



The significance of recent glacial history for the limno-terrestrial microfauna in Trygghamna (Svalbard, High Arctic)

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Abstract

The diversity and spatial distribution of microscopic invertebrates in the Arctic have yet to be studied in detail. Knowledge of this is especially important in the context of glacier shrinking, one of the most visible environmental consequences of climate change. To understand how time since deglaciation shapes the communities of limno-terrestrial microfauna, we analysed samples of moss collected during the summer of 2021 in forefields of Trygghamna (Svalbard), where glaciers thought to have started to recede at the beginning of the twentieth century. We estimated the taxonomic and trophic composition and abundance of all microfauna groups (with a specific focus on little-known bdelloid rotifers) in two areas, which correspond to the different stages of the glacial retreat. The impact of 14 other environmental parameters (distance from the sea, moisture, moss structural complexity, soil nutrient, and isotopic composition) was considered. Thirty-seven microfauna taxa were found, wherein Dorylaimida nematodes (Dorylaimida, Nematoda) dominated both in frequency (present at all sites) and abundance ($50 \pm 21\%$ from all individuals). Less prevalent bdelloid rotifers (Bdelloidea, Rotifera) were followed by tardigrades (Tardigrada), which, in contrast to others, were more abundant in the later deglaciated area. In general, environmental parameters explained 81.8% of the microfauna distribution. Time since deglaciation was the most significant factor (9.5%). Among the variables that act at a fine scale, the most important were moisture in the habitat (6%), presence of ground in the samples (4%), and $\delta^{15}\text{N}$ (4%). The moss structural complexity did not have a significant effect, and neither did most of the variables characterising soil nutrient and isotopic composition. However, some variability was observed for different lower taxa.

Keywords Deglaciation · Nematodes · Bdelloid rotifers · Tardigrades · Polar · Nutrient · Isotopic N, C composition

Introduction

In recent decades, better knowledge of polar ecosystems has been seen as important because of the impact of climate change, compared to other regions (Rantanen et al. 2022). In polar areas, the most obvious consequence of global warming is glacier retreat, which in turn drives significant changes in local biodiversity (Fell et al. 2017; Stibal et al. 2020; Losapio et al. 2021).

Microfauna communities (micrometazoan or microinvertebrate communities) can reach high densities and species richness in many terrestrial and limno-terrestrial polar ecosystems but the data of how they are affected by warming and glacier retreat is still controversial and incomplete. In their global review of consequences of glacier retreat on species richness and abundance in ice-adjacent habitats, Cauvy-Fraunié and Dangles (2019) provided only 51 records of nematodes (Nematoda), tardigrades (Tardigrada), and rotifers (Rotifera) in glacier-fed freshwater and glacier forefields in the Antarctic and alpine ecosystems, among more than 1500 given for all living organisms. In this study, microfauna was indicated as rather ‘losers’ than ‘winners’ in terms of ice receding. The anticipation of the extinction for many cold-adapted species, especially tardigrades (Zawierucha and Shain 2019), co-exists with the general assumptions of increasing in abundance and productivity of polar terrestrial invertebrates as a respond to warming (Convey and

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Peck 2019). Recent meta-analysis of soil biota responses to deglaciation over a prolonged time span (up to 500 years) showed increased abundance of nematodes, especially omnivores (Pothula and Adams 2022).

On the other hand, there is a general view of glacial forefield succession patterns, which, apart from the time since deglaciation, can be resulted from site conditions (Wojcik et al. 2021). Regarding microscopic organisms in polar ecosystems, the conditions of the site can include a huge number of factors, many of which can function on a very small scale, referring to the concept of the patchy distribution of microfauna (e.g. Adams et al. 2006; Velasco-Castrillon et al. 2014). Thus, in the Antarctic, microfauna communities depend on the type of habitat, e.g. moss, soil, lichen, and algae (Heatwole and Miller 2019), and can display variability even in close and homogeneous biotopes (Adams et al. 2006). Arctic tardigrades are strongly affected by the ornithogenic nutrient input (Zawierucha et al. 2016), while the abundance of nematodes in Antarctic soils correlates with elemental composition (Zawierucha et al. 2019b) and moisture (Andriuzzi et al. 2018). The same was demonstrated for less studied rotifers (Smykla et al. 2018). There are no particular data for polar regions, but generally, the structural complexity of mosses and associated water content favour species richness and abundance of moss-dwelling rotifers (Hirschfelder et al. 1993). Altitude is also important for microfauna distribution in polar regions (Zawierucha et al. 2015b, 2019b), so variables which do not relate to nutrient content or microhabitat structure should not be excluded either.

The present study deals with the question how concept of patchy distribution relates to the expected significant impact of glacial history on polar limno-terrestrial microfauna. We hypothesise that the distribution of microfauna in glacier-adjacent ecosystems is not determined only by processes related to the time since ice retreated (colonisation, immigration, extinction), but is also driven by conditions of the site, i.e. environmental variables sometimes act on a very small scale, like microstructure of the habitat, nutrient, and isotopic composition in particular place.

We performed the study at Svalbard archipelago, where one of the vastest reductions of ice mass in the world happens (Noel et al. 2021; Wang et al. 2021; Geyman et al. 2022), with the annual decreasing of the glacierized area by an average of 80 km² during last decades (Nuth et al. 2013). A location well suited to ascertaining the answer to the research question was identified in 2021 in Isfjorden (West Spitsbergen). The forefields of Trygghamna were chosen, since the glacial history of this region reflects the overall trend of deglaciation in Svalbard and is well documented (Aradóttir et al. 2019), making it possible to identify places that became free from ice cover in the very beginning, in the middle, and in the end of twentieth century. We estimated

diversity, taxonomic, and trophic structure of microinvertebrates residing in limno-terrestrial mosses (a habitat that has been studied much less compared to soil) in two areas differing by their time since deglaciation, and, in parallel, determined a set of environmental variables there. Assuming large variability in relation to different microfauna taxa, as they have different features of their biology and different level of knowledge, we mostly focussed on one of the oddest and most poorly studied microfauna group—parthenogenetic bdelloid rotifers (subclass Bdelloidea). Despite being widely presented in various environments, including wet mosses and other vegetation, they are frequently ignored in ecology, biodiversity and soil biology studies. With that, they have extremely high capacities for passive dispersal (Fontaneto and Ricci 2006; Debortoli et al. 2018) and some species—very wide ecological tolerance (Ricci 1987). All these make bdelloids an attractive object for understanding the importance of glacial history in recent past on communities of microfauna in the Arctic.

Materials and methods

Sample collection

All field materials were collected on 30 July 2021. The study area was the inner part of Trygghamna (the northern side of Isfjorden, Spitsbergen, Svalbard archipelago). The Kjerulfbreen and Harrietbreen glaciers, currently laying exclusively on land, in the vicinity of the study area, previously drained into the bay and then have been receding since the beginning of the twentieth century (started approximately in period of 1890–1910). The overall retreat along the proposed major flow line from the position of the maximal advance up to 2016 is 2.8 and 2.4 km, respectively. Six ice-marginal positions in forefields of Trygghamna corresponding to the dates 1909/1910, 1936, 1968, 1990, 2007, and 2016 are known from the old aerial photos, geomorphological archives of Norwegian Polar Institute, and satellite imagery (Aradóttir et al. 2019).

All sampling activities were performed between Lovenvatnet lake and the seacoast, i.e. within the area that had been glacierized previously. We established seven sampling plots across the \approx 980-m transect along the watercourse which connects Lovenvatnet lake and the seacoast and is surrounded by large moss patches (Fig. 1a). Plots, corresponding to the biggest moss patches (Fig. 1b–e), were distanced between each other by 162.7 ± 22.9 m $n = 6$. Sampling plot # 1 was located very close to the shore of Lovenvatnet, then sampling plot # 2 was located, and so forth to sampling plot # 7, which was about 160 m from the Trygghamna bay coastline (Fig. 2).

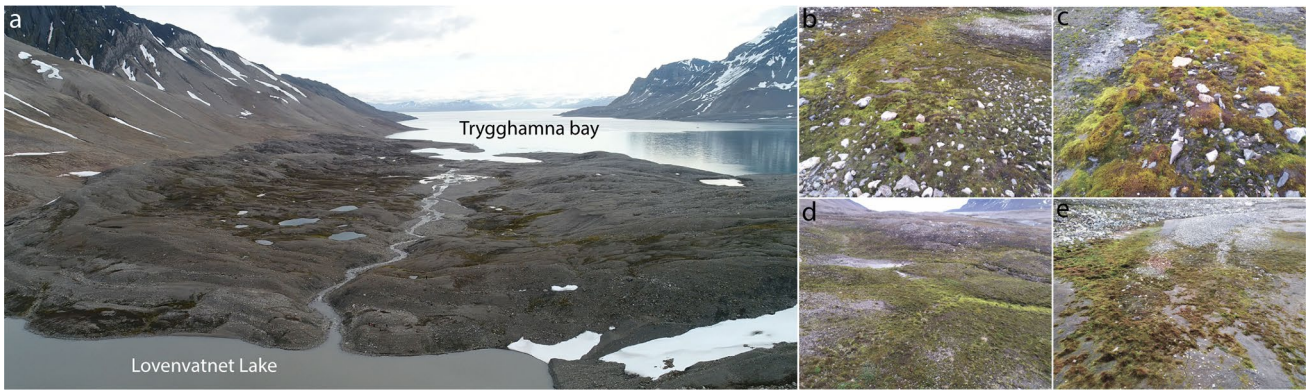


Fig. 1 Study area in Trygghamna: **a** sampling transect (drone photo by Jonas Gintauskas) and examples of moss patches at **b** sampling plot # 1, **c** sampling plot # 2, **d** sampling plot # 3, **e** sampling plot # 4 (photos by Dzmitry Lukashanets)

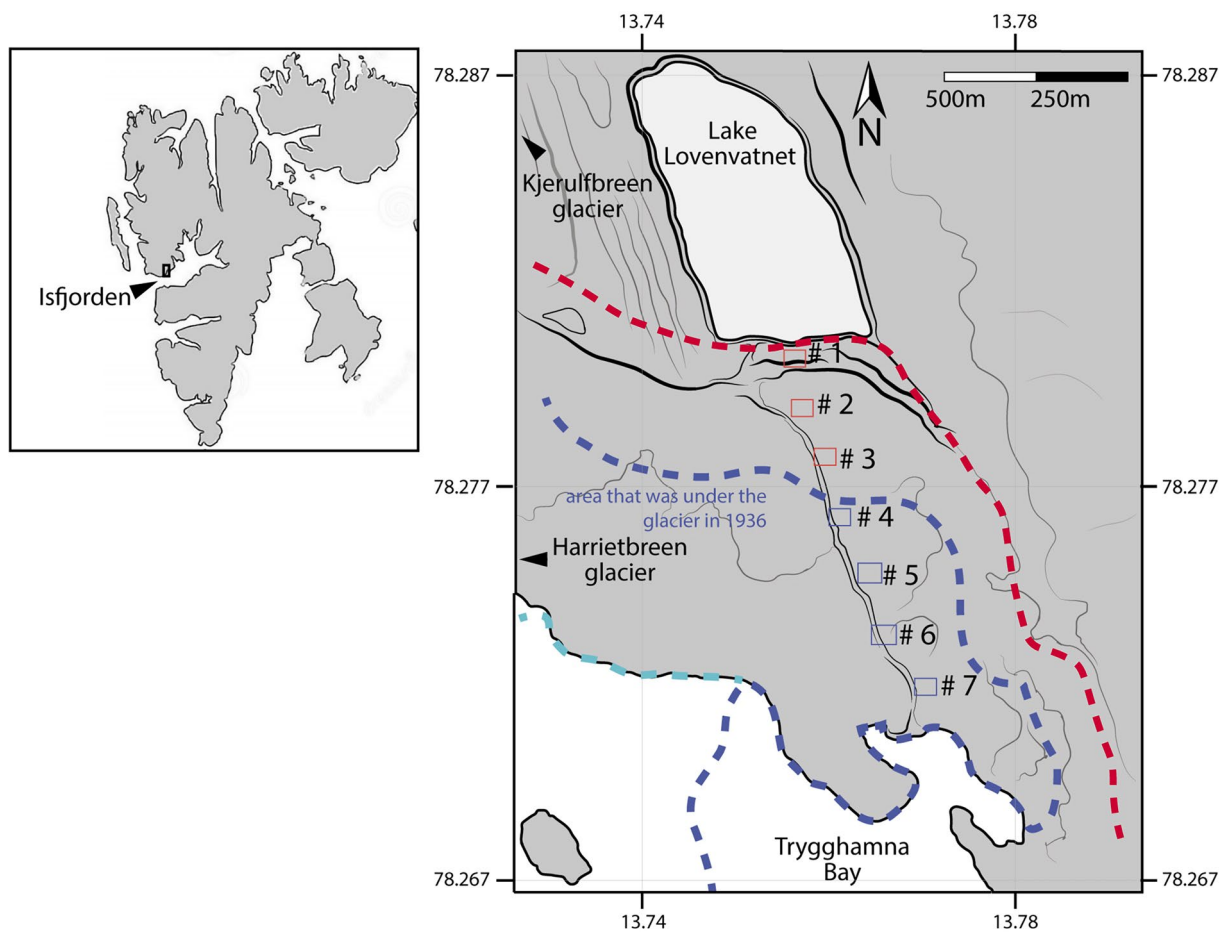


Fig. 2 Study area in Trygghamna overlaid with known margins of the glacier in 1936 (dark blue dash line), 1968 (light blue dash line), and terminal moraine (red dash line) (Aradóttir et al. 2019)

For identification of the areas corresponding to different stages of the glacier retreat, we referred to the reconstruction of the glacier margins in Trygghamna (Aradóttir et al. 2019). Plots ## 1–3 were in the area, which is located between line of the terminal moraine (the margins of maximal advance

of glacier, 1890–1909/1910) and glacier margin of 1936 and was deglaciated during this interval (hereinafter referred to as area of early 20th c. deglaciation). This area, elevated above sea level from 10 to 26 m, is lying on kame hill with kettles. The area where other four plots are located was

Table 1 Characteristics of the sampling area and sampling sites in Trygghamna

Sampling area	Sampling plots	Sampling sites	Altitude, m	Latitude	Longitude	Distance to sea (along the transect), m
Early 20th c. deglaciation	1	early1, early2, early3	26	78.2801	13.7554	1080
	2	early4, early5, early6	26	78.2790	13.7564	941
	3	early7, early8, early9	10	78.2777	13.7581	797
Middle 20th c. deglaciation	4	late1, late2, late3	2	78.2764	13.7610	656
	5	late4, late5, late6	2	78.2749	13.7641	465
	6	late7, late8, late9	2	78.2734	13.7654	276
	7	late10, late11, late12	1	78.2724	13.7709	163

limited by the glacier margins of 1936 and was deglaciated much later, between 1936 and 1990 (hereinafter referred to as area of middle 20th c. deglaciation). This part of study area is less elevated (average altitude is 1.75 m) represented mostly by fluted till plain with crevasse-squeeze ridges or outwash plain (Aradóttir et al. 2019) (Fig. 2).

Within one plot, we collected mosses at three sites, which were on one 1.5–2.0 m line and referred to the distal end of the line, the proximal end, and the middle of the line. Depending on the area ('early 20th c. deglaciation' or 'middle 20th c. deglaciation'), we considered the sites as 'early' (sites early1–early3 for plot #1, etc.) and 'late' (sites late1–late3 for plot #4, etc.), respectively (Table 1).

At each site, two cores with a 3.5-cm diameter and a few cm of length were collected using plastic tubes and tweezers (designating the boundaries of the core by tube followed by picking up by tweezers). The cores were combined in one sample and placed in a plastic 100-mL jar. At the same sites, just beneath moss cores, some amount of soil and ground were collected by plastic spatula and placed into plastic sterile 20-mL tubes. All samples were frozen without using any fixative chemicals.

Moss sample processing

After delivery to the laboratory, samples were slowly defrosted by keeping them under 5–6 °C for several hours and then under room temperature. All moss samples were weighed moistened and after drying.

A set of environmental variables were estimated during the primary processing of the samples. First, we calculated the moisture (water content in moss) using the formula:

$$\text{Moisture} = \frac{M - m}{m} \times 100\%,$$

where M is the mass of the moistened moss, m is the mass of the dry moss.

The presence of the ground/soil particles was estimated visually and expressed in percent proportion for each sample

(e.g. 0%—clean moss, 50%—moss with ground constituting one half of the sample volume).

The level of the complexity of the moss (moss structural complexity) was estimated by precise examination of moss thalli parts under light microscopy. The measuring of the following parameters is suggested being most essential:

- the mean number of lateral branches;
- the mean number of phyllids (leaves) present at 5 mm of the caulid (stem);
- the mean length of phyllids;
- the mean maximal width of phyllids.

The caulid length was not estimated as a distinct parameter as caulid can be easily torn into separate parts during sampling or primary sample processing.

Microfauna isolation and identification

To assess the animal numbers, three small moss sub-samples (5–7 cm³ moss particles) from each sample were taken. Microfauna was extracted using the method of multiple washing (Peters et al. 1993 with some modifications). The sub-sample was placed into a glass vial with 20 ml of distilled water and kept there for 24 h. After the vial with moss particles had been shaken vigorously the water was poured into gridded Petri dish for animal isolation, sorting, and counting using the dissecting microscopy (binocular microscopes Olympus SZ61 and NR.3 Nikon SMZ1000 with bottom light). The procedure is repeated several times (up to 10) till no animal individuals can be recorded in the water from washing. Moss parts (stems) were precisely collected after finishing the animal extraction and subsequently dried and weighed on electronic scales with 0.001 g accuracy.

Taxonomic identification was carried out under light microscopy (Nikon Eclipse Ts2R equipped with a digital camera Nikon DS-Ri2 and NIS Elements BR analysis 5.10.00 software). The identification was carried out to the

species level for bdelloid rotifers and to higher taxa—for other microfauna groups (e.g. nematodes and tardigrades).

We used the following identification keys: Donner (1965) and Kutikova (2005) for bdelloid rotifers; Kutikova (1970), Nogrady et al. (1995), and De Smet and Pourriot (1997) for monogonont rotifers (Monogononta, Rotifera); Ramazzotti and Maucci (1983), Fontoura and Pilato (2007), Pilato and Binda (2010), Bingemer and Hohberg (2017) for tardigrades; Zullini (2010) for nematodes; Wells (2007) for harpacticoids (Harpacticoida, Arthropoda). Also, for bdelloid rotifers, body dimensions and morphometry estimation methods developed by Iakovenko et al. (2013) were used.

Soil nutrient and isotope composition

To characterise the site conditions in terms of their nutrient and stable isotope composition, we analysed only soil and ground samples collected just beneath the moss cores. These characteristics in polar vegetation and in surrounding soil or water correlate with each other (Royles et al. 2016; Zmudczyńska-Skarbek et al. 2017); moreover, the amount of collected moss was insufficient for both nutrient/stable isotope analysis and for assessing the microfauna that should be extracted from undisturbed moss samples.

The organic carbon (hereinafter referred to as OC) and total nitrogen (TN) content in the soil samples was determined in Center for Physical Science and Technology (Vilnius, Lithuania) using an elemental analyser Thermo Flash EA 1112. Standard sulphanimide (Merck, cat. #111799) was used for calibration. Long-term standard measurements were performed with a precision of < 1% for N and < 1.5% for C. Before analysis, carbonates were removed. The samples were acidified with 1 M HCl, then rinsed in deionized water to a neutral pH, and dried at 60 °C in a drying oven overnight.

Soil samples were analysed for stable carbon and nitrogen isotopes using a Thermo Flash EA 1112 elemental analyser interfaced with a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer (IRMS). All the results of the stable isotope ratio measurements were expressed relative to a standard using delta notation in units of per mils (‰):

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3,$$

where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$, $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ in the sample or in the standard. The stable carbon isotope ratios were expressed relative to the international Vienna Pee Dee Belemnite (V-PDB) reference standard. IAEA600, IAEA-N-1, IAEA-CH-3 were used to calibrate the laboratory standards for sample measurements. Long-term reference material measurements were performed with a precision of < 0.15‰ for C in organic matter, and < 0.2‰ for N.

Analysis for total phosphorus (hereinafter referred to as TP), total inorganic phosphorus (TIP), total organic phosphorus (TOP), and organic matter (OM) was performed in the Coastal Environment and Biogeochemistry Laboratory of Klaipėda University. Samples for TP and TIP were dried at 60 °C for 48 h and ignited at 550 °C for 4 h (only TP). TP and TIP pools were extracted with 37% HCl and measured spectrophotometrically after neutralisation with 10 N NaOH, following Valderrama (1981). TOP was calculated as the difference between TP and the sum of sedimentary P pools that are considered TIP. OM content was calculated by mass loss after ignition where sediment was ignited at 550 °C for 4 h.

Data analysis

To estimate the abundance of microfauna in different sites, we used two different approaches. First, like in several studies of moss tardigrades (Zawierucha et al. 2016) and microinvertebrates from other substrates (Sohlenius et al. 2004; Sohlenius and Boström 2005, 2008), we displayed it as individuals in 1 g of dry weight (hereinafter referred to as ind gdw^{-1}) calculating mean value from three sub-samples with known dry weight. However, expressing in individuals per square unit is also applicable, e.g. in the canonical work of Peters et al. (1993), where the method for quantitative extraction of moss-dwelling rotifers was proposed. Heatwole and Miller (2019), who studied micrometazoans in different terrestrial habitats of the Antarctic and sampled them in a manner very similar to the present study, calculated the sample volume from the sampler mouth square and core length. In the case of our samples, the core diameter was constant, but the measurements of the core length would not be precise because of protrusions of moss branches, variations in surface, and deformations of cylindrical shape. Therefore, the second approach based on extrapolating the overall number taken from all sub-samples to the sample square ($\approx 10 \text{ cm}^2$ in accordance with the formula $\pi r^2 \times 2$, where $\pi = 3.14$, r = radius of the tube) was considered less accurate.

To describe the peculiarities of microfauna distributional and diversity patterns, we established the following explanation (environmental) variables (Table 2). The main factor is related to glacial history and determines whether the site is ‘early’ or ‘late’, meaning located in the area of early 20th c. deglaciation or in the area of middle 20th c. deglaciation, respectively. The significance of the time since deglaciation was compared with that of other environmental variables, both large scale (the straight distance to the sea), and small scale, which are supposed to act much more locally. Altitude was not included in the analysis as this variable strongly reflects the division of the study transect on the area of early 20th c. deglaciation and the area of middle 20th c. deglaciation (first is more elevated while the second is more lowland).

Table 2 Environmental variables used for explaining the microfauna distributional patterns

Variables	Description	Unit of measurement	
Glacial history			
1	Time since deglaciation (Early/Late site)	Whether the site located in the area of early 20th c. deglaciation (Early site), or in the area of middle 20th c. deglaciation (Late site)	–
Other			
Large-scale variables			
2	Distance to sea	Position of the site on the transect line connecting sea and Lovenvatnet lake	m
Small-scale variables			
Microhabitat structure			
3	Moisture	Mass proportion of water in the moss sample	%
4	Ground presence	Volume proportion of ground (soil) in the sample	%
5	Moss structural complexity #1	Lateral branching of the caulid (moss stem)	nbr
6	Moss structural complexity #2	Number of phyllids (moss leaves) present at 5 mm of the caulid	nph
7	Moss structural complexity #3	Length of the of phyllids	mm
8	Moss structural complexity #4	Maximal width of phyllids	mm
Soil nutrient and isotopic composition			
9	TN	Content of total nitrogen in the soil	%
10	OC	Content of organic carbon in the soil	%
11	C/N	Ratio of carbon to nitrogen in the soil	–
12	TP	Content of the total phosphorus in the soil	mg kg ⁻¹
13	OM	Organic matter content in the soil	%
14	δ ¹⁵ N	Proportion of nitrogen-15 isotope in the soil	‰
15	δ ¹³ C	Proportion of carbon-13 isotope in the soil	‰

nbr number of branches, *nph* number of phyllids

Spearman rank correlation was applied for analysis of data obtained by different methods of abundance estimation. To describe the differences in species composition between sites we built pair-wise matrix of Sørensen distances. The analysis of similarities ANOSIM was used for comparing the differences in species diversity between sites within one plot with the differences in species diversity between plots. The values of microfauna abundances and environmental variables between early and late sites were compared by the non-parametrical Mann–Whitney *U* test. Since the main idea was to establish the significance of the time since deglaciation on microinvertebrate distribution patterns that simultaneously might be affected by other environmental parameters, the relationships between microfauna and all explanatory variables listed in Table 2 were considered complexly, by methods of ordination (no additional analyses like regression analysis with separate variables as predictors were performed). To reveal how microfauna taxa are dispersed along the variation of all environmental parameters we used transformation-based redundancy analysis (tBRDA). All graph plotting and statistical tests were performed using R Statistical Software (R Core Team 2021), with ‘vegan’ (v2.5-4; Oksanen et al. 2020) and ‘Hmisc’ (v4.7-1; Harrell 2022) packages for

tBRDA and ANOSIM, and ‘labsdv’ (v1.5-0; Roberts 2013) package for Hellinger transformation of data.

Results

Environmental variables

Several parameters describing microhabitat structure were characterised by significant variability. The ground presence in the sample ranged from 0% (clean moss) to 90% (ground volume exceeds over the moss volume in nine times). In more than one half of the samples, ground particles that interspersed moss stems and leaves constituted 30–70% of the entire volume. Moisture varied from 17% (almost completely dry sample of moss) to more than 90% (completely wet moss, enriched with water). The variability in moss structural complexity was significant only in the case of lateral branching (13.1 ± 6.9 $n=21$), other parameters did not disperse much (Online Resource 1).

Estimated characteristics of the soil (nutrient and isotope composition) showed following ranges ($n=21$): TN— $0.2 \pm 0.1\%$; OC— $3.1 \pm 1.7\%$; δ¹⁵N— 1.8 ± 0.8 ‰; δ¹³C— -25.8 ± 0.6 ‰; C/N— 14.5 ± 2.1 ;

Table 3 Comparing of microhabitat structure, soil nutrient and isotopic composition (Mann–Whitney *U* test) between early and late sites

Environmental variables	<i>W</i>	<i>p</i>
Moisture	55.5	0.94
Ground presence	67.5	0.35
Moss structural complexity #1	27.0	0.059
Moss structural complexity #2	12.0	0.0032
Moss structural complexity #3	55	0.97
Moss structural complexity #4	49.5	0.77
TN	49.0	0.73
OC	59.0	0.75
C/N	61.0	0.64
TP	31.0	0.11
OM	48.5	0.72
δ ¹⁵ N	80.0	0.069
δ ¹³ C	49.5	0.78

All variable abbreviations are explained in Table 2

TP—1015.3 ± 259.9 mg kg⁻¹; OM—7.4 ± 3.7% (Online Resource 2).

Most of the environmental factors were not statistically different between early and late sites with the only exception of the moss structural complexity # 2, or number of phyllids (Mann–Whitney test: *W* = 12, *p* = 0.0037; Table 3, Fig. 3). Two areas were not compared by the distance from sea as the difference between is obvious: area of early 20th deglaciation is located much more distantly from the coast then the area of middle 20th deglaciation (Fig. 2).

Microfauna abundance and structure

The abundances of all microfauna groups calculated using two approaches (Online Resource 3) were compared for main microfauna groups across all sites. For all microfauna taxa, average numbers in gdw⁻¹ occurred to have strong positive correlation with the numbers obtained from extrapolation of combined sub-samples to 10 cm² (Spearman rank correlation: *r* = 0.91, *n* = 131, *p* < 0.0001).

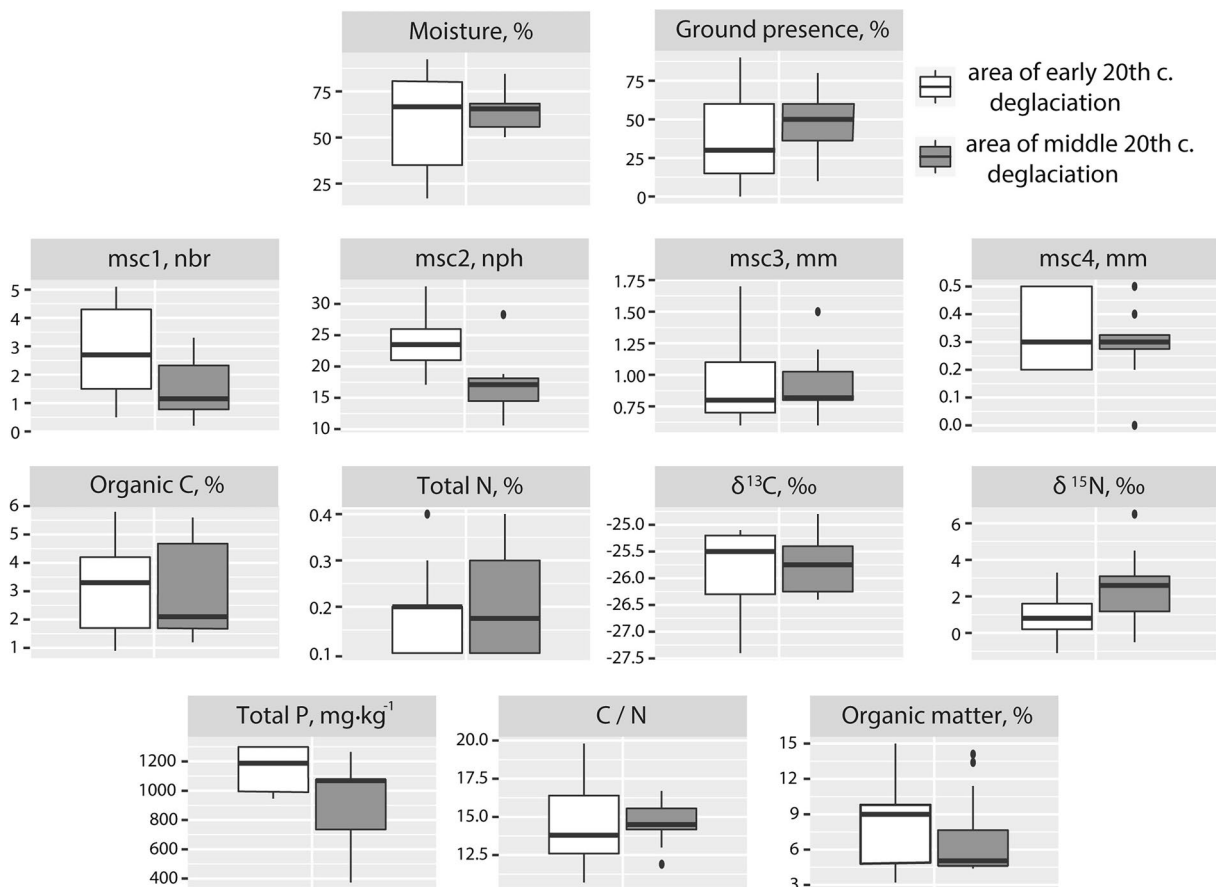


Fig. 3 Differences in environmental variables depending on the time since deglaciation (early sites *n* = 9, late sites *n* = 12). Boxes represent interquartile ranges, box central lines—median, whiskers—max

and min, spots—outliers. msc1–4—moss structural complexity #1–4, respectively, nbr—number of branches, nph—number of phyllids

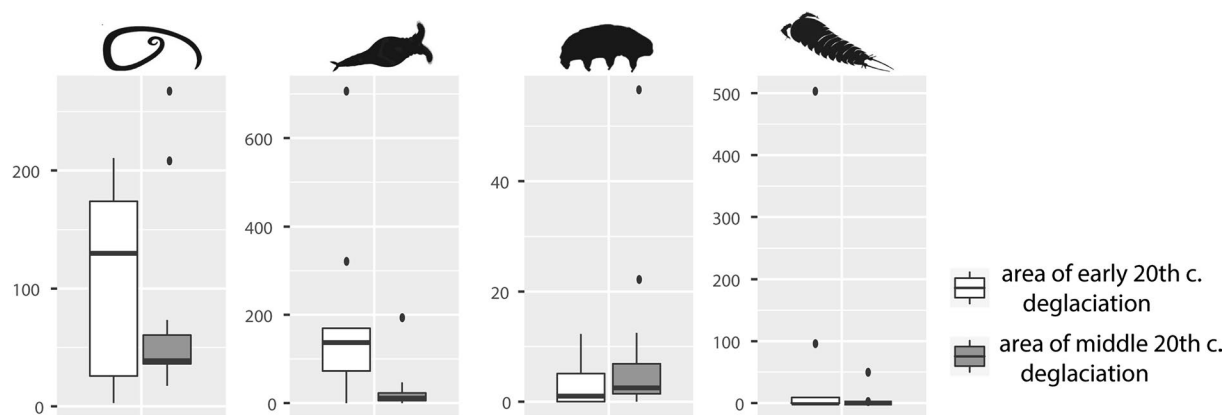


Fig. 4 Differences in abundance of Nematoda, Rotifera, Tardigrada, and Harpacticoida (from left to right) depending on the time since deglaciation (early sites $n=9$, late sites $n=12$). Boxes represent interquartile ranges, box central lines—median, whiskers—max and min, spots—outliers

Because the per gram approach seems to be more relevant (explained in “Materials and methods: Data analysis”), only values in ind gdw^{-1} will be further addressed and statistically analysed. Both types of data for all taxa are given in table at Online Resource 3.

Microscopic invertebrates were found in each site ranging from 3.8 ind gdw^{-1} (early8) to $865.3 \text{ ind gdw}^{-1}$ (early6). In general, early sites provide higher values and higher dispersion comparing to late sites— $263.2 \pm 260.7 \text{ ind gdw}^{-1} n=9$ and $112.2 \pm 144.4 \text{ ind gdw}^{-1} n=12$, respectively.

Nematodes inhabit all sites and represent about 49.5% from all individuals recorded in the present study making it the most distributed and abundant group in limno-terrestrial mosses of Trygghamna. The microfauna structure remains nematode-dominating if consider both area separately: in early sites, nematodes constituted $105.3 \pm 80.7 \text{ ind gdw}^{-1}$, or $47.4 \pm 18.9\% n=9$ from all individuals, and in late they were recorded with abundance of $74.3 \pm 78.5 \text{ ind gdw}^{-1}$, or $77.0 \pm 15.1\% n=12$ (Fig. 4). Rotifers were absent only in a one early and in one late site, with statistically different (Mann–Whitney test: $W=17.5, p=0.01$) abundances in corresponding areas: $81.8 \pm 52.2 \text{ ind gdw}^{-1}$, or $35.4 \pm 21.2\% n=9$, and $24.2 \pm 53.6 \text{ ind gdw}^{-1}$, or $15.7 \pm 11.2\% n=12$. Tardigrades, third microfauna group, were found in more than 75% of the sites, numbering $3.7 \pm 5.0 \text{ ind gdw}^{-1}$, or $5.6 \pm 8.9\% n=9$ in early sites and $9.1 \pm 16.2 \text{ ind gdw}^{-1}$, or $5.9 \pm 5.7\% n=12$ in late sites. In less than one-third of the sites, microfauna communities also included harpacticoid copepods. They contribute significantly to the communities of the early sites ($67.5 \pm 166.3 \text{ ind gdw}^{-1}$, or $9.1 \pm 16.2\% n=9$), but were not so abundant in the late ones presenting only $4.4 \pm 14.2 \text{ ind gdw}^{-1} n=12$, that is less than 1% of the community structure (Fig. 4). Ciliates (Ciliophora) found to be less distributed and did not contribute much to the community structure ($\approx 1\text{--}1.5\%$ in both areas). Their abundances in early sites ($4.9 \pm 8.7 \text{ ind gdw}^{-1} n=9$) were significantly

higher (Mann–Whitney test: $W=29, p=0.038$) than in late ones ($0.2 \pm 0.5 \text{ ind gdw}^{-1} n=9$).

Several taxa of invertebrates of larger sizes (Chironomidae, Collembola, Oligochaeta, Mesostigmatida) were also present in the samples. As they were out of the focus of the study, we indicated only its presence/absence in the sample. Collembola individuals were found in one early site and four late, while oligochaetes and chironomids—only in the area of middle 20th c. deglaciation. Only mesostigmatid mites were distributed across two areas equally—five early sites and five late.

Microfauna taxonomic diversity

All microfauna communities in limno-terrestrial of Trygghamna included 37 smallest identified taxa, 25 of which were recorded in early sites and 27 in late (Fig. 5; Online Resource 3). The numbers of taxa recorded only in early sites and only in late were 10 and 12, respectively. Overall number of microfauna taxa in one site varied from 2 to 18 without significant differences between early and late sites ($6.4 \pm 3.1 n=9$ and $6.2 \pm 4.1 n=12$, respectively; Mann–Whitney U test: $W=48.5, p=0.72$).

Sorensen distance between assemblages in two areas constitutes 0.567%. In pair-wise matrix of distances for all microfauna taxa and all sites, Sorensen distance was 0.75 and higher in 37.6% of cases. For bdelloid rotifers, which had been identified to species level, 81.3% of distance were 0.75 and higher, and in 75.4% no overlap at all was observed. Comparing the assemblages within one plot and between different plots showed that microfauna communities in neighbouring sites are more similar than in distant sites (ANOSIM: $R=0.325, p=0.0015$, number of permutations=9999). The same was shown for bdelloid species only (ANOSIM: $R=0.272, p=0.0031$, number of permutations=9999). However, the sites showed little clustering

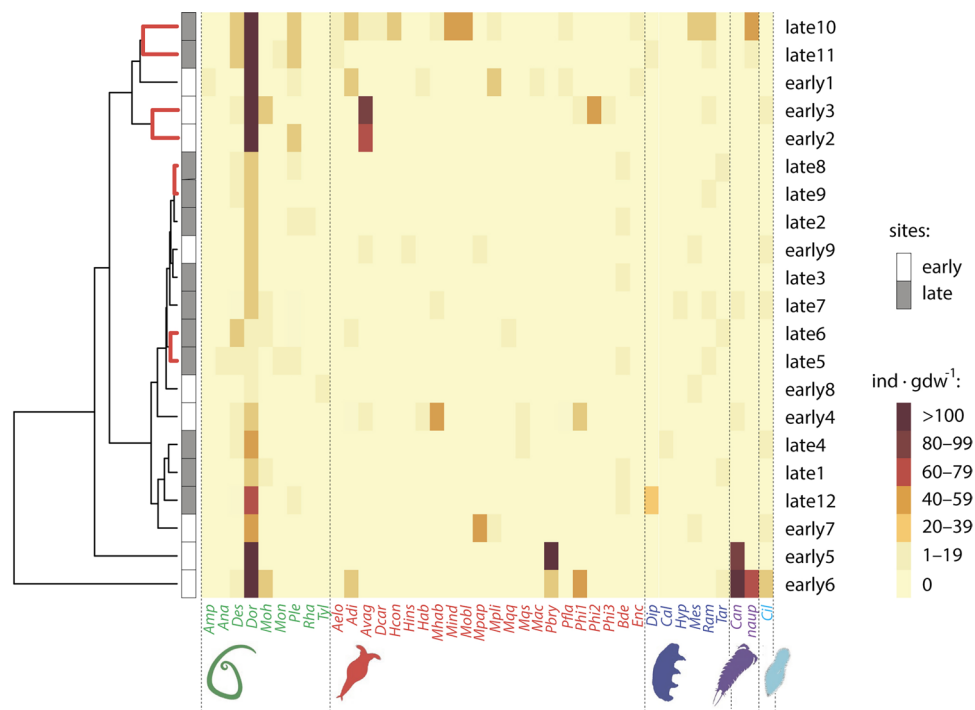


Fig. 5 Heat map of the microfauna community composition and their clustering. The darker shading represents the increase of abundances. Sampling sites from one sampling plot, which were well clustered, are shown in red. *Amp*—*Amphidelus* sp., *Ana*—*Anatonchus* sp., *Des*—*Desmodoridae* sp., *Dor*—*Dorylaimida* sp., *Mon*—*Mononchidae* sp., *Moh*—*Monhysteridae* sp., *Ple*—*Plectus* sp., *Rha*—*Rhabditidae* sp., *Tyl*—*Tylenchidae* sp., *Aelo*—*Adineta elongata*, *Adi*—*Adineta* sp., *Avag*—*Adineta vaga*; *Dcar*—*Didymodactylos carnosus*; *Hcon*—*Habrotrocha constricta*; *Hins*—*Habrotrocha insignis*, *Hab*—*Habrotrocha* sp., *Mhab*—*Mactotrachela habita*, *Mind*—*Macrotrachela*

induta, *Mobl*—*Macrotrachela oblita*, *Mpap*—*Mactotrachela papillosa*, *Mpli*—*Mactotrachela plicata*, *Mqq*—*Macrotrachela quadricornifera quadricornifera*, *Mqsc*—*Macrotrachela quadricornifera scutellata*, *Mac*—*Macrotrachela* sp., *Pbry*—*Pleuretra brycei*, *Pfla*—*Philodina flaviceps*, *Phi1*—*Philodina* sp.1, *Phi2*—*Philodina* sp.2, *Phi3*—*Philodina* sp.3, *Bde*—*Bdelloidea* sp. unident., *Enc*—*Encentrum* sp., *Dip*—*Diphascion* sp., *Cal*—*Calohypsibiidae* sp., *Hyp*—*Hypsibius* sp., *Mes*—*Mesocrista* sp., *Ram*—*Ramazottius* sp., *Can*—*Canthocampitidae* sp. copepodites and adults, *naup*—*Harpacticoida* sp. nauplii, *Cil*—*Ciliophora* sp

according to their position (Fig. 5). Some pairs of sites from one plot were clustered (e.g. early2 and early3, late5 and late6, etc.) as well as some sites that located nearby (e.g. late3 and early9).

Nematodes were represented by nine taxa identified to levels from order to genus reflecting their feeding strategy (Fig. 5; Online Resource 3). The most distributed were plant eating, stylet-bearing *Dorylaimida* spp. (100% occurrence frequency), followed by *Plectus* sp., and *Desmodoridae* sp., which both were recorded in ten sites. *Dorylaimida* nematodes also predominated by abundance over others, especially in late sites ($58.6 \pm 21.4\%$ $n = 12$ from all individuals comparing to $38.7 \pm 13.1\%$ $n = 9$ in early) reaching maximum of 194 ind gdw^{-1} (late11). *Monhysteridae* sp. were found only in five sites, *Mononchidae* sp. in two sites. Other nematodes taxa were represented by single records.

Rotifers included one monogonont taxon (*Encentrum* sp.), which was found in two sites, and 20 bdelloid species

(Fig. 5). *Adineta vaga* (Davis, 1873)¹ had the highest occurrence frequency (five sites, four of which are in the area of early 20th c. deglaciation) and in some sites large abundance (e.g. $84.7 \text{ ind gdw}^{-1}$ in early3). Four species were recorded in three sites, other species were doubletons or singletons. Unlike nematodes, rotifer abundance and distribution were not in alignment—highest number ($137.2 \text{ ind gdw}^{-1}$) was recorded for relatively rare *Pleuretra brycei* (Weber, 1898).

The most frequent tardigrades were members of *Ramazottius* sp. and *Mesocrista* sp. recorded in six sites and four sites, respectively (Fig. 5). All tardigrade taxa were less than 20 ind gdw^{-1} except *Ramazottius* sp. in late10 ($26.2 \text{ ind gdw}^{-1}$).

Unidentifiable bdelloid rotifers and tardigrades comprised approximately 4.5% and 11.5% from all individuals of the

¹ Identification is not completely clear; its morphology in general matches *Adineta vaga*, which probably consists of dozens of the distinct species.

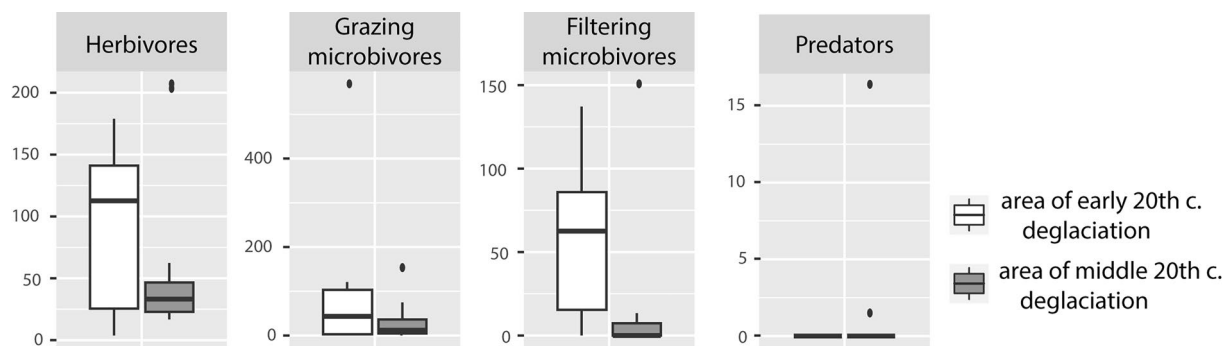


Fig. 6 Differences in abundance of trophic groups of microfauna depending on the time since deglaciation (early sites $n=9$, late sites $n=12$). Boxes represent interquartile ranges, box central lines—median, whiskers—max and min, spots—outliers

phyla, respectively. Noteworthy, all *Bdelloidea* sp. were recorded in late sites.

Harpacticoids were presented by Canthocamptidae family having about 30% occurrence frequency with some variability if consider different stages (Fig. 5). Adult forms have maximal abundance more than 430 ind gdw^{-1} , while nauplii numbered a maximum of $65.1 \text{ ind gdw}^{-1}$.

Microfauna trophic structure and diversity

Microfauna in the mosses of Trygghamna included herbivores, microbivores, or bacteria and unicellular algae eaters, and predators. First two groups have higher abundances in early sites compared to late (Fig. 6). Herbivores, presented by plant-sucking dorylaimida and tylenchida nematodes and tardigrades of genera *Mesocrista*, *Hypsibius*, *Ramazzottius*, numbered $93.4 \pm 67.6 \text{ ind gdw}^{-1}$ $n=9$ in the area of early 20th c. deglaciation and $60.5 \pm 68.8 \text{ ind gdw}^{-1}$ $n=12$ in the area of middle 20th c. deglaciation. Microbivores in turn included two large groups in respect to the consumption mechanism: ‘grazers’ (bacterivorous nematodes Desmodoridae sp., Monhysteridae sp., Amphidelus sp., Rhabditidae sp., *Plectus* sp., tardigrades of genus *Diphascoen*, scapping *Adineta* rotifers, and harpacticoids, grazing on biofilm) and filtrators (non-*Adineta* bdelloid rotifers and single monogonont rotifer). The former numbered $107.6 \pm 179.2 \text{ ind gdw}^{-1}$ $n=9$ in early sites and $30.4 \pm 44.6 \text{ ind gdw}^{-1}$ $n=12$ in late sites. In the case of the sediment filtration feeding type, the statistical difference (Mann–Whitney test: $W=23$; $p=0.022$) was observed between early ($56.0 \pm 45.2 \text{ ind gdw}^{-1}$ $n=9$) and late sites ($14.9 \pm 43.0 \text{ ind gdw}^{-1}$ $n=12$).

Predators, which consisted of nematodes taxa (Mononchiidae sp. and *Anatonchus* sp.), were presented only in the area of middle 20th c. deglaciation, but with minor abundance (less than 20 ind gdw^{-1}).

Despite the predomination of herbivores in both areas, some differences of proportion for the feeding strategies were recorded. In early sites the average relative abundance

decreased as follows: herbivores (48.2%), filtrators (27.2%), and grazing microbivores (24.5%). In the microfauna structure for late sites, the proportion of the herbivores was higher than that of grazers to a much extent (61.2% against 22.5%), while filtrators numbered only 6.6%, and predators 0.7%.

Microfauna distributional patterns

Microfauna distribution occurred to be significantly determined (81.8%) by environmental variables (RDA, scaling type II—Fig. 7). The first two axes explain 36.7% of the entire variation and 44.8% of the constrained variation. The results of the RDA analysis were statistically significant (permutation test: $F_{15}=1.49$, $p=0.03$). The factor of glacial history (whether the site located in the area of early 20th c. deglaciation, or in the area of middle 20th c. deglaciation) was the most important environmental variable (explains 9.5% of the variation, $p=0.001$). Other significant parameters were moisture (explains 6.0% of the variation, $p=0.006$), ground presence (4.3%, $p=0.021$), and soil $\delta^{15}\text{N}$ (4.1%, $p=0.023$). Also, the distance from the sea was statistically significant ($p=0.043$) but does not contribute much to the microfauna variation (2.7%).

We revealed the significant variability in the responses of different microfauna taxa and even different species to environmental parameters (Fig. 7). While nematodes were mostly independent in relation to the time since deglaciation, Dorylaimida sp., the most distributed taxon, was strongly positively correlated with the presence of ground particles in the moss samples. Other frequently occurred nematode taxa were linked to different variables: *Plectus* sp., was strongly positively correlated with $\delta^{15}\text{N}$, Desmodoridae sp. and Monhysteridae sp. increased with increasing moisture in the sample. Several rotifer species demonstrated very clear, but different tendencies. *Adineta* spp., *Philodina flaviceps* Bryce, 1906, *Philodina* sp.1, *Macrotrachela habita* (Bryce, 1894) were strongly negatively correlated with ground presence; *P. brycei* and *Macrotrachela plicata* (Bryce, 1892) were

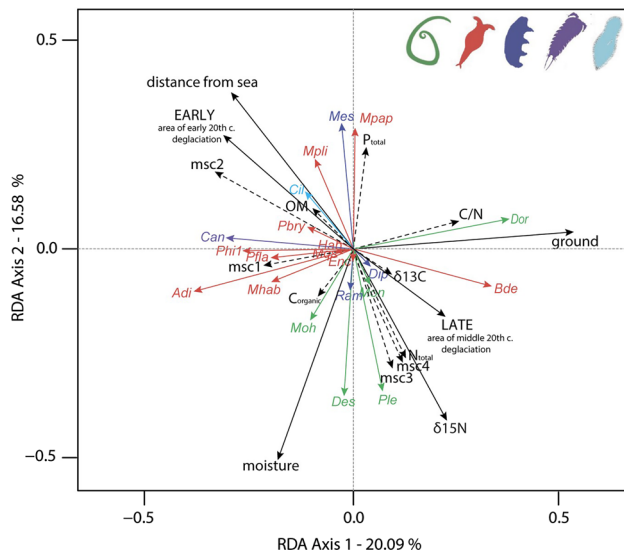


Fig. 7 tbRDA analysis of microfauna taxa with respect to all environmental variables. Coloured arrows represent response variables: Nematoda (green arrows), Rotifera (red), Tardigrada (dark blue), Harpacticoida (purple), Ciliophora (light blue). Black arrows represent explanatory variables: significant (Monte Carlo test: $p < 0.05$; solid lines) and not-significant (Monte Carlo test: $p > 0.05$; dash lines). *Des*—Desmodoridae sp., *Dor*—Dorylaimida sp., *Mon*—Mononchiidae sp., *Moh*—Monhysteridae sp., *Ple*—Plectus sp., *Adi*—Adineta spp., *Hab*—Habrotracha sp., *Mhab*—Mactotrachela habita, *Mpap*—Mactotrachela papillosa, *Mpli*—Mactotrachela plicata, *Mqsc*—Mactotrachela quadricornifera scutellata, *Phil*—Philodina sp.1, *Pfla*—Philodina flaviceps, *Pbry*—Pleuretra brycei, *Bde*—Bdelloidea sp. unident., *Enc*—Encentrum sp. Tardigrada taxa: *Dip*—Diphoscon sp., *Mes*—Mesocrista sp., *Ram*—Ramazzottius sp., *Can*—Canthocamptidae sp., *Cil*—Ciliophora sp. msc1–4—moss structural complexity ##1–4, respectively. Species found only in one site were excluded. All Adineta members were combined in Adineta spp.

negatively correlated with $\delta^{15}\text{N}$, and increased in early sites and along the transect from the seacoast; *Macrotrachela papillosa* (Thompson, 1892) like one of the most distributed tardigrade taxa, *Mesocrista* sp., was negatively correlated with $\delta^{15}\text{N}$ and moisture. Another tardigrade taxon, *Ramazzottius* sp., has positive correlation with moisture. Ciliates were positively correlated with the distance from sea and more related to the area of early 20th c. deglaciation. Canthocamptidae sp. was characterised by the tendencies very similar to that for *Adineta* spp. and some *Philodina* species (negative correlation with ground presence).

Discussion

Since Svalbard is the best inventoried area for invertebrates in the Arctic, the present study in Trygghamna did not reveal new records for monogonont rotifers, nematodes, tardigrades, and harpacticoids. The representatives of these groups have been previously reported in Svalbard (Loof

1971; Coulson and Refseth 2004; Coulson 2007; Zawierucha et al. 2015b), or have cosmopolitan distribution, including in many Arctic territories (Tsalolikhin 2014). Nevertheless, a very limited number of studies in Svalbard have addressed bdelloid rotifers (Coulson et al. 2014). Only nine species found in this study overlap with the previously produced species list, derived from Kaya et al. (2010), Ávila-Jiménez et al. (2019), and older surveys (Bryce 1897, 1922; Summerhayes and Elton 1923)—Online Resource 3.

The understanding of microfauna responses to deglaciation (Cauvy-Fraunié and Dangles 2019) can be used for predicting what kind of difference can be observed between microinvertebrate communities in the forefields that exist different periods of time. Hypothetically, when the impact from other environmental factors can be ruled (i.e. all sites were subjected to the same environmental conditions differing only by their age), at sites without a glacier for a longer period comparing to sites deglaciated later, the following are to be expected: (i) a smaller proportion or lack of cold-adapted species; (ii) increasing the presence of opportunistic species; (iii) a greater species diversity (the same was shown for arthropods in several locations of Svalbard—Gwiazdowicz et al. 2020). The processes that account for the effects mentioned are, in order, (i) the low tolerance of psychrophiles that have survived in the polar region for millions of years; (ii) mechanisms enabling broad ecological tolerance in species; and (iii) colonisation of the area by animals capable of dispersal.

Some of these processes are partially exemplified in the present study. The total abundance of all large groups of microfauna, excluding tardigrades, is greater in early sites. The taxa that thought to be opportunistic (found in both areas, as well as most distributed ones, like Dorylaimida sp. *Plectus* sp., *M. habita*, and some other bdelloids) showed the same trend. Late sites were characterised by a set of specific taxa (mostly tardigrades and rotifers), which were not recorded in the area of early 20th deglaciation. The fact that there were fewer species overall in the area of early 20th deglaciation (contradicting the aforementioned theoretical assumptions) can be explained by incomplete identification of nematodes and tardigrades. Herewith, the trophic composition of the microfauna in area of middle 20th deglaciation was more uneven, with herbivores predominating, followed by grazing microbivores and filtrators in considerably smaller numbers. According to the larger proportions of all microbivorous microinvertebrates in the area of early 20th deglaciation, it can be suggested that it takes more time for bacterial and algal communities to emerge in mosses following glacier retreat.

Despite microfauna communities in forefield of Trygghamna are affected substantially by the time since deglaciation, other environmental variables are also important, making distribution of microscopic animals a result of the

interaction of different factors. RDA analysis showed glacial history explains only 9.5% of the variation, and only a few taxa, mainly infrequently occurring ones, are strongly aligned with either early or late sites (Fig. 7). Ciliates were found to be strongly related to the area of early 20th c. deglaciation, as well as only two bdelloids: widely distributed *M. plicata* and *P. brycei* (a species of the poorly studied and rare genus, with some representatives known to be present in alpine ecosystems—Kutikova 2005). It is worth noting that unidentified bdelloids (*Bdelloidea* sp.) demonstrated the opposite ecological preferences, being positively related to late sites. It may mean that despite rotifers mostly benefit from the glacial retreat, there are some cold-adapted species, which were not identified at the species level. Failure to identify *Bdelloidea* sp. allowed us to consider them as distinct cold-adapted species: probably, because of sensitivity to increasing temperature, these rotifers could not withstand gradual warming during sample processing. Among other microinvertebrates, only some tardigrade taxa were characterised by a strong relation with late sites. The strong association of tardigrades with the area of middle 20th c. deglaciation corresponds to the fact that many species of this phylum are glacial relics and psychrophiles (Zawierucha et al. 2015a, 2018, 2019a), which are expected to become extinct because of warming (Zawierucha and Shain 2019). According to redundancy analysis, the trophic groups were not associated with the environmental variables (e.g. herbivorous nematodes and the two most widely distributed herbivorous tardigrade taxa demonstrated quite different relations), making the taxonomic context more important than the feeding strategy.

Among environmental variables included in the analysis and supposed to affect the microfauna communities, only four were significant: distance from sea, moisture, ground presence, and $\delta^{15}\text{N}$. As all of them demonstrated no statistical differences, if areas of early 20th c. deglaciation and middle 20th c. deglaciation (Table 3) were compared, we can assume these variables as generally independent of the glacial history that is necessary for further interpretation.

Some microfauna taxa (*M. plicata*, ciliates) were found to increase in numbers with increasing distance from the sea, along the watercourse connecting the coast with Lovenvatnet Lake. However, the total abundance and number of species do not increase in this direction. With this, water content (moisture) itself has a significant impact on microfauna distribution, with several taxa strongly associated with wet mosses and a few (*M. papillosa*) associated with dry ones. Moisture is known to be critical for the abundance of many micrometazoans in soils in polar regions (Andriuzzi et al. 2018; Smykla et al. 2018; Zawierucha et al. 2019b) and supposedly in mosses in temperate zones (Hirschfelder et al. 1993). In polar regions, liquid water is often considered to be a major driver of life expansion (Block et al. 2009; Convey

et al. 2014) and, together with a temperature that fuels biological processes, a primary limiting factor for terrestrial invertebrates (Coulson et al. 2014). However, we found that several nematode bacterivorous taxa benefited most from moisture, while rotifers (which are filtrators and alternate swimming with movements) were mostly independent of this variable or were even negatively correlated with it.

The branched, three-dimensional structure of mosses provides suitable living conditions for rotifers and other microfauna demanding attention to this type of habitat. It is usually accepted that the more complex structure of moss provides better conditions for microfauna (rotifers) to thrive (Hirschfelder et al. 1993). However, no qualitative estimation of that was performed. The present study showed a total lack of importance of moss structural complexity for moss-dwelling microfauna. Nevertheless, the suggested set of parameters of structural complexity could be used (taking a broad perspective) to investigate the possible relations between habitat and microfauna using incidence data accumulated during previous years and numerous datasets relating to moss-dwelling microfauna.

The ground is a type of physical environment that also provides living conditions. Some differences in species diversity and abundance between moss samples containing different amounts of ground particles were expected. The assemblages of bdelloid rotifers living in soil include many exclusive species (Devetter 2007, 2009; Devetter et al. 2017). Only a few of the species found (like *M. habita*, *M. plicata* and some others) were typical of both mosses and soil (Ricci et al. 2003; Devetter 2007). The other bdelloid taxa found in the present study were mostly moss inhabitants (Donner 1965; Fontaneto and Melone 2003; Kutikova 2005; Kaya et al. 2010; Lukashanets 2018; Zeng et al. 2020). Their avoidance of the samples with ground supports the fact that bdelloids require high levels of oxygen, as found in the previous studies (Bērziņš and Pejler 1989; Pejler and Bērziņš 1993). In contrast, some micrometazoans positively correlated with the ground present in the samples, e.g. dorylaimida nematodes, which are soil inhabitants but feed on the roots of plants.

Among the variables characterising nutrient and isotope composition, the only important finding for microfauna distribution was $\delta^{15}\text{N}$ (Fig. 7). In the Arctic, when there is no ornithogenic nutrient input, which significantly affects soil- and vegetation-dwelling invertebrates (Zmudczyńska et al. 2012; Zawierucha et al. 2016; Zmudczyńska-Skarbek et al. 2015, 2017), the main nitrogen source is atmospheric deposition and primary N_2 fixation from the atmosphere (Skrzypek et al. 2015). The $\delta^{15}\text{N}$ values that we measured are within the range had been recorded previously for Alaska (Liu et al. 2018) and correspond with the estimated values for Svalbard (Amundson et al. 2003). They were lower in the area of early 20th c. deglaciation than in the area of

middle 20th c. deglaciation with no statistical difference recorded. However, little is known about $\delta^{15}\text{N}$ patterns in respect of climatic gradients in regions with a mean annual temperature below 9.8 °C (Craine et al. 2015a, b). With that, to explain the observed differences in $\delta^{15}\text{N}$ between the two areas and the strong, mostly negative, correlation of some taxa with this variable, some indirect effects of glacier retreat can be taken into account. It is known that changes in initial signatures by enriching $\delta^{15}\text{N}$ are possible because of specific microbial activities in the soil (Ansari et al. 2013). However, mosses, which provide a layer of thermal insulation on top of the soil, can inhibit microbial activity, reduce soil N availability, and retard nitrogen cycling (Koranda and Michelsen 2020). In the studied region, although moss patches covered all the transects, they were older in the area which had been exposed, without an ice covering, for longer. It therefore follows that their negative impact on soil microbial activity will be greater. This allows us to consider $\delta^{15}\text{N}$ in moss-covered post-glacial area as a function of the time that has elapsed since the area became free of the glacier. As the presence of microfauna in mosses is expected to be also time-dependent (the more time passes, the more colonisation occurs), its increase with a decrease in $\delta^{15}\text{N}$ becomes more understandable.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-023-03192-y>.

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Author contributions DL designed the study, performed fieldwork and identification of microfauna, carried out all statistical analyses, and prepared the manuscript. JP carried out analysis for phosphorus and organic matter content in the soil. RB estimated isotope ratios, and organic carbon and total nitrogen composition in the samples.

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Data availability The authors declare that the data supporting all findings of this study (microfauna abundances in each sampling site, data on measured environmental variables) are available within the paper and its supplementary information (Online Resources 1, 2, and 3).

Declarations

Conflict of interest The author declare that they have no conflict of interest.

Ethical approval All sampling activities strictly followed Svalbard Environmental Protection Act.

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