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Significant impact of allochthonous nutrient loads on microarthropods in forest soils

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Abstract

Aim of study: To investigate the impact of allochthonous material from piscivorous birds on forest soil microarthropod communities.

Area of study: Six study zones in the Curonian Spit peninsula (western Lithuania) were designated in *Pinus sylvestris* stands with nesting sites of the great cormorants, taking into account the relief and the duration of the ornithogenic impact.

Materials and methods: The total abundance of mites and Collembola and the species richness and diversity of Oribatida and Gamasina mites were assessed and compared.

Main results: The abundance of Collembola, Tarsonemidae and Acaridae mites positively correlated with ornithogenic activity, while Oribatida and Gamasina mites decreased significantly. The structure of microarthropod communities was similar in most of the studied zones, except for the active nesting zone and the abandoned part of the colony on the dune slope. The greatest species richness of Oribatida and Gamasina was found in the unaffected forest in the dune hollow, whereas the lowest value was found in the active nesting area and in the abandoned part of the colony on the dune slope. Of the environmental parameters studied, soil pH (r = - 0.725) and tree layer (r = 0.827) were those most significantly related to the changes of microarthropod communities.

Research highlights: We found that cormorant colonies have a strong impact on forest ecosystems and soil properties, leading to significant changes in soil microarthropod communities. Birds thus create a natural disturbance experiment that can help reveal the factors that determine the diversity and composition of natural microarthropod communities.

Additional key words: Oribatida; Gamasina; mites; Collembola; piscivorous birds; great cormorants; pine forest

Abbreviations used: EDXRF (energy dispersive x-ray fluorescence); MRPP (multi-response permutation procedure); NMDS (non-metric multidimentional scaling).

Authors' contributions: Field work: AP, DM and RT. Data collection: AP, RT and DM. Statistical analysis: RI and RT. Drafting of the manuscript: JM and AP. Critical revision of the manuscript: JM. Supervising the work: JM. Coordinating the research project: JM.

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Supplementary material (Table S1) accompanies the paper on *FS*'s website.

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Introduction

Soil is one of the most biologically rich habitats on Earth, and soil biodiversity is essential for ecosystem-level processes and functions, such as decomposition, mineralization and nutrient cycling, and associated ecosystem services (Bakker *et al.,* 2019). Biota of soils encompass a variety of life forms such as fungi, bacteria, archaea, and various invertebrates (Briones, 2014). Hyperdiverse array of soil fauna performs, in parts, such ecosystem functions as decomposition and nutrient mineralization (Meehan *et al.,* 2020). The dominant soil fauna includes the microarthropods, primarily mites (Acari) and springtails (Collembola), which are the most abundant and diverse faunal group of terrestrial ecosystems (Petersen & Luxton, 1982). Diversity within Collembola (Liiri *et al.,* 2002; Lenoir *et al.,* 2007) and mites (Heneghan & Bolger, 1998) has been reported to be positively related to increased mineralization and trophic interactions between organisms, allowing nutrient supply for root uptake. Consequently, diversity of microarthropod communities is considered a good indicator of environmental quality (Ponge *et al.,* 2003; Cassagne *et al.,* 2006; Blasi *et al.,* 2013; Urbanovičová *et al.,* 2014; Reis *et al.,* 2016). Soil microarthropods are sensitive to seasonal climatic changes and variations in soil moisture, organic matter content, pH, and concentrations of certain chemical elements, and their abundance

and diversity can change significantly following shifts in these factors (Tousignat & Coderre, 1992; Eisenhauer *et al.,* 2012).

Colonies of piscivorous birds alter terrestrial ecosystems through chemical and mechanical effects (Ellis, 2005, and the literature cited therein). Among the fish-feeding avian fauna, cormorants have the greatest impact on nesting sites due to the large size of colonies, dense nesting and large amounts of guano (Kameda *et al.,* 2000). As a result, they cause degradation of the ecosystems they invade, destroying the original vegetation and changing the properties of the soil. In this way, the cormorants create natural experimental sites that simulate enhanced nutrient inputs along with subsequent plant cover changes and soil exposure. These sites allow us to study the effects of allochthonous material on various organisms inhabiting bird-affected areas, including soil biota such as fungi (Osono *et al.,* 2002; Osono, 2012; Kutorga *et al.,* 2013; Motiejūnaitė *et al.,* 2021), myxomycetes (Adamonytė *et al.,* 2013), bacteria and archaea (Domínguez *et al.,* 2017). In Lithuania, the largest and oldest colony of great cormorants *(Phalacrocorax carbo sinensis)* is located on the Curonian Spit. In 25 years, since the first nests appeared in 1989 (Žydelis *et al.,* 2002), the colony has expanded to an area of 6.82 ha by the end of 2014 (Matulevičiūtė *et al.,* 2018). The aim of this study was to investigate the effect of a cormorant colony on the abundance and diversity of soil-inhabiting microarthropod communities. The specific objectives were: 1) to establish the abundance of soil microarthropods in a gradient of the duration and intensity of cormorant colony impact; 2) to establish changes in the percentage of different groups of microarthropods in the study zones; 3) to assess the existence of a significant correlation between soil microarthropod communities, plant coverage and soil chemical parameters.

Material and methods

Study site and design

The study area was situated in the Curonian Spit peninsula in western Lithuania (55°31′N 21°06′E). The peninsula is an elongated stretch of sand dunes surrounded by brackish water bodies, specificaly the Baltic Sea to the west and the Curonian Lagoon to the east. The climate on the Spit is intermediate between maritime and continental with an average annual rainfall of ≈ 700 mm, and the average annual temperature ranges from 17.8 °C in August to -1.7 °C in January and February (Bukantis, 2013). Seventy percent of the Spit is covered by forests, mostly conifers (80 %). Old-growth pine (*Pinus sylvestris* L.) and mixed pine-hardwood stands occur, but only in patches and only on parabolic dunes close to Juodkrantė settlement (Morkūnaitė *et al.,* 2011).

The study was conducted in 2010 in the great cormorant colony, established on the east-facing (leeward) slope of the dune, from the hollow to ridge (altitude ranging from 0 to 34 m). The dune ridge and terrace are characterized by dry conditions and dry arenosol soils, while the soils of the dune hollow are wetter and become swampy at the lowest elevations (Gudelis, 1998; Peyrat, 2007). The upper part of the cormorant colony area was originally occupied by a 110-year old pine forest approximately, whereas the terrace of the slope was occupied by a 230-year old pine forest. Dune hollows were formerly occupied by a 230-year old pine and spruce forest (Jončys & Paulaitis, 1987). At the time of the study, most of the conifers on the slopes of the dune and in the hollow were dead or dying.

Six zones were selected for the study, taking into account forest type, age, slope exposure, and different timespan of bird colony activity. Three repetition plots (100 m^2 each) were established in each of the zones (Fig. 1). The selected zones (called A, B, C, D, E and F) were characterized as follows:

− A, was the oldest, abandoned part of the colony in the dune hollow, formerly was a pine and spruce forest on mesotrophic temporarily wet soil. All of the mature coniferous trees have already died, and there were only a few young, stunted *Picea abies, Quercus robur* and *Betula pubescens.* Most of the area was overgrown with tall herbs, and shrubs *Sambucus* nigra and *S. racemosa.*

− B, was the oldest, abandoned part of the colony on the dune terrace: there were no living trees, a few standing dead, barkless trees of *P. sylvestris.* The litter consisted of twigs, larger and smaller pieces of pine bark, fish scales and bones. Nitrophilous plant communities began to form here, with few remaining mesotrophic plants. The moss layer was absent.

− C, was the most active part of the colony with the highest concentration of nests, on the upper dune terrace: pines dead or dying but still with bark, low shrub cover formed by *Sorbus aucuparia* and *Sambucus* spp., with sparse dying individuals of *Juniperus communis.* Herb layer coverage reached 10% with a predominance of nitrophilous species. The moss layer was absent.

− D, was the edge of the colony with the very recent and still rather few nests in 2010, on the upper part of the dune, pine trees were alive, but their crowns had thinned. The shrub layer was somewhat thickened by *S. aucuparia* and young *Sambucus* spp. while *J. communis* appeared weakened. The herb layer was depauperate due to the disappearance of some oligotrophic plants, patches of bare soil appeared and the moss layer was thinned.

− E, was a relatively undamaged oligotrophic pine forest on top of the dune with typical pine forest vegetation and very few mesotrophic and eutrophic plants. It represents the control area outside the colony.

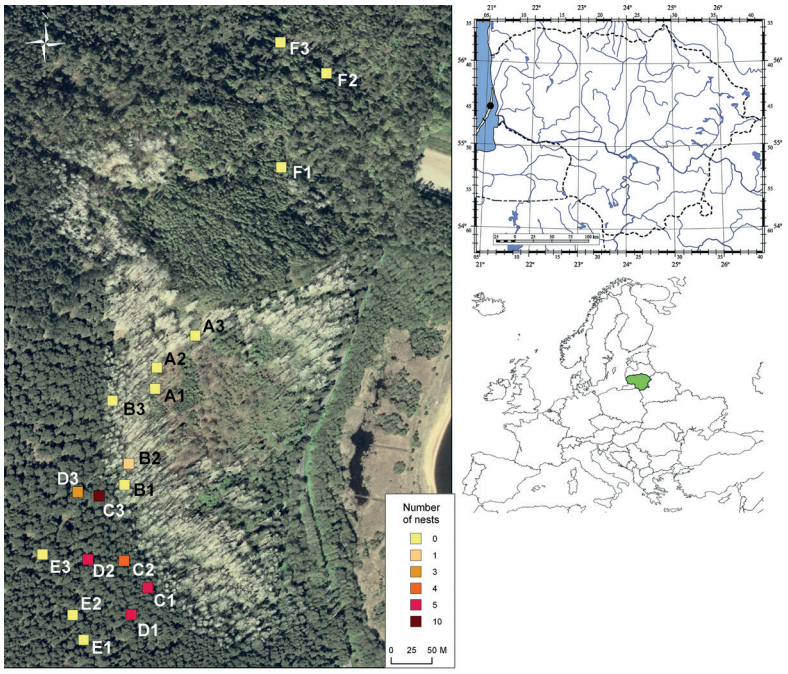

Figure 1. Map of the study plots in the cormorant colony with the location of the study area in Lithuania (black dot) and in Europe. Scale of the study area is presented in the legend. The colors of the squares indicate the number of cormorant nests per plot, the letters refer to the zones, the numbers refer to the repetitions of the study plots. The study zones have been described in the text.

− F, was a mesotrophic mixed forest in a dune hollow. Trees were predominantly *P. sylvestris* and *P. abies,* with some admixture of *B. pubescens* and *Q. robur*. Control area outside the colony.

A detailed description of the vegetation in each zone is provided by Matulevičiūtė *et al.* (2018).

Environmental parameters

Topsoil samples were taken for analysis from each repetition plot in six zones. At five points (four corners and one central point) in each plot, five soil sub-samples (15 × 4.5 cm) were taken with a round soil core (25 sub-samples per plot). From each subsample, 5 cm of topsoil was collected and merged into one sample per plot (3 plots × 6 zones = 18 samples). Two parts were separated from each sample: the first one was used to determine soil pH, total nitrogen, and total carbon, and the second one was used to measure P, K, Mg, Ca, Al, Na, and Cl concentrations. The contents of P, K, Mg, Ca, Al, Na and Cl were analysed by EDXRF method. For a detailed description of the laboratory procedure see Matulevičiūtė *et al.* (2018). The rest of the analyses were performed at Labtarna Chemical Laboratory in Vilnius. Total nitrogen (N) was measured following the Kjeldahl method. The samples were prepared following the standard method ISO 6498:1998, the total N content was determined following the standard method LST EN ISO 5983-1:2005. A Tecator 2200 Kjeltec Auto Distillator and a Schott TitroLine 96 titrator were employed for distillation and titration of the sample solutions, respectively. Total carbon (C) was determined after dry combustion following the standard method ISO 10694:1995; pH was measured following the standard method ISO 10390:2005.

Vegetation was studied during the first ten days of September by the *relevé* method (Braun-Blanquet, 1964) in the same repetition plots where the soil samples were collected. The vertical structure of the vegetation was investigated by assessing the coverage of tree, shrub, field, and bottom layers. Values were rounded to two decimal points in cases with coverage < 1%, to one decimal point in cases with coverage of 1-10%, and to whole numbers in cases with coverage > 10%.

Microarthropod sampling

To assess the microarthropod communities, the topsoil (0–5 cm) was collected from the experimental zones A–F, from each repetition plot, in August 2010. Five samples were taken (four corners and one central point) in each plot by a round soil corer 5 cm × 5 cm × 5 cm. The samplings were performed nearby the soil sampling sites for chemical analysis. In each plot, the samples were processed separately (5 samples × 3 plots × 6 zones = 90 soil samples). The soil samples were placed in individual plastic bags and taken to the laboratory. Each sample was

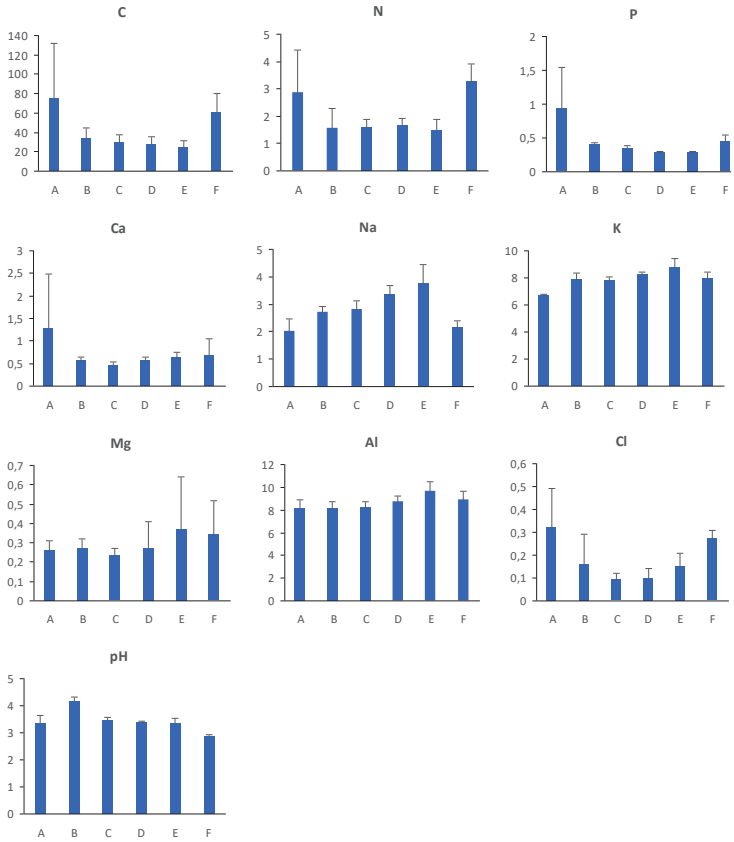

Figure 2. Soil parameters of the zones A–F. Mean values and standard deviations are presented. Elemental concentrations in topsoil (A0-5) are in g/kg. The study zones have been described in the text.

transferred to a modified Berlese-Tulgren funnel for removal of microarthropods over a 5-day period. The extracted microarthropods were stored in 70 % ethanol for further sorting and identification.

The specimens were classified into the following groups: (1) Collembola, (2) Mesostigmata (Gamasina), (3) Oribatida, (4) Astigmata (Acaridae), (5) Prostigmata (Tarsonemidae) and other mites. Only Oribatida and Gamasina, the most abundant groups of mites, were identified to the genus or species level. The microarthropods were morphotyped under dissecting microscope (Nikon SMZ 800). Representative (adult) individuals were slide-mounted in Euparal and identified under a compound microscope (Nikon Eclipse Ci) using keys from Ghilarov & Krivolutsky (1975), Ghilarov & Bregetova (1977) and Balogh & Balogh (1992).

Data analysis

Abundance of all microarthropods and species richness of Oribatida and Gamasina in each study zones were calculated. The community structure of microarthropods per zone was expressed with percentages. To estimate the species diversity of Oribatida and Gamasina, Shannon diversity index (H') (Shannon, 1948) was calculated. Multi-response permutation procedure (MRPP) was applied to test whether there were significant differences among the groups (zones A, B, C, D, E, F) of sample units based on similarities within group (i.e., environmental parameters, microarthropod abundance or species richness). In the analysis, "A" is a measure of effect size and indicates the extent to which the same sample units within a group are similar to each other. The value of "A" can range from 0 to 1. As the similarity of sample units within groups (zones) increases, "A" increases. A low p-value (<0.05) indicates that sample units belonging to a group (zone) are statistically more similar to each other than would be expected if they belonged to other groups (McCune & Grace, 2002). To investigate the impact of the study zones on the composition of Oribatida and Gamasina communities, non-metric multidimensional scaling (NMDS) was used, applying Sørensen (Bray-Curtis) dissimilarity. We used species abundance in the main matrix. Species with abundance below five individuals were excluded from analysis.

NMDS was also used to determine the relationship between microarthropod species composition in the experimental zones and environmental variables (soil and vegetation characteristics). A secondary matrix with soil and vegetation variables which differed significantly among the zones (Table 1) was used as an overlay on

main matrix. Spearman's rank correlation was used to identify significant correlations of ordination (axes 1 and 2) with vegetation cover and soil parameters. Parameters that showed a significant correlation with configuration ($r \geq 0.5$) were presented as vectors. All statistical analyses were performed using PC-ORD ver. 6.0 (McCune & Mefford, 2011).

Results

Environmental parameters

The studied environmental parameters are shown in Figs. 2 and 3. Analysis of the chemical elements in the topsoils showed the existence of gradients from the zones of the bird colony to the control zones (Table 1, Fig 2). The highest content of total C was recorded in the zones of dune hollow (A and F). The peak of P content was found in the zone A, where soil was originally richer and was supplemented by both long-term bird influence and runoff from the more elevated parts of the colony. Conversely, the levels of K and Na were highest in the control zone E. No significant differences were found for N contents in individual zones.

As occurred for the acidity of the topsoil, the highest pH values were found in the zones of longest bird influence (zones A and B). Acidic soils are typical of pine-dominated forests, and they remained acidic in all the studied zones. However, in the zones of long-term bird influence A (dune hollow) and B (dune terrace), the pH values increased significantly compared to the respective control zones F and E.

Ornithogenic impact on plant cover was evident in all layers except the shrub layer (Table 1), which can be explained by the replacement of mesotrophic shrub species by eutrophic and nitrophilous shrubs. Significant ($p < 0.05$) changes in the tree layer showed a gradient from the unaffected forest and edge of the cormorant colony (zones E and D, respectively) to areas of short-term (zone C) and long-term (zones A and B) bird impact (Table 1, Fig. 3), due to bird-caused damage and subsequent tree mortality. The tree layer was dense in the non-impacted zones, sparse in zone C, while in zones A and B old trees were dead and there were no young trees or solitary stunted individuals. Decreased cover of the field and bottom layers and an increase in the percentage of open forest cover were indicators of the short-term impact of birds. Significant changes were observed at the edge of the colony (zone D) and in the area of highest nest concentration (zone C), where the original pine forest vegetation disappeared, but eutrophic plants did not colonise large areas yet. In the abandoned parts of the colony (zones A and B), the area of open forest floor decreased, while the area of the field layer increased again following the emergence of eutrophic and nitrophilous herbaceous plants.

Abundance and species richness of microarthropods

A totality of 65,028 specimens of Oribatida, Gamasina, Acaridae, Tarsonemidae, other unidentified mites and Collembola, has been collected. The highest number of individuals (15,344) was found at the margin of the colony (zone D), whereas the lowest (6,637) was found in the oldest, abandoned part of the colony (zone A) (Fig. 4).

The abundance of microarthropods differed across the study zones (Table 2). Oribatid mites showed a distinct gradient of abundance from unaffected forest (zones E and F) to the sites of long-term impact (zones A and B) (Fig. 4). The abundance of Gamasid mites and Collembola also varied as a result of ornithogenic impact, but the gradient was not as obvious. Zones D and A stood out not

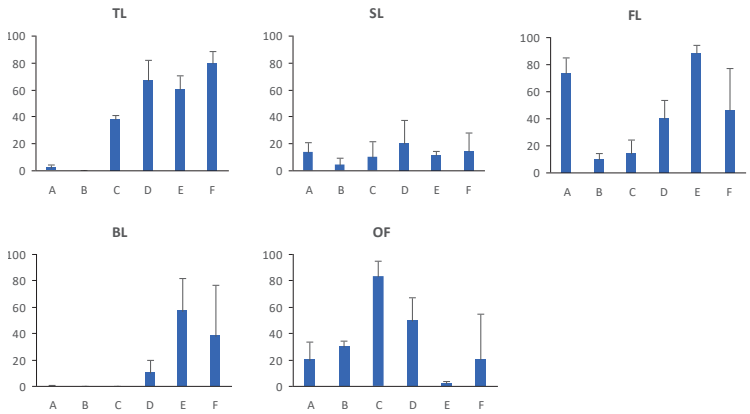

Figure 3. Vegetation parameters of the zones A–F. Mean values and standard deviations are presented. Coverage of vegetation layers in study zones are presented in percents. Abbreviations of the layers are as follows: TL = tree layer; SL = shrub layer, FL = field layer; BL = bottom layer; OF = open forest floor. The study zones have been described in the text.

Table 1. Results (A-values) of multiple response permutation procedure (MRPP) testing for differences of soil parameters and vegetation coverage between the studied zones (A, B, C, D, E and F), are shown. The MRPP test for pairwise comparisons between zones was not performed for those variables where the MRPP test comparing all zones was > 0.05, *i.e.* not significant (shown as – in the Table). The study zones have been described in the text.

Zones	Soil parameters						Vegetation coverages[1]			
	pH	C	P	K	Na	Cl	TL	FL	BL	OF
All	0.465***	0.162*	0.359***	0.339**	0.320**	0.212*	0.628***	0.389**	0.483**	0.424**
A-B	0.333*	0.158ns	0.206*	0.365*	0.159ns	0.095ns	0.167ns	0.489*	-	0.063ns
A-C	-0.063ns	0.126ns	0.238*	0.429*	0.079ns	0.349*	0.481*	0.422*	-	0.365*
A-D	0.098ns	0.079ns	0.238*	0.429*	0.349*	0.302*	0.429*	0.235*	0.087ns	0.252*
A-E	-0.111ns	0.111*	0.238*	0.429*	0.381*	0.143*	0.489*	0.194*	0.489*	0.405*
A-F	0.319*	0.032ns	0.048ns	0.429*	-0.095ns	0.000ns	0.490*	0.048ns	0.388*	0.111ns
B-C	0.428*	-0.105ns	0.146ns	-0.095ns	-0.063ns	-0.095ns	0.740*	-0.095ns	-	0.429*
B-D	0.489*	-0.032ns	0.428*	-0.048ns	0.302*	-0.048ns	0.643*	0.381*	0.046ns	0.184*
B-E	0.428*	-0.048ns	0.429*	0.079ns	0.238*	-0.063ns	0.740*	0.489*	0.643*	0.489*
B-F	0.489*	0.413*	-0.048ns	-0.127ns	0.238*	0.079ns	0.740*	0.262*	0.524*	0.143ns
C-D	0.184ns	-0.032ns	0.349*	0.111ns	0.127*	-0.095ns	0.405*	0.116ns	0.095ns	0.258ns
C-E	-0.088ns	-0.088ns	0.365*	0.222*	0.159*	0.079ns	0.560*	0.439*	0.643*	0.489*
C-F	0.489*	0.381*	-0.000ns	-0.063ns	0.254*	0.429*	0.560*	0.056ns	0.523*	0.206*
D-E	-0.012ns	-0.063ns	0.016ns	0.048ns	-0.032ns	0.032ns	-0.037ns	0.371*	0.191*	0.560*
D-F	0.560*	0.254*	0.286*	0.048ns	0.429*	0.397*	0.002ns	-0.095ns	-0.048ns	0.116ns
E-F	0.456*	0.428*	0.270*	0.063ns	0.413*	0.190*	0.267ns	0.218*	-0.117ns	-0.081ns

[1] TL = tree layer; FL = field layer; BL = bottom layer; OF = open forest floor. p-values: * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001, ns > 0.05.

only by the total number of individuals, but also by the average (per sample) abundance of microarthropods. Significant variation between samples ($p < 0.05$) was recorded in the zones C and B.

Oribatid mites predominated in all the studied zones, ranging from 83.3% to 40.4% of individuals, except for the zone B, where their percentage decreased (Fig. 5). In this zone, they accounted only for the 16.3% of all

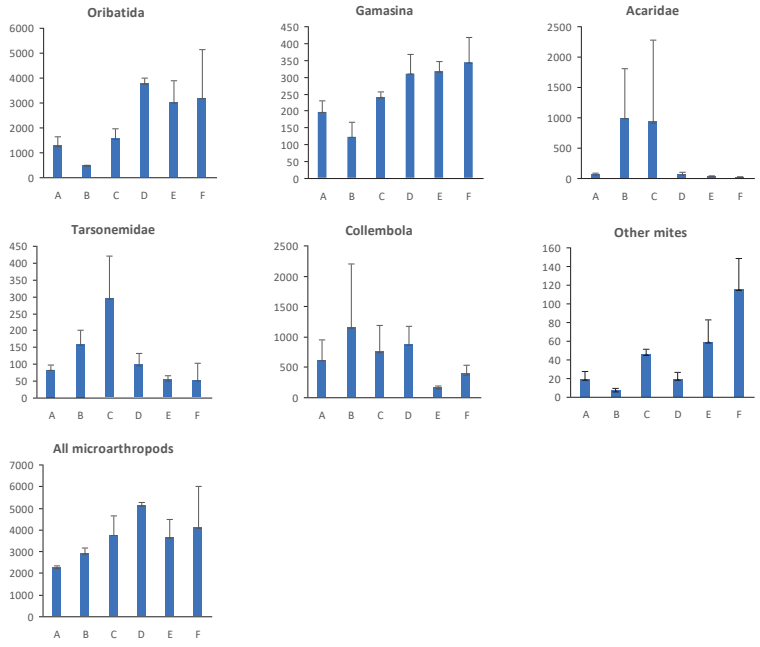

Figure 4. Abundance of microarthropod groups (individuals per zone) sorted among the study zones. Mean values and standard deviations are presented. The study zones have been described in the text.

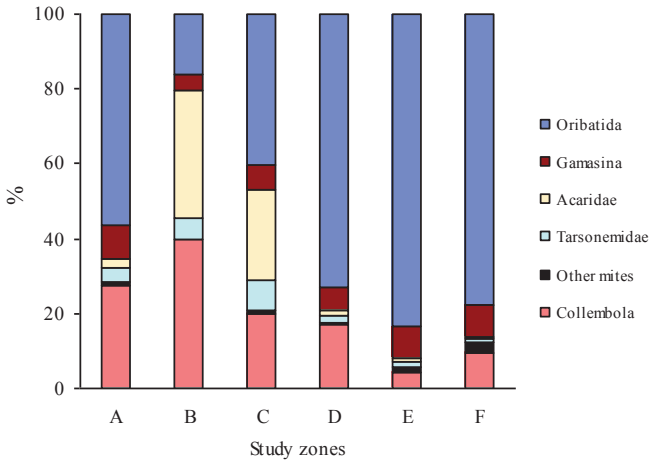

Figure 5. Structure of the microarthropod communities (% of individuals) in the study zones.

microarthropods. Acarid mites and Collembola dominated in the zone B, accounting for the 34% and 39.8% of all the microarthropods, respectively (Fig. 5). The percentage of Collembola was generally higher in all the areas affected by the birds, being at the peak in the oldest, abandoned parts of the colony (zones A and B). The percentage of Gamasid mites was similar in all study zones, with a slight decrease in bird-influenced areas of the dune terrace, especially in zone B. Tarsonemid mites were spread in all studied zones, although their presence was more pronounced in all areas affected by birds. Other unidentified mites accounted for a small fraction of the remaining microarthropods (from 0.23% to 2.81%). Changes in Oribatida abundance correlated positively ($p < 0.05$) with changes in Gamasina and negatively with Acaridae abundance, while Acaridae correlated positively with Collembola and Tarsonemidae abundance.

In the two predominant suborders of mites (Oribatida and Gamasina), the 37.3% and 51.3 % of specimens, respectively, contained juvenile stages (*i.e.* larvae and nymphs). Out of a total of 26,992 adults of both groups, 72 species of Oribatida and 50 species of Gamasina were identified (Table S1 [suppl]). In these two groups, species richness (MRPP, A = 0.433, $p \leq 0.001$) and abundance (MRPP, A = 0.455, $p \leq 0.001$) differed between studied zones. The highest species richness was found in zone F (83 species), while the lowest was found in zone B (41 species). Accordingly, the highest mean species abundance was found in zone F (2855 ± 653) and the lowest in zone B (457 ± 208). The mean Shannon diversity index (H') between Oribatida and Gamasina was 2.702 ± 0.244), and the diversity indices did not differ between zones (MRPP, A = 0.071, $p = 0.214$).

Correlation between Oribatida and Gamasina communities and environmental parameters

Of all the tested environmental parameters, field ($r = 0.621$), tree ($r = 0.827$), bottom layer coverage ($r = 0.684$), and soil pH ($r = -0.725$) were significantly associated with differences in arthropod communities across the zones studied, as shown by NMDS ordination (Fig. 6). All these factors strongly correlated with axis 1 (80 % of variations) and reflected bird influence, especially the long-term one. Percent of open forest floor ($r = 0.532$), amounts of Na ($r = 0.602$), K ($r = 0.506$), and Cl ($r = -0.666$) correlated with axis 2 (explaining 7% of variation) and reflected the combined effects of topography and bird impact. In the ordination, microarthropod communities were grouped separately for all study zones, but a clear separation was noted only for areas under the longer influence of birds (zones A–C). Three species, *Macrocheles penicilliger, Rhodacarellus silesiacus* (both Gamasina) and *Furcoribula furcillata* (Oribatida) showed preference for the zones under ornithogenic influence. Environmental preferences of oribatids *Oribatula tibialis, Scheloribates confundatus* and *Eniochthonius minutissimus* correlated with axis 2 in the upper part of the ordination, where plots of D zone are grouped (Fig. 6).

Discussion

The impact of cormorant colonies on forest soils is complex, and the factors involved are difficult to disentangle. Cormorant excreta, which can contain up to 14% of P and 14.5% of N, and can result in annual loads of 181–1,120 kg/ha of N and 112–786 kg/ha of P, depending on bird density (Klimaszyk & Rzymski, 2016), significantly affect soil chemistry. In addition, eggshells, dead birds, bird pellets and regurgitated fish, as well as forest litter generated from the activities of cormorants, also changed soil chemistry (Sanchez-Piñero & Polis, 2000). This situation increases the content of nutrients and other elements (*e.g.,* Ca and Na) and raises the pH of the soil surface, the latter mainly due to the decomposition of uric acid in bird feces, which rapidly decomposes into ammonia (Bachrach, 1957). These changes, along with the direct impact of birds, such as mechanical damage to trees, lead to radical transformation in the quality and quantity of vegetation cover (Matulevičiūtė *et al.,* 2018), as well as in the structure and functioning of soil fungi and myxomycete communities (Osono, 2012; Adamonytė *et al.,* 2013; Kutorga *et al.,* 2013; Motiejūnaitė *et al.,* 2021). All these ecosystem elements are also crucial for microarthropods because they provide habitat and food. It was found that soil microarthropod diversity and community structure depend on the structure and diversity of plant, soil fungi and myxomycete communities (Hågvar, 1982; Klironomos & Kendrick, 1995; Kataoka & Nakamori, 2020). Our study showed significant changes in soil microarthropod abundance and community structure in a complex gradient of cormorant colony impact.

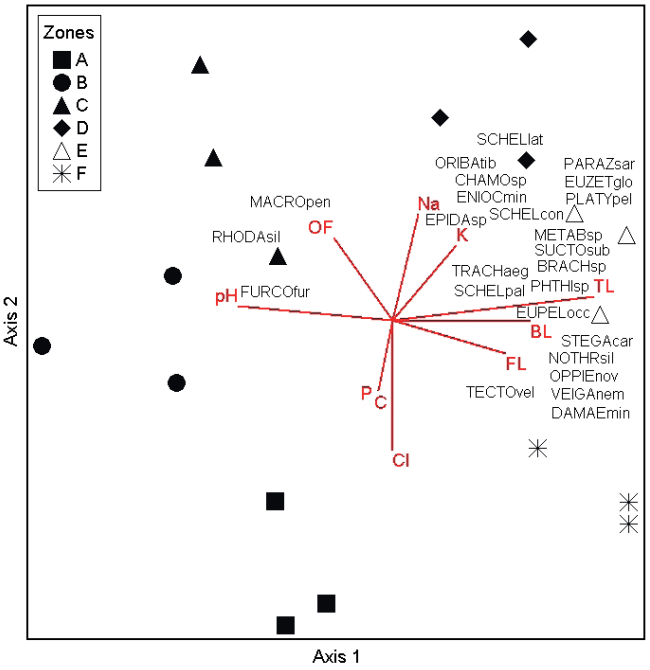

Figure 6. Two-dimentional solution of non-metric multidimentional scaling (NMDS) ordination with final stress value of 8.189 (67 iterations) of the plots across the zones (A, B, C, D, E and F) based on the Oribatida and Gamasina mite community. Environmental variables (soil parameters and vegetation) and mite taxa, which had significant correlation ($r^2 \geq 0.5$) in the ordination configuration, are shown. First axis explains 80% of variables; second, 7%. Abbreviations for environmental variables: TL, tree layer; FL, field layer; BL, bottom layer; OF, open forest floor. Mite species: BRACHsp, *Brachychthonius* sp.; CHAMOsp, *Chamobates* sp.; DAMAEmin, *Damaeobelba minutissima;* ENIOCmin, *Eniochthonius minutissimus;* EPIDAsp, *Epidamaeus* sp.; EUPELocc, *Eupelops occultus;* EUZETglo, *Euzetes globulus;* FURCOfur, *Furcoribula furcillata;* MACROpen, *Macrocheles penicilliger;* METABsp, *Metabelba* sp.; NOTHRsil, *Nothrus silvestris;* OPPIEnov, *Oppiella nova;* ORIBAtib, *Oribatula tibialis;* PARAZsar, *Parazercon sarekensis;* PHTHIsp, *Phthiracarus* sp.; PLATYpel, *Platynothrus peltifer;* RHODAsil, *Rhodacarellus silesiacus;* SCHELcon, *Scheloribates confundatus;* SCHELlat, *Scheloribates latipes;* SCHELpal, *Scheloribates pallidulus;* STEGAcar, *Steganacarus carinatus;* SUCTOsub, *Suctobelbella subtrigona;* TECTOvel, *Tectocepheus velatus;* TRACHaeg, *Trachytes aegrota;* VEIGAnem, *Veigaia nemorensis.*

Collembola are among the most widespread and numerous terrestrial arthropods, characteristic of organic-rich substrates. Together with other members of the soil fauna, they are important for soil formation as well as for conversion and decomposition processes, playing a role in two key stages of ecosystem functioning: soil organic matter dynamics and nutrient mineralization (Jucevica & Melecis, 2005; Cassagne *et al.,* 2006). In this study, Collembola abundance was significantly higher in zones with ornithogenic influence, compared to unaffected forest on the dune slope, reaching a peak abundance in zone under the longest bird influence on the dune terrace. Towns *et al.* (2009) and Zmudczynska *et al.* (2012) reported similar results in their studies of the islands of New Zealand and Spitsbergen, although Kolb *et al.* (2010) found that in the Stockholm Archipelago, the density of Collembola decreased on active cormorant islands. In a more recent work, Kolb *et al.* (2015) stated that the density of Collembola in litter samples near cormorant nests was lower than in samples taken 3-20 m away from the nests. Kolb *et al.* (2015) suggested that the differences between their results and those of Towns *et al.* (2009) and Zmudczynska *et al.* (2012) are due to the different nesting behaviour of seabirds in different systems and habitat conditions. The guano of tree-nesting species is deposited directly under the nests in Stockholm archipelago, meanwhile in the case of ground-nesting species in islands of New Zealand and Spitsbergen, guano is spread more uniformly over the area. Collembola numbers were five-fold higher in the plots with the highest nest density compared to unaffected forest, but lower than in abandoned parts of the colony and at the colony edge, which is consistent with the findings of Kolb *et al.* (2015). It is to be noted, however, that initial input of guano at the edge of the colony and its residual effect in the oldest, abandoned zones stimulated abundance of Collembola.

In agreement with the study by Kolb *et al.* (2015), we found that the abundance of acarid mites increased significantly in areas with intensive and long-term bird impact on the dune slope. Acarids are mostly fungivorous and commonly occur in decaying organic matter. Many other species are facultatively phytophagous or are associates of various insects, or inhabitants of vertebrate nests. This group also includes parasites of birds and mammals (Proctor & Owens, 2000) and therefore the presence of cormorants may benefit them.

Tarsonemid mites are predominantly free-living fungivores, inhabiting dung, bird and small mammal nests, many of them being found in the above-ground layer (Kaliszewski *et al.,* 1995). In our study, the abundance of this group of mites was significantly higher in areas of intensive and short-term cormorant influence, with a peak in the active zone.

Oribatid mites are among the most abundant and diverse microarthropods in forest soils, and they contribute significantly to the decomposition process as microbial grazers and saprophages (Hansen, 2000). The diversity and composition of oribatid communities are largely determined by local habitat attributes, being also considered indicators of clean, naturally-formed soil (Hansen, 2000). In the present study, oribatid abundance was two-fold higher in unaffected forest compared to areas with long-term ornithogenic impact, which is consistent with the results obtained by Kolb *et al.* (2015). However, the highest abundance of these mites was recorded at the edge of the colony, where changes in vegetation were significant, although soil chemistry was comparatively stable. Oribatid species richness was highest at the edge of the colony and outside of it. Ruf & Beck (2005) stated that species numbers and oribatid abundance in general decline rapidly in

Table 2. The results (A-values) of multiple response permutation procedure (MRPP) testing for differences in microarthropod abundance between studied zones (A, B, C, D, E and F) are shown. The study zones have been described in the text.

Zones	Oribatidae	Gamasina	Acaridae	Tarsonemidae	Collembola	Other mites
All	0.332***	0.132***	0.099***	0.088***	0.145***	0.245***
A-B	0.241***	0.042*	0.042ns	-0.021ns	0.042ns	0.091**
A-C	0.023ns	0.000ns	0.118***	0.120**	-0.013ns	0.042ns
A-D	0.343***	0.098**	-0.003ns	-0.004ns	-0.016ns	0.009ns
A-E	0.281***	0.114***	-0.005ns	-0.000ns	0.201***	0.161***
A-F	0.144**	0.064*	0.005ns	0.011ns	0.051*	0.229***
B-C	0.235***	0.101***	0.016ns	0.083*	0.020ns	0.243***
B-D	0.466***	0.219***	0.013ns	-0.008ns	0.024ns	0.215***
B-E	0.448***	0.245***	0.067**	-0.002ns	0.093***	0.305***
B-F	0.301***	0.150***	0.109***	0.021ns	0.104***	0.327***
C-D	0.205***	0.041ns	0.063**	0.076*	-0.014ns	0.027ns
C-E	0.137***	0.069*	0.153***	0.209***	0.238***	0.023ns
C-F	0.078 *	0.032ns	0.236***	0.201***	0.054*	0.094**
D-E	0.010 ns	-0.002ns	0.017ns	0.031ns	0.231***	0.172***
D-F	0.020 ns	0.004ns	0.056*	0.067*	0.071*	0.253***
E-F	0.024 ns	0.009ns	-0.018ns	-0.004ns	0.268***	0.023ns

p values: * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001, ns > 0.05.

the sequence from forest to grassland or arable land, while Kitazawa & Kitazawa (1980) and Bielska & Paszewska (1997) showed that application of compost and manure can sometimes stimulate oribatid populations in the soil. These outputs may explain the significant decrease in oribatid abundance in zone with no tree layer and the increase at the edge of the colony, where initial guano fertilization took place.

Gamasid mites, which are known to be predators that regulate populations of other microarthropod groups (Huhta *et al.,* 1998), were most abundant in the unaffected forest. Their abundance gradually declined as bird impact increased, as well as their species richness. This contradicts the findings of Kolb *et al.* (2015), who found a higher abundance of these mites near cormorant nests. The abundance pattern of the gamasid mites in our study corresponded to the abundance of their potential prey, oribatid mites. However, the abundance of gamasids did not follow the abundance pattern of Collembola, another group of arthropods that gamasid mites feed on (Koehler, 1999).

Only three mite species showed a clear preference for ornithogenic effects: *Macrocheles penicilliger*, *Rhodacarellus silesiacus* (Gamasina) and *Furcoribula furcillata* (Oribatida). *Macrocheles penicilliger* is a typical coprophilous mite, often found in grazing areas where it forms coprophilous communities, feeding on eggs and larvae of flies, nematodes and other mites of the community. Along with other coprophilous mites, *M. penicilliger* colonises habitats where dung and carrion are present (Niogret *et al.,* 2007). *Rhodacarellus silesiacus* is characteristic of a range of xerothermophilous habitats (Manu *et al.,* 2016). *Furcoribula furcillata* typically inhabits coniferous forests, being frequently found on dead wood (Huhta *et al.,* 2012); which is abundant in cormorant-affected zones (Iršėnaitė *et al.,* 2019), but also on bird plumage (Krivolutsky & Lebedeva, 2004).

Three oribatid mites, *Oribatula tibialis*, *Scheloribates confundatus* and *Eniochthonius minutissimus*, preferred the edge of the colony, where ornithogenic impact was short-term and limited. These species are ubiquitous fungivorous mites, also known from ornithogenic environments (Krivolutsky & Lebedeva, 2004). *Oribatula tibialis* is a phytotophagous species (Skubala & Kafel, 2004) that lives in moss cushions, deadwood, leaf litter (Brückner *et al.,* 2017) and pine wood (Klimek & Chachaj, 2018). *Scheloribates confundatus* is a secondary decomposer, feeding predominantly on fungi, litter (Schneider *et al.,* 2004), and in bird feathers (Krivolutsky & Lebedeva, 2004). *Eniochthonius minutissimus* is very abundant in compost piles (Seniczak *et al.,* 2009), mainly feeding on fungi, but also on forest litter (Schneider *et al.,* 2004).

Regarding soil chemical parameters, pH was the factor that most significantly affected microarthropod communities. That pH is a key factor in changes in microarthropod abundance and community structure has also been demonstrated by Hågvar & Amundsen (1981), Hågvar (1990), Klironomos & Kendrick (1995), etc. In addition to the direct ornithogenic impact, which led to changes in soil chemistry, other factors related to the impact of birds, such as reduced tree cover and subsequent mortality, a reduction in the field and bottom layers, and an increase in the percentage of open floor, have also had a significant

impact on the soil microarthropod communities. This can be partly explained by changes in litter type and quality, which is known to strongly influence microarthropod communities (Hansen, 2000). It is also known that the loss of tree cover and increased areas without plant cover affect the composition and abundance of the microarthropod community (Lindo & Visser, 2004; Meloni *et al.,* 2020). In our study, topography also played a role in microarthropod abundance and community composition because the colony (especially the abandoned parts) was located on a dune slope and in a dune hollow, where the initial soil type and humidity differed. Although the experimental design was not replicated, and it was not possible to establish how similar the forest plots and microarthropod communities were before the appearance of the colony, it is clear that any inherent differences would have been relatively insignificant compared to the subsequent impact of birds.

Cormorant colonies have a strong impact on forest ecosystems, including a very obvious impact on vegetation, microbial species and soil properties, leading to changes in soil microarthropod communities. Birds thus create a natural disturbance experiment that can help in revealing the factors that determine the diversity and composition of natural microarthropod communities. This knowledge contributes to the study of soil fauna under ecological disturbance, the need for which has been pointed out by Parisi *et al.* (2005) for assessing soil quality. We found that different groups of soil microarthropods responded differently to cormorant colony activity: while the abundance of Collembola, Tarsonemidae and Acaridae mites was positively correlated with ornithogenic activity, the abundance of Oribatida and Gamasina mites, which are dominant in undisturbed forest soils, was reduced significantly. Both direct effects of birds (changes in soil chemistry, especially pH) and indirect effects (changes in vegetation cover) have had a significant impact on microarthropod communities.

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