80	30	130
Total nitrogen (mgN/L)		<1	6	<1	9	8	25	112
Total phosphorus (mgP/L)		<0.5	0.73	<0.5	<0.5	<0.5	<0.5	1.55
Calcium (mgCa/L)		1.5	2.1	4.3	7.5	0.9	5.1	1.2
Total organic carbon (mgC/L)	TOC	24	38	16	22	73	14	99
Vegetation characteristics (per 25 m <sup>2</sup> )								
Bush cover b (%)		5	5	5	1	15	20	10
Vascular plant cover c (%)		30	70	70	70	40	60	60
Moss cover d (%)		100	100	90	100	70	100	100
Number of species		18	20	23	9	17	23	17
Dominant <i>Sphagnum</i> subgenus		<i>Sphagnum</i>	<i>Cuspidata</i>	<i>Sphagnum</i>	<i>Cuspidata</i>	<i>Cuspidata</i>	<i>Cuspidata</i>	<i>Cuspidata</i>
Some characteristics of arthropods								
Number of species of Oribatida		35	23	29	38	21	30	27
Number of species of Mesostigmata		8	1	5	8	2	8	3
Shannon index of Oribatida		-2.368	-0.966	-1.676	-2.119	-1.104	-2.232	-1.786
Shannon index of Mesostigmata		-1.629	0.000	-1.376	-1.626	-0.045	-1.176	-0.777

<sup>a</sup> After Nowicka (2014).

into 70 % ethanol and Oribatida and Mesostigmata were sorted out from the samples under stereomicroscope. Oribatida were mounted on slides in lactic acid and adult specimens were identified using the keys of Ghiljarov and Krivolutskij (1975), Pérez-Íñigo (1993, 1997) and Weigmann (2006), while juveniles were identified based on publications listed in Norton and Ermilov (2014) and Seniczak et al. (2018). The nomenclature of oribatid species follows Schatz (2020) and Schatz et al. (2021) and partly Norton and Ermilov (2014), Subías (2004, 2021) and Weigmann (2006). The data on Oribatida from pond Z1 were previously used in publications, but analyzed from a different perspective (this pond was named pond 'Z' in Seniczak et al., 2016 and 'Zakrę' in Seniczak et al., 2019).

Mesostigmata mites were either prepared as semi-permanent (using lactic acid) or permanent (using Hoyers medium) microslides. Adult and juvenile specimens were identified based on Karg (1993), Mašán (2001), Mašán and Fend'a (2004) and Gwiazdowicz (2007). The taxonomic classification and nomenclature of mesostigmatid species follows Lindquist et al. (2009). Full names of species are given in Appendix 2; abbreviations are used in figures. The arrangement of genera within families and the arrangement of species within genera are alphabetical.

## 2.5. Statistical analyses

For the analyses the abundance of adults and juveniles of a particular species were pooled. The oribatid and mesostigmatid communities were characterized by abundance ( $A$ ; ind./500 cm<sup>3</sup>), species richness ( $S$ , number of species in pond) and the Shannon ( $H'$ ) diversity index (Odum, 1982). The basic statistical descriptors were the mean values and standard deviation. Normality of the distribution was tested with Kolmogorov-Smirnov test, while equality of variance in different samples with Levene test. The assumption of normality or equality of variance was not met, so the non-parametric Kruskal-Wallis test by ranks was used, and in case of significant

differences between medians, a multiple comparison test between mean ranks was applied. Spearman rank order correlations coefficient was calculated between number of plant species, Oribatida and Mesostigmata species. The significance of Shannon diversity index among the ponds was tested with Kruskal-Wallis test. The level of significance for all statistical tests was accepted at  $\alpha = 0.05$ . These calculations were carried out with STATISTICAL2.5 software.

PCA analysis was carried out on  $\log(n+1)$  transformed abundances of each species in each of the 70 subsamples collected. Redundancy analysis (RDA) with forward selection was used to examine the relationships between plants, Oribatida and Mesostigmata and the environmental factors measured. The sums of the ten subsamples of each species of mite from each pond were used in these analyses. These analyses were carried out using CANOCO for Windows (version 5) (Ter Braak and Šmilauer, 2012). The environmental variables used were water colour (values 30, 40, 80, 90, and 130 mgPt/dm<sup>3</sup>), pond area (ha), pH, conductivity, N, P, Ca, TOC, mean annual temperature and annual precipitation in 1998–2007 and in the year of sampling (2007).

Procrustes analysis was used to investigate the degree of concordance between the patterns of variation of plants, Oribatida and Mesostigmata. The input to the analysis were the scores for the sites on the first four principal components of untransformed plant data and  $\log(n+1)$  transformed mite species abundances. Procrustes analysis was performed using the Procrustes and Protest functions in the 'Vegan' package (Oksanen et al., 2012) of the R software v.4.0.0 (R Core Team, 2020).

## 3. Results

### 3.1. Abiotic factors of studied ponds

The abiotic features of each pond are given in Table 1. In four ponds (Z1, Z2, SB and L) the water parameters were characteristic of dystrophic water

bodies (high content of organic carbon, high value of water colour, low pH, low content of calcium); pond L was very small (more advanced stage of succession) and had highest values of organic carbon and water colour, and in addition higher content of nitrogen and phosphorus. The other three ponds (Z3, G and K) differed from typical dystrophic ponds: they had higher pH and calcium content and lower colour value and content of organic carbon.

3.2. Vegetation

In total, 46 plant species were recorded. Species characteristic of bogs from class *Oxycocco-Sphagneteta* and species characteristic of fens and transitional mires from class *Scheuchzerio-Caricetea fuscae* dominated. The plant richness varied from nine species in pond G to 23 species recorded at ponds Z3 and K (Table 1, Appendix 1). Only one species, *Betula pubescens* Ehrh. was found at all ponds. The number of plant species was highly correlated with water conductivity ( $r_s = -0.95$ ) and with pond area ( $r_s = 0.76$ ).

RDA showed that annual precipitation (1998–2007) was the main environmental variable associated with the variation in the plant community compositions in the different ponds accounting for 29.1 % of the variation (Pseudo  $F = 2.1, p = 0.046$ ) (Fig. 2). In this case ponds Z1, Z2 and Z3, which are located further east than the others and relatively close together and have similar rainfall, are separated from the other four ponds. The shores of ponds K and L had the highest cover of small trees in the bush layer. These included Scots pine (*Pinus sylvestris* L.) and downy birch (*Betula pubescens*) which were also abundant at SB. The bush cover was also highest (10–20 %) at these three ponds (Appendix 1). The lowest moss cover (70 %) and the highest number of associate species (i.e., species occurring in a plant community but not characteristic of it, Matuszkiewicz, 2006) were observed at pond SB.

*Sphagnum divinum* Flatberg et Hassel was recorded for the first time from Poland. Previously it was erroneously considered *S. magellanicum* Brid., which as shown by Hassel et al. (2018), does not occur in Europe.

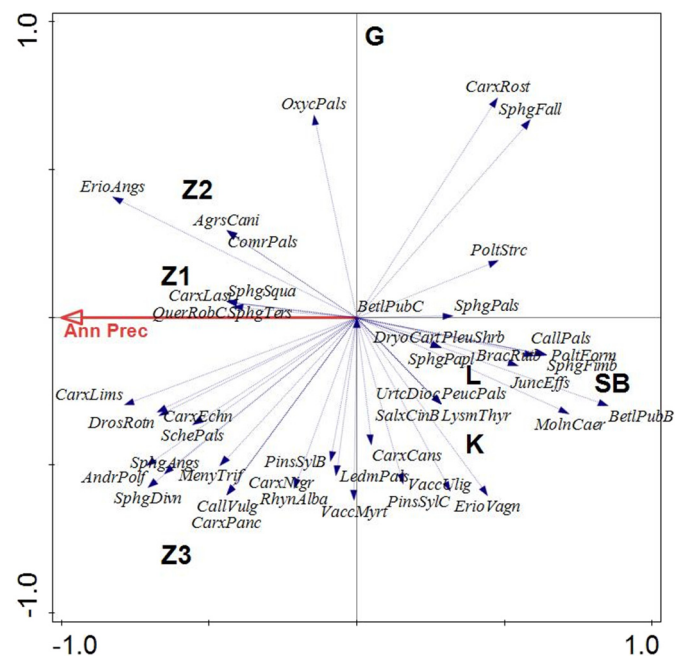


Fig. 2. Redundancy analysis (RDA) of the plant communities at ponds in peatlands in North-eastern Poland and the abiotic parameters (red); Zakrę 1 (Z1), Zakrę 2 (Z2), Zakrę 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L); Annual Precipitation (AnnPrec) accounts for 29.10 % of the variation; see Table 1 and Appendix 1 for abbreviations.

3.3. Oribatida

In total, 63,635 specimens of Oribatida, represented by 56 species from 25 families, were found at the ponds studied. The number of species ranged from 21 at pond SB to 38 at pond G (Table 1, Appendix 2). The number of Oribatida species was highly correlated with the number of Mesostigmata species ( $r_s = 0.93$ ) and with the mean annual temperature in the years 1998–2007 and in 2007 (in both cases the coefficient was  $r_s = -0.80$ ). The abundance of Oribatida differed significantly between the ponds studied ( $H = 26.948, p = 0.0001$ ). It was highest at pond L, followed by SB, and lowest at Z3 (Fig. 3). There were significant differences in Shannon diversity index among the ponds ( $H = 35.63, p < 0.0001$ ), and the values were higher in ponds Z1, G and K. The dominant species of Oribatida differed among the ponds (Fig. 4) and PCA showed a high degree of consistency in the composition of the subsamples for each pond (Fig. 5). Ponds L, SB and Z2 were most similar to each other (Fig. 4) having a predominance of the aquatic species [*Limnozetes* spp., *Tyrphonothrus* spp., and *Trhypochthoniellus longisetus* (Berlese)] (Fig. 4). Aquatic genera of Oribatida were less abundant in the other ponds where a generalist species, *Oppiella nova* (Oudemans), and species with lower dominance ( $<1$ ) represented large proportions of the oribatid communities.

Redundancy analysis using forward selection of environmental variables showed that oribatid community structure was significantly associated with concentrations of organic carbon (Pseudo- $F = 2.4, p = 0.024$ ) which accounted for 32.4 % of the variation while pond area was the next most important variable accounting for 21.3 % of the variation but this was not significant at the 0.05 level (Pseudo- $F = 1.8, p = 0.084$ ) (Fig. 6).

Organic carbon content was highest in ponds SB, L, and Z2 (to a lesser extent) where *Limnozetes foveolatus* Willmann was most abundant (Fig. 4). Other species that distinguished these ponds were *Hydrozetes lacustris* (Michael), *H. octosetosus* Willmann, and *Trhypochthoniellus longisetus* and *Tyrphonothrus foveolatus* (Willmann). Ponds with more diverse oribatid

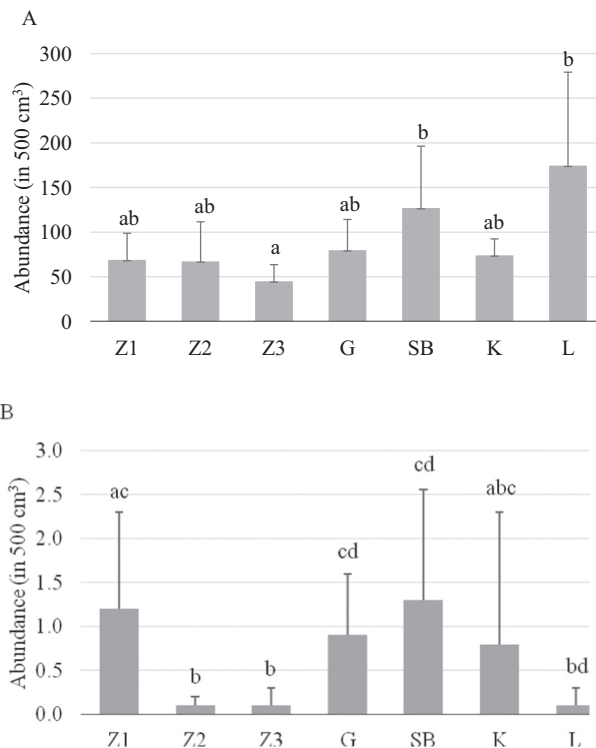
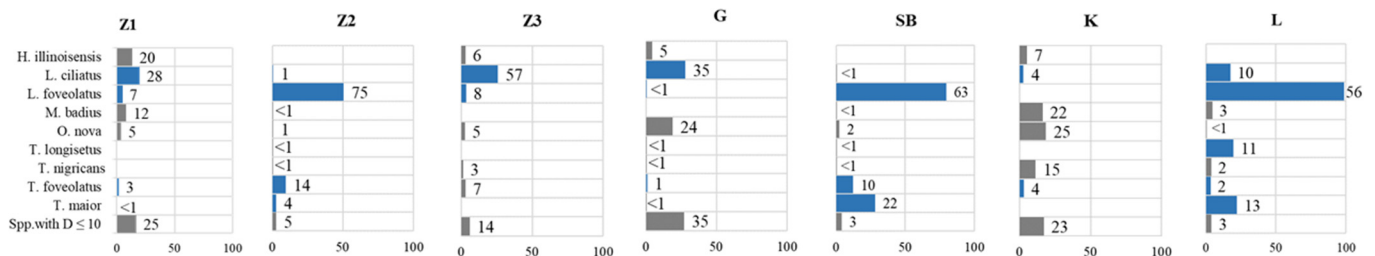


Fig. 3. Average abundance of mites (bars) with standard deviation (whiskers) at ponds in peatlands in North-eastern Poland: Zakrę 1 (Z1), Zakrę 2 (Z2), Zakrę 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L); A – Oribatida, B – Mesostigmata; different letters indicate significant differences at  $p < 0.05$ .



A



B

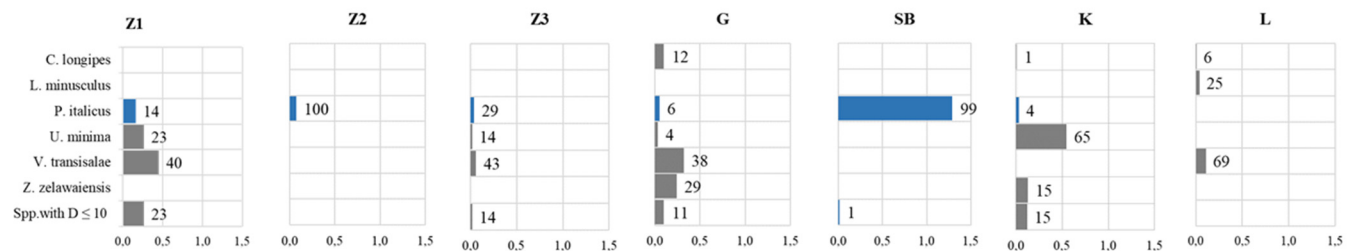


Fig. 4. Average abundance (in 500 cm<sup>3</sup>) of species at ponds in peatlands in North-eastern Poland: Zakrę 1 (Z1), Zakrę 2 (Z2), Zakrę 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L); A – Oribatida, B – Mesostigmata; letters next to bars indicate the dominance of species in communities of Oribatida and Mesostigmata; aquatic species are marked in blue.

communities (K, Z1, Z3, G) were characterized by a number of species different from the species mentioned above (Fig. 6), with more abundant *Hoplophthiracarus illinoisensis* (Ewing), *Oppliella nova*, *Mainothrus badius* (Berlese), and *Trhypochthonius nigricans* Willmann (Fig. 4).

### 3.4. Mesostigmata

Overall, 448 specimens of Mesostigmata represented by 15 species belonging to seven families were found. The number of species varied between ponds, from 1 species found at Z2 up to 8 species at ponds Z1, G and K (Table 1, Appendix 2). The number of Mesostigmata species was only correlated with the number of Oribatida species ( $r_s = 0.93$ ). Mesostigmata were most abundant at SB, and occurred abundantly at Z1, G, and K, while at other ponds (Z2, Z3 and L) their abundance was significantly lower ( $H = 34.530, p = 0.0000$ ). Species diversity of Mesostigmata

was equally high at Z1 and G, and lowest in Z2 (Fig. 3). There were significant differences in Shannon diversity index among the ponds ( $H = 28.95, p < 0.0001$ ), and higher values were in ponds Z1, G and K. In contrast to the oribatids, PCA analysis suggests that the Mesostigmata communities were not different between ponds and the samples from the ponds overlap extensively (Fig. 7). Pond K, where *Uroobovella minima* (C.L. Koch) was most abundant (Fig. 4), was most different from other ponds (Fig. 7). Pond SB and pond Z2, were somewhat different from other ponds, and were highly dominated by the aquatic species *Platyseius italicus* (Berlese). In turn ponds Z1, Z3, G and L were characterized by a high relative abundance of *Veigaia transisalae* (Oudemans). None of the environmental variables were significantly associated with variation in the Mesostigmata communities. Calcium concentration was most important in the RDA but, although associated with 26.5 % of the variation, did not show significant association with the community structure (Pseudo-F 1.8,  $p = 0.1$ ) (Fig. 8).

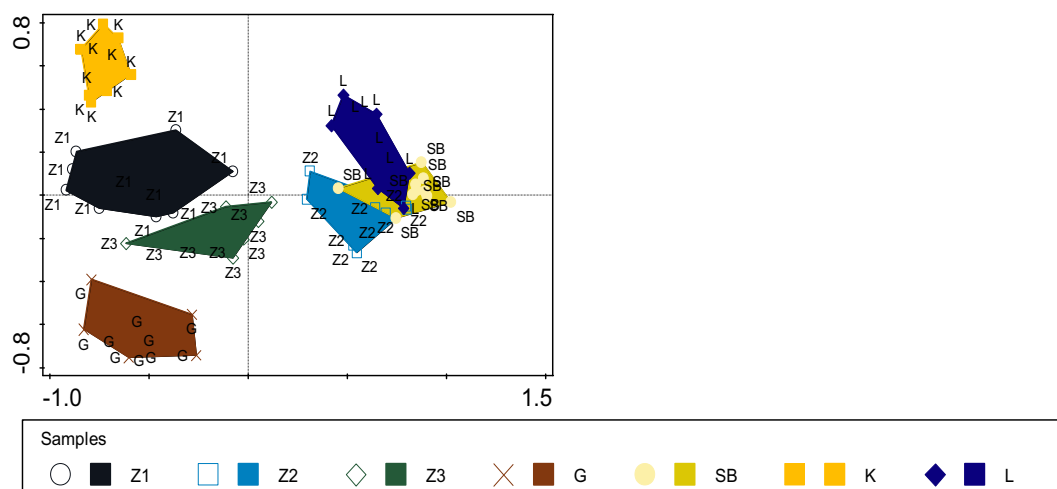


Fig. 5. PCA of oribatid communities in the subsamples grouped by pond: Zakrę 1 (Z1), Zakrę 2 (Z2), Zakrę 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L); species abundances were log transformed. Axis 1 accounts for 40.16 % of the variation and Axis 2 13.24 %.

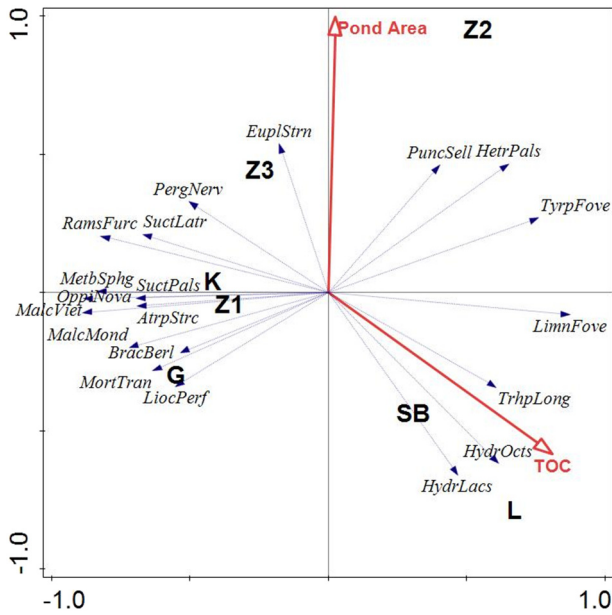


Fig. 6. Redundancy analysis (RDA) using forward selection of log transformed species totals of Oribatida (represented by 20 best fitted species) at ponds in peatlands in North-eastern Poland and the abiotic parameters (red); total organic carbon (TOC) accounts for 32.40 % of variation and pond area for 21.30 %; see Table 1 and Appendix 2 for abbreviations.

3.5. Comparisons between the responses of the different taxa

Procrustes analysis was used to determine whether the patterns of variation of the plants and the two taxa of mites were similar. This showed that there was no correlation between the variation between the plant communities in the ponds and either taxon of mite (in Procrustes) rotations for plants with oribatids (correlation = 0.69,  $p = 0.77$ ) for plants with Mesostigmata (correlation = 0.765,  $p = 0.397$ ), (Fig. 9 a,b). However, although the correlation was not significant, the patterns of variation between the two mite taxa showed greater similarity (correlation = 0.8611,  $p = 0.068$ ) (Fig. 9c).

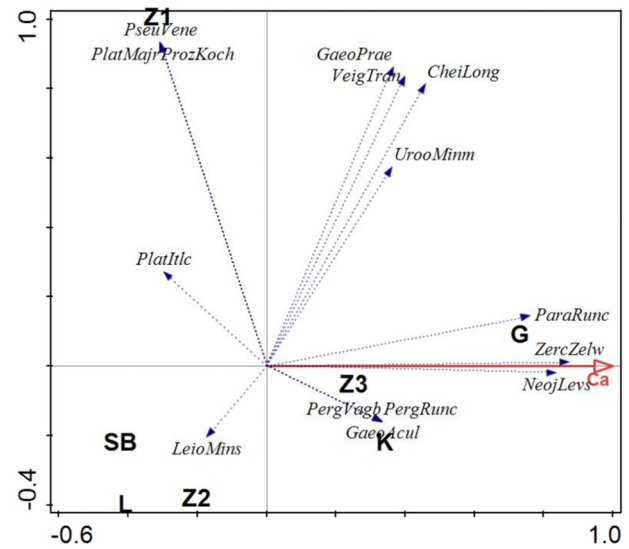


Fig. 8. Redundancy analysis (RDA) of log transformed species totals of Mesostigmata at ponds in peatlands in North-eastern Poland and the abiotic parameters (red); see Table 1 and Appendix 2 for abbreviations.

4. Discussion and conclusions

Procrustes analysis shows that the patterns of variation of the three taxa studied are different, and the taxa respond in different ways to the environmental factors as indicated by RDA. They thus provide complimentary information about the development and environmental conditions in peatland ponds what supports our first hypothesis. The vegetation in the ponds was significantly associated with annual precipitation in the years 1998–2007 (accounting for 29.1 % of their variation), while Oribatida communities were significantly associated with the content of organic carbon in water (it accounted for 32.4 % of variation of this group), and none of the abiotic properties measured were significantly associated with the variation in Mesostigmata.

Precipitation is an important factor for plant communities and for the functioning of peatland (Radu and Duval, 2018). Increasing global

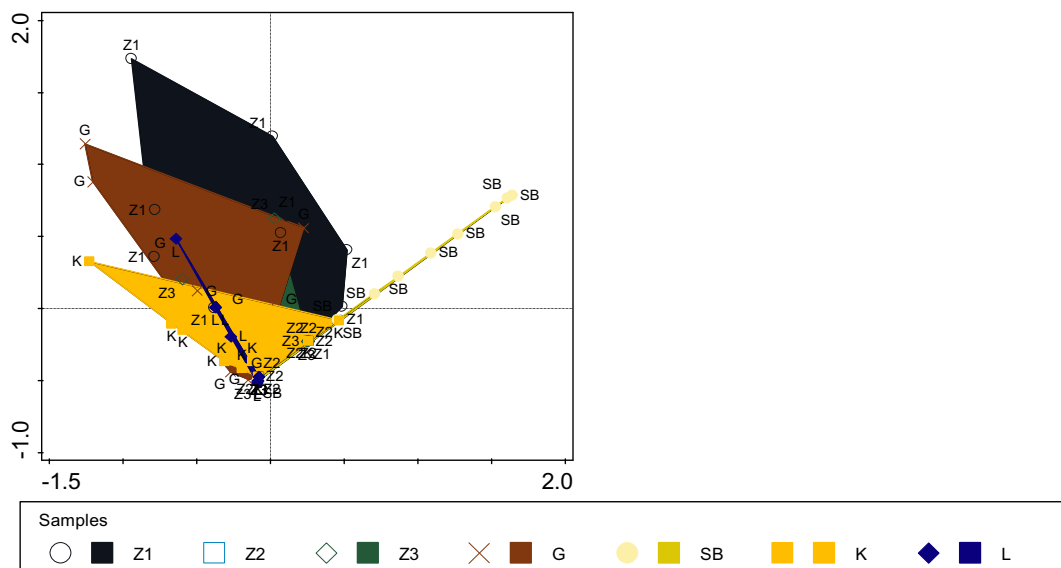


Fig. 7. PCA of Mesostigmata communities in the subsamples grouped by pond: Zakrę1 (Z1), Zakrę2 (Z2), Zakrę3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łąbędź (L). Species abundances were log transformed. Axis 1 accounts for 33.72 % of the variation and Axis 2 25.00 %.

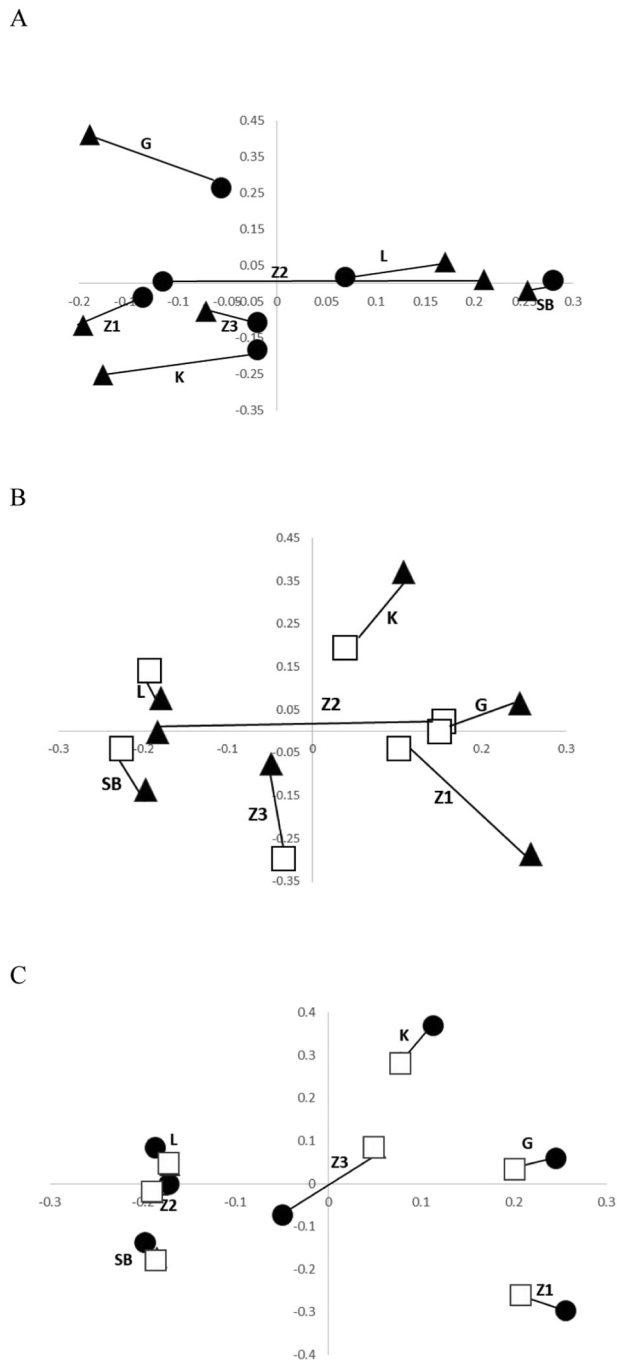


Fig. 9. Procrustean superimposition plot of the PCA ordinations based on plants (triangles), Oribatida (circles) and Mesostigmata (squares) at each site. A – plants and Oribatida, B – plants and Mesostigmata and C – Oribatida and Mesostigmata.

temperatures are driving greater evapotranspiration rates that leads to more intense rainfalls (Westra et al., 2014). Although peatlands are on the one hand dependent on precipitation, increased rainfall may lead to changes in the composition of plant communities and vascular plant encroachment which could have large consequences for their carbon-sink function (Radu and Duval, 2018; Barel et al., 2021). In the present study the vegetation communities at three ponds (Z1, Z2, and Z3) located in Zakręć reserve, where annual precipitation in the years 1998–2007 was highest (672 mm) are well separated from the other ponds studied (with precipitation varying between 562 and 617 mm). It is also evident that in Zakręć reserve the precipitation in the years 1998–2007 increased most comparing to the long-term annual precipitation before this period

(Table 1); in other ponds the increase was less distinct, or the decrease of rainfall was observed.

In addition, vegetation in previously disturbed peatlands K, L and SB clearly differed from near-natural ones in having greater bush cover and the presence of small trees (common pine and downy birch). The appearance of trees indicates changes in the humidity conditions as a delayed effect after drainage of these peatlands in the past. Lowering of the water level in drained peatland favours the establishment and growth of trees, such as pine and birch, and decreases *Sphagnum* cover (Gunnarsson et al., 2002; Murphy et al., 2009; Talbot et al., 2010). At the same time, encroaching trees take up more and more water through their root systems, which contributes to further drying out of the peatland. Often, as part of the active protection of peatlands, it is recommended that trees are removed (Czerepko et al., 2018). However, only persistent changes in the depth of the water table resulted in obvious changes in vegetation, while no observable effects of drainage were observed with transient lowering of the water table (Talbot et al., 2010) or during short-term experimental drought (Andrews et al., 2021). The effects of long-term (10 yrs) drought were different on different plant groups: ericaceous shrubs such as *Calluna vulgaris* (L.) Hull were affected by it, while *Sphagnum* was unaffected (Andrews et al., 2021). On the other hand some studies show that a short-term water table change may still impact the vegetation and carbon dynamics of peatland (Morris et al., 2013; Planas-Clarke et al., 2020).

Due to the specific habitat conditions (e.g., low pH), well-preserved peatlands belong to floristically poor ecosystems, where there are specific plant species with narrow ecological preferences (Rydin and Jeglum, 2013). The encroachment of ecologically alien species, i.e., species of other habitats, may indicate disturbances. Such a situation can be observed at pond SB, where the lowest moss cover (70 %) and the largest number of associate species were recorded. Peatland SB was destroyed in the past by peat exploitation and despite it is protected since 1993 it is surrounded only by a narrow forest buffer zone and is located in the vicinity of farmland (Fig. 1). The presence of alien plant species at this pond, likely from the nearby agricultural ecosystems is an example of the negative effect of the close proximity of agriculture. Opinions vary on the effect of water chemistry on plants. Extensive studies in several countries showed vegetation to be less correlated with hydrochemical variables and water table than were testate amoebae for example (Mitchell et al., 2000; Lamentowicz et al., 2010). In the current study the number of plant species was correlated with water conductivity and with pond area but the variability of plant communities was not associated significantly with any of the other water chemistries assessed. This lack of correlation between water chemistry and vegetation has been explained by the fact that in many cases water parameters were measured close to the surface while for deep-rooted plants such as *Carex* spp. and *Eriophorum* spp. the chemistry of water near the ground water table may be more important (Mitchell et al., 2000). Some other authors observed however the strong linkage among vegetation and water chemistry in peatlands (Arsenault et al., 2019).

For Oribatida, the most important factor was the concentration of organic carbon in water. Higher concentration of organic carbon, accompanied by brownish colour of water and acidic pH occurred in ponds Z1, Z2, SB and L. These features are characteristic of dystrophic water bodies and have ecological consequences resulting in lower species diversity (Kostrzewska-Szlakowska and Jasser, 2011). Indeed, most ponds mentioned above, except Z1, were characterized by low species richness and low diversity of Oribatida ( $S = 21\text{--}27$ ,  $H_s = 0.97\text{--}1.46$ , respectively).

At the dystrophic ponds the aquatic Oribatida highly dominated (making 92–85 % of this group) and the most abundant was *Limnozetes foveolatus* (it made 56–75% of Oribatida) as seen at nine dystrophic ponds in natural bogs in northern Poland (Seniczak, 2011). This species seems to be restricted to dystrophic water bodies, as, for example, it was absent at oligotrophic (Seniczak et al., 2010) and mesotrophic ponds (Seniczak, 2011). In heavily degraded bogs that were not protected, and still disturbed to some extent by peat exploitation, *L. foveolatus* occurred in low densities (Seniczak et al., 2016), while in present study it occurred abundantly at previously degraded but now recovering peatlands. This indicates that



Oribatida communities can recover relatively quickly after peatland's disturbance, as long as water parameters resemble those of dystrophic water bodies.

As with all *Limnozetes* species, *L. foveolatus* is truly aquatic, i.e., with reproduction and all stages of life cycle occurring in water or at its margins (Schatz and Behan-Pelletier, 2008). It lives in dripping-wet habitats (Behan-Pelletier and Bisset, 1994; Donaldson, 1996; Seniczak, 2011) but seems to have narrower ecological tolerance than its congener, *L. ciliatus* (Schränk). For example, it reacts quickly to seasonal changes, and at pond Z1 it was only dominant among the Oribatida in spring, while in summer and autumn it was less abundant and in winter was nearly absent (Seniczak et al., 2019). By contrast, the abundance of *L. ciliatus* remained relatively constant throughout the year, although it was much less abundant in winter (Seniczak et al., 2019). We speculate that changes in the abundance of *L. foveolatus* might be driven by the food resources. Many peatland Oribatida feed on the bacterial biofilm on *Sphagnum* mosses (Lehmitz and Maraun, 2016). In dystrophic ponds bacterial biomass is related to the concentration of organic matter, expressed in dissolved organic carbon units (Kostrzewska-Szlakowska and Jasser, 2011), which may change seasonally (Arsenault et al., 2019) further affecting bacteriophagous Oribatida. In turn, species with wider spectrum of food types will not depend so much on the season. *Limnozetes ciliatus* seems to feed on different food types and the analyses of its gut content documented presence of fungal hyphae, conifer pollen and even arthropod fragments (Behan-Pelletier and Hill, 1983). It cannot be excluded that the mite communities were also affected by some transient water scarcity, that was not noticeable during sampling, since all samples were collected from water-soaked habitat at the pond edge. According to Lehmitz et al. (2020) oribatid mites are the best predictors of moisture in peatlands, better than spiders or vegetation.

Mesostigmata had far less bioindicator value as was observed from a forest pond in Norway (Seniczak et al., 2021). However, as with Oribatida, Mesostigmata had low diversity in dystrophic ponds ( $S = 1-3$ ,  $H_s = 0.00-0.78$ ) and at most of these ponds the aquatic species, *Platyseius italicus* was most abundant. This species is not restricted to peatlands and is found in other submerged habitats like streams, reservoirs, and fens (Bolger et al., 2018). In turn, *P. major* (Halbert) is a typical mesostigmatid mite species found in various types of peatlands (Bregotova, 1977; Gwiazdowicz, 2007). However, it appeared quite sporadically in these ponds.

One dystrophic pond in near-natural peatland (Z2), hosted abundant oribatid fauna highly dominated by specialists and few Mesostigmata represented by aquatic species. However, quite surprisingly, at another dystrophic pond in the same peatland (Z1) the mite communities were different, so our second hypothesis was only partially supported. The mite communities in Z1 resembled those from ponds that were not typical dystrophic (Z3, G and K, which had higher pH and calcium content and lower colour value and content of organic carbon), i.e., the species diversity of Oribatida and Mesostigmata was higher, and a shift to species with wider ecological tolerance was observed. For example, among Oribatida, *Mainothrus badius* and *Oppiella nova* occurred abundantly, and among Mesostigmata, *Veigaia transisalae* dominated. *Mainothrus badius* is considered a peatland species (Weigmann et al., 2015), found in raised bogs, transitional mires and fens, but sometimes also occurs in other moist habitats like meadows and springs (Seniczak et al., 1998; Ermilov and Chistyakov, 2007; Schatz, 2020). Although it is not frequently reported (Olszanowski et al., 1996; Ermilov and Chistyakov, 2007; Weigmann et al., 2015), at peatland pond edges it is quite common (it was found at nine out of 16 investigated ponds, Seniczak, 2011). It has wider ecological tolerance and in seasonal studies at pond Z1 it was abundant in winter when it replaced aquatic species (Seniczak et al., 2020). *Oppiella nova* is a semicosmopolitan generalist (Weigmann, 2006; Schatz, 2020) and mesostigmatid *Veigaia transisalae* is known from different ecosystems, including bogs (Salmane and Brumelis, 2010). It is remarkable, that at pond Z1 the moss cover was dominated by *Sphagnum divinum* that represents subgenus *Sphagnum*, characterized by higher species diversity of Oribatida and higher participation of generalists (Minor et al., 2016; Seniczak et al., 2020). By contrast, at dystrophic ponds where *Sphagnum fallax* (subgenus *Cuspidata*) dominated mite

communities were abundant but less diverse, and dominated by peatland specialists [e.g., *Limnozetes foveolatus*, *Tyrphonostrus foveolatus*, *T. maior* (Berlese)] (Donaldson, 1996; Seniczak, 2011). Interestingly, a similar pattern has been also observed in microbial communities (Opelt et al., 2007; Bragina et al., 2012), which were more diverse in subgenus *Sphagnum* than in subgenus *Cuspidata*. Possibly more diverse food resources created by more diverse microbial communities attract richer oribatid communities. Present results confirm the importance of microhabitat created by *Sphagnum* to oribatid mites (Minor et al., 2016; Seniczak et al., 2020).

Oribatida and Mesostigmata of disturbed but now recovering peatlands only sometimes differed from near-natural peatlands, so, our third hypothesis that disturbed peatlands have more diverse oribatid and mesostigmatid fauna comparing to natural peatlands, was not universally supported. Water properties in pond L (drained peatland) and SB (pond in cutaway peat) were similar to those of natural dystrophic ponds, and contained similar Oribatida and also similar Mesostigmata in the case of SB, as occurred at natural ponds. Ponds in cutaway peat have considerable allochthonous input of humic substances what makes them similar to natural dystrophic water bodies (Kalinowska, 2000). As with Oribatida and Mesostigmata, phytoplankton in such ponds resembles that in natural, dystrophic lakes and ponds (Rychert et al., 2021). Only at pond K were Oribatida and Mesostigmata communities more diverse with a greater abundance of peatland species with wider tolerance (like *M. badius*) and generalists (like *O. nova*).

The taxa studied here have been shown to have complementary bioindicators value in the peatland assessment. Vegetation differed between ponds in peatlands unaffected by human activity and those in disturbed peatlands. By contrast, mites did not respond consistently to such changes. Oribatida, however, have been shown to be effective bioindicators reacting quickly to water conditions (Lehmitz et al., 2020), seasons (Seniczak et al., 2019), and microhabitat created by *Sphagnum* mosses (Minor et al., 2016; Seniczak et al., 2020), and this study shows that oribatid communities are significantly affected by the concentration of organic carbon in water – a key parameter and indicator of the proper condition and functioning of dystrophic lakes and ponds. Changes in this parameter mean that the water body loses its dystrophic character and are accompanied by different oribatid communities. The reaction of Mesostigmata is less pronounced, but often supports the results of Oribatida (e.g., with disturbance of dystrophic water body a shift to generalists is often observed in both groups).

#### CRediT authorship contribution statement

AS and SS planned the study, AS and SS identified Oribatida, JCI and TB carried out statistical analyses, DJG identified Mesostigmata, BWR identified vegetation, KIF contributed to identification of *Sphagnum*, AS and TB wrote the manuscript with support of all authors.

#### Data availability

Data will be made available on request.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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**Appendix 1. Plant communities at ponds in Poland: Zakrę 1 (Z1), Zakrę 2 (Z2), Zakrę 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L); † – associate species are listed under the table with the abbreviation of the name and of pond where they occurred; abbreviations of species for RDA analysis**

Species	Abbreviation	Z1	Z2	Z3	G	SB	K	L
Ch. <i>Oxycocco-Sphagneteta</i> Br.-Bl. et R. Tx. 1943 and * <i>Sphagnetalia magellanici</i> (Pawłowski et al.1928) Kästner et Floßner 1933								
* <i>Sphagnum divinum</i> Flatberg et Hassel	<i>SphgDivn</i>	3	2b	4			2b	2a
* <i>Eriophorum vaginatum</i> L.	<i>ErioVagn</i>	2 m	1	2 m		3	2 m	4
* <i>Andromeda polifolia</i> L.	<i>AndrPolf</i>	2a	2 m	2b			2a	
<i>Drosera rotundifolia</i> L.	<i>DrasRotn</i>	2 m	1	2 m	+		2 m	1
<i>Sphagnum fallax</i> (H.Klinggr.) H.Klinggr.	<i>SphgFall</i>	2b	3		5	4	4	3
* <i>Oxycoccus palustris</i> Pers.	<i>OxycPals</i>	2a	2a		3		2b	1
* <i>Polytrichum strictum</i> Brid.	<i>PoltStrc</i>				+		+	1
<i>Sphagnum papillosum</i> Lindb.	<i>SphgPapl</i>							2b
Ch. <i>Scheuchzeria-Caricetea fuscae</i> (Nordhagen 1936) R. Tx. 1937 and * <i>Rhynchosporion albae</i> W. Koch 1926								
* <i>Scheuchzeria palustris</i> L.	<i>SchePals</i>	2a	2 m	1			2 m	2 m
* <i>Carex limosa</i> L.	<i>CarxLims</i>	3	2 m	2 m			1	+
<i>Eriophorum angustifolium</i> Honck.	<i>ErioAngs</i>	1	2b	1	1			
<i>Carex rostrata</i> Stokes	<i>CarxRost</i>		1		4	2a		2 m
* <i>Rhynchospora alba</i> (L.) Vahl	<i>RhynAlba</i>		+	2 m			2a	
<i>Menyanthes trifoliata</i> L.	<i>MenyTrif</i>		1	2 m			1	
<i>Carex echinata</i> Murray	<i>CarxEchn</i>		1	2 m				
<i>Carex lasiocarpa</i> Ehrh.	<i>CarxLasi</i>	1	1				1	
<i>Sphagnum teres</i> (Schimp.) Ångstr.	<i>SphgTers</i>	2b						
<i>Carex canescens</i> L.	<i>CarxCans</i>	+		+		1		
<i>Agrostis canina</i> L.	<i>AgrsCani</i>		2 m					
<i>Carex panicea</i> L.	<i>CarxPanc</i>			1				
Ch. <i>Vaccinio-Piceetea</i> Br.-Bl. in Br.-Bl. et al. 1939								
<i>Pinus sylvestris</i> L. b	<i>PinsSylB</i>	+	+	1	r		2a	2 m
<i>Pinus sylvestris</i> L. c	<i>PinsSylC</i>		+	+		+	+	1
<i>Ledum palustre</i> L.	<i>LedmPals</i>	+		1		1		
<i>Vaccinium uliginosum</i> L.	<i>VaccUlig</i>			1		1		
<i>Vaccinium myrtillus</i> L.	<i>VaccMyrt</i>			1		+		
<i>Pleurozium schreberi</i> (Willd.) Mitten.	<i>PleuShrb</i>							1
Other species								
<i>Betula pubescens</i> Ehrh. b	<i>BetlPubB</i>					2 m	+	2 m
<i>Betula pubescens</i> Ehrh. c	<i>BetlPubC</i>	+	+	+	+	+	+	+
<i>Sphagnum palustre</i> L.	<i>SphgPals</i>			1	1	2 m		
<i>Sphagnum angustifolium</i> (C.E.O.Jensen ex Russow) C.E.O.Jensen	<i>SphgAngs</i>	1		2a				
<i>Calla palustris</i> L.	<i>CallPals</i>		+			2b	+	
<i>Sphagnum squarrosum</i> Crome	<i>SphgSqua</i>	2 m						
<i>Calluna vulgaris</i> (L.) Hull.	<i>CallVulg</i>			1				
<i>Sphagnum fimbriatum</i> Wilson	<i>SphgFimb</i>					1		
<i>Juncus effusus</i> L.	<i>JuncEfff</i>		+			+	+	+
<i>Molinia caerulea</i> (L.) Moench s.str.	<i>MolnCaer</i>					+	+	

†Ch. *Scheuchzeria-Caricetea fuscae* (Nordhagen 1936) R. Tx. 1937: *Carex nigra* Reichard – *CarxNigr* (Z3), *Comarum palustre* L. – *ComrPals* (Z3); Other associate species: *Quercus robur* L. c – *QuerRobC* (Z1), *Lysimachia thyrsiflora* L. – *LysmThyr* (K), *Peucedanum palustre* (L.) Moench – *PeucPals* (K), *Salix cinerea* L. b – *SalxCinB* (K), *Urtica dioica* L. – *UrtcDioc* (K), *Dryopteris carthusiana* (Vill.) H. P. Fuchs – *DryoCart* (L), *Brachythecium rutabulum* (Hedw.) Schimp. – *BracRutb* (SB), *Polytrichastrum formosum* (Hedw.) G.L. Smith – *PoltForm* (SB).

**Appendix 2. Oribatida and Mesostigmata at ponds in Poland: Zakrę 1 (Z1), Zakrę 2 (Z2), Zakrę 3 (Z3), Galwica (G), Świńskie Bagno (SB), Kociołek (K) and Łabędź (L); A – average abundance (thousand individuals per 500 cm<sup>3</sup>), D – dominance (%); – – species absent; abbreviations of species included in RDA analyses.**

Order/suborder family	Species	Abbreviation	Z1	Z2	Z3	G	SB	K	L					
Oribatida			A	D	A	D	A	D	A	D	A	D	A	D
Brachychthoniidae	<i>Brachychthonius berlesei</i> Willmann, 1928	<i>BracBerl</i>	5.2	<1	–	0.3	<1	0.1	<1	–	1.9	<1	0.5	<1
	<i>Liochthonius alpestris</i> (Forsslund, 1958)		20.7	3	–	26.4	6	17.7	2	8.8	<1	46.7	6	18.9
	<i>L. furcillatus</i> (Willmann, 1942)		–	–	–	–	–	0.4	<1	–	–	–	–	–
	<i>L. peduncularius</i> (Strenzke, 1951)		1.1	<1	10.5	2	2.3	<1	41.8	5	1.3	<1	0.2	<1
Hypochthoniidae	<i>L. perfuscatorius</i> Moritz, 1976	<i>LiocPerf</i>	8.2	1	–	0.1	<1	16.7	2	–	–	–	0.3	<1
	<i>Hypochthonius rufulus</i> C.L. Koch, 1835		–	–	–	–	0.8	<1	–	–	–	–	0.1	<1
Phthiracaridae	<i>Atropacarus striculus</i> (C.L. Koch, 1835)	<i>AtrpStrc</i>	4.6	<1	–	0.8	<1	1.4	<1	–	–	–	–	–
	<i>Hoplophthiracarus illinoisensis</i> (Ewing, 1909)		135.0	20	–	28.9	6	42.8	5	–	50.8	7	0.2	<1
Crotoniidae	<i>Platynothrus peltifer</i> (C.L. Koch, 1839)		–	0.2	<1	–	50.5	6	0.4	<1	–	–	7.8	<1
Malaconothridae	<i>Malaconothrus monodactylus</i> (Michael, 1888)	<i>MalcMond</i>	5.4	<1	–	–	3.1	<1	–	–	0.2	<1	–	–
	<i>M. tardus</i> (Michael, 1888)		–	–	–	–	0.1	<1	0.1	<1	0.3	<1	–	–
	<i>M. vietsi</i> (Willmann, 1925)	<i>MalcViet</i>	0.2	<1	–	0.2	<1	1.7	<1	–	1.3	<1	–	–
	<i>Tyrphonothrus foveolatus</i> (Willmann, 1931)	<i>TyrypFove</i>	19.0	3	95.1	14	29.9	7	7.8	<1	122.6	10	30.4	4

(continued)

Order/suborder family	Species	Abbreviation	Z1	Z2	Z3	G	SB	K	L							
	<i>T. maior</i> (Berlese, 1910)		0.1	<1	25.6	4	0.5	<1	1.3	<1	282.1	22	0.3	<1	222.8	13
Nanhermanniidae	<i>Nanhermannia coronata</i> Berlese, 1913		19.8	3	–	–	4.3	<1	12.9	2	–	–	22.0	3	0.6	<1
Nothridae	<i>Nothrus pratensis</i> Sellnick, 1928		25.7	4	–	–	7.9	2	9.9	1	–	–	6.9	<1	0.6	<1
Trhypochthoniidae	<i>Mainothrus badius</i> (Berlese, 1905)		80.7	12	1.7	<1	0.4	<1	0.2	<1	0.4	<1	162.9	22	47.0	3
	<i>Trhypochthoniellus longisetus</i> (Berlese, 1904)	<i>TrhpLong</i>	–	–	3.1	<1	0.1	<1	2.4	<1	0.2	<1	0.3	<1	197.2	11
	<i>Trhypochthonius nigricans</i> Willmann, 1928		–	–	0.9	<1	11.7	3	3.0	<1	0.2	<1	111.7	15	37.7	2
Damaeidae	<i>Metabelba sphagni</i> Strenzeke, 1950	<i>MethSphg</i>	7.4	1	–	–	1.4	<1	1.4	<1	–	–	0.3	<1	–	–
Liacaridae	<i>Dorycranosus acutus</i> Woolley, 1969		0.1	<1	–	–	–	–	–	–	–	–	–	–	–	–
Carabodidae	<i>Carabodes labyrinthicus</i> (Michael, 1879)		–	–	–	–	–	0.1	<1	–	–	–	–	–	–	–
Oppiidae	<i>Moritzoppia translamellata</i> (Willmann, 1923)	<i>MortTran</i>	2.6	<1	–	–	–	66.1	8	–	–	–	0.2	<1	0.1	<1
	<i>Oppiella nova</i> (Oudemans, 1902)	<i>OppiNova</i>	37.9	5	7.5	1	24.9	5	189.9	24	23.4	2	185.3	25	5.5	<1
	<i>O. propinqua</i> Mahunka et Mahunka-Papp, 2000		–	–	–	–	–	–	–	–	0.1	<1	–	–	–	–
	<i>Ramusella furcata</i> (Willmann, 1928)	<i>RamsFurc</i>	10.6	1	0.1	<1	2.7	<1	0.6	<1	–	–	28.8	4	–	–
Quadropiidae	<i>Quadropia maritilis</i> Lions, 1982		–	–	–	–	–	0.5	<1	–	–	–	–	–	0.1	<1
Suctobelbidae	<i>Suctobelbella latirostris</i> (Strenzeke, 1950)	<i>SuctLatr</i>	–	–	–	–	4.4	<1	1.0	<1	–	–	5.9	<1	–	–
	<i>S. longirostris</i> (Forsslund, 1941)		0.3	<1	–	–	–	–	–	–	–	–	–	–	0.1	<1
	<i>S. palustris</i> (Forsslund, 1951)	<i>SuctPals</i>	1.8	<1	–	–	–	0.4	<1	–	–	–	18.1	2	–	–
	<i>S. subcornigera</i> (Forsslund, 1941)		–	–	–	–	–	0.6	<1	–	–	–	–	–	–	–
Tectocepheidae	<i>Tectocephus velatus</i> (Michael, 1880)		4.2	<1	–	–	1.0	<1	11.6	1	–	–	1.1	<1	0.1	<1
Hydrozetidae	<i>Hydrozetes lacustris</i> (Michael, 1882)	<i>HydroLacs</i>	0.4	<1	–	–	–	–	–	–	3.3	<1	–	–	0.8	<1
	<i>H. longisetosus</i> Seniczak et Seniczak, 2009		–	–	2.7	<1	0.2	<1	–	–	0.1	<1	–	–	1.2	<1
	<i>H. octosetosus</i> Willmann, 1931	<i>HydroOcts</i>	–	–	–	–	–	–	–	–	25.3	2	–	–	3.6	<1
Limnozeteidae	<i>Limnozetes ciliatus</i> (Schränk, 1803)		196.6	28	6.8	1	257.6	57	279.9	35	0.2	<1	27.4	4	174.5	10
	<i>L. foveolatus</i> Willmann, 1939	<i>LimmFove</i>	49.9	7	505.0	75	35.4	8	1.3	<1	796.1	63	0.3	<1	985.3	56
	<i>L. rugosus</i> (Sellnick, 1923)		–	–	0.2	<1	–	–	–	–	–	–	–	–	–	–
Phenopelopidae	<i>Eupelops occultus</i> (C.L. Koch, 1835)		3.0	<1	0.2	<1	–	–	–	–	–	–	0.9	<1	–	–
	<i>E. strenzkei</i> (Knülle, 1954)	<i>EuplStrm</i>	0.2	<1	3.3	<1	0.3	<1	3.6	<1	–	–	0.6	<1	0.2	<1
Achipteriidae	<i>Achipteria coleoptrata</i> (Linnaeus, 1758)		0.3	<1	–	–	–	–	–	–	–	–	–	–	–	–
Scheloribatidae	<i>Hemileius initialis</i> (Berlese, 1908)		–	–	0.1	<1	–	–	–	–	–	–	–	–	–	–
	<i>Scheloribates laevigatus</i> (C.L. Koch, 1835)		4.4	<1	–	–	–	–	–	–	1.4	<1	–	–	–	–
	<i>S. latipes</i> (C.L. Koch, 1844)		13.1	2	0.3	<1	1.5	<1	–	–	0.3	<1	1.1	<1	–	–
	<i>S. pallidulus</i> (C.L. Koch, 1841)		–	–	–	–	–	–	2.2	<1	–	–	–	–	–	–
Ceratozetidae	<i>Diapterobates humeralis</i> (Hermann, 1804)		–	–	–	–	–	–	0.9	<1	–	–	–	–	–	–
	<i>Fuscozetes fuscipes</i> (C.L. Koch, 1844)		–	–	–	–	–	–	2.9	<1	–	–	–	–	–	–
	<i>Trichoribates berlesei</i> Jacot, 1929		0.4	<1	0.5	<1	0.4	<1	–	–	–	–	1.0	<1	0.5	<1
	<i>T. novus</i> (Sellnick, 1928)		0.2	<1	–	–	–	–	–	–	–	–	–	–	–	–
Chamobatidae	<i>Chamobates pusillus</i> (Berlese, 1895)		–	–	–	–	0.1	<1	–	–	–	–	–	–	–	–
Punctoribatidae	<i>Punctoribates sellnicki</i> Willmann, 1928	<i>PuncSell</i>	0.1	<1	5.8	<1	0.1	<1	–	–	1.4	<1	5.5	<1	0.3	<1
Zetomimidae	<i>Heterozetes palustris</i> (Willmann, 1917)	<i>HetrPals</i>	–	–	0.7	<1	–	–	–	–	0.4	<1	–	–	–	–
	<i>Zetomimus furcatus</i> (Warburton et Pearse, 1905)		0.1	<1	1.9	<1	–	–	–	–	–	–	–	–	–	–
Galumnidae	<i>Galumna tarsipennata</i> Oudemans, 1914		–	–	–	–	–	0.3	<1	–	–	–	–	–	–	–
	<i>Pergalumna nervosa</i> (Berlese, 1914)	<i>PergNerv</i>	1.4	<1	0.3	<1	0.1	<1	0.3	<1	–	–	0.1	<1	–	–
	<i>Pilogalumna tenuiclava</i> (Berlese, 1908)		27.1	4	0.4	<1	5.1	1	18.9	2	2.4	<1	27.4	4	3.4	<1
Mesostigmata																
Urodynchidae	<i>Uroobovella minima</i> (C.L. Koch, 1844)	<i>UrooMinm</i>	2.6	23	–	–	0.2	14	0.3	4	–	–	5.5	65	–	–
Zerconidae	<i>Prozerccon kochi</i> Sellnick, 1943	<i>ProzKoch</i>	0.1	<1	–	–	–	–	–	–	–	–	–	–	–	–
	<i>Zercon zelawaiensis</i> Sellnick, 1944	<i>ZercZelw</i>	–	–	–	–	–	2.4	29	–	–	–	1.3	15	–	–
Parasitidae	<i>Paragamasus runciger</i> (Berlese, 1904)	<i>ParaRunc</i>	–	–	–	–	–	0.1	1	–	–	–	–	–	–	–
	<i>Pergamasus runcatellus</i> (Berlese, 1903)	<i>PergRunc</i>	–	–	–	–	–	–	–	–	–	–	0.2	2	–	–
	<i>P. vagabundus</i> (Karg, 1968)	<i>PergVagb</i>	–	–	–	–	–	–	–	–	–	–	0.2	2	–	–
Veigaiidae	<i>Veigaia transisalae</i> (Oudemans, 1902)	<i>VeigTran</i>	5.5	40	–	–	0.6	43	3.2	38	–	–	–	–	1.1	69
Ascidae	<i>Leioseius minusculus</i> Berlese, 1905	<i>LeioMins</i>	–	–	–	–	0.1	7	–	–	0.1	1	–	–	0.4	25
	<i>Neojordensia levis</i> (Oudemans et Voigts, 1904)	<i>NeojLevs</i>	–	–	–	–	–	0.6	7	–	–	–	0.7	8	–	–
Blattisociidae	<i>Cheiroseius longipes</i> (Willmann, 1951)	<i>CheiLong</i>	0.9	8	–	–	–	1.0	12	–	–	–	0.1	1	0.1	6
	<i>Platyseius italicus</i> (Berlese, 1905)	<i>PlatItlc</i>	1.6	14	1.0	100	0.4	29	0.5	6	12.9	99	0.3	4	–	–
	<i>P. major</i> (Halbert, 1923)	<i>PlatMajr</i>	0.2	2	–	–	–	–	–	–	–	–	–	–	–	–
Laelapidae	<i>Gaeolaelaps aculeifer</i> (Canestrini, 1883)	<i>GaeoAcul</i>	–	–	–	–	–	–	–	–	–	–	0.1	1	–	–
	<i>G. praesternalis</i> (Willmann, 1949)	<i>GaeoPrae</i>	0.4	3	–	–	0.1	7	0.3	4	–	–	–	–	–	–
	<i>Pseudoparasitus venetus</i> (Berlese, 1904)	<i>PseuVent</i>	1.0	9	–	–	–	–	–	–	–	–	–	–	–	–

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