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Soil conditions under cormorant colonies favor for mites excepting Oribatida

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Original research

ABSTRACT

Over the last few decades, the population of the great cormorant (*Phalacrocorax carbo* L., 1758) in Europe has been rising. The formation of large nesting and roosting colonies in relatively small areas, their rapid metabolism and the excretion of significant amounts of guano can have a marked environmental impact. This study aimed to investigate how cormorants affect the biodiversity and density of soil mites under breeding colonies. Soil samples from three cormorant colonies located on lake islands were compared to samples from adjacent areas unaffected by birds. Soil from colonies was characterised by a higher concentration of nitrogen, phosphorus and organic matter as well as the abundance of mites (except Oribatida). The abundance and diversity of adult Oribatida in soil under the colonies were lower than in their control sites.

Keywords fertilization; island; soil mites; soil microvertebrate

Introduction

The great cormorant (*Phalacrocorax carbo* L., 1758) is a seabird with a global distribution. It is an apex predator with a diet almost exclusively based on fish. The growth of the European population of these birds has raised concerns due to their impact on the land and water environment. Cormorants breed and rest on land but forage on water and can, therefore, represent a very important intermediate link in ecosystems and food webs. Their fish-based diet and behaviour result in the transport of nutrients and other chemical elements between terrestrial and aquatic environments (Marion *et al.* 1994; Klimaszyk and Rzymiski 2016). They deposit large amounts of guano (20–50 g per day), mainly beneath their roosts and nests, leading to acidification of the soil and accumulations of N and P loads to extreme levels. These changes in the chemical properties of the soil can decrease plant biodiversity and promote the growth of nitrophilous species. Cormorants also have a significant impact on the trees in their colonies, as these usually become defoliated because the birds break off twigs to build their nests, thus making the trees more susceptible to a pest invasion (Klimaszyk and Rzymiski 2016).

The high allochthonous input and changes in soil chemistry and plant vitality, diversity and density also have a significant impact on food webs and the diversity of other groups of organisms. Previous studies found that the abundance, density or species richness of Collembola, Coleoptera (herbivores), Thysanoptera and litter spiders in breeding colonies of cormorants were lower than in reference sites (Kolb *et al.* 2010, 2012, 2015). Breeding colonies of cormorant are also characterised by a higher abundance and density of Astigmata (Acari), bacteriophage nematodes, some herbivores (Aphidoidae and Lepidoptera larvae) and

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their natural enemies, such as Hymenoptera, Neuroptera and Coccinellidae (Kolb *et al.* 2010, 2012, 2015; Pen-Mouratov and Dayan 2019).

This study aimed to determine how the transformations of habitat by cormorants affect the populations of soil mites, mainly Oribatida, which are one of the most common soil arthropods. Their abundance can reach up to 200 000 ind./m². Most Oribatida are saprophagic, feeding mainly on dead plant material and fungi, but some species also eat, among other things, algae, lichen, mosses, and even nematodes. They digest dead organic material, which returns it into the circulation of nutrients (Magilton *et al.* 2019). Also, some species belonging to Nothoidea or Ptyctima, due to their sensitivity to soil disturbance, may serve as potential bioindicators of soil conditions (Gulvik 2007).

Additionally, the study collected data on the abundance of other soil mites (without distinguishing between species), which have different ecologies and functions. Mesostigmata are mostly predators, Astigmata are saprophagous, fungivorous, or graminivorous, while Prostigmata have a broad range of feeding habits, e.g. being predators, fungivores-microbivores, parasites, or omnivores (Potapov *et al.* 2022). These taxa are also considered to be potential bioindicators of soil conditions. For example, previous studies showed that disturbing the soil causes a decrease in the densities or percentage abundance of Oribatida, as well as an increase of Prostigmata (Gulvik 2007). These changes were due to the difference in life strategies of these mites. Most Oribatida use the *K*-strategy, while most Prostigmata use the *r*-strategy. Thus, the latter can colonise new habitats faster and react to change faster (Gulvik 2007).

Knowledge of the impact of cormorants on soil mites (Oribatida, among others) is still limited. Kolb *et al.* (2015) found a higher abundance of Astigmata and a lower abundance of moss mites in breeding colonies, but individuals were not identified to the species level. There are few publications on the impact of European cormorants on soil mites. Many works do not include Oribatida (e.g. Kolb *et al.* 2012) or focus on other bird species (e.g. Zmudczynska-Skarbek *et al.* 2017), which have different diets, nesting behaviours, or habitat preferences.

In summary, a hypothesis was formulated that the change in the soil habitat caused by cormorants results in a decrease in the abundance and diversity of Oribatida (adults and juveniles), and an increase in the abundance of Astigmata.

Material and methods

Study sites

The samples were collected on three sites (Fig.1):

Lake Chrzypsko

Samples were collected in July 2018 from the following sites:

- Col. I - The cormorant colony (52°36'57"N, 16°13'23"E) has existed since the beginning of the 21st century. Cormorants occupy the most northward island of the lake, with an area of 0.9 ha. The island is slightly elevated above the lake level. It is overgrown mainly with alder (*Alnus glutinosa* (L.) Gaertn., 1791) and willow (*Salix cinerea* L., 1753). In sites where nests are concentrated, the herbaceous vegetation is very poor or represented by nitrophilous species like the nettle (*Urtica dioica* L., 1753) or elderberry shrubs (*Sambucus nigra* L., 1753). The forest canopy is bald and many of the trees are dead. In recent years, over 160 pairs of cormorants have been nested on the island.
- Con. I - Control island (52°36'44"N, 16°13'24"E) is located about 400 m South of the cormorant colony. The island elevation is insignificant, and its area is about 1.4 ha. The island is unaffected by cormorants and is overgrown with dense alder, willow and ash (*Fraxinus excelsior* L., 1753) forest.

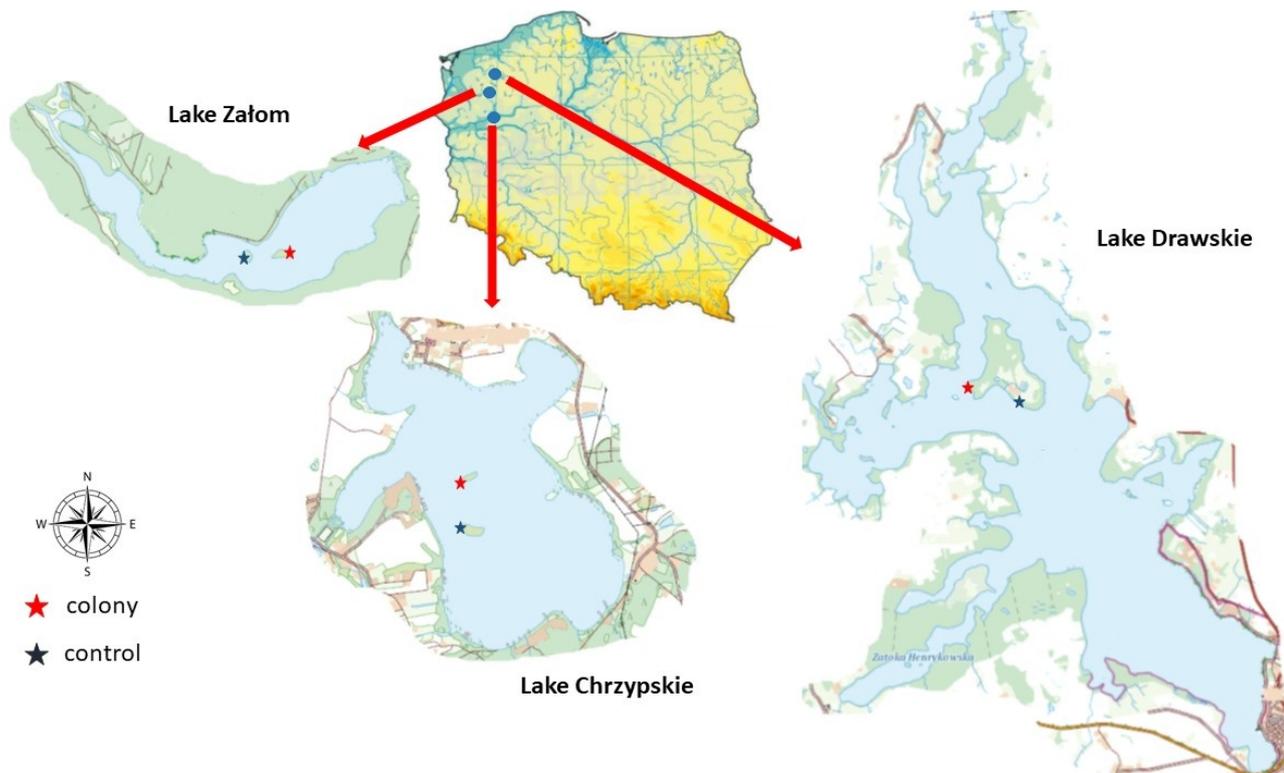


Figure 1 Map of sampling sites.

Lake Załom

Samples were collected in May 2019 from the following sites:

- Col. II - The cormorant colony (53°04'58"N, 16°03'35"E) is located on the eastern island with an area of 0,6 ha. Inhabited by cormorants since the second decade of the 21st century. Overgrown with alders, oaks, birches and willows. In areas with cormorant nests, the tree canopy is sparse, herbaceous vegetation is absent and forest litter is accumulated. During the surveys over 200 nests were occupied by cormorants.
- Con. II - Control island (53°04'59"N, 16°03'49"E) is unaffected by cormorants, it is about 150 m West of the colony. It is similar to the colony island regarding morphology. Vegetation showed no symptoms of cormorant impact.

Lake Drawskie

The colony and control sites were located on Bielawa Island. The island surface is about 8 ha and is mainly covered by forest. Samples were collected in June 2019.

- Col. III – The cormorant colony (53°36'11"N, 16°09'44"E) was established in the first decade of the 21st century on the western part of the island. Today, almost 800 pairs of cormorants are nesting there. The area of the colony is overgrown with alder, willow and elderberry shrubs. Herbaceous vegetation is sparse.
- Con. III - control site (53°36'05"N, 16°10'24"E) is located 500 m from the colony in an alder forest unaffected by cormorants.

Sampling

Sampling of soil for chemical analyses

Soil samples for chemical analyses were taken simultaneously and from the same sites as the soil fauna samples. The collected soil samples were air-dried and sieved using a 2-mm sieve to separate gravel (particle size >2 mm) and non-soil components and were stored in a freezer at -20 °C prior to analysis.

Sampling of soil for studying mite communities

In total, 25 soil samples were collected from random sites in the central part of each island using a metal core (10 cm in depth, 4 cm in diameter). Samples were collected from under nests in breeding colonies of cormorants. Invertebrates were extracted with a Tullgren funnel and preserved in 75% ethanol. Soil mites were divided into the following groups: Astigmata, Mesostigmata, Prostigmata, and adult and juvenile Oribatida.

Chemical analyses of soil

The total amount of nitrogen (N_{t_K}) in soils was determined using the Kjeldahl method (van Reeuwijk 1995), constituting the sum of N_{org} and $N-NH_4$. Contents of $N-NO_3^-$ and $N-NH_4^+$ were determined after extraction in CH_3COOH (0.03 mol L^{-1}) using the Nessler method, whereas $N-NO_2^-$ was analysed using a method with phenoldisulphonic acid (Prince 1955). TP content in soils was determined at 850 nm using a Shimadzu UV-1610 spectrophotometer (molybdate method) after burning the samples at 550 °C and mineralized in suprapure HNO_3 (14 mol L) and H_2SO_4 (18 mol L) (Sobczyński and Joniak 2009). The amount of organic matter in soil samples was measured as a percentage weight loss through the combustion at 550 °C for 3 h following drying at 50 °C for 24 h (Wang *et al.* 2011).

Identification of soil mites

To classify individuals, adult Oribatida mites were macerated with 80% lactic acid. Subsequently, they were placed on a microscope cavity slide and covered by a coverslip. A drop of lactic acid was also used as the medium. The following keys were used for the identification: Olszanowski (1996), Weigmann (2006), Niedbała (2008), and Krantz and Walter (2009). The abundance, constancy, density, and dominance were estimated for each species. Up-to-date taxon names were used according to Subías (2004, updated 2021).

Data analysis

Diversity and abundance of mites

To compare study sites, the following indices were used according to Krebs (2011), Carmo *et al.* (2013), Pen-Mouratov and Dayan (2019):

- Abundance: number of individuals per sample
- Density: number of individuals per m^2
- Dominance: $DOM=(i/t)*100$, where i = abundance of taxa and t = total abundance of all taxa
- Constancy: $CON=(p \times 100)/N$, where p = number of samples in which the taxa is present; N = total number of samples
- Species richness: $SR=[(S-1)/\ln(N)]$, where S is the number of species and N is the number of individuals identified

- Shannon-Wiener diversity index: $H' = [-\sum P_i (\ln P_i)]$, where P_i is the proportion of individuals in the taxon
- Species evenness: $J' = H'/H_{\max}$, where $H_{\max} = \ln S$
- Modified Simpson's dominance index: $D = 1/(\sum P_i^2)$

Additionally, we used a modified ratio of the dominance index of Oribatida and Prostigmata, which is based on the ratio of the relative abundance of Oribatida and Prostigmata (Gulvik 2007). To avoid dividing by zero (many samples lacked Prostigmata), 1 was added to the dominance values of both groups.

$O+1/P+1$, where O = dominance value of Oribatida, P = dominance value of Prostigmata.

Statistical analysis

Data about soil chemistry and mites were assessed with the Shapiro–Wilk tests. Due to the lack of normality of the distributions in most cases and unsuccessful attempts at transformation, Mann–Whitney U test was applied on the untransformed data.

A canonical correspondence analysis (CCA) was conducted to identify species and site arrangements in relation to environmental factors. The analyses used untransformed data for average soil chemistry (pH, organic material content, and nitrogen content in mineral and organic form), the number of cormorant pairs, and mean abundance of species whose dominance after rounding up was $\geq 5\%$ on at least one island. Data about each species of Oribatida were transformed using: $\log(x+1)$, where x is the mean abundance.

Statistical software

Statistical analyses about soil chemistry were performed with the program Statistica (StatSoft Inc. 2007). The significance of any difference in the data for soil mites was calculated with the *base* and *stats* R packages (R Core Team 2020). A graphical interface was also used (RStudio Team 2020). The CCA was run using the PAST software package (Hammer *et al.* 2001).

Results

Soil chemistry

Cormorants exerted a significant influence on the chemistry of the soils under their colonies. Very high concentrations of nitrogen, phosphorus, and potassium were recorded, as well as soil acidification. Among nitrogen forms, organic nitrogen predominated in all colonies, accounting for between 60% and 70% of the total pool of accumulated nitrogen. Regardless of the colony, compared to control sites, which were not exposed to bird impact, soils under colonies were characterised by 4 to more than 10 times higher nitrogen concentrations. The differences between colonies and control sites were even greater for total phosphorus concentrations. Soils

Table 1 Content of nutrients and pH in (\pm SD) under cormorant colonies (Col) and control sites unaffected by birds (Con). Asterisk signifying p-value of Mann–Whitney U test for given pairs of islands: * $p < 0.05$, ** $p < 0.001$, *** $p < 0.001$.

	Lake Chrzypskie			Lake Załom		Lake Drawskie	
		Col I	Con I	Col II	Con II	Col III	Con III
pH		4.6-5.2	7.9-8.2	4.7-4.9	7.4-8.2	5.2-6.0	7.4-7.9
P	mgP kg	3210 \pm 1214	*** 36.2 \pm 11.5	3630 \pm 1511	*** 192.8 \pm 26.8	2932 \pm 811	*** 48.6 \pm 11.6
N org.	mgN kg	1456.8 \pm 421.2	*** 182.6 \pm 25.3	1712.8 \pm 311.2	*** 281.1 \pm 71.2	1517 \pm 221.6	*** 197.2 \pm 44.2
N min.	mgN kg	920.6 \pm 158.9	*** 99.2 \pm 11.6	498.5 \pm 58.7	*** 152.1 \pm 11.6	724.8 \pm 102.3	*** 137.5 \pm 23.3
K	mgK kg	186.2 \pm 55.2	* 45.8 \pm 21.6	162.3 \pm 24.1	** 30.1 \pm 9.6	241 \pm 31.4	** 72 \pm 11.8

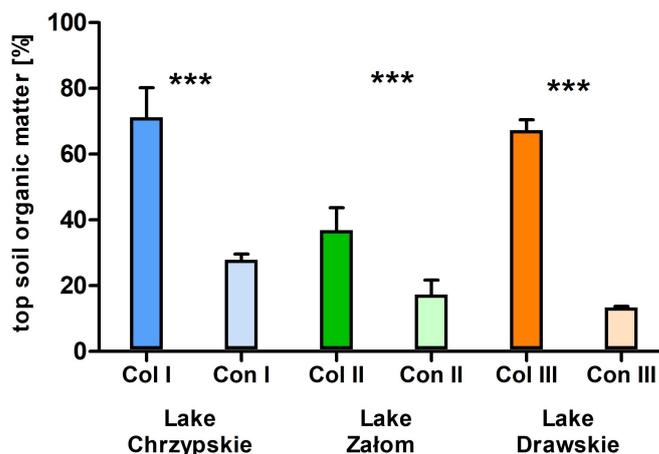


Figure 2 Organic matter comparisons between studied islands. Asterisk signifying p-value of Mann-Whitney U test for given pairs of islands: * p<0.05, ** p<0.001, *** p<0.001.

under the colonies were characterized by 20 times (Lake Załom) to almost 90 times (Lake Chrzypskie) higher concentrations of this element than the control sites. The differences for potassium were not as high, but like nitrogen and phosphorus, the soils under the colonies were characterised by statistically significantly higher concentrations of potassium (Table 1). The soil reaction at the control sites was neutral or slightly alkaline, while the soil under the colonies was strongly acidic (Table 1). Moreover, the content of organic matter in the soil under the cormorant colonies was statistically higher compared to the control sites (Figure 2).

The abundance of soil mites

In total, 3 191 individuals of adult Oribatida were found. The highest abundance of Oribatida was in control site II (Con. II), where 1679 specimens were found (Table 2). The lowest abundance was detected in colony site III (Col. III). The abundance of juveniles was lower than that of adults. In all cormorant colonies, fewer Oribatida (both adults and juveniles) were recorded than in the corresponding control sites. This difference is statistically significant for Oribatida from the islands in Lake Drawskie and the population of adult mites in Lake Załomie (Table 2).

Among other soil mite groups (Table 3), the most numerous were Mesostigmata (955 individuals), while the least abundant were Prostigmata (209 individuals). Mesostigmata

Table 2 Abundance (A), mean density (D) and constancy (C) of Oribatida (adult and juvenile) with standard error (SE). Asterisk signifying p-value of Mann-Whitney U test for given pairs of islands: * p<0.05, ** p<0.001, *** p<0.001.

Site	Total				Adult				Juvenile			
	A	D	C(%)	P-value	A	D	C(%)	P-value	A	D	C(%)	P-value
Col.I	137	4215.38 ± 714.90	92	0.306	111	3415.38 ± 658.85	72	0.48	26	800 ± 271.89	40	0.059
Con.I	223	13015.38 ± 2104.25	100		162	4984.62 ± 1161.61	76		61	1876.92 ± 536.87	72	
Col.II	1003	30861.54 ± 3938.71	100	0.057	788	24246.15 ± 3192.42	76	0.026*	215	6615.38 ± 1326.41	100	0.66
Con.II	1940	52061.54 ± 8376.11	100		1679	51661.54 ± 8349.93	100		261	8030.77 ± 1556.36	80	
Col.III	105	4707.69 ± 1671.98	80	p<0.001***	92	2830.77 ± 1687.48	40	p<0.001***	13	400 ± 231.28	20	p<0.001***
Con.III	402	12369.23 ± 1672.33	100		359	11046.15 ± 1751.24	96		43	1323.08 ± 487.56	40	
Total abundance					3810				3 191			619

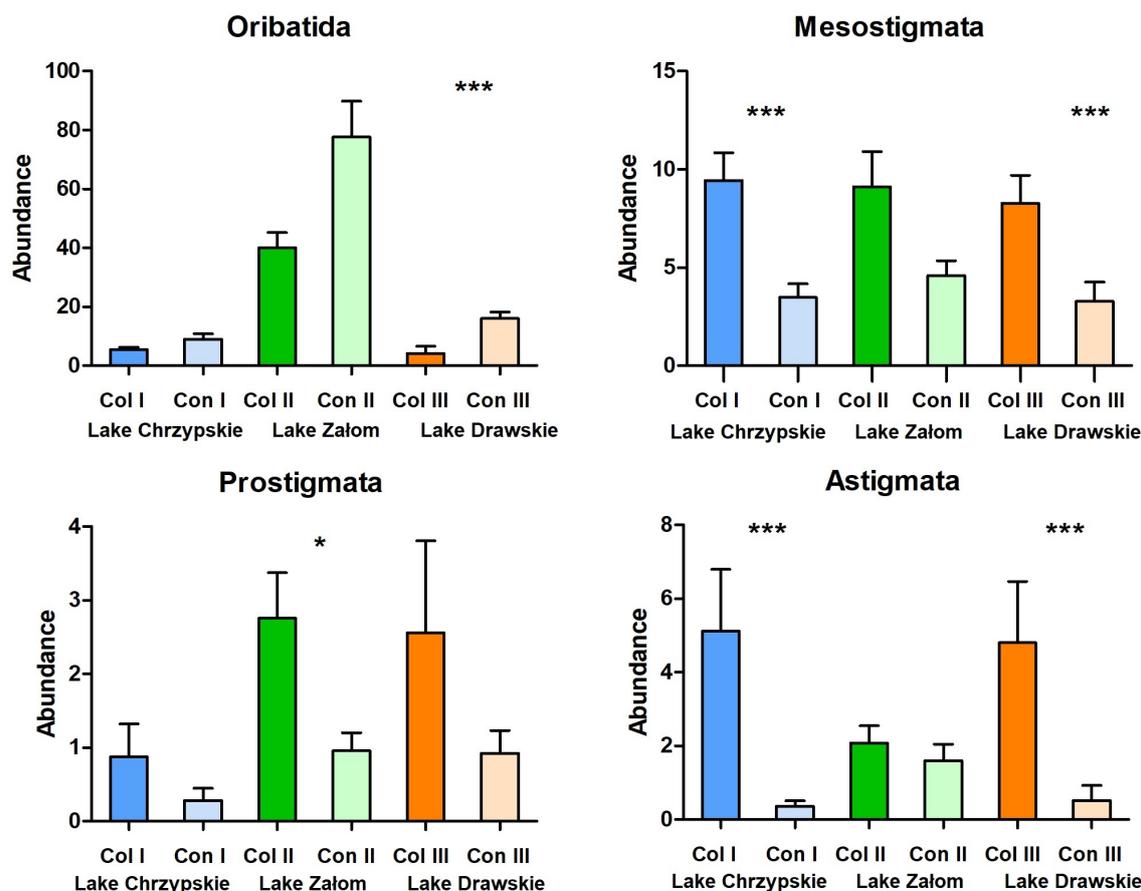


Figure 3 Comparison of abundance of mite groups in soil under cormorant colonies and control sites. Asterisk signifying p-value of Mann–Whitney U test for given pairs of islands: * p<0.05, ** p<0.001, *** p<0.001. box – mean, whisker – SE.

were identified in most samples from all sites. Their constancy was $\geq 80\%$. Astigmata and Mesotigmata were mostly significantly more abundant in colonies than at reference sites (Figure 3). The only exception was an island in Lake Zalomie. Populations of Prostigmata were also greater in areas occupied by cormorants but only the difference between Col. II and Con. II was statistically significant. The ratio of Oribatida and Prostigmata dominance was significantly lower in all colonies (Table 4).

Table 3 Abundance (A), mean density (D) and constancy (C) of other mites (Astigmata, Mesostigmata and Prostigmata) with standard error (SE). Asterisk signifying p-value of Mann–Whitney U test for given pairs of islands: * p<0.05, ** p<0.001, *** p<0.001.

Site	Astigmata				Mesostigmata				Prostigmata			
	A	D	C (%)	P-value	A	D	C (%)	P-value	A	D	C (%)	P-value
Col.I	128	3938.46 ± 1288.18	68	0.0004***	236	7261.54 ± 1079.74	92	0.0004***	22	676.92 ± 339.16	24	0.42
Con.I	9	276.92 ± 116.49	24		87	2676.92 ± 542.33	80		7	215.38 ± 129.63	16	
Col.II	52	1600 ± 360.58	68	0.39	228	7015.38 ± 1370.53	92	0.06	69	2123.08 ± 476.84	68	0.018*
Con.II	40	1230.77 ± 344.01	60		115	3538.46 ± 577.35	80		24	738.46 ± 185.68	52	
Col.III	120	3692.31 ± 1282.56	60	0.0002***	207	6369.23 ± 1092.85	92	0.0019***	64	1969.23 ± 960.85	36	0.82
Con.III	13	400 ± 317.53	8		82	2523.08 ± 747.8	68		23	707.69 ± 242.93	40	
Total abundance					362				955			209

Species diversity of Oribatida

In total, 78 species from 32 families were recorded (Table Supplement). The richest number of species was found at the control site on the island in the Lake Drawskie, where 39 species were found (Table 4). In all cormorant colonies, fewer species were recorded than at control sites. Furthermore, most samples from colonies had lower values for species richness, evenness, Shannon-Werner index and Simpson index. In most cases, these differences were statistically significant. Exceptions were the islands in Lake Chrzypsko where no difference was significant (except Simpson index). Among control sites, the highest values of all indicators (except *J'*) were found in Con. II.

In Cols. II and III, the dominant species were *Rhinoppia nasuta* (Moritz, 1965) and *Acrogalumna longipluma* (Berlese, 1904). Their dominance values ranged from 3.60% to 55.43% and from 4.50% to 21.70%, respectively (Table Supplement). Both species also occurred in Col. I (constancy values 8% and 12%), but the most common species was *Scheloribates laevigatus* (Koch, 1835), which was absent in other colonies of cormorants. The dominance and constancy of this species were 61.26% and 80%. For comparison, in reference sites (Cons.I, II, III) *Atropacarus striculus* (Koch, 1835), *Oppiella nova propinqua* Mahunka & Mahunka-Papp, 2000; *Oppiella nova* (Oudemans, 1902) and *Suctobelbella baloghi* (Forsslund, 1950) were the most common species. *Oppiella nova* also occurred frequently in colonies of cormorants, and three individuals of *A. striculus* were found in Col.II. The dominance of *A. striculus* at control sites ranged from 11.37% to 34.36%, while its constancy range was from 48% to 96%. No specimens of *R. nasuta* were recorded at the reference sites.

CCA was used to analyse the Oribatida communities in relation to habitat type (Figure 4). The first eigenvalue axis is about 0.71 and explains 46.63% of the variance. The permutation test shows that the eigenvalue of the first axis is significant ($p= 0.035$; $N= 999$). It is positively correlated with the pH, while organic material (Om), number of cormorants pairs (Cor), and mineral and organic nitrogen (N min and N org) were negatively correlated with this axis. Cor and N org had the strongest correlation with the axis (the smallest angles between the axis and the vector). For the second axis, the eigenvalue is 0.59 and explains 38.64% of the variance. CCA divided the studied sites into three groups of points. Along the first axis, Cols. II and III are separated from their reference sites. These colonies are positively correlated with Cor and all soil parameters apart from pH and have the highest abundances of *S. pallidulus*, *S. latipes*, *H. rufulus*, *A. longipluma* and *R. nasuta*.

The next group of points are reference sites, which are positively correlated with the pH and characterised by the highest abundance of *A. striculus*, *P. clavatus*, *M. monodactylus*, *O. nova*, *O. nova propinqua*, *Q. hammerae*, *S. baloghi*, *S. forsslundi*, and *T. velatus sarekensis*. Colony I stands out the most among the islands. This site is characterised by the highest abundance of *S. laevigatus* and is the only site where *C. subglobulus* and *O. tibialis* were found. *O. nova* is close to the central portion of the triplot. These species occur in nearly all sites; however, it was more abundant at the reference sites.

Table 4 Number of species, mean species richness (SR), Shannon-Werner index (*H'*) evenness(*J'*) and Simpson index (D) of samples, mean dominance ratio of Oribatida and Prostigmata (O/P) with standard error (SE). Next to the value of colonies indices are asterisk signifying p-value of Mann–Whitney U test for given pairs of islands: * $p<0.05$, ** $p<0.001$, *** $p<0.001$, ns – non-significant.

Sites	Number of species	SR	<i>H'</i>	<i>J'</i>	D	O/P (%)
Col. I	9	1.02 ± 0.24 ^{ns}	0.59 ± 0.13 ^{ns}	0.44 ± 0.09 ^{ns}	0.33 ± 0.06*	24.87 ± 4.99***
Con. I	31	2.41 ± 0.65	1.07 ± 0.2	0.57 ± 0.09	0.51 ± 0.07	70.39 ± 6.19
Col. II	23	1.42 ± 0.13***	1.91 ± 0.12***	0.76 ± 0.05 ^{ns}	0.66 ± 0.03**	34.53 ± 6.93*
Con. II	32	2.48 ± 0.16	2.61 ± 0.13	0.79 ± 0.02	0.76 ± 0.03	57.22 ± 6.98
Col. III	17	1 ± 0.42***	0.20 ± 0.11***	0.28 ± 0.16***	0.07 ± 0.04***	21.94 ± 5.31**
Con. III	39	1.92 ± 0.14	1.90 ± 0.13	0.82 ± 0.04	0.75 ± 0.03	47.23 ± 7.67

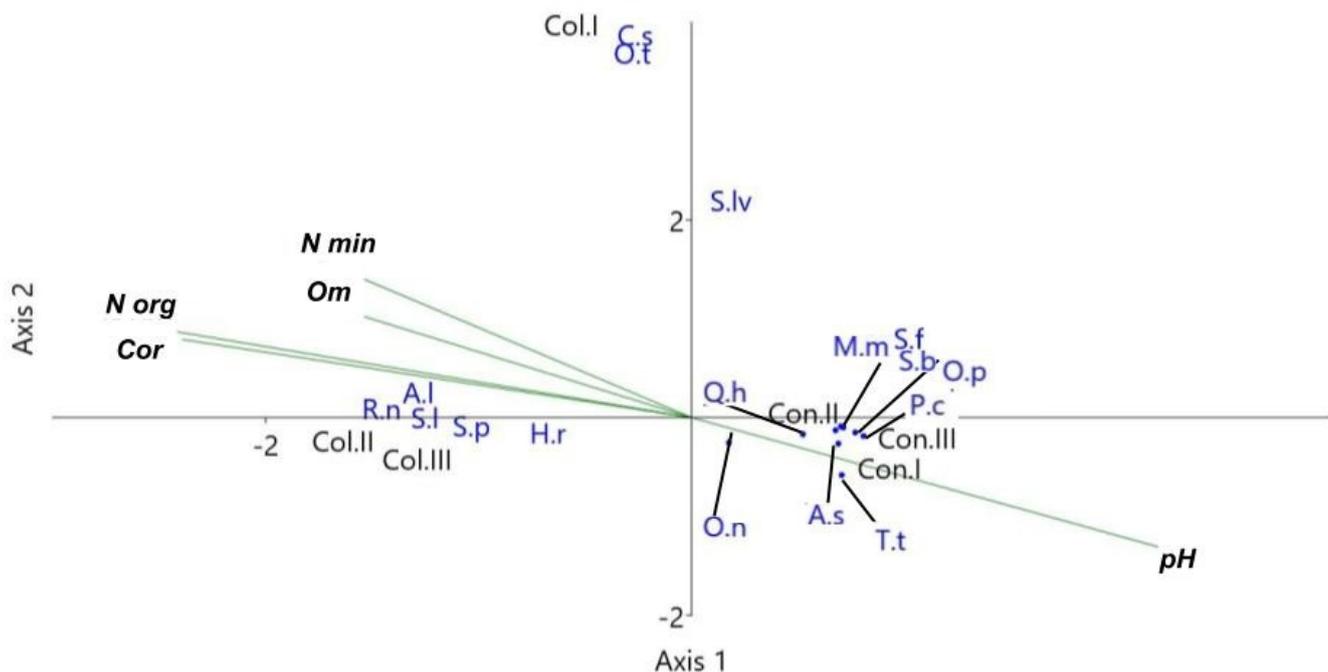


Figure 4 CCA with scaling type 2 of the relationship between site fauna and chemical parameters of soil: Cor – number of cormorants pairs, Om – soil organic matter, N min. – mineral nitrogen, N org – organic nitrogen, pH – value of pH, H.r – *Hypochothonius rufulus*, A.s – *Atropacarus striculus*, P.c – *Phthiracarus clavatus*, M.m – *Malaconothrus monodactylus*, R.n – *Rhinoppia nasuta*, O.n – *Oppiella nova*, O.p – *Oppiella nova propinqua*, Q.h – *Quadroppia hammerae*, S.b – *Suctobelbella baloghi*, S.f – *Suctobelbella forsslundi*, T.t – *Tectocepheus velatus sarekensis*, O.t – *Oribatula tibialis*, C.s – *Chamobates subglobulus*, S.p – *Scheloribates pallidulus*, S.lv – *Scheloribates laevigatus*, S.l – *Scheloribates pallidulus latipes*, A.l – *Acrogalumna longipluma*.

Discussion

This study demonstrated that cormorants cause significant alterations in biotopes and biocenoses under their colonies. The soil under all the surveyed colonies contained significantly higher loads of nitrogen (both the organic and mineral form), phosphorus and potassium compared to the control sites. Fertilisation of areas under cormorant colonies and roosts results mainly from the deposition of nutrient-rich guano (Marion *et al.* 1994; Ligęza and Smal 2003; Klimaszyk 2012). The faeces-originating nitrogen occurs primarily in the form of uric acid (Mizutani and Wanda 1988; Mulder and Keall 2001) which acidifies soils under the colonies (Kameda *et al.* 2000; Breuning-Madsen *et al.* 2008). In the case of the surveyed colonies, strong soil acidification was also noted. Moreover, additional loads of chemical substances are deposited under colonies with cormorants' pellets, which contain fish remains, along with the bird-induced accumulation of plant debris (Hobara *et al.* 2001; Osono 2006a). In dense colonies, cormorants may be responsible for the accumulation of as much as 2000 kg ha⁻¹ of forest litter per month (Klimaszyk and Rzymiski 2016). This usually results in the topsoil horizon becoming enriched with organic matter (Osono *et al.* 2006a; Breuning-Madsen *et al.* 2008; Klimaszyk 2012), which was also reported in the studied colonies.

In addition to their chemical properties, soils beneath the colonies differed from the control sites with respect to the diversity and abundance of mites. Similar to Kolb *et al.* (2015),

we found that the abundance of oribatid mites was lower in soil under cormorant colonies, but Astigmata were more frequent in the areas than at the control sites unaffected by birds. However, contrary to the above-mentioned work, Mesostigmata mites were significantly more abundant in soils under cormorant pressure. Most Mesostigmata are predators, thus an increase in their abundance might be caused by the higher availability of prey, such as bacteriophage nematodes, which are also more abundant in these habitats (Pen-Mouratov and Dayan 2019) or other invertebrates. Isotopic studies in the Westland petrels (*Procellaria westlandica* Falla, 1946) colony showed that one mesostigmatid species likely feeds on guano decomposers or their eggs (Hawke *et al.* 2013).

Astigmata, which include species associated with carrion, guano and nests as well as parasites of birds, likely filled appropriate microhabitats in cormorants colonies (Krantz and Walter 2009). Previous studies also show a correlation between the density of Astigmata and the concentration of N, for which the source could be guano (Kolb *et al.* 2015).

For all the studied colonies, the dominance ratios of Oribatida and Prostigmata were lower than at their control sites. This is in accordance with previous studies, which showed that a change in the ecosystem (e.g. the transformation of woodland into an arable field) leads to a decrease of Oribatida and an increase in Prostigmata abundance (Gulvik 2007). Prostigmata were more abundant in the colonies in this study, but statistical significance was achieved only in the samples from islands on Lake Załomie. Most individuals likely belonged to Heterostigmata (e.g. Scutacaridae), which are among other things fungivorous, phytophagous and algophagous mites (Krantz and Walter 2009). However, Kolb *et al.* (2015) did not demonstrate any statistically significant differences in the density of Prostigmata between colonies and their reference sites.

Zmudczynska-Skarbek *et al.* (2017) also revealed the significant negative effect of a colony of planktivorous little auks (*Alle alle* (L., 1758)), on decomposers' diversity (oribatid mites and springtails) and a positive one on the density of predator (mesostigmatid mites and one spider species) and the number of invertebrate species. However, other studied birds, such as the predatory glaucous gull (*Larus hyperboreus* Gunnerus, 1767) and great skua (*Stercorarius skua* (Brünnich, 1764)), did not have any significant impact on invertebrates populations. Contrary to the above-mentioned works and present results, the studies of Orwin *et al.* (2015), showed a positive effect of seabirds' burrow density on the abundance of oribatid and mesostigmatid mites. Similarly, Ilieva-Makulec *et al.* (2015) also found a higher abundance of mites (the authors did not separate the mites into groups) from soil under corvid roosts.

The results obtained indicate that cormorants have a significant effect on the biodiversity of Oribatida. In all colonies, the abundance, numbers of species and values of diversity indices were lower than those at control islands unaffected by birds. In the case of Lake Chrzypsko, no diversity indices were statistically significant (except Simpson's dominance index), although the difference in the number of species between the colony and control islands was the highest. However, in Con. I most species had constancy lower than 25%, thus the diversity indices values were low. The lowest abundance, constancy and diversity indices of Oribatida were for Col. III, which could have been caused by the substantial impact of cormorants because that island was occupied by the highest number of bird pairs during the study.

Species composition also differed among the studied islands. Many species (e.g. *Galumna obvia* (Berlese, 1915) were found only at the control sites. This is similar to the findings of previous studies that showed this taxon is sensitive to a high dose of organic fertilisation (Wasińska-Graczyk *et al.* 2009). Suctobelbidae, Phthiracaridae (e.g. *A. striculus*) and Nothrina (Malaconothridae, Crotoniidae, Nothridae), as well as others, turned out to be the groups most sensitive to guano fertilisation. In the control sites, they are the most abundant and diverse soil mites, while in colonies, they were found sporadically. A similar result was obtained by Lebedeva *et al.* (2006), as no species from Suctobelbidae or Phthiracaridae were found in soil from the breeding sites of the Arctic tern (*Sterna paradisaea* Pontoppidan, 1763) and snow bunting (*Plectrophenax nivalis* (L., 1758)). Nothrina and Phthiracaridae are known for their sensitivity to soil disturbance and are considered potential bioindicators of soil quality (Gulvik

2007). Moreover, in some studies, *Suctobelbella* sp. reacted by decreasing in abundance due to soil fertilisation (Lindberg and Persson 2004; Cao *et al.* 2011).

The reason for the decrease in Oribatida diversity is not known; however, it is most likely to be the result of combination of several factors, interacting with individual species in different intensities. The first potential factor is the harmful effect of guano's compounds, including ammonia, which is toxic to most animals (Weihrauch *et al.* 2012). However, the effect of the cormorant colony could be less direct. The low abundance of *A. striculus* might be due to decreased plant cover and diversity because the abundance of this species is correlated with these factors (Skubała and Maślak 2010). Guano also has a significant impact on the abundance and species composition of bacteria, lichen and fungi, which are sources of food for oribatid mites (Osono *et al.* 2002, 2006a,b; Kutorga *et al.* 2013; Magilton *et al.* 2019; Motiejūnaitė *et al.* 2014; Pen-Mouratov and Dayan 2019). Thus, faecal fertilisation may decrease the availability of the food preferred by mites. For example, high concentrations of phosphorus inhibit the development of mycorrhizal hyphae, while excess nitrogen interferes with the activity of the lignin-degrading enzymes of ligninolytic fungi (Osono *et al.* 2002, 2006b; Cao *et al.* 2011). Kolb *et al.* (2015) also noticed a negative correlation between the density of Oribatida and soil P concentration in cormorant colonies. According to Lemanski and Scheu (2004), fertilisation of the soil weakens the trophic links between microorganisms and microbial grazers and leads to changes in the diet of soil invertebrates. Most Oribatida are characterised by high trophic plasticity; however, the type of food affects their fertility and mortality. Thus, the reduced availability of food might limit the abundance of some species (Seniczak *et al.* 2017; Maraun *et al.* 2020). The enrichment of potassium in colonies was not huge; thus its effect on mites is likely masked by the influence of phosphorus and nitrogen.

Although cormorants create hostile habitats for most Oribatida species, some tolerate or maybe prefer such an environment. Among the taxa recorded in the colonies were for examples, *Punctoribates punctum* (Koch, 1839) and *Scheloribates laevigatus* which according to Seniczak *et al.* (2006) and Wasińska-Graczyk *et al.* (2009) showed a significant tolerance or even increased abundance in the presence of ammonia water and high dose of liquid pig manure (for second species small and medium dose caused opposite effect). Another example is *O. pectinate*, which are mites associated mostly with nests of for examples, birds (Rajski 1968; Skubała and Kalinka 2006).

The presence of cormorants can create optimal conditions for scavengers due to the availability of dead plant and animal remains. Also, a higher density of nematodes in topsoil may be beneficial mites that feed on nematodes (Pen-Mouratov and Dayan 2019). An example of a scavenger mite is *H. rufulus*, which is one of the most common species in colonies (Magilton *et al.* 2019). *Acrogalumna longipluma* is considered a secondary decomposer or fungivore. However, Melguizo-Ruiz *et al.* (2017) suggest that this species may function in part, as a predator, scavenger or omnivore. Oppiidae (e.g. *O. nova*) are also known for feeding on nematodes. According to Eissfeller *et al.* (2013), the densities of both groups are correlated.

Rhinopia nasuta occurred only in cormorant colonies and was the dominant species in Cols. II and III. This is a rare species. In Poland, it has been found only in one cave (without bats and guano) according to Maślak and Barczyk (2011). *Rhinopia nasuta* is known mostly from beech forests and soil with low pH and high C/N ratio and humus mass (Weigmann and Kratz 1981; Arabuli 2007; Eissfeller *et al.* 2013). Thus the fertilisation and acidification of soil by cormorant guano may create optimal conditions for *R. nasuta* populations. The density of *R. nasuta* is also associated with the density of nematodes. Thus like other Oppiidae, this species may be predatory (Eissfeller *et al.* 2013).

Although *R. nasuta* occurred in all the colonies, its abundance on each island was different. This species was the most common mite, in Cols. II and III. However, its constancy was low in Col. III (8%) because most samples were free of Oribatida. The colony on Lake Drawskie was the biggest (800 pairs); thus, its impact may be too strong for most Oribatida. *Rhinopia nasuta* was also identified in Col. I, although only four specimens were found. A more common species was *S. laevigatus*. This could be because of the specificity of the island. In contrast to

Col. II, the colony on Chrzypsko has very poor herbaceous vegetation, the forest canopy was bald and many of the trees were dead (the conditions on Col. III were intermediate between the mentioned colonies). These factors might lead to better insolation of soil and thus, to a change in soil temperature and moisture (Kunkel *et al.* 2016). This could explain the dominance of *S. laevigatus*, as this species is common in similar habitats such as meadows (Rajski 1967). On the other hand, it could create less optimal conditions for *R. nasuta* due to for example the lower humidity of the soil. Progressive deforestation in the colonies may lead to the replacement of *R. nasuta* by *S. laevigatus*. If this hypothesis is true, these mites could be used as bioindicators of cormorant activity and the development stage of a colony.

Another species common in the islands studied is *A. longipluma*, which was found in all colonies. One individual was found in Con. II. According to Rajski (1968), this is a rather rare species, being known from various microhabitats, like tree hollows, mosses, lichen or ant nests. They are also found in tree hollows with bird guano (Żbikowska-Zdun *et al.* 2006; Seniczak *et al.* 2012). A decrease in the abundance of some Oribatida due to the transformation of soil by cormorants may make accessible niches for *A. longipluma* and other more resistant species, which would explain, why they became the dominant species.

The influence of ornithogenic input on oribatid mite diversity has been poorly studied and the results do not display clear dependencies. Zmudczynska-Skarbek *et al.* (2017) found *T. velatus* in sites occupied by auks and gulls. Of the colonies studied only one individual of *T. velatus sarekensis* was found. It was from Col. III *Oribatula tibialis*, which was found in Col. I has also been recorded in soil from a colony of gulls and skuas. However, in both colonies, this species occurred in only one plot (Zmudczynska-Skarbek *et al.* 2017). *Oribatula tibialis* has also been found in ornithogenic soils from the breeding sites of the Svalbard Arctic tern (*Sterna paradisaea*) and snow bunting (*Plectrophenax nivalis*).

In summary, the transformation of soil by cormorants leads to a drastic change in the abundance of soil mites, Oribatida diversity and species compositions. Since the samples from each pair of islands (colony and reference site) were collected on the same day, thus we could exclude any seasonal variation. However, this does not apply overall, as the soil samples Załomie and Drawskie were collected in different months (May and June). Moreover, the fieldwork in Chrzypsko was in different years. Oribatida may display seasonal fluctuations of abundance (e.g. Seniczak *et al.* 2006). Thus, the sampling date may be an important factor. Additionally, cormorants are migratory birds. They leave colonies at the end of summer and come back in spring; thus, the impact of these birds is not constant over the year. For example, cormorants generally have a negative impact on trees; however, Molina-Montenegro *et al.* (2013) noticed the increased growth of trees on an island abandoned by these birds due to, among other things, the accumulation of organic material. This leads to the hypothesis that some species of Oribatida may recolonise islands during the cormorants' absence (between autumn and spring) and that their abundance gradually decrease, when new colonies form. This hypothesis could be verified in further studies, such as on the relation between seasonal dynamics of Oribatida and cormorants.

According to our results, the best potential indicators of the impact of cormorants on soil would be *R. nasuta* and members of Scherloribates, Suctobelbidae, Phthiracaridae and Nothrina. However, this work should be treated as a pilot study due to the small number of samples and because each island was sampled on only one day. More seasons and samples should be included in further research to confirm the observations of this study.

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