Turkish Journal of Zoology

http://journals.tubitak.gov.tr/zoology/

Research Article

Turk J Zool
(2020) 44: 303-311
© TÜBİTAK
doi:10.3906/zoo-2003-24

Impact of overwintering cormorants (*Phalacrocorax carbo*) on springtail (Hexapoda: Collembola) communities of the Azov and Black Sea coastal forests

Ruslan A. SAIFUTDINOV[1,2,*], **Daniil I. KOROBUSHKIN**[1]
[1]A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia
[2]Kazan (Volga Region) Federal University, Kazan, RT, Russia

Received: 16.03.2020 • **Accepted/Published Online:** 22.03.2020 • **Final Version:** 13.07.2020

Abstract: Nesting water bird colonies may act as important drivers of aquatic-terrestrial nutrient turnover in coastal ecosystems. By depositing a large amount of guano, they induce changes in the structure of soils, flora, and fauna. However, little is known about how nesting water bird colonies influence soil fauna, especially in a Mediterranean type of coastal landscape. In this study, focus was placed on how time had elapsed since the last overwintering activity of cormorant colonies, as a factor that affects the structure of springtail communities and edaphic parameters in the Black and Azov Sea coastal forest ecosystems. Black Sea coastal forests with active overwintering cormorant colonies have been characterized by a decreased total abundance, genus richness, and an abundance of certain functional groups of springtails. In contrast, in the coastal forests of the Azov Sea, where the last cormorant overwintering activity was observed 8 years ago, the total abundance of collembolans, and particularly epiedaphic species, had increased in comparison with the control sites. It was concluded that the overwintering activity of cormorants had a negative effect on springtails in previously undisturbed areas within the Mediterranean coastal forests. Nevertheless, the long-term absence of cormorant colonies may lead to the recovery of collembolan total abundance and genus richness in the previously affected areas.

Key words: Soil fauna, seabirds, disturbance, functional traits, aquatic subsidy, nutrient flux

1. Introduction

Water birds may act as important carriers of organic material from aquatic to terrestrial ecosystems (Ellis et al., 2006). Feeding on fish and aquatic invertebrates, they concentrate and transport organic matter through guano, food remains and dead bodies to terrestrial nesting and overwintering areas (Polis et al., 1997). This can significantly change vegetation, soil properties, and ecosystem functioning. Overwintering and nesting sites of bird colonies (such as the Great Cormorant, *Phalacrocorax carbo*) are usually confined to coastal cliffs or other biotopes closely located near the coastline. These biotopes are inhabited by a specific complex of plant and animal species (Anderson and Polis, 1999; Klimaszyk and Rzymski, 2016). However, due to the lack of suitable areas or anthropogenic impact, birds can shift to forest ecosystems that do not have direct contact with marine ecosystems. In this case, a large amount of allochthonous organic matter enters the forest ecosystem, which can lead to direct and indirect changes in the properties of the soil, vegetation, and soil fauna (Balčiauskas et al., 2015; Kolb et al., 2015).

The long-term impact of water bird presence on soil macro- and meso-invertebrates has been fairly well-studied with a focus on the higher latitudes (Kolb et al., 2010, 2012; Zmudczyńska et al., 2012). However, the effects reported were region-specific and often contradictory. Among the soil fauna, a negative effect was shown in the densities of microbial communities, oribatid mites, springtails, and few insect groups (Hemiptera), and conversely, the presence of water bird colonies was positively correlated with the density of Mesostigmata and Diptera, among others (Kolb et al., 2015). However, such effects have remain poorly studied for southern regions and Black Sea coastal forests, in particular (Korobushkin and Saifutdinov, 2019), where colonies of the great cormorant have increased their nesting and overwintering activity over recent decades (Bregnballe et al., 2014).

Herein, a study was conducted in the Mediterranean pine forests on the Black and Azov Sea coasts, which are disturbed by great cormorant (*P. carbo*) overwintering colonies. Selected forests differed in the amount of time that had elapsed since the last cormorant overwintering activity. This allowed for the tracking of changes in the

* Correspondence: saifutdinov@biogeo.ru

belowground communities under colonies that had been abandoned within the previous 8 years. Springtails (Hexapoda: Collembola) were selected as a model group for this. Collembolans are one of the most widespread and numerous taxa of soil mesofauna, and they play a key role in detrital food webs (Hopkin, 1997; Coulibaly et al., 2019). They inhabit different soil horizons and can be easily divided into different functional traits according to their life history strategies (Potapov et al., 2016; Saifutdinov et al., 2018). It was hypothesized that the overwintering activity of cormorant colonies should lead to a reduction in the abundance and taxonomic richness of springtails in the forests when compared with the control forest sites. It was also assumed that in forests that have had no overwintering activity for a long period (>8 years), collembolan abundance may reach a level similar to that at the control sites, which had never been affected by this bird species.

2. Material and methods

2.1. Sampling area and samples collection

The material was collected in the summer of 2018 at 8 forest sites along the Azov and Black Sea coastal areas. The distance between the 2 coastal areas was approximately 160 km. The studied forests differed in terms of the time that had elapsed since the last cormorant overwintering activity. In the coastal forests of the Black Sea, cormorant colonies overwintered from 2015 to 2017. In the forests of the Azov Sea, the last overwintering activity of cormorants was observed in 2010. Thus, the sites can be divided into 2 blocks: forests with active overwintering colonies at the Black Sea (hereinafter referred to as active overwintering colonies) and Azov Sea forests without cormorant overwintering activity (hereinafter referred to as abandoned forests). Within each block type, 4 sites that were covered by pine forests were selected, wherein 2 sites represented overwintering colonies (hereinafter referred to as impact sites) and 2 control sites (further mentioned as control sites) located in the vicinity near the impact sites.

Sampling sites in the forests with active overwintering colonies near the Black Sea coast were located on the Abrau Peninsula (44.7175 N, 37.4439 E), within the Utrish State Nature Reserve. The study sites were located on a cliff with a height of about 13 m. The vegetation at both the impact and control sites was represented by xerophytic communities of the sub-Mediterranean type (Seregin and Suslova, 2007), with the prevalence of *Pinus brutia* var. *pityusa* and single trees of *Juniperus excelsa*, *Carpinus orientalis*, and *Quercus pubescens*; the shrub layer was represented by *Ruscus ponticus*; the grass layer was dominated by cereals *Hordeum leporinum* and *Bromus sterilis*. The projective grass cover of the impact sites reached 80%, yet it did not exceed 20% within the control sites. The litter depth within the impact and control sites was similar (Table 1). However, visually, needle litter prevailed at the impact sites. The soil and plants at the impact sites were covered with bird guano, feathers, and food residues (fish, scales, and bones). Tree and shrub vegetation were strongly depressed and desiccated (see also Dzhangirov

Table 1. Edaphic parameters (mean ± SE, n = 2) at the impact and control sites of forests with active overwintering cormorant colonies (Black Sea) and abandoned forests (Azov Sea).

Parameter	Active overwintering colonies		Abandoned forests	
	Impact	Control	Impact	Control
Litter depth, cm	3.6 ± 0.7	3.8 ± 0.2	3.4 ± 0.5	3.6 ± 0.3
Soil pH	5.9 ± 0.3**	7 ± 0.1	7.6 ± 0.2	7.5 ± 0.2
Al, mg kg^{-1}	0.8 ± 0.0***	1 ± 0.0	1.5 ± 0.3	2.2 ± 0.7
P, mg kg^{-1}	1.7 ± 0.05***	0.14 ± 0.01	0.6 ± 0.1*	0.1 ± 0.02
S, mg kg^{-1}	0.24 ± 0.2***	0.11 ± 0.1	0.3 ± 0.1**	0.1 ± 0.05
K, mg kg^{-1}	1380.5 ± 46.3	1615.9 ± 162.1	2918 ± 937	1300 ± 219
Ca, mg kg^{-1}	2178.4 ± 4.1	2346.2 ± 7.6	42299 ± 10560	26420 ± 7106
Mn, mg kg^{-1}	18.2 ± 0.7*	25 ± 3.3	0.6 ± 0.1**	0.1 ± 0.03
Fe, mg kg^{-1}	10107 ± 365.6	9524 ± 1501.1	1908 ± 457	3306 ± 1153
C, %	13.5 ± 0.5	10.8 ± 2.4	4.1 ± 1	6.1 ± 0.8
N, %	1.0 ± 0.1**	0.6 ± 0.1	0.2 ± 0.07	0.3 ± 0.05

Values differed significantly between the control and impact sites according to the ANOVA analysis: *P < 0.05; **P < 0.01; ***P < 0.001.

and Suvorov, 2015). Based on the personal observations and published data (Bregnballe et al., 2014), the total number of overwintering cormorants did not exceed 100 individuals within the impact sites.

Sampling sites in the abandoned forests at the Azov Sea coast were located near the Kazantipsky Nature Reserve (45.4172 N, 35.8661 E). According to the Nature Reserve monitoring data (verbal communication from the National Reserve officer) and personal observations, overwintering of the great cormorant colonies at the studied sites was observed until 2010. The total number of *P. carbo* breeding pairs was estimated at 20,000 (Bregnballe et al., 2014). However, during the sampling period, no active nests, guano on the soil surface, or food residuals were observed in the studied forests. Both the impact and control sites were approximately 300 m away from the sea and separated by a sandy beach, a coastal meadow, and a country road. The vegetation at all of the control sites was represented by communities of *Pinus nigra* subsp. *pallasiana* with a small fraction of *Robinia pseudoacacia* in the shrub layer; the grass layer was absent (projective cover <1%). The vegetation at the impact sites during sampling was represented by solitary and severely damaged pine trees. Undergrowth and shrubs were represented by *Populus sp.* and *R. pseudoacacia*, respectively. Xerophilous sereals and sagebrush species dominated in the grass cover. The grass foliage cover of the impact sites reached 75%. Pine needles prevailed in the litter layer of both the control and impact sites. At the impact sites, numerous dry pine tree trunks and branches were observed on the ground.

To collect collembolans, 5 intact soil samples were randomly collected within each site using a steel soil corer that was 5 cm in diameter, down to the depth of 10 cm. For each soil sample, the litter depth (cm) was measured directly in the field (Table 1). To avoid the edge effect, samples were collected in the center of a 10 × 10 plot. Afterwards, the sampling soil was sealed in plastic bags and delivered in isothermal containers at a temperature of 9 ± 1 °C to the laboratory of A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow.

2.2. Samples processing

Within 1–3 days after the delivery of the samples to the laboratory, soil fauna were extracted into a mixture of alcohol, water, and ethylene glycol (80:15:5) for 7 days using Tullgren extractors. After extraction, the collembolans were separated from the other animals and identified down to the genus level using the applicable keys (Fjellberg, 1998, 2007). In total, 2414 individuals belonging to 27 genera were collected. After identification, all of the springtails were allocated into different functional traits according to their vertical distribution (Saifutdinov et al., 2018) (epiedaphic, hemiedaphic, euedaphic), and further by adding information about their feeding preferences (Potapov et al., 2016). The following trait combinations were identified: euedaphic microorganism consumers (EMC), hemiedaphic microorganism consumers (HMC), epiedaphic plant and microorganism consumers (EPMC), epiedaphic animal and microorganism consumers (EAMC).

Additionally, for each soil sample, the pH of the soil solution (H_2O ratio of 1:5) and total C and N contents (%) were determined using a Flash 1112 elemental analyzer (Thermo Electron, Germany) at the Joint usage center, Instrumental Methods in Ecology, of the A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences. Total Al, P, S, K, Ca, Mn, and Fe contents (mg kg^{-1}) were estimated using an X-ray fluorescence analyzer (S2 PICOFOX Bruker, USA).

2.3. Statistical analysis

Within each study site, the 5 soil samples collected were considered as pseudo-replicates and averaged to form the mean value per site. Accordingly, the abundance of springtails (ind. m^{-2}) in the text was given as the mean between the forests with an active overwintering colony and the abandoned forests for both the control (n = 2) and impact (n = 2) treatments ± standard error of the mean (SE). Total abundance, number of genera, abundance of springtails with specific traits, and soil parameters were selected as dependent variables and compared between the control and impact sites using nested design ANOVA (sample nested within site). Before the analysis, the potential collinear effects of the sampling regions on the dependent variables were checked using one-way ANOVA, by including all of the sites into the model as independent groups. The effect of the sampling region was stronger than that of the cormorant overwintering activity, as demonstrated by the Tukey HSD test ($P < 0.01$). Thus, further analyses were performed, separately, for 2 regions. To avoid false discoveries during the multiple trait comparisons, the Benjamini-Yekutieli controlling procedure (Benjamini and Yekutieli, 2001) was applied. Prior to the analyses, all of the quantitative data were log-transformed.

To compare the abundance, the genus richness and abundance of the functional groups of springtails (n = 8 for each parameter) between forests with active overwintering colonies and abandoned forests, the relative total abundance, genus richness, and abundance of functional groups between the impact and control sites (abundance at the impact sites divided by abundance at the control sites) were calculated. Furthermore, parameters were compared between forests with active overwintering colonies and abandoned forests using one-way ANOVA using log-transformed data.

To visualize the relationship between the abundance of springtails belonging to different genera and the descriptive variables (the impact of birds and edaphic parameters), principal component analysis (PCA) was performed. Edaphic parameters were chosen as active variables, while data on springtail genera abundance were chosen as the supplementary (passive) variables. Prior to the PCA, the data were z-transformed to standardize the effects. To avoid the influence of region-specific genera on the model, only the genera found in both studied regions were used.

Statistical hypotheses were tested and $P < 0.05$ was accepted as significant. Data processing was performed using Statistica 13.3 (TIBCO Software Inc., Palo Alto, CA, United States), licensed to the coauthors.

3. Results

The total abundance and average number of springtail genera (Table 2) at the control sites in forests with active overwintering colonies were significantly higher in comparison with the impact sites (ANOVA, $F = 28.04$, $P < 0.0007$ and $F = 38$, $P < 0.0003$, respectively). The abundance of epiedaphic and euedaphic collembolans (Figure 1) was higher at the control sites than at impact sites (ANOVA, $F = 62.28$, $P < 0.00005$ and $F = 14.32$, $P < 0.006$, respectively). The abundance of hemiedaphic springtails did not differ significantly between the study sites. Among the trophic groups, the abundance of EPMC, EAMC, and EMC significantly differed between the study sites (ANOVA, $F = 21.32$, $P < 0.002$; $F = 32.25$, $P < 0.005$, and $F = 18.52$, $P < 0.003$, respectively), where it was higher at the control sites when compared to the impact sites (Table 2, Figure 1).

In the forests abandoned by the cormorant colonies, the total collembolan abundance at the impact sites did not differ when compared to the controls (Table 2). The total number of genera was higher at the control sites, while the average number of genera was higher at the impact sites (Table 2). The abundance of epiedaphic collembolans at the impact sites was 8 times higher than at the control sites ($F = 27.93$, $P < 0.001$) (Figure 2). Similarly, the abundance of EAMC springtails was higher at the impact sites in comparison to the control sites ($F = 21.64$, $P < 0.002$). The remaining functional groups of collembolans did not differ in abundance between the impact and control sites.

In the PCA, the first 2 axes explained approximately 54% of the total variance (Figure 3). The soils at impact sites with active overwintering cormorant colonies were characterized by a high content of P, N, and S, and positively correlated with the abundance of *Pseudosinella* and *Cryptopygus* species. In the abandoned forests, the impact sites were enriched with K and Ca, with a higher abundance of *Isotomiella* species. In contrast, the control forests were characterized by higher litter content and were represented by many other taxa included in the analysis (Figure 3).

The springtail abundance and genus richness (Figure 4) at the impact sites relative to the controls were higher in the abandoned forests than in the forests with active overwintering colonies ($F = 8.66$, $P < 0.01$, and $F = 11.24$, $P < 0.005$, respectively). Among the functional groups, relative abundance (Figure 4) of epiedaphic, HMC, EAMC, and EPMC were higher in the abandoned forests than in those with active overwintering cormorants ($F = 45.57$, $P < 0.00001$, $F = 12.64$, $P < 0.005$, $F = 37.77$, $P < 0.00001$, and $F = 8.96$, $P < 0.01$, respectively).

4. Discussion

This study revealed that the overwintering activity of cormorants in coastal forests of the Black and Azov Seas can significantly change the taxonomic structure and functional composition of springtail communities. The studied Black Sea coastal forests, used for overwintering by cormorants, were significantly depleted in total abundance and genus richness of springtails in comparison with the forests of Azov Sea, abandoned 8 years ago. Generally, springtails prefer soils with low nitrate concentrations (Birkhofer et al., 2012), while soils under active cormorant colonies are usually enriched with organic nitrogen (Klimaszyk et al., 2015; Kolb et al., 2015). This can lead to the loss of plant diversity, which in turn leads to a decrease of springtail habitat heterogeneity, and subsequently affects soil fauna communities (Klimaszyk and Rzymski, 2016). The results supported the findings of Kolb et al. (2010, 2015). However, others (Zmudczyńska et al, 2012; Bokhorst and Convery, 2016) found that in nutrient-poor polar terrestrial ecosystems, allochthonous nutrients delivered by the birds in both Arctic and Antarctic played an important role in soil animal communities and in particular, may have led to an increase in the total abundance of springtails. Thus, the negative effect on the soil animal communities in the presence of water birds was determined to not only be by direct influence, but also by nutrient availability in the soils.

It was found that epiedaphic species had the most active reaction to the recent cormorant overwintering activity, which was most likely to be explained by the fact that this functional group inhabits the litter layer and feeds largely on microorganisms, animals, and plant residues (Hopkin, 1997). Presumably, the decline of abundance observed in the forests with active overwintering colonies was caused by an excessive amount of guano, which is known to greatly modify plant diversity and litter quality (Kolb et al., 2012; Korobushkin and Saifutdinov, 2019). After several years, as in the abandoned forests of Azov Sea, bird guano will degrade and the associated nutrients will be leached away, which might allow epiedaphic species to recover.

The positive correlation of epiedaphic species (e.g., from *Lepidocyrtus* and *Isotoma* genera) with the litter depth

Table 2. Abundance of springtails (ind. $m^{-2} \pm$ SE, n = 2) at the impact and control sites of forests with active overwintering cormorant colonies (Black Sea) and abandoned forests (Azov Sea).

Genus	Active overwintering colonies		Abandoned forests	
	Impact	Control	Impact	Control
Mesaphorura sp.	2253 ± 2150	8960 ± 2202	2458 ± 1126	9421 ± 7475
Metaphorura sp.	0 ± 0	0 ± 0	0 ± 0	51 ± 51
Protaphorura sp.	1024 ± 922	922 ± 819	0 ± 0	0 ± 0
Willemia sp.	0 ± 0	870 ± 666	0 ± 0	0 ± 0
Pseudachorutes sp.	358 ± 51	34253 ± 12646	9062 ± 8141	0 ± 0
Hypogastrura sp.	0 ± 0	0 ± 0	410 ± 307	205 ± 205
Friesea sp.	51 ± 51	0 ± 0	0 ± 0	0 ± 0
Neanura sp.	0 ± 0	1638 ± 717	0 ± 0	0 ± 0
Xenylla sp.	0 ± 0	2458 ± 1741	154 ± 154	0 ± 0
Micranurida sp.	0 ± 0	0 ± 0	0 ± 0	154 ± 154
Folsomia gr. *quadrioculata* sp.	102 ± 102	102 ± 102	0 ± 0	512 ± 512
Parisotoma sp.	717 ± 307	11725 ± 1075	102 ± 0	51 ± 51
Isotomiella sp.	717 ± 307	51 ± 51	922 ± 922	819 ± 819
Isotomodes sp.	0 ± 0	0 ± 0	51 ± 51	0 ± 0
Cryptopygus sp.	6963 ± 6963	102 ± 0	0 ± 0	102 ± 102
Isotoma sp.	51 ± 51	717 ± 717	0 ± 0	51 ± 51
Desoria sp.	0 ± 0	0 ± 0	0 ± 0	51 ± 51
Cyphoderus sp.	0 ± 0	102 ± 102	0 ± 0	0 ± 0
Orchesella sp.	0 ± 0	0 ± 0	51 ± 51	51 ± 51
Lepidocyrtus sp.	1997 ± 51	8960 ± 2918	870 ± 768	0 ± 0
Pseudosinella sp.	2714 ± 256	666 ± 256	102 ± 102	0 ± 0
Entomobrya sp.	512 ± 102	1997 ± 154	1792 ± 461	973 ± 51
Pygmaarhopalites sp.	0 ± 0	51 ± 51	0 ± 0	0 ± 0
Sphaeridia sp.	0 ± 0	2662 ± 409	0 ± 0	0 ± 0
Sminthurides sp.	0 ± 0	0 ± 0	0 ± 0	51 ± 51
Sminthurinus sp.	0 ± 0	102 ± 0	0 ± 0	0 ± 0
Megalothorax sp.	51 ± 51	1280 ± 154	0 ± 0	0 ± 0
General characteristics of the springtail communities				
Total abundance	17510 ± 10035***	77619 ± 16282	15974 ± 10547	12493 ± 6042
Total number of genera	13	19	11	13
Average number of genera per site	5.2 ± 0.4***	9.8 ± 0.8	4.3 ± 0.5	3.3 ± 0.7

Values differed significantly between the control and impact sites according to the ANOVA analysis: *P < 0.05; **P < 0.01; ***P < 0.001.

and control sites near forests with active overwintering colonies underlined the importance of this edaphic parameter for the litter-dwelling species of springtails. This was supported by many other studies, in which a decline in litter depth was accompanied by a reduction of epiedaphic species (Ponge et al., 1993; Saifutdinov et al., 2018). On the other hand, positive correlation of some mobile euedaphic species (genera *Pseudosinella*, *Isotomiella*) with impact sites probably indicates that the cormorant activity mainly influences upper soil horizons, being less adverse for soil-dwelling species.

In conclusion, the impact of cormorants on soil microarthropods is the strongest when the colony is active and decreases over time, since the birds abandon the area. Sites with recent cormorant overwintering activity (1 year after overwintering), in comparison with long-abandoned

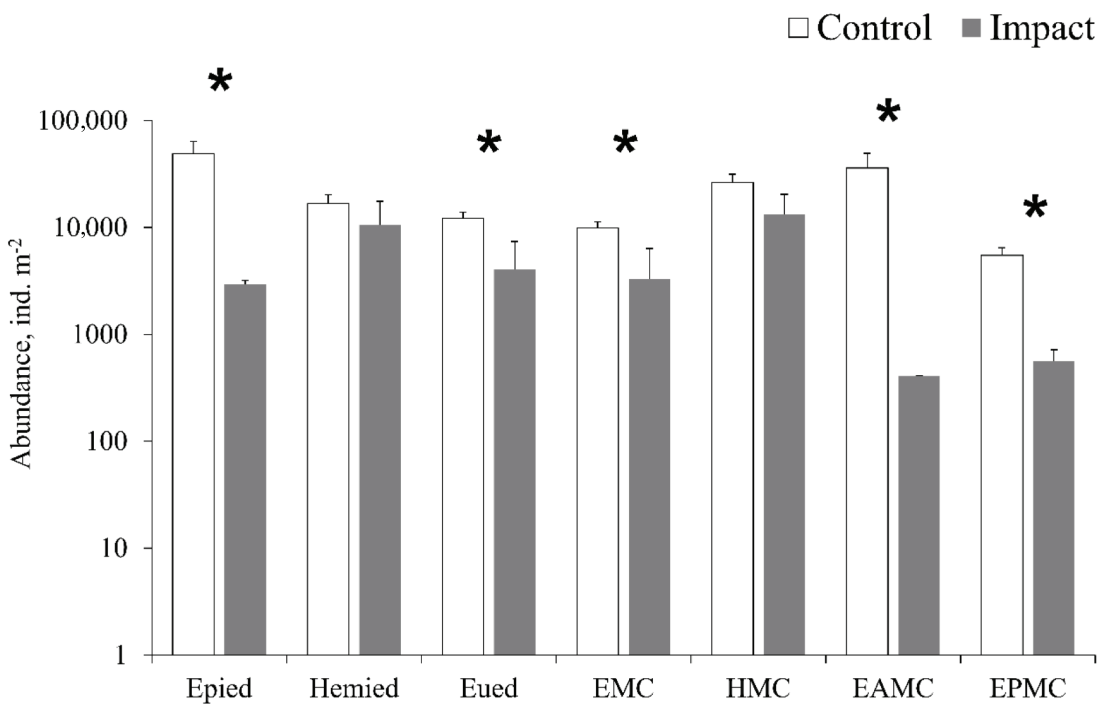

Figure 1. Abundance of different functional groups of springtails (ind. $m^{-2} \pm$ SE, n = 2 at the control and impact sites of forests with active overwintering cormorant colonies (Black Sea). Epied: Epiedaphic, Hemied: Hemiedaphic, Eued: Euedaphic, EMC: Euedaphic microorganism consumers, HMC: Hemiedaphic microorganism consumers, EPMC: Epiedaphic plant and microorganism consumers, EAMC: Epiedaphic animal and microorganism consumers. *: Statistically significant differences between the control and impact sites according to the Tukey HSD test.

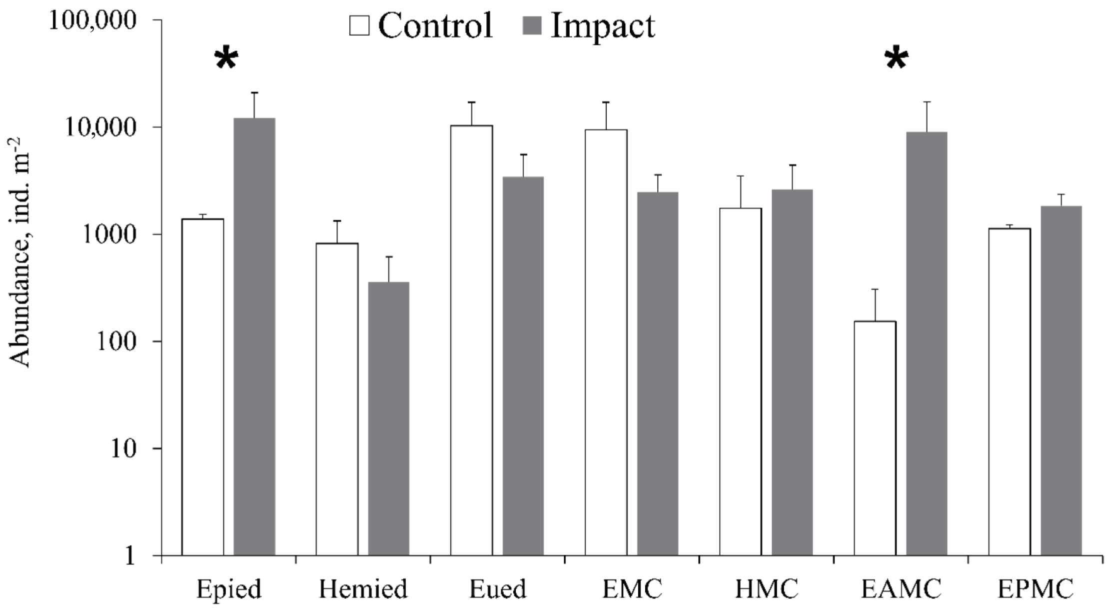

Figure 2. Abundance of different functional groups of springtails (ind. $m^{-2} \pm$ SE, n = 2) at the control and impact sites of forests abandoned by cormorants (Azov Sea). Epied: Epiedaphic, Hemied: Hemiedaphic, Eued: Euedaphic, EMC: Euedaphic microorganism consumers, HMC: Hemiedaphic microorganism consumers, EPMC: Epiedaphic plant and microorganism consumers, EAMC: Epiedaphic animal and microorganism consumers. *: Statistically significant differences between the control and impact sites according to the Tukey HSD test.

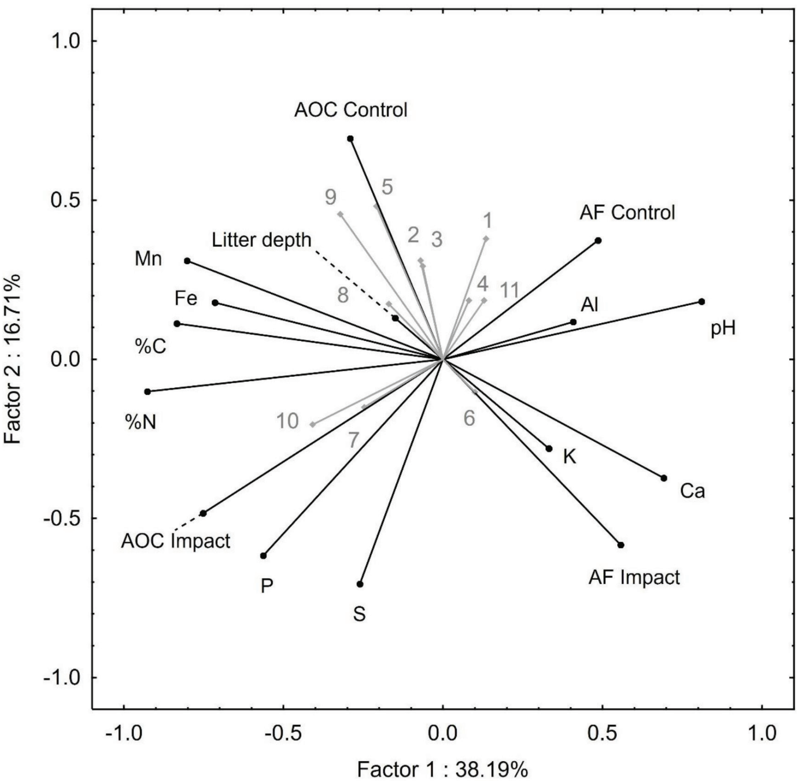

Figure 3. PCA of the relationship between springtail genera abundance (shown as gray lines and diamond-shaped symbols) and edaphic parameters (black lines and dots). AOC impact: Impact sites with active overwintering colonies (Black Sea), AOC control: Control sites close to active overwintering colonies (Black Sea), AF impact: Impact sites in abandoned forests (Azov Sea), AF control: Control sites in abandoned forests (Azov Sea). 1) *Mesaphorura*, 2) *Pseudachorutes*, 3) *Xenylla*, 4) *Folsomia* gr. *quadrioculata*, 5) *Parisotoma*, 6) *Isotomiella*, 7) *Cryptopygus*, 8) *Isotoma*, 9) *Lepidocyrtus*, 10) *Pseudosinella*, 11) *Entomobrya*.

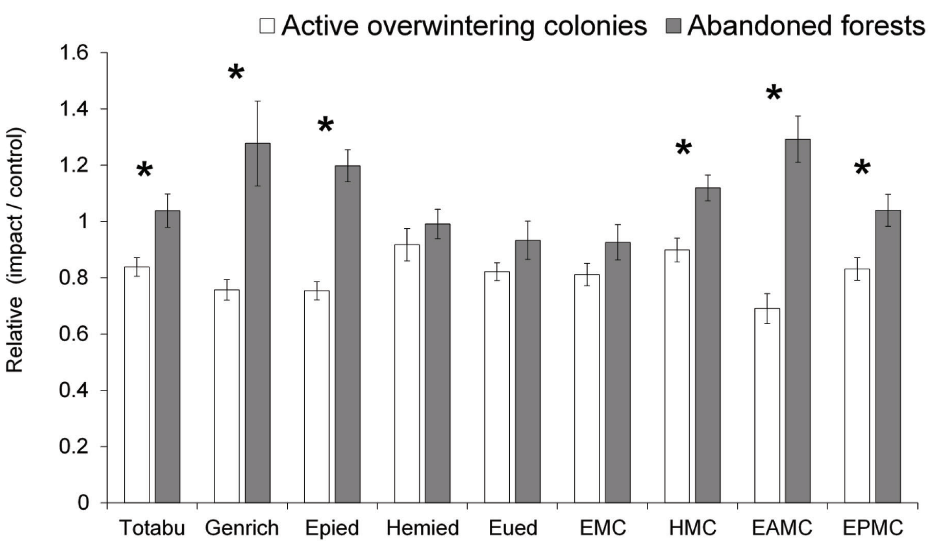

Figure 4. Relative total abundance, genus richness, and abundance of the different functional groups of springtails (abundance in impact sites/abundance in controls ± SE) in forests with active overwintering cormorant colonies (Black Sea) and abandoned forests (Azov Sea). Totabu: Total abundance, Genrich: Genus richness, Epied: Epiedaphic, Hemied: Hemiedaphic, Eued: Euedaphic, EMC: Euedaphic microorganism consumers, HMC: Hemiedaphic microorganism consumers, EPMC: Epiedaphic plant and microorganism consumers, EAMC: Epiedaphic animal and microorganism consumers. *: Statistically significant differences between the control and impact sites according to the Tukey HSD test.

forests (8 years after overwintering), are defined by depleted and less diverse collembolan communities, which is most strongly exhibited for surface-dwelling species. Further research is needed to understand how overwintering and nesting of water birds affect other collembolan traits, as well as assess changes in trophic relationships with other groups of soil animals.

Acknowledgments

We are grateful to O.N. Bykhalova, the Deputy Director of the Utrish State Nature Reserve, for the support given during the fieldwork. We thank L.A. Pelgunova for the elemental soil analysis and A. Tarasov for the measurements of the soil pH. We also thank Ksenia Speranskaya for improving the language. The collection of material, processing, and identification of collembolans was supported by the Russian Foundation for Basic Research (project # 18-34-00573). Determination of the soil parameters, statistical data processing, and identification of the taxa were performed using software and equipment funded by the Russian Science Foundation (project # 19-74-10104).

References

Anderson WB, Polis GA (1999). Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118: 324-332. doi: 10.1007/s004420050733

Balčiauskas L, Balčiauskienė L, Jasiulionis M (2015). Mammals under a colony of great cormorants: Population structure and body condition of yellow-necked mice. Turkish Journal of Zoology 39: 941-948. doi: 10.3906/zoo-1407-27

Benjamini Y, Yekutieli D (2001). The control of the false discovery rate in multiple testing under dependency. The Annals of Statistics 29: 1165-1188. doi: 10.1214/aos/1013699998

Birkhofer K, Schöning I, Alt F, Herold N, Klarner B et al. (2012). General relationships between abiotic soil properties and soil biota across spatial scales and different land-use types. PLoS ONE 7: e43292. doi: 10.1371/journal.pone.0043292

Bokhorst SF, Convey P (2016). Impact of marine vertebrates on Antarctic terrestrial micro-arthropods. Antartic Science 28: 175-186. doi: 10.1017/S0954102015000607

Bregnballe T, Lynch J, Parz-Gollner R, Marion L, Volponi S et al. (editors) (2014). Breeding numbers of Great Cormorants *Phalacrocorax carbo* in the Western Palearctic, 2012-2013. No 99. Aarhus, Denmark: Aarhus University.

Coulibaly SFM, Winck BR, Akpa-Vinceslas M, Mignot L, Legras M et al. (2019). Functional assemblages of Collembola determine soil microbial communities and associated functions. Frontiers in Environmental Science 7: 52. doi: 10.3389/fenvs.2019.00052

Dzhangirov MYu, Suvorov AV (2015). Current state of Pitsunda pine (*Pinus pityuosa* Steven) phytocenoses in the Utrish Nature Reserve. In: Ogureeva GN, Gongalsky KB (editors). Conservation of the Biota in the Utrish State Nature Reserve. Volume 3. Maykop, Russia: Polygraph-South LLC, pp. 129-141 (in Russian).

Ellis JC, Fariña JM, Witman JD (2006). Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. Journal of Animal Ecology 75: 565-574. doi: 10.1111/j.1365-2656.2006.01077.x

Fjellberg A (1998). Collembola of Fennoscandia and Denmark: Poduromorpha. Part I. Leiden, Netherlands: Brill.

Fjellberg A (2007). Collembola of Fennoscandia and Denmark: Entomobryomorpha and Symphypleona. Part II. Leiden, Netherlands: Brill.

Hopkin S (1997). Biology of the Springtails (Insecta: Collembola). Oxford, UK: Oxford University Press.

Klimaszyk P, Piotrowicz R, Rzymski P (2015). Changes in physico-chemical conditions and macrophyte abundance in a shallow soft-water lake mediated by a Great Cormorant roosting colony. Journal of Limnology 74: 114-122. doi: 10.4081/jlimnol.2014.994

Klimaszyk P, Rzymski P (2016). The complexity of ecological impacts induced by great cormorants. Hydrobiologia, 771: 13-30. doi: 10.1007/s10750-015-2618-1

Kolb GS, Jerling L, Hambäck PA (2010). The impact of cormorants on plant-arthropod food webs on their nesting islands. Ecosystems 13: 353-366. doi: 10.1007/s10021-010-9323-8

Kolb GS, Jerling L, Essenberg C, Palmborg C, Hambäck PA (2012). The impact of nesting cormorants on plant and arthropod diversity. Ecography 35: 726-740. doi: 10.1111/j.1600-0587.2011.06808.x

Kolb GS, Palmborg C, Taylor AR, Bååth E, Hambäck PA (2015). Effects of nesting cormorants (*Phalacrocorax carbo*) on soil chemistry, microbial communities and soil fauna. Ecosystems 18: 643-657. doi: 10.1007/s10021-015-9853-1

Korobushkin DI, Saifutdinov RA (2019). Influence of seabird colonies on soil macrofauna communities at the Black Sea coast forests. Russian Journal of Ecology 50: 567-573. doi: 10.1134/S1067413619060080

Polis GA, Anderson WB, Holt RD (1997). Toward an integration of landscape ecology and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28: 289-316. doi: 10.1146/annurev.ecolsys.28.1.289

Ponge JF, Arpin P, Vannier G (1993). Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem. European Journal of Soil Biology 29: 141-153.

Potapov AA, Semenina EE, Korotkevich AY, Kuznetsova NA, Tiunov AV (2016). Connecting taxonomy and ecology: Trophic niches of collembolans as related to taxonomic identity and life forms. Soil Biology and Biochemistry 101: 20-31. doi: 10.1016/j.soilbio.2016.07.002

Saifutdinov RA, Gongalsky KB, Zaitsev AS (2018). Evidence of a trait-specific response to burning in springtails (Hexapoda: Collembola) in the boreal forests of European Russia. Geoderma 332: 173-179. doi: 10.1016/j.geoderma.2017.07.021

Seregin AP, Suslova EG (2007). Vascular plant flora in the environs of Malyi Utrish village. In: Gongalsky KB, Leontieva OA, Suslova EG (editors). Landscape and Biological Diversity in the Northwestern Caucasus. Moscow, Russia: Lomonosov Moscow State University, pp. 104-174 (in Russian).

Zmudczyńska K, Olejniczak I, Zwolicki A, Iliszko L, Convey P et al. (2012). Influence of allochtonous nutrients delivered by colonial seabirds on soil collembolan communities on Spitsbergen. Polar Biology 35: 1233-1245. doi: 10.1007/s00300-012-1169-4