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Influence of allochtonous nutrients delivered by colonial seabirds on soil collembolan communities on Spitsbergen

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Abstract Despite a widespread recognition of the role of seabird colonies in the fertilization of nutrient-poor polar terrestrial ecosystems, qualitative and quantitative data documenting any consequential influence on soil invertebrate communities are still lacking. Therefore, we studied community structure and abundance of springtails (Collembola) in ornithogenic tundra near two large seabird colonies in Hornsund, south-west Spitsbergen. We found considerably (5–20×) higher densities and biomass of Collembola in the vicinities of both colonies (the effect extending up to ca. 50 m from the colony edge) than in comparable control areas of tundra not influenced by allochtonous nutrient input. The most common springtails observed in the seabird-influenced areas were *Folsomia quadrioculata*, *Hypogastrura viatica* and *Megaphorura arctica*. The latter species appeared the most resistant to ornithogenic nutrient input and was found commonly closest to the bird colonies. Collembolan abundance decreased with increasing distance from the seabird colonies. However, relationships between collembolan density and specific physicochemical soil parameters and vegetation characteristics were weak. The most important factors were the cover of the nitrophilous green alga *Prasiola crispa*, total plant biomass and soil solution conductivity, all of which were correlated with distance from the colony and estimated amount by guano deposition. Community composition and abundance of springtails showed no evidence of being influenced of seabird diet, with no differences apparent between communities found in ornithogenic tundra developing in the vicinity of planktivorous and piscivorous seabird colonies. The study provides confirmation of the influence of marine nutrient input by seabirds on soil microfaunal communities.

Introduction

Arctic terrestrial ecosystems experience severe environmental conditions and generally low nutrient availability, resulting in low primary production. This contrasts strongly with the adjacent marine environment, where high near-surface nutrient concentrations exist due to vertical mixing of water masses, and the predominance of diatoms and the 24 h polar day support high primary production during summer (Cocks et al. 1998; Stempniewicz 2005; Stempniewicz et al. 2007).

Seabirds constitute a major link between these two environments. They feed at sea and breed on land, often in very large colonies. During the summer reproductive season, seabirds deposit considerable amounts of guano, along with feathers, egg shells and carcasses, which locally provide the main sources of nutrients for tundra plants (Lindeboom 1984; Erskine et al. 1998; Ellis 2005; Stempniewicz 2005). For example, during one breeding season

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in Hornsund, south-west Spitsbergen, little auks (*Alle alle*) deliver ~60 tonnes of guano dry mass km^{-2} of colony area (Stempniewicz [1990](#), [1992](#)). In comparison, over the three month austral summer period on Anchorage Island, maritime Antarctic, guano input contributed ca. 100 mg N m^{-2}, the vast majority of the external nitrogen input at this location (Bokhorst et al. [2007a](#)). Smith and Froneman ([2008](#), Tables 7.1 and 7.2) provide a detailed description of vertebrate (and other marine-derived) nutrient inputs into the terrestrial ecosystems of sub-Antarctic Marion Island. This island has large populations of seals and various birds including penguins, albatrosses, petrels and burrow-nesting species. Total bird guano production is estimated at 4,279 tonnes year^{-1}, of which about 15% by mass is nitrogen. As well as guano, additional sources of nutrients include food remnants and feathers, and dead eggs, chicks and adults deposited close to colonies (Polis et al. [1997](#); Anderson and Polis [1999](#); Ellis [2005](#); Smith and Froneman [2008](#))—feathers alone account for somewhat less than 10% of the input values of guano on Marion Island (Smith and Froneman [2008](#), Table 7.2). Higher concentrations of ions crucial for plant growth (NO_3^-, NH_4^+, PO_4^{3-}, K^+), which are present in soil in the vicinity of seabird colonies and even individual nest burrows compared to areas beyond their impact, enhance primary production (Smith [1976](#); Anderson and Polis [1999](#); García et al. [2002](#); Stempniewicz et al. [2006](#)). Substantial guano deposition close to seabird colonies increases nutrient content in the soil (Ryan and Watkins [1989](#); Wainright et al. [1998](#); Anderson and Polis [1999](#); Stempniewicz et al. [2006](#)) and plant biomass (Anderson and Polis [1999](#); Zmudczyńska et al. [2008](#)), as well as causing changes within plant communities (Vidal et al. [2003](#); Ellis et al. [2006](#); Zmudczyńska et al. [2009](#)). This feeds through the local food web, with more intensive use of such areas by invertebrate and vertebrate herbivores (Jakubas et al. [2008](#)), predators and scavengers (Croll et al. [2005](#)).

Soil invertebrates together with microorganisms play a crucial role in decomposition processes and nutrient flows in polar terrestrial ecosystems (e.g. Cragg and Bardgett [2001](#); Hodkinson et al. [2002](#); Hopkin [2002](#); Bokhorst et al. [2007b](#)). Invertebrates perform and regulate mineralization of fresh organic residues, mostly acting in their physical breakdown or as grazers of the microflora, whereas microorganisms are responsible for the chemical degradation of complex molecules. The most important soil invertebrates in the Arctic are springtails, mites, enchytraeids and dipteran larvae, all of which benefit from organic resources (Filser [2002](#)). However, springtails (Collembola) often exceed all other groups both in abundance and species richness (e.g. Uvarov and Byzova [1995](#); Birkemoe and Leinaas [2000](#)). Typically, collembolan

biomass in the tundra ecosystem reaches 150 mg dry mass m^{-2}, a value that is high in comparison with other biomes such as temperate and tropical grasslands and forests (Rusek [1998](#)). Due to feeding on soil microbiota (fungi, bacteria, actinomycetes, algae), in at least some cases selectively (Worland and Lukešová [2000](#)), springtails potentially influence microbial population dynamics and thereby indirectly affect the overlying macroscopic plant community. They also play important roles in mixing and channelling detritus, dispersing microbial propagules and excreting nutrient-rich wastes (Bardgett and Chan [1999](#)).

In spite of widespread recognition of the important role of seabird colonies in enriching otherwise nutrient-poor polar terrestrial ecosystems (Smith [1979](#); Joly et al. [1987](#); Ryan and Watkins [1989](#); Hodkinson et al. [1994](#), [1998](#); Byzova et al. [1995](#); Uvarov and Byzova [1995](#); Sømme and Birkemoe [1999](#)), qualitative and quantitative data documenting any consequential impacts on their soil invertebrate communities are still limited. The aims of this study were, therefore:

(1) To measure species composition, density and biomass of springtails in the vicinity of two seabird colonies and compare them with non-enriched areas.
(2) To assess the relationship between the level of guano deposition and collembolan species abundance and community composition along a gradient of guano deposition between the colonies and the coast.

Materials and methods

Study area

The study was conducted on the north coast of Hornsund (south-west Spitsbergen, Svalbard) in an area of tundra between two seabird colonies and the coast:

(1) A colony of little auks (*Alle alle*, a planktivorous species) situated on Ariekammen mountain (77°00′N 15°31′E) (Transect 1, Fig. [1](#)a). The study area (effectively a ca. 1,000 m transect) ranged from the mountain slope (inclination 25°–45°) consisting of vegetation covered rock debris, where the colony was located, to near-horizontal tundra approaching the seashore.

(2) A mixed colony of Brunnich's guillemots (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*) (both piscivorous species) situated on Gnålberget cliff (77°01′N 15°52′E) (Transect 2, Fig. [1](#)b). This study area included ca. 500 m between the nesting cliff and seashore, initially with an inclination of 40°–50° directly under the cliff itself and again terminating with the flat plain at the coast.
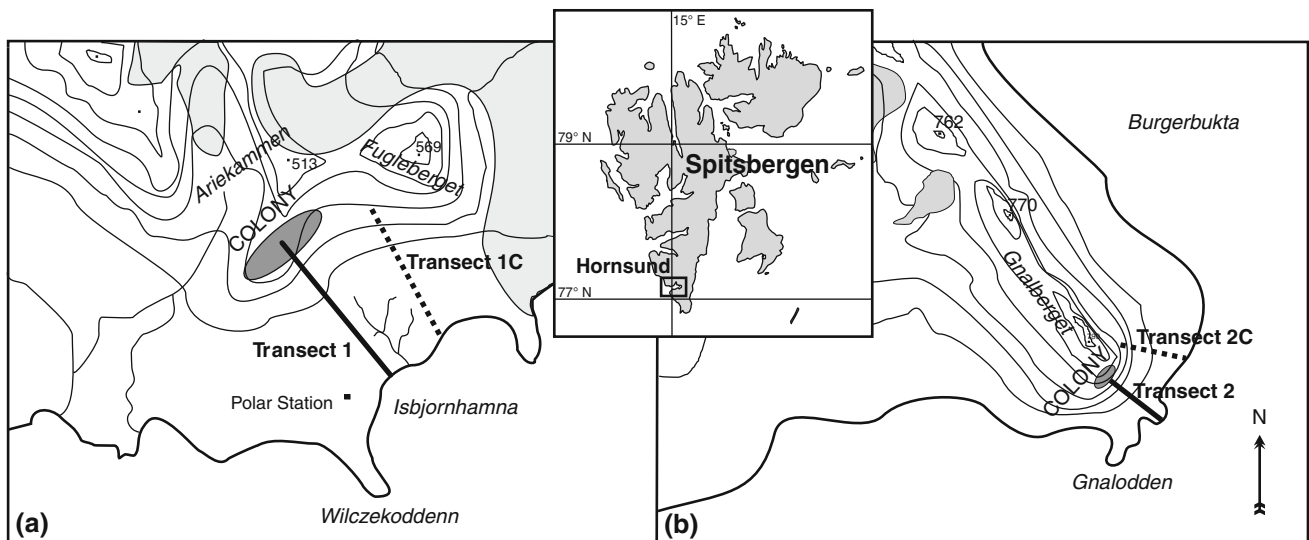
Fig. 1 Location of the study transects in Hornsund, Spitsbergen: **a** Transect 1 and its control Transect 1C, **b** Transect 2 and its control Transect 2C

Both transects were oriented towards (exposed to) the south-east and covered an altitudinal range from sea level to ca. 200 m asl.

Plant communities occurring in these study areas were characteristic of well-fertilized bird-cliff vegetation (Rønning 1996), with vegetation cover typically 90–95% across the transects, excepting the seashore itself and sites directly under the cliff in Transect 2 that were damaged mechanically by falling rocks. Well-developed vascular plants and algal mats predominated over mosses. The zonal character of vegetation along the colony-sea axis was clearly defined (Zmudczyńska et al. 2009). In the centre of the little auk colony (i.e. in the area under greatest ornithogenic impact), a *Deschampsia alpina-Prasiola crispa* community was present, which gradually changed to vegetation dominated by a *Cerastium arcticum-Chrysosplenium tetrandum* community towards the edge of the colony, and then to a wet *Sanionia uncinata-Straminergon stramineum* community on flat tundra. The transect sector closest to the sea was characterized by a *Saxifraga oppositifolia-Sanionia uncinata* community. On the talus slope beneath the kittiwake and guillemot community (Transect 2), the following plant communities were successively represented down the slope: *Cochlearia groenlandica-Prasiola crispa*, *Cerastium arcticum-Poa alpina*, *Saxifraga caespitosa*, *Festuca rubra* and, as in Transect 1, *Saxifraga oppositifolia-Sanionia uncinata* in the zone adjacent to the shore (Wojtuń unpublished data).

We established control areas on topographically similar transects to those on the ornithogenic tundra sites, but that were not impacted by seabirds (Fig. 1, Transect 1C and Transect 2C, respectively). Both control transects covered the same altitudinal range (from sea level to ca. 200 m asl) and had similar aspect (Transect 2C was offset by no more than 25° from Transect 2). Vegetation in these control areas was limited with lower total cover, a higher proportion of mosses, lichens and cyanobacteria, and with no zonation observed. Vegetation along Transect 1C was almost entirely represented by a *Sanionia uncinata-Salix polaris* community, except immediately adjacent to the coast, where it was again characterized by a *Saxifraga oppositifolia-Sanionia uncinata* community. Transect 2C included *Sanionia uncinata-Straminergon stramineum* and *Sanionia uncinata-Tortula ruralis* communities (Wojtuń unpublished data).

Sampling and analyses

The study was conducted during July and August 2005. Additionally in late July 2006, we replicated guano deposition analyses, and from early June to late August 2006, we measured soil temperature. In both study areas, a line transect was traced down the slope between the colony and seashore consisting of 10–12 sample plots (160 × 160 cm each). The little auk colony covered a large area of the relatively shallow slope and had a less clear-cut boundary than in the case of the cliff-nesting species. Therefore, Transect 1 commenced from the colony centre, while Transect 2 commenced just beneath the nesting cliff; in both cases we considered these points (sampling plot 1) as being the most influenced by seabirds. Subsequent sampling plots were located at increasing distance from the transect starting points as follows: plot 2 (6 m), 3 (15 m), 4 (29 m), 5 (49 m), 6 (79 m), 7 (125 m), 8 (193 m),

9 (296 m), 10 (449 m), 11 (680 m) and plot 12 (1,026 m). Transect 1 ($\sim$1,000 m long), therefore, consisted of 12 and Transect 2 ($\sim$500 m long) of 10 sample plots. Along each transect, more sampling plots were situated in the zone of expected strong impact of the colony where the greatest variation in vegetation was observed, than in the coastal area that was less influenced by seabirds and where the vegetation was more homogenous.

Similarly, Transect 1C included 12 sampling plots and Transect 2C 11 sampling plots. Thus, all sampling plots along the ornithogenically influenced transects had corresponding plots in the appropriate control transect.

Springtail sampling

We collected three soil cores from three sites along the same diagonal of each sampling plot (one from the centre and two from the corners of each square) ($N = 135$ cores in total). Samples were taken with a cylindrical probe (diameter 6 cm) from the soil surface (mainly organic) layer containing vegetation covering the area, down to a soil depth of ca. 5 cm. In the laboratory, each sample was placed for 48 h in a modified Tullgren apparatus illuminated with 60 W bulbs (Barton 1995). Extracted animals were preserved in 96% ethanol and identified to species level following Fjellberg (1998, 2007). We recorded and extrapolated their abundance to calculate total density (all species) and densities of particular species (number of individuals m^{-2}). Biomass (g m^{-2}) of the most abundant species (*Folsomia quadrioculata* and *Hypogastrura viatica*) was calculated using species specific formulas relating their body mass and length (Dunger 1968).

Since there were distinct differences in springtail density between the upper part of the ornithogenic transects close to the colony and the lower, seashore, part of each transect (Fig. 2), we divided each transect into two sectors. The upper sector consisted of the 5 sample plots adjacent to the colony in Transect 1 and 2 or their equivalents in 1C and 2C. The seashore sector consisted of 5 (in Transect 2) or 6 (all remaining transects) sample plots.

Guano deposition

To estimate seabird guano deposition along the studied transects, we placed a black plastic sheet (150 × 150 cm) adjacent to each sample plot. A digital picture of each sheet was taken every 24 h (Canon PowerShot A95, resolution 5.0 million pixels), on each occasion being cleaned before being re-exposed (Transect 1 and 1C, 6 days in total; Transect 2, 9 days in total; Transect 2C, 1 day). We estimated the area covered with guano by analysing the
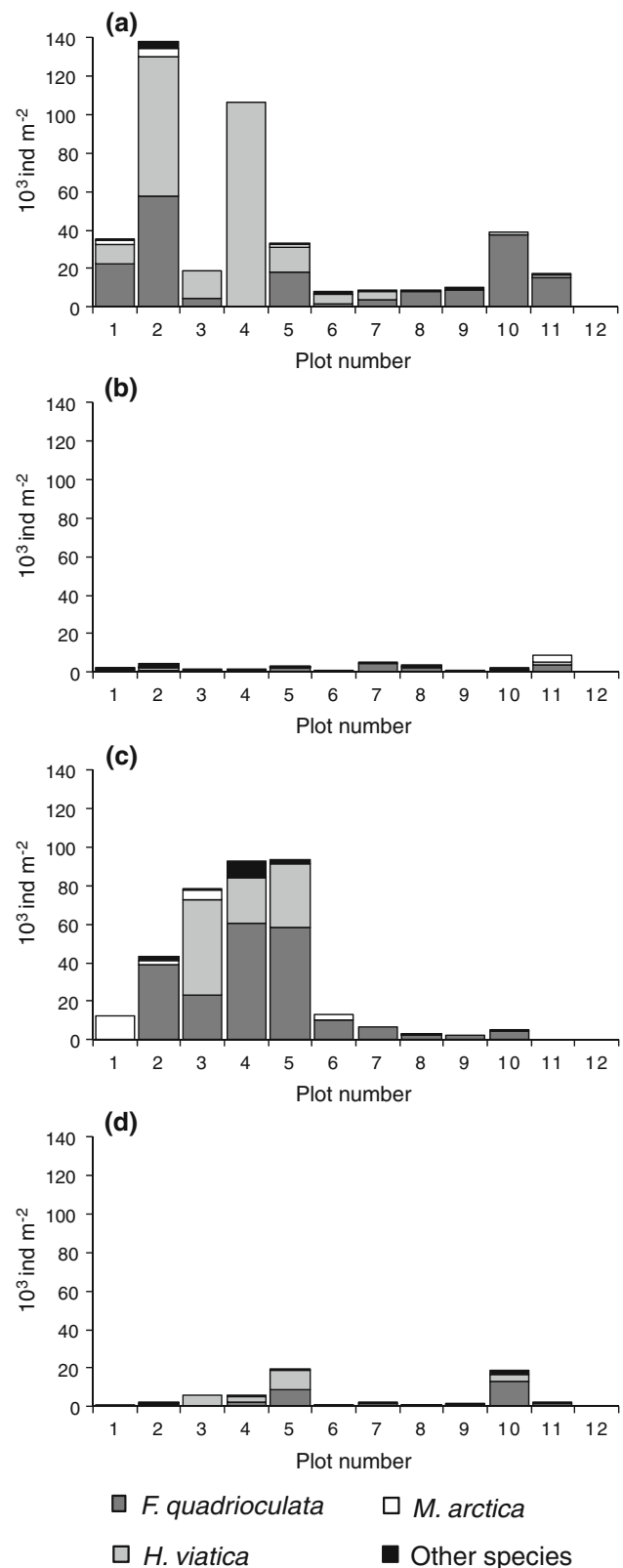
Fig. 2 Density of springtails within each plot of individual transects: **a** Transect 1, **b** Transect 1C, **c** Transect 2, **d** Transect 2C

pictures with SigmaScan Pro 5.0.0. software. Using an earlier calibration (drying and weighing 41 sheets of known guano-covered area, and calculating regression equations separately for planktivores ($y = 0.003\ x$, $R^2 = 0.7$, $N = 31$) and piscivores ($y = 0.008\ x$, $R^2 = 0.7$, $N = 10$); data not shown, Zwolicki unpublished), we estimated dry mass (DM) of guano deposited over time ($g\ m^{-2}\ day^{-1}$).

Soil physicochemical analyses

We took samples of soil for physicochemical analyses adjacent to the same collection sites as used for collembolan sampling ($N = 123$, 12 samples were lost during analyses). Each sample was taken with a shovel from the soil surface layer (to a depth of ca. 5 cm) and contained ca. 500 cm^3 of soil. At sampling locations with very compact vegetation, we removed and discarded the upper layer of live and dead, poorly decomposed, plant material. We prepared the soil samples for analyses in the laboratory immediately after return from the field. Each sample was divided into 3 sub-samples, 80 cm^3 each, and weighed with electronic scales (precision 0.1 g) before assessment of:

(1) Water content per unit dry mass (%)—Soil sub-samples were ground and dried at 40–60°C to constant mass. Water content (W) was defined as: $W = (m_w\ m_s^{-1})$ 100%, where m_w was the mass of water and m_s the dry mass of soil (Myślińska 1998)

(2) Conductivity and pH—Soil sub-samples were mixed with 160 cm^3 of distilled water and mixed by shaking for about 20 min, before being filtered through a sieve (0.5 mm diameter mesh). We measured conductivity (μS) and pH in this filtrate using a pH/conductance/salinity metre CPC-401 (Elmetron)

(3) Content of nitrogen (NO$_3^-$, NH$_4^+$), potassium (K$^+$) and phosphorus (PO$_4^{3-}$)—Soil sub-samples were mixed with 200 cm^3 of 0.03 N acetic acid. Closed vessels were left for ca. 60 min, being shaken every 10 min. The solution was filtered through a sieve (0.5 mm diameter mesh) and then through a filter paper (MN 640 w, Macherey–Nagel). We analysed the filtrate, diluted with distilled water in the case of sub-samples with very high concentrations, with a photometer LF205 (Slandi) following standard procedures (Cygański 1994)

(4) Soil organic matter content (%) in dried sub-samples was measured at the Institute of Soil Science and Plant Cultivation (State Research Institute), Puławy, Poland, by measuring loss on ignition (Ostrowska et al. 1991; Heiri et al. 2001).

Finally, to provide a description of the soil thermal microenvironment, temperature loggers (Dallas Thermochron iButton DS1921Z-F5, recording range −5°C to +26°C, ± 1°C accuracy, 0.1°C resolution) were buried at a depth of 5 cm next to the centre of each sampling plot in both ornithogenically influenced transects, recording data every hour from early June to late August.

Vegetation analysis

Within all sampling plots along each transect, we identified vascular plants and mosses and measured their percentage contribution to total vegetation cover. Along the second diagonal of each sample plot, we collected five samples of vegetation (20 × 20 cm) for assessment of biomass of live above-ground parts of plants and mosses. The samples were manually divided into vascular plant and moss components, dried to constant mass and weighed. Total biomass, and biomass of the specific vegetation layers, was extrapolated to be expressed per m^2.

Statistical analysis

Shannon's diversity index (Shannon and Weaver 1949) was used to describe springtail species diversity ($H' = \Sigma_i (n_i\ N^{-1}) \ln (n_i\ N^{-1})$, where n_i is the number of individuals of species i, and N is the total number of individuals) and evenness ($J' = H'\ (\ln S)^{-1}$, where S is the number of species). Hutcheson's test was used for diversity comparison between transects (Hutcheson 1970). Springtail density and biomass were compared between transects and between sectors within each transect using the Mann–Whitney's U test. We analysed relationships between springtail abundance and the various environmental factors using Spearman's rank correlation. These non-parametric tests were used due to the non-normal distributions of data obtained and the relatively low number of sampling plots. Numerical ordination methods were used to describe total (qualitative and quantitative) variability of springtail communities independent of the environmental variables (linear indirect gradient analysis—Principal Component Analysis (PCA)) and in relation to the environmental factors (linear direct gradient analysis—Redundancy Analysis (RDA)). All species data and most environmental data (except soil water and organic matter content, soil solution pH, guano deposition and distance from the colony) were log-transformed to normalize and smooth their distributions. After RDA, a Monte Carlo permutation test was performed (with 499 permutations) to identify which of the factors significantly influenced the model (ter Braak and Šmilauer 2002). We calculated parametric Pearson's correlations between selected springtail species as well as between the species and environmental variables from all the sample plots (all transects) when it concerned RDA results as data were log-transformed in that case.

Data were processed using the following software: DIVer 10.o1 (AZB analysis & software (2010). DIVer (diversity indices analysis software), version 10.o1, http://www.azb.com.pl), STATISTICA 8.0 (StatSoft, Inc. (2008). STATISTICA (data analysis software system), version 8.0. http://www.statsoft.com.) and CANOCO 4.5 (ter Braak and Šmilauer 2002).

Results

Species composition, density and biomass of springtails

We found seven Collembola taxa in the study area (five identified to species, plus one representative of the genus *Isotoma* and one of the family Entomobryidae) (Table 1). Four taxa (*Folsomia quadrioculata*, *Hypogastrura viatica*, *Megaphorura arctica* and *Isotoma* sp.) occurred in all the transects, both ornithogenically influenced and controls. *F. quadrioculata* and *H. viatica* were generally found most commonly (in 73–91% of sampling plots of each transect), with the exception of the Transect 2 where *H. viatica* occurred in only 50% of plots. *Tetracanthella arctica* occurred in all the transects except for Transect 2C, while *Lepidocyrtus lignorum* and the unidentified entomobryid were only encountered occasionally, at most in two sample plots within a transect, and only within the control areas. The most abundant species found in the study area were *F. quadrioculata*, *H. viatica* and, in sites adjacent to the bird colonies, *M. arctica* (Fig. 2), whose numbers far exceeded all the other taxa encountered.

The diversity of the springtail community (Shannon's index), based on the number of individuals obtained in each sampling plot, was lower (Hutcheson's test; $t = 6.73$, $p < 0.001$, $df = 887$) in both seabird-influenced transects (combined data; $H' = 0.95$) compared with the control transects (combined data; $H' = 1.18$). The index of evenness based on Shannon's formula showed no differences between areas, being only slightly lower in the seabird-influenced Transects 1 and 2 (combined data; $J' = 0.59$)

comparing with the control transects (combined data; $J' = 0.60$). When comparing the transects individually, the diversity was lower ($t = 9.57$, $p < 0.001$, $df = 296$) in Transect 1 ($H' = 0.86$) than in its control (Transect 1C: $H' = 1.40$). The index values obtained within Transect 2 ($H' = 1.00$) and its control (Transect 2C: $H' = 0.95$) were similar. The index value was significantly higher in Transect 2 than in Transect 1 ($t = 7.47$, $p < 0.001$, $df = 5,847$). The index of evenness showed similar differences between transects, being lower in Transect 1 ($J' = 0.53$) than in Transect 1C ($J' = 0.72$), but similar between Transect 2 ($J' = 0.62$) and Transect 2C ($J' = 0.59$).

No consistent linear decrease of Collembola density along the colony-sea axis was observed (Fig. 2). However, there were distinct differences between the upper part of the ornithogenic transects close to the colonies and the lower, seashore, part of each transect. Total springtail density (and that of *H. viatica* considered separately) in both study areas was much higher adjacent to the colony in comparison with the seashore sectors ($p < 0.05$, detailed statistics in Table 2). *F. quadrioculata* density within Transect 2 was similarly higher in the section adjacent to the colony ($p < 0.01$). No differences were evident in the control areas, except for the case of *H. viatica* in Transect 2C. Moreover, the seashore sectors of all four transects did not differ significantly in either total collembolan density or that of *H. viatica* or *F. quadrioculata* separately (all $p > 0.05$).

Comparing only the sectors adjacent to the bird colonies, total collembolan density, and that of *F. quadrioculata* considered separately, were significantly greater in both ornithogenically influenced transects in comparison with their controls ($p < 0.05$, detailed statistics in Tables 3 and 4). In case of *H. viatica,* this difference was statistically significant for Transect 1 and its control ($p < 0.05$). The comparison was not significant for Transect 2, but the overall trend was similar, with the mean and median density values being 4–5 times higher in Transect 2 compared with 2C. We did not find significant differences between the two ornithogenically influenced transects. The frequency of *M. arctica* was too low to detect any differences between

Table 1 List of Collembola taxa recorded in the current study, and their frequency of occurrence along each transect

Total number of sampling plots along transect	Transect 1 12	Transect 1C 12	Transect 2 10	Transect 2C 11
	Number of plots with occurrence (%)			
Folsomia quadrioculata (Tullberg, 1871)	10 (83)	10 (83)	9 (90)	10 (91)
Hypogastrura viatica (Tullberg, 1871)	10 (83)	10 (83)	5 (50)	8 (73)
Megaphorura arctica (Tullberg, 1876)	4 (33)	5 (42)	6 (60)	4 (36)
Isotoma sp.	4 (33)	6 (50)	4 (40)	4 (36)
Tetracanthella arctica Cassagnau, 1959	4 (33)	3 (25)	2 (20)	–
Lepidocyrtus lignorum Fabricus, 1793	–	2 (17)	–	1 (9)
Entomobryidae	–	1 (8)	–	–

Table 2 Springtail density comparison for each study transect between the sectors adjacent to each bird colony, or their equivalent sectors in control transects, and the seashore sectors of each transect (z, Mann–Whitney's test)

	Transect 1 ($N_1 = 15$, $N_2 = 21$)	Transect 1C ($N_1 = 15$, $N_2 = 21$)	Transect 2 ($N_1 = 15$, $N_2 = 15$)	Transect 2C ($N_1 = 15$, $N_2 = 18$)
F. quadrioculata	ns	ns	2.59**	ns
H. viatica	2.89**	ns	2.41*	2.24*
All species	2.65**	ns	3.32***	ns

N_1, N_2—number of samples from seabird colony/upper ($_1$) and seashore ($_2$) sector of a transect

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

ns no significant correlation ($p > 0.05$)

Table 3 Density (10^3 ind m^{-2}) of the three dominant springtail species and all species taken together, and biomass (g m^{-2}) of *Folsomia quadrioculata* and *Hypogastrura viatica* (see "Materials and methods" for means of estimation), in the sectors of individual transects adjacent to bird colonies or their equivalent sectors in control transects

	Transect 1		Transect 1C		Transect 2		Transect 2C	
	Median	Mean ± SE	Median	Mean ± SE	Median	Mean ± SE	Median	Mean ± SE
F. quadrioculata								
Density	9.6	20.7 ± 7.3	0.7	0.8 ± 0.3	19.5	36.4 ± 11.1	0.0	2.4 ± 1.2
Biomass	0.10	0.21 ± 0.07	0.00	0.01 ± 0.003	0.19	0.36 ± 0.11	0.00	0.02 ± 0.01
H. viatica								
Density	14.2	43.1 ± 20.8	0.0	0.6 ± 0.2	12.0	21.4 ± 5.9	2.8	4.1 ± 1.4
Biomass	0.18	0.50 ± 0.18	0.00	0.01 ± 0.002	0.27	0.50 ± 0.20	0.02	0.05 ± 0.02
M. arctica								
Density	0.0	1.9 ± 1.0	0.0	0.1 ± 0.1	0.0	3.9 ± 2.6	0.0	0.1 ± 0.1
All species								
Density	37.2	66.5 ± 23.6	2.1	2.5 ± 0.6	47.8	64.3 ± 15.0	2.8	6.7 ± 2.4

Number of samples analysed in each transect: $N = 15$

SE standard error

Table 4 Comparison of springtail density and biomass between the sectors of each transect adjacent to bird colonies or their equivalent sectors in control transects (z, Mann–Whitney's test, number of samples analysed: N_1 and $N_2 = 15$)

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

ns no significant correlation ($p > 0.05$)

	Transect 1 versus Transect 1C	Transect 2 versus Transect 2C	Transect 1 versus Transect 2	Transect 1C versus Transect 2C
F. quadrioculata				
Density	2.22*	3.15***	ns	ns
Biomass	2.32*	3.15***	ns	ns
H. viatica				
Density	2.82**	ns	ns	−2.09*
Biomass	3.73***	ns	ns	−2.05*
All species				
Density	3.03**	3.44***	ns	ns

transects, but its occurrence was clearly limited to plots situated close to the bird colonies (Fig. 3).

The biomass of *F. quadrioculata* and *H. viatica* showed similar differences between transects as seen with density, with significantly higher values found in sampling plots influenced by both colonies compared with their respective control areas, and no differences between the two colonies (Tables 3, 4).

Environmental factors affecting collembolan abundance

Total collembolan density, and density of *H. viatica* considered alone, decreased substantially with the distance from the two colonies ($r_S = -0.45$, $p < 0.001$, $N = 66$ and $r_S = -0.41$, $p < 0.001$, $N = 66$, respectively). Significant correlations were present between springtail
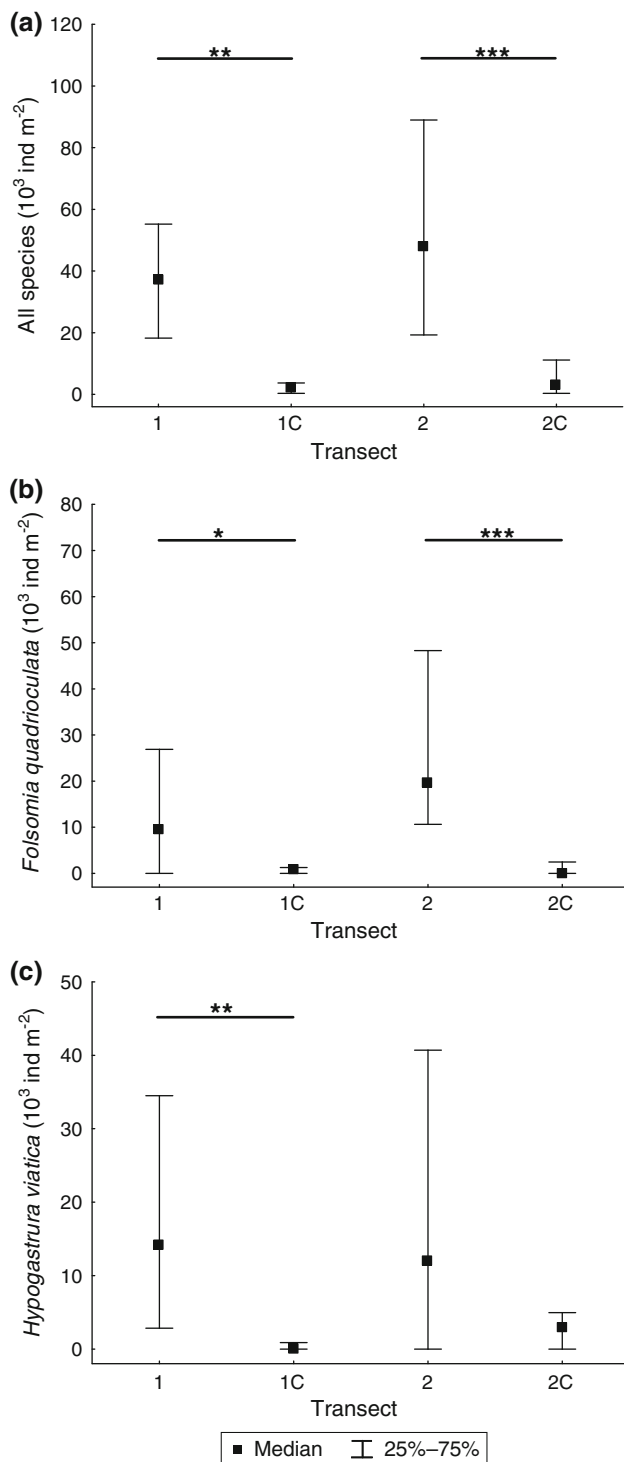
Fig. 3 Comparison of springtail density (median ± quartile) found on the sectors of transects adjacent to bird colonies and their equivalent control sectors: **a** all species in total, **b** *Folsomia quadrioculata* and **c** *Hypogastrura viatica* (Mann–Whitney's test; *p < 0.05; **p < 0.01; ***p < 0.001)

density and guano deposition, and most of the environmental factors examined, as well as with plant cover and biomass (Table 5). Soil temperature, measured only within

the ornithogenically influenced transects, was not correlated either with total springtail density or with density of individual species.

Principal Component Analysis (PCA), which is independent of environmental variables (i.e. soil and plant characteristics), showed that 59.6% of the total variability of Collembola species composition in the studied plots was explained by two main hypothetical gradients expressed by two axes. Guano deposition used as a sole environmental variable (axis 1 in Redundancy Analysis (RDA)) significantly explained 6.7% ($F = 3.44$, $p = 0.006$) of that variability (Fig. 4a). Unidentified factors, represented by the other RDA axes, explained a larger proportion of the species variability: axis 2 = 32.4%, axis 3 = 21.7%, axis 4 = 14.1%. The RDA model testing all environmental variables except for those showing high levels of autocorrelation with each other (inflation factor >20; guano deposition, vascular plant, moss and *C. groenlandica* cover, phosphorus and both nitrogen ion concentrations), explained 53.7% ($F = 1.78$, $p = 0.002$) of springtail community variability. The strongest effect was exerted by *Prasiola crispa* cover (explaining 11.0% of the total variability, $p = 0.002$), total plant biomass (9%, $p = 0.002$) and soil solution conductivity (6%, $p = 0.01$) (Fig. 4b). Densities of the most abundant species, *F. quadrioculata*, *H. viatica* and *M. arctica*, best fitted the model. *F. quadrioculata* abundance was significantly positively correlated with total plant biomass ($r = 0.56$, $p < 0.001$, $N = 44$). *H. viatica* abundance increased with increasing *P. crispa* cover ($r = 0.46$, $p < 0.01$, $N = 44$) and total plant biomass ($r = 0.34$, $p < 0.05$, $N = 44$), and *M. arctica* abundance was positively correlated with conductivity ($r = 0.39$, $p < 0.01$, $N = 44$). *F. quadrioculata* and *H. viatica* densities were positively correlated with each other ($r = 0.32$, $p < 0.05$, $N = 44$) and were independent of that of *M. arctica* ($p > 0.05$, $N = 44$) (Fig. 4b).

Both *P. crispa* cover and conductivity were strongly and positively correlated with guano deposition (*P. crispa*: $r = 0.67$, conductivity: $r = 0.64$, $p < 0.001$, $N = 44$), and significantly decreased with increasing distance from the seabird colony (*P. crispa*: $r = -0.53$, $p < 0.05$; conductivity: $r = -0.54$, $p < 0.01$, $N = 22$) along the ornithogenically influenced transects (Fig. 4b).

Discussion

Arctic terrestrial ecosystems, generally characterized by chronic nutrient deficiency, can profit from allochtonous matter of marine origin deposited by seabirds, often in large amounts in the vicinity of their colonies. This deposition can facilitate plant and invertebrate community development although, on the other hand, locally excessive

Table 5 Spearman's rank correlation coefficient (r_S) for density of *Folsomia quadrioculata*, *Hypogastrura viatica* and total collembolan density with distance from seabird colony (only data from the sampling plots from the two ornithogenically influenced transects included), and with each specific environmental factor examined (data from all sampling plots included)

Factor	F. quadrioculata	H. viatica	All species	N
Distance	ns	0.41***	0.45***	66
Guano DM	0.35***	0.35***	0.44***	123
NH_4^+	0.37***	0.22***	0.43***	122
NO_3^-	0.37***	0.26***	0.46***	120
K^+	0.29**	ns	0.36***	122
PO_4^{3-}	0.39***	0.26**	0.48**	121
pH	ns	−0.22*	−0.25**	123
Conductivity	0.19*	ns	0.23**	123
Soil water content	0.29***	ns	0.35***	123
Organic matter content	0.32***	0.24**	0.41***	123
Soil temperature	ns	ns	ns	60
Vascular plant cover	0.26***	0.28**	0.32***	135
Moss cover	ns	−0.17*	−0.20***	135
Total plant biomass	0.42***	0.21*	0.32***	135
Vascular plant biomass	0.31**	ns	ns	99
Moss biomass	0.37***	0.27**	0.37***	117

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

ns no significant correlation ($p > 0.05$)

N number of samples analysed

tundra fertilization may limit the occurrence of some plants and soil invertebrates to those with the greatest tolerance.

In our study area, two to three Collembola species were encountered commonly and in large numbers, with the remainder being found occasionally and often only within control areas not affected by birds (Table 1; Fig. 2). The two most abundant species, *F. quadrioculata* and *H. viatica*, are both widespread in Svalbard (Sømme and Birkemoe 1999; Herzberg et al. 2000). Their densities and biomass, as well as total collembolan density, were 5–20 times higher in parts of both ornithogenically influenced transects compared with their controls (Tables 3, 4; Fig. 3), indicating improved feeding conditions (cf. Hodkinson and Wookey 1999; Bokhorst et al. 2007b). In spite of differences in physicochemical soil parameters and vegetation structure being reported between the ornithogenic tundra developing close to planktivorous and piscivorous seabird colonies (Stempniewicz et al. 2006), we found similar abundance and species composition of springtail communities in the sampling plots influenced by the two representatives of these colony types examined in this study.

Guano fertilization can be excessive in the direct proximity of a bird colony (deposition reaching ca. 1.2–1.5 g m^{-2} day^{-1}, Zwolicki unpublished data) and such conditions probably only permit the most tolerant species to survive. Springtails existing under these conditions may avoid or limit the associated extreme stresses by,

for example, vertical stratification in the soil or the neutralization of high ammonium concentration through increased water uptake (Jensen et al. 2006). They may then benefit from the subsequent tundra plant development providing directly and indirectly an important food resource for them. Such sites here were dominated by *M. arctica,* a species known for its occurrence close to bird cliffs (Hodkinson et al. 1994), and presumably the collembolan most resistant to high guano deposition.

The density and biomass of springtails did not show a simple linear gradient along the transects from the seabird colonies to the coast, but there were very clear differences between groups of sampling plots close to and remote from the bird colonies. The contrast between these two groups of sample plots indicates that seabird impact on soil invertebrate community composition, while potentially very large, is also spatially limited, here being restricted to within ca. 50 m (i.e. to sample plot 5) of each bird colony (Fig. 2).

Notwithstanding the clear localized colony impact, we found an overall negative relationship between collembolan density and distance from the bird colonies, and a positive correlation with rate of guano deposition and various physicochemical properties of the soil and vegetation characteristics (Table 5). The decrease in springtail density and biomass with increasing distance from the colony distance was clearly not linear (Fig. 2). This probably relates to the most abundant species achieving their

Fig. 4 Multivariate analyses of relationships within the springtail community with respect to: **a** guano deposition and **b** environmental and biotic factors (RDA, all transects included). *Full tip arrows*—variables, *open tip arrows*—springtail species; *bold solid lines*—significant variables (Monte Carlo permutation test, $p < 0.05$), *regular solid lines*—insignificant variables ($p > 0.05$), *dashed lines*—supplementary variables (not tested due to high correlations with other variables, not influencing the ordination)
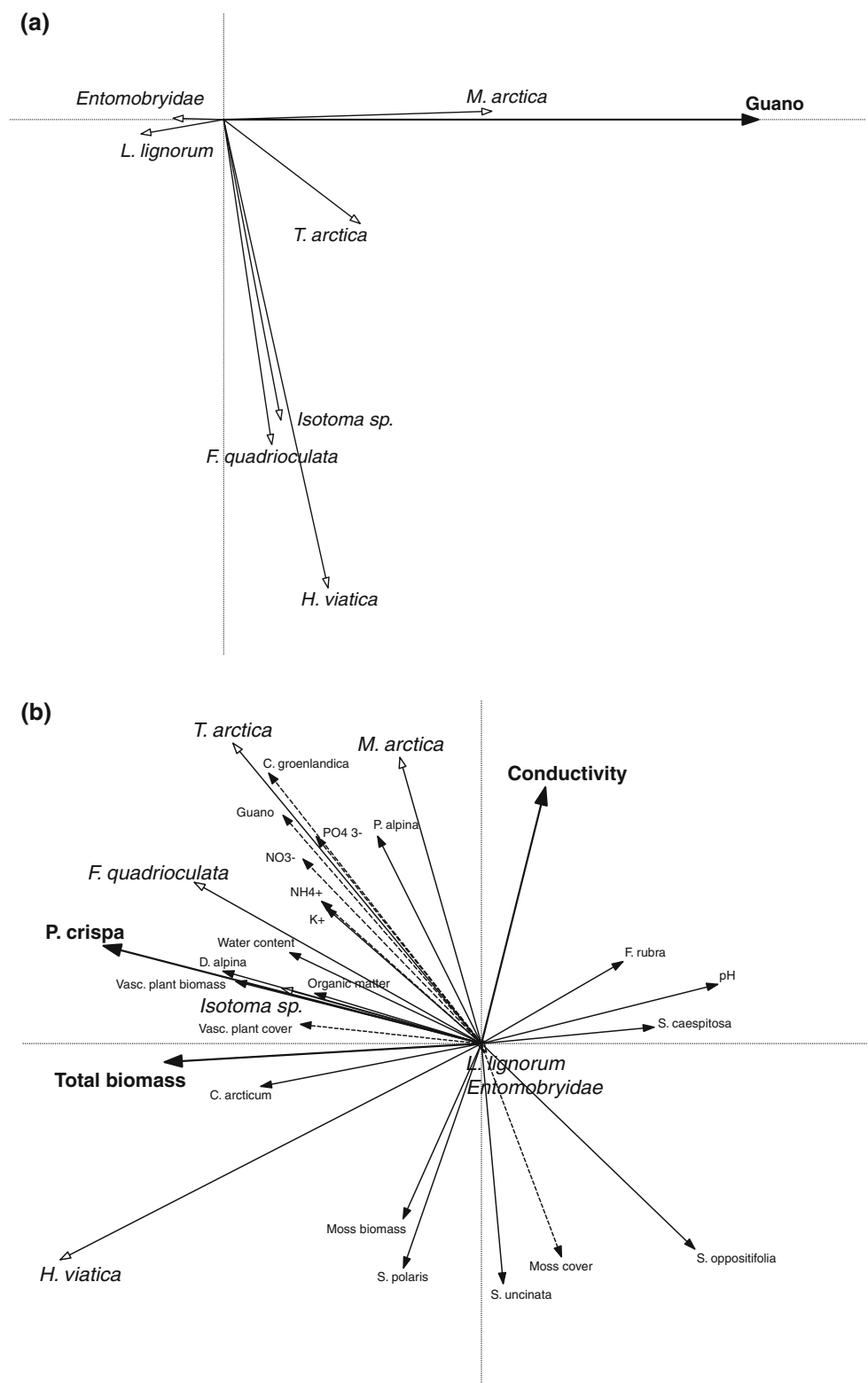
optimum occurrence at points below the maximum seabird influence (guano deposition), as suggested by Sømme and Birkemoe (1999). Our data are consistent with previous observations that springtail abundance is not directly dependent on a single factor but is likely related to a suite of complex environmental conditions, such as habitat moisture, temperature, acidity, organic matter content, vegetation cover, soil structure and composition (Hodkinson et al. 1998; Herzberg et al. 2000; Filser 2002; Cassagne et al. 2003; Dollery et al. 2006; Caruso et al. 2007).

Springtail distribution and density often reflect the patchy nature of their habitat, especially in earlier vegetation succession stages (Caruso and Bargagli 2007). Notwithstanding this influence of habitat, microarthropod distributions in polar soils and vegetation profiles are characteristically patchy or uneven, even in otherwise apparently uniform habitats (Usher and Booth 1984, 1986). Distinct springtail assemblages with one or two dominant species may be found in combination with particular plant species or communities and, consequently, be related to specific environmental conditions forming below or near to this vegetation (Herzberg et al. 2000; Ims et al. 2004; Dollery et al. 2006; Caruso and Bargagli 2007). Such relationships between soil properties and vegetation type and invertebrate distribution also impact springtail communities and may involve a form of feedback. Selective habitat choice by Collembola may be connected with food availability, so the litter type or fungal species therein may strongly influence springtail community structure, especially that of microphytophagous and fungivorous species. Moreover, feedback effects may also occur if microarthropod grazing affects decomposition rates and, thereby, the fungal and plant communities themselves (Coulson et al. 2003).

These potentially complex springtail-habitat interactions are partially reflected in the RDA results (Fig. 4). The only factors significantly influencing the springtail community were the cover of the green nitrophilous alga *P. crispa*, total plant biomass and soil conductivity. *P. crispa* is known for its growth directly on guano-covered sites close to marine bird and mammal aggregations both in Arctic and Antarctic (Matuła et al. 2007; Smykla et al. 2007). Algal cover and soil conductivity, which is indirectly connected with content of several ions, changed along the seabird colony-sea axis and guano deposition gradient. Herzberg et al. (2000) recognized plant cover as the most important variable explaining density of some collembolans, such as *F. quadrioculata*. Since in our study area total plant cover was homogeneous and very high across virtually the entire transects (with the exception of plot 1 of Transect 2, directly below the bird cliff, and some plots of Transect 2C), cover values were not included in the RDA. Instead, total plant biomass was used as a measure of vegetation abundance, and appeared to be a significant factor influencing Collembola community composition. Many studies have linked plant biomass and cover increase with seabird presence in the polar regions (e.g. Ellis 2005; Wait et al. 2005; Maron et al. 2006), and our results provide further support to the hypothesis that seabirds impact indirectly on springtail (and other soil invertebrate) community composition and variability, this being mediated through vegetation changes.

Our study has confirmed the locally strong influence of nutrient input from seabird colonies on the springtail communities developing in these areas on High Arctic Svalbard. While the strongest effects were clearly apparent within a relatively short distance—tens of metres—of the colony, it is important also to recognize that springtail distribution shows significant correlations with a range of physical and biological environmental factors and, thus, that a complex suite of these factors and their interactions is likely to underlie these distributions. Furthermore, while impacts of over-fertilization in the immediate vicinity of colonies are likely to be directly limiting to springtails, many of the factors influencing springtail distribution will act indirectly through their consequences for local vegetation and microbial community composition, structure and biomass.

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