

1 Biotope and biocenosis of cryoconite hole ecosystems on Ecology Glacier in the
2 maritime Antarctic

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23 **Abstract:** Despite recent great interest in glacier ecosystems in the continental Antarctic, little is known about
24 their maritime counterparts. Our study presents descriptive data on cryoconite sediments and cryoconite holes on
25 Ecology Glacier (King George Island) to accomplish three main objectives: (a) to identify main eukaryotic (algae,
26 invertebrates) and prokaryotic (cyanobacteria) components of microbial communities; (b) to provide a “baseline”
27 of community composition, organic matter and artificial contamination; and (c) identify key abiotic factors that
28 might be important in community assembly. Cryoconite holes were sampled along an altitudinal gradient of

29 Ecology Glacier in January, mid Austral Summer 2017. Cryoconite holes located in lower altitude were deeper
30 than those located in the middle and the highest altitude. Seventeen species of algae and cyanobacteria with
31 biomass of 0.79 to 5.37 $\mu\text{g}/\text{cm}^3$ have been found in sediments. Dominant species were cyanobacterial
32 *Pseudanabaena frigida* and Bacillariophyceae *Microcostaus* sp. Biomass of Bacillariophyceae was significantly
33 higher than that of Chlorophyta and Cyanobacteria. We found three species of rotifers (two potentially new to
34 science) and for the first time a glacier dwelling Acari (suspension feeder, *Nanorchestes nivalis*). Organic matter
35 content ranged from 5.4% to 7.6%. Investigated artificial radionuclides included ^{137}Cs , ^{238}Pu , $^{239+240}\text{Pu}$ and ^{241}Am .
36 ^{210}Pb seems to be related to organic matter content. Overall, cryoconite holes on Ecology Glacier present unique
37 habitats that serve as biodiversity hotspots of psychrophiles, source of organic matter, matrices for radioactivity
38 tracking and model for observing changes in supraglacial ecosystems in Maritime Antarctic.

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40 **Keywords:** algae, Antarctic cryoconite, biodiversity, contamination of polar regions, Acari and Freshwater
41 Rotifera, glacial ecosystems, microbial communities

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49 **1. Introduction**

50 For years glaciers have been considered as unproductive and mostly lifeless systems. Over the
51 last two decades, a new view of glaciers as the coldest of Earth's biomes and biodiversity
52 hotspots of psychrophiles has emerged (Anesio & Laybourn-Parry 2012, Stibal et al. 2020).
53 Glaciers' biological activity peaks during summers (Hodson et al. 2008, Anesio & Laybourn-

54 Parry 2012) when liquid water accumulates on the surface of glaciers (supraglacial zone)
55 providing habitable space for microbial communities. Most of the organisms within those
56 communities are unique and highly adapted to cope with extreme cold, frequent cycles of
57 melting and freezing, flushing of nutrients, and high UV radiation (e.g., Hodson et al. 2008,
58 Zawierucha et al. 2019, Samui et al. 2018). Through their activity, they can affect local carbon
59 and iron budgets, and rates of ice melting (Anesio et al. 2009, Tedstone et al. 2017, Williamson
60 et al. 2018).

61 The most biologically diverse, active, and productive glacial communities are those
62 associated with cryoconite holes (Takeuchi et al. 2010, Stibal et al. 2015, 2020, Cook et al.
63 2015, Zawierucha et al. 2015). They form when supraglacial sediment (mineral debris deposited
64 on the surface of ice by wind, water, and rockfall) along with microorganisms (e.g., bacteria,
65 algae, and invertebrates) (Takeuchi et al. 2001a, Hodson et al. 2008, Cook et al. 2015) absorb
66 more solar radiation than the surrounding ice and melt into the ice. Cryoconite holes are
67 considered biodiversity hotspots, bioreactors producing organic matter, and potential sinks of
68 heavy metals and other contaminants (Wharton et al. 1985, Stibal et al. 2010, Baccolo et al.
69 2017, Łokas et al. 2016, 2018, 2019, Zawierucha et al. 2018). Many species are associated
70 exclusively with these unique glacial ecosystems (Dastyh et al. 2003, Edwards et al. 2013,
71 Zwierucha et al. 2015, 2016a). Although the seedbank of cryoconite communities originates
72 from habitats surrounding glaciers (e.g., soils, supraglacial gravel and streams) (Franzetti et al.
73 2017), they develop their own distinct signatures (Franzetti et al. 2017, Stibal et al. 2020,
74 Zawierucha et al. 2016a). Even though studies on biological and ecological characteristics of
75 glaciers have been conducted worldwide (Franzetti et al. 2017, Segawa et al. 2017, Stibal et al.
76 2015, Zawierucha et al. 2019) including Antarctica, the knowledge on glaciers in the Maritime
77 Antarctica remains scarce. Despite the fact that Antarctica is the most extensive ice covered
78 part of the world, its glacier ecosystems seem to be poorly known, with comprehensive studies

79 conducted only on few glaciers (Porazinska et al. 2004; Sommers et al. 2019; Stanish et al,
80 2013).

81 Antarctica is the only continent covered by 97% ice, and thus it constitutes the largest
82 freshwater reservoir on Earth. Glaciers play an important role in Antarctic ecosystems as a
83 source of water and nutrients for forefields in polar deserts (Bagshaw et al. 2013) but also as a
84 source of nutrients for aquatic systems (Hodson et al. 2017). Despite a long history of studies
85 on glacial ecosystems in the Continental Antarctic, special attention has been given only to
86 microbial diversity and its function, cryoconite holes morphology and biochemistry mostly on
87 McMurdo Dry Valley glaciers (Bagshaw et al. 2007, 2011, 2013, Fountain et al. 2004, Mueller
88 et al. 2001, Porazinska et al. 2004, Sommers et al. 2019, Wharton et al. 1985), the knowledge
89 on glacial ecosystems in the Maritime Antarctica remain scarce. Maritime Antarctica,
90 especially the Antarctic Peninsula, is a transition zone, where climatic conditions vary between
91 a temperate north and more polar-influenced south. Therefore, specifically the Antarctic
92 Peninsula is characterized by unique conditions including climate and isolation from human
93 impact. Owing to its remote location, the Antarctic Peninsula has been suggested as an area
94 suitable for monitoring the effects of climate change (Braun & Gossman 2002) and air pollution
95 (Artaxo et al. 1992). Given that cryosphere is one of the fastest changing biomes (Quayle et al.
96 2002, Robinson et al. 2003, Convey 2013), physical and biological description of supraglacial
97 habitats for developing a better understanding of glacial ecosystem functioning, their
98 biodiversity, human impact and organic matter losses from ice to downstream ecosystems is
99 urgent..

100 The present study lays out groundwork on cryoconite hole ecosystems of Ecology
101 Glacier in Maritime Antarctic. Specifically, it identifies diversity and composition of microbial
102 eukaryotes (algae, invertebrates) and prokaryotes, characterizes abiotic conditions, and
103 describes the extent of biotic/abiotic interactions.

104

105 **2. Material and methods**

106 *2.1 Study area*

107 *2.1.1. King George Island*

108 King George Island (KGI) is located between 61°54'-62°16'S and 57°35'-59°02'W in the South
109 Shetland archipelago (West Antarctica, Figure 1). This island was formed on a crustal block
110 with a thickness of 30-32 km separated from the Antarctic Peninsula (Birkenmajer et al. 1991).
111 The KGI rocks (Igneous rock) are mainly rich in both calcium and alkali metals and there is a
112 low abundance of trace elements. More than 90% of the land is covered by ice with the highest
113 point being 650 m a.s.l. with the glacier equilibrium-line at about 100 m a.s.l (Bintanja 1995).
114 The whole island is characterised by a typical maritime climate with low annual amplitudes of
115 air temperature (2°C), high humidity (82%) (Martianov & Rakusa-Suszczewski 1989) as well
116 as constant cloud cover (Rakusa-Suszczewski et al. 1993, Knap et al. 1996, Braun et al. 2001,
117 Ferron et al. 2004). The average annual (1977-1998) sum of precipitation at the Arctowski
118 station is 499.8 mm with two maxima in March and September (58.3 mm and 47.4 mm
119 respectively), and two minima in August and December (28.2 mm and 34.7 mm respectively)
120 (Marsz et al. 2000).

121 *2.1.2. Ecology Glacier*

122 Ecology Glacier (62°11'S, 58°28'W) is located in the southern part of the KGI. The glacier is
123 an outlet from the Warszawa Icefield flowing north-east. The central part of the front empties
124 into the Suszczewski Cove of the Admiralty Bay while lateral parts of the lobe terminate on
125 land forming marginal moraines. The surface area of the basin of Ecology Glacier is 5.21 km²
126 (Pełlicki et al. 2017). Overall glacier mass balance is driven by both frontal and surface ablation,
127 which over the last 40 years has been negative (Pełlicki et al. 2017). This reflects a concurrent

128 climate warming trend of 0.19°C per decade (Sobota et al. 2015, Kejna et al. 2012). Recently,
129 observed positive net surface mass balance (Sobota et al. 2015), similar to other glaciers in the
130 Antarctic Peninsula (Navarro et al. 2013, Oliva et al. 2017), may be explained by a regional
131 cooling recorded in the last few years (Turner et al. 2016, Pętllicki et al. 2017). The temporal
132 variation of climatic conditions is expressed in surface lowering rate since 1979, ranging from
133 -1.7 m y⁻¹ (1979-2001) to -0.5 m y⁻¹ (2002-2016) (Pętllicki et al. 2017). The same pattern is
134 noted in the frontal retreat rate that has decelerated after 2002, however the main driver of
135 glacier front displacements is subglacial/ submarine topography at the glacier cliff (Pętllicki et
136 al. 2017). Overall frontal changes of Ecology Glacier are moderate with the average rate ca.
137 0.019 km² y⁻¹ measured in the periods 1961-1996 and 2007-2012 (Kejna et al. 1998, Sobota et
138 al. 2015). Most ice masses of King George Island located below 400 m a.s.l. are at the pressure
139 melting point (Blindow et al. 2010). Shallow temperature profiles confirm the existence of
140 temperate ice on Ecology Glacier (Sobota et al. 2015).

141

142 2.2. Sampling

143 In total, 23 melted cryoconite holes were sampled on Ecology Glacier during fieldwork of
144 January 2017. Cryoconite holes were located at three altitudes all within the ablation zone
145 (Figure 1) including: 1. 128 - 142 m a.s.l. with 7 holes, 2. 168 - 172 m a.s.l. with 6 holes, and
146 3. 201 - 221 m a.s.l. with 9 holes. Altitudes and measurements of the depth and height of the
147 water column were made for 22 cryoconite holes. Additional parameters, such as depth,
148 diameter, length and width of cryoconite holes, were measured when possible (diameter for
149 spherical holes, width and length for irregularly shaped holes) with a ruler. Cryoconite material
150 (0.5 to 1.3 cm³) was collected using sterile plastic Pasteur pipettes and transferred to 15 cm³
151 tubes and immediately preserved with 96% ethylene alcohol. Samples were stored frozen and
152 transported to laboratories in Poland. All 23 samples were used for faunistic analysis and

153 organic matter measurements. For phycological and radiometric analysis, 12 and 10 samples
154 were used, respectively. In the laboratory, after the cryoconite material had settled in the tubes
155 (i.e., after at least 30 min), only the sediment was collected for analysis. The amount of sediment
156 used for analysis was estimated based on the measure of the plastic tube.

157 *2.3. Organic matter*

158 The amount of organic matter in cryoconite was measured as a percentage weight loss through
159 combustion at 550°C for 3 hours following drying at 50°C for 24 hours.

160 *2.4. Microscopic observations and estimation of cyanobacteria and algae biomass*

161 Cyanobacteria and algae were identified, counted, and measured with a Nikon Eclipse TE2000-
162 S digital microscope. Taxa were archived through NIS (Imaging Software NIS – Elements BR
163 on VGA). The biomass of cyanobacteria and algae for each hole was calculated as the total cell
164 volume per unit area (standard coverslip). Mean cell volume was estimated by measuring the
165 size of 50–100 cells for each species. To ensure accuracy of measurements, each sample was
166 counted three to six times and thus cell concentrations (cells/cm³) are mean values of the
167 repeated counts. The biomass of cyanobacteria and algae for each sample was calculated as the
168 total cell volume per unit area (standard coverslip). Every time under standard coverslip 100 µl
169 of the cryoconite was mounted (after Yoshimura et al. 1997, modified). The taxonomy of
170 cyanobacteria and algae is based on Hoek et al. (1995) and identification of cyanobacterial and
171 algal species followed Krammer & Lange-Bertalot (1991a, b), Hindak (1996), Komárek &
172 Anagnostidis (2005), Coesel & Meesters (2007), Van de Vijver et al. (2010) and John & Rindi
173 (2015). Figure S2 contains diatom shells without chloroplast for better visibility of diagnostic
174 features.

175 *2.5. Microfauna extraction and identification*

176 The material was homogenised by shaking the vials and transferred into Petri dishes (\varnothing 8.5 cm)
177 and entire cryoconite material was scanned for microfauna using a stereomicroscope (Olympus
178 BZ51). On the bottom of each Petri dish, parallel thin lines at 5-mm intervals were drawn with
179 a black marker for precise scanning (5 mm corresponds to a visible image at 30x magnification).
180 The entire cryoconite material was scanned for microfauna using a stereomicroscope (Olympus
181 BZ51). Subsequently, all individuals were isolated and counted. The density of animals was
182 calculated per 1 cm³ of cryoconite.

183 Representatives of the nanorchestid mite populations were cleared in KOH or Nesbitt's fluid,
184 mounted on microslides in Hoyer's medium, examined using an Olympus BX50 phase-contrast
185 microscope and subsequently identified following the keys of Strandtmann (1982) and Booth
186 (1984).

187 To delimit rotifer species, total genomic DNA was extracted from 14 separate individuals
188 (selected from six cryoconite holes) using the method described in Dabert et al. (2008) and
189 Mironov et al. (2012). DNA was isolated with the DNeasy Blood and Tissue Kit (Qiagen
190 GmbH, Hilden, Germany) following the protocol of Dabert et al. (2008). A fragment of the
191 mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified with a LCO1490
192 forward primer (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 reverse
193 primer (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994).
194 Amplification of DNA fragments (PCR) for a total volume of 10 μ L was carried out with the
195 following protocol: 5 μ L Type-it Microsatellite PCR Kit (Qiagen), 0.25 μ M of each primer, 4
196 μ L of the DNA template and 0.5 μ L water. For PCR, a thermocycling profile with one cycle of
197 5 min at 95°C followed by 5 steps of 30 s each at 95°C, 60 s at 45°C, 1 min at 72°C, and 30
198 steps 30 s at 95°C, 60 s at 50°C and 60 s at 72°C with a final step of 5 min at 72°C for all
199 amplicons. Samples containing single, uniform 700-bp bands were purified with exonuclease I
200 and fast alkaline phosphatase (Fermentas). The amplicons were sequenced with the BigDye

201 Terminator v3.1 kit and ABI Prism 3130xl Genetic Analyzer (Applied Biosystems) following
202 the manufacturer's instructions. The identity of COI sequences was verified with BLAST
203 (Altschul et al. 1990) against the NCBI database. Sequences were processed in BioEdit ver.
204 7.2.5 (Hall 1997). Pairwise distances between nucleotide sequences were calculated via a
205 distance model for all codon positions as implemented in MEGA 7 (Tamura et al. 2013).
206 Delimitation and identification of the rotifer species as independently evolving entities (IEEs)
207 was conducted employing the GMYC model (Pons et al. 2006, Fujisawa & Barraclough 2013)
208 on both ultrametric trees constructed in BEAST 1.10.4 and Bayesian trees constructed in
209 MrBayes 3.2, and then converted to ultrametric ones using the `chronopl` function in RStudio
210 software (R Core Team 2018). GMYC analysis was performed in RStudio using the 'paran'
211 and 'splits' packages (Supplementary Material, Appendix A, Fig. 5 and 6). The following
212 sequences were utilised in the analysis: KJ543594-KJ543597 and KP869999 belongs to
213 *Macrotrachela jankoi* Iakovenko et al., 2015, and KP870000 belongs to *Macrotrachela* aff.
214 *jankoi*, and as an out group, *Floscularia melicerta* GenBank ID EU499896 (FLM) was used
215 (Iakovenko et al. 2015). The remaining sequences are new and described in the results.
216 Slides with animals are deposited in the Department of Animal Taxonomy and Ecology, Adam
217 Mickiewicz University in Poznań, Poland.

218 2.6. Identification and measurements of radionuclides

219 Owing to location and separation by cold oceanic waters of Antarctic Peninsula, it is a suitable
220 region for analysing transport of contaminants in the environment. The Antarctic ecosystem is
221 of great interest in estimating global environmental pollution caused by nuclear detonation tests
222 and accidents. In order to identify radionuclides, time of their deposition and links between
223 biotic and abiotic characteristics of supraglacial ecosystems, we identified radionuclides in
224 glacier of Maritime Antarctic for the first time. ^{137}Cs and ^{210}Pb activity was determined with a
225 broad energy germanium detector (BEGe), BE5030. The activities of ^{137}Cs were determined

226 using its emission peak at 662 keV, and the emission peak at 46.6 keV was employed to
227 determine the activities of ^{210}Pb . The activities of the ^{238}Pu , $^{239+240}\text{Pu}$, ^{241}Am , $^{234,238}\text{U}$ and
228 $^{230,232}\text{Th}$ radionuclides were determined in 0.48 to 0.85 g of the dried samples. The samples
229 were dissolved with mineral acids and resultant liquid samples underwent radiochemical
230 separation and concentrations of all alpha isotopes. The procedure is extensively described
231 elsewhere by Łokas et al. (2010, 2013, 2018). The full sequential radiochemical procedure and
232 gamma analyses were verified employing soil reference material (IAEA 385). The results were
233 in strong agreement with the recommended values. After further radiochemical purification
234 procedure, the $^{240}\text{Pu}/^{239}\text{Pu}$ atomic ratio was measured through a Neptune MC-ICP-MS in
235 accordance to Łokas et al. (2018). The reference date for ^{210}Pb and ^{137}Cs activities is 1 January
236 2017.

237

238 *2.7. Data processing*

239 We tested relations between continuous variables using Spearman-rank correlation (assumption
240 for the Pearson correlation were violated). To test differences of the mean for elevations groups
241 we used a Kruskal-Wallis rank-sum test. In case of significant results of Kruskal-Wallis, we
242 used post hoc Dunn's test with Bonferroni-corrected alpha level. To determine central tendency
243 we used mean and the standard error (SE) for normally distributed data, while for the variables
244 with the distribution that deviated from normal we used the median. To asses variance for
245 normally distributed data, we used Standard Deviation (SD), while the variables with the
246 distribution that deviated from normal we used the Interquartile Range (IQR). Moreover, we
247 tested evenness of a community of algae using Pielou Diversity index J based on the Shannon-
248 Wiener index. The analysis was processed using R software (R Core Team 2018) and MVSP
249 3.1 software (Kovach 1985-1999).

250 **3. Results**

251 Mean diameter and total depth for sampled cryoconite holes on Ecology Glacier in January
252 2017 were 10.0 ± 2.5 , 95%CI (14.98, 16.21) and 15.9 ± 4 , 95%CI (10.48, 11.22) cm. All
253 measurements of cryoconite holes are presented in the Table S1. The collected cryoconite
254 consisted mostly of fine mineral grains and infrequent minute cryoconite granules (Figure S3).
255 Cryoconite holes located in lower altitude were deeper than those located in the middle and the
256 highest altitude (Dunn's test, $p = 0.014$ and $p = 0.002$, respectively).

257 Organic matter varied between 5.4% and 7.6% ($median = 6.72$, $IQR = 0.79$, $n = 23$), but without
258 any clear gradient with the elevation (Figure S1). There was no significant correlation between
259 organic matter content and depth of cryoconite holes ($\rho = 0.21$, $df = 20$, $p = 0.14$). Likewise,
260 there was no correlation between organic matter and total photoautotrophic biomass ($\rho = -$
261 0.077 , $p = 0.8119$). However, a significant difference in means of organic matter were found
262 between first and second group (lowest and middle altitude) of samples, with higher organic
263 matter content in middle (Kruskal-Wallis $X^2 = 8.026$, $df = 2$, $p = 0.02$; Dunn's test $p = 0.0089$).

264 Each cryoconite hole was characterized by relatively low biodiversity (4 to 10 species). Overall,
265 4 species of Chlorophyta, 4 species of Cyanobacteria, 7 species of Bacillariophyceae and 2
266 unidentified cysts (Figure 2, S2; Tables S2, S3) were found with relatively even distribution
267 (Diversity index (J')) 0.347 to 1.013. In most cryoconite holes, the predominant cyanobacterial
268 species included *Pseudanabaena frigida*, *Leptolyngbya* sp. 1, *Leptolyngbya* sp. 2 and
269 *Komvophoron* sp., diatoms *Microcostatus* sp., and filamentous green algae *Klebsormidium*
270 *flaccidum*. *Microcostatus* sp. and *Pseudanabaena frigida* dominated all holes (Figure S2). The
271 biomass of Bacillariophyceae was significantly higher than that of Cyanobacteria (Dunn's test,
272 $p < 0.001$) and Chlorophyceae (Dunn's test, $p = 0.004$). However, there were no differences
273 between Chlorophyta and Cyanobacteria biomass (Dunn's test, $p = 0.052$) (Figure 2, Tables S2,
274 S3). There were no differences in total biomass of photoautotrophs among 3 elevational patches
275 (Kruskal-Wallis $X^2 = 1.2603$, $df = 2$, $p = 0.5325$).

276 Among invertebrates, only 3 species of Rotifera (according to the GenBank search using
277 BLAST algorithm and our sequence data: representatives of Philodinavidae family, relative
278 of *Adineta* sp. and *Macrotrachela* aff. *jankoi* Iakovenko et al. 2015) and 1 species of Acari
279 (*Nanorchestes nivalis* (Trouessart, 1914) sensu Judson (1995)) were observed, but while
280 rotifers were present in every hole ($median = 37, IQR = 60.5, n = 23$), mites were found in 30%
281 of the holes ($median = 0, IQR = 1, n = 23$) (Figures 3, 4, 5 Table S1). Sequences for rotifers
282 obtained in this study are deposited in GenBank under accession numbers: MT181011-
283 MT181018; MT180985-MT180987; MT180992-MT180993. Two rotifer species did not 100%
284 match any rotifer sequences in GenBank and may potentially be new to science (Figures 5, S5,
285 S6). We found a marginally significant differences in densities of rotifers among elevational
286 groups (*Kruskal-Wallis* $X^2 = 6.0825, df = 2, p = 0.05$, Figure 4).

287 Artificial and natural radionuclides observed in the samples included ^{137}Cs , $^{239+240}\text{Pu}$, ^{241}Am ,
288 ^{210}Pb , $^{234,238}\text{U}$ and $^{230,232}\text{Th}$ (Table 1, Figure S4). Significantly higher concentrations of ^{210}Pb
289 (Dunn's test, $p = 0.0131$) were associated with samples located at middle elevation than the
290 lowest one. Isotopic ratios of $^{238}\text{Pu}/^{239+240}\text{Pu}$, $^{239+240}\text{Pu}/^{137}\text{Cs}$ $^{241}\text{Am}/^{239+240}\text{Pu}$ indicate that
291 analysed cryoconite material could be of about 60-70 years old.

292

293 **4. Discussion**

294 Our study presents baseline data on biotic and abiotic characteristics of cryoconite holes for a
295 glacier in Maritime Antarctica. Herein, we present data on morphology, organic matter content,
296 primary producers, top consumers and contamination of radionuclides (proxy for long-range
297 transport of anthropogenic originated contaminations) for cryoconite holes on Ecology Glacier
298 sampled in 2017. Ecology Glacier is located close to the Polish Antarctic Station, "Arctowski",
299 on King George Island (thus supporting easy logistics) and for years was in the focus of
300 biologists (e.g., Dziewit et al. 2013, Mieczan et al. 2013, Grzesiak et al. 2015), ecologists

301 (Zawierucha et al. 2019), glaciologists (e.g., Bintaja 1995, Sobota et al. 2015, Pełlicki et al.
302 2017) and geomorphologists (Sziło et al. 2017) (Table S5). Taking into account the entirety of
303 the literature on the biota of Ecology Glacier published until now, as well as the present study,
304 4 cyanobacteria taxa, 11 algae, 20 ciliates and 4 metazoans (Rotifera, Acari) have been reported
305 (Table S4; see also subsequent results and discussion).

306

307 *4.1. Cryoconite holes*

308 The results of this study showed that cryoconite holes located at lower elevations on the
309 Ecology Glacier have larger depth. The same phenomenon was observed in the Thule Area,
310 (Greenland) by Gajda (1958), who showed various depths of cryoconite holes at different
311 distances from the terminus of valley glacier. Following Gajda (1958), this effect could be
312 caused by more energy available for melting at lower elevations of a glacier. Nevertheless, our
313 study on Ecology Glacier and the study by Gajda (1958) cover a distance of less than 1 km. An
314 opposite pattern but at a larger scale (4 km on valley glacier – Sermikavsak, Greenland) was
315 shown by Gribbon (1979), who found deeper cryoconite holes in the upper part of glaciers. The
316 results of this study and that of Gajda's (1958) may stem from local variations of their surface
317 structure: samples were taken from visually different types of ice, as opposed to Gribbon
318 (1979), who made measurements in each location on visually similar ice patches. Summarising
319 the aforementioned results, cryoconite holes located further from the edge of a glacier are
320 characterised by moving their equilibrium-depths deeper into the ice. A detailed explanation of
321 these phenomena has been proposed by Gribbon (1979), however we did not observe this
322 pattern, which in case of our sampling, might be related to smaller elevational gradient. Detailed
323 formation of cryoconite holes, their forms, and depths were earlier discussed by Sharp (1949).
324 Cryoconite holes on Ecology Glacier are smaller in diameter and size, and with thin layer of ice
325 lid (or lacking such) during sampling, compared to those in the Antarctic McMurdo Dry Valleys

326 (Fountain et al. 2004). However, they are similar in size and depth as well as being open (or
327 with very thin layer of ice) to those in Arctic Svalbard archipelago (Zawierucha et al. 2016b).
328 This indicates that physical processes like flushing, ablation, solar radiation influencing size
329 and shape of cryoconite holes in maritime Antarctic are similar to those found in Arctic insular
330 climate.

331 *4.2. Organic matter*

332 The organic matter content in cryoconite holes from around the world can vary from <2% (e.g.,
333 Tyndal Glacier, Patagonia) to >18% (e.g., Thule Ice Ramp, Greenland) (Gerdel & Drouet 1960,
334 Takeuchi et al. 2001a). However, an average organic matter (7%) content in cryoconite from
335 holes (Cook et al 2015) is similar to that found in our study (6.7%). Although relatively low in
336 our cryoconite samples, the content of organic matter has been shown to play a key role in many
337 geochemical and biological processes in the cryosphere. Not only does it provide substrates for
338 heterotrophic organisms, but also lowers ice albedo and binds various pollutants (Cook et al.
339 2015, Łokas et al. 2016, 2018). Contrary to other observations (Porazinska et al. 2004, Stibal et
340 al. 2010, Langford et al. 2014), we did not observe elevational pattern of organic matter content.
341 These findings might reflect relative flatness of sampling elevational gradient on Ecology
342 Glacier, small sampling area, and possibly the timing of sampling. Significantly higher organic
343 matter content in holes at the middle elevation is hard to explain. It is possible that opposing
344 forces drive the productivity of organic matter (like an autochthonous and allochthonous input),
345 and wash-out (removal) operate across elevations. Lower elevations may have more organic
346 matter, but stronger wash-out obscures this, while wash-out is lower at higher elevations, along
347 with lower productivity. This could result in intermediate effect.

348 *4.3. Algae and cyanobacteria*

349 We observed that cryoconite holes on Ecology Glacier are mostly algae-dominated systems.
350 These findings were rather unexpected as cyanobacteria are considered cryoconite hole

351 ecosystem engineers (Takeuchi et al. 2001a, 2001b, Hodson et al. 2008, Cook et al. 2015). They
352 produce extracellular polymeric substances that stick together mineral and organic matter on
353 glaciers to form granules commonly observed in Arctic and High Alpine (Takeuchi et al. 2001a,
354 Hodson et al. 2010, Langford et al. 2014, Cook et al. 2015). We observed only small and rare
355 cryoconite granules under a stereomicroscope, suggesting that binding properties of
356 cyanobacteria to form granules are marginal on Ecology Glacier (Figure S3). This likely reflects
357 communities and biomass dominated by algae over cyanobacteria. The dominance of algae over
358 cyanobacteria in holes is generally not common, or perhaps not well known, since studies of
359 cryoconite communities generally focus on their diversity rather than biomass (Pittino et al.
360 2018). We cannot exclude that inland ice sheets and small valley glaciers with significantly big
361 inputs of dust or englacial outcropping minerals may favor cyanobacteria that bind particles
362 and form granules; tide-water glaciers located in big fjords may receive more aqueous nutrients
363 that favor algae. However such assumptions need further studies.

364 The number of taxa of cyanobacteria and algae on Ecology Glacier appears consistent with
365 previous studies in Continental Antarctica (Wharton et al. 1981, Porazinska et al. 2004,
366 Sommers et al. 2017). Slightly higher numbers of cyanobacterial taxa were found in previous
367 studies on cryoconite holes in Continental Antarctic. Wharton et al. (1981) and Porazinska et
368 al. (2004) reported seven and six taxa of cyanobacteria, respectively. However, it should be
369 taken into account that the authors investigated few glaciers (Wharton et al. 1981, Porazinska
370 et al. 2004), thus differences may be attributed to broader study sites. In the case of algae,
371 Porazinska et al. (2004) did not describe them in glaciers located in the McMurdo Dry Valleys.
372 However, Sommers et al. (2017) recently showed five taxa of algae via environmental
373 sequencing. Among all taxa of cyanobacteria and algae revealed in our study, only one was
374 previously found in cryoconite holes on Continental Antarctica (*Pseudanabaena frigida*
375 (Fritsch)) by Sommers et al. (2017, 2019). We did not found any of the diatom taxa reported by

376 Stanisch et al. (2012) from glaciers in Antarctic Taylor Valley, who found the two dominant
377 cryoconite hole genera, *Diadlesmis* and *Muelleria*. In turn, the observed taxa of cyanobacteria
378 and algae on Ecology Glacier corresponds better to that found on Chilean and Arctic glaciers
379 than to Continental Antarctic cryoconite holes (Takeuchi et al. 2001a, Porazinska et al. 2004,
380 Stibal et al. 2006, Sommers et al. 2017, 2019, Zawierucha et al. 2018).

381 Certain taxa of algae may be specially adapted to life within the cryoconite holes, other are
382 opportunistic (Cameron et al. 2012, Mueller et al. 2001, Yallop and Anesio 2010). In the Arctic,
383 where the holes are frequently hydrologically connected and lacking an ice lid, the community
384 function and composition appears to be influenced by surface hydrology (Zawierucha et al.
385 2018). Ecology Glacier in maritime Antarctica might be such equivalent example.

386 Stanisch et al. (2013) have proven that cryoconite holes in McMurdo Dry Valleys located on
387 glaciers with most productive hydrological basin and is closest to the Ross Sea, had the highest
388 diatom richness. Authors claimed that glaciers at the coastal end of the Antarctic Taylor valley
389 receive more aeolian inputs from the local area and probably collect more biological material,
390 including diatoms, from stream beds and exposed lake shores (Stanisch et al. 2013). It supports
391 our observations on biotic community on Ecology Glacier, which due to proximity of sea sprays
392 bearing nutrients and delivery of mineral matter from surrounding mountains may favor
393 diatoms.

394 The dominance of algae over cyanobacteria in cryoconite holes from Ecology Glacier which
395 are mostly shallow and with thin and fragile ice lid (or without lid) potentially negatively affect
396 cyanobacterial survivorships in quickly changing and unstable environment. Compared to
397 Bacillariophyceae, Cyanobacteria are slow growing and more sensitive to disturbance like
398 sediment load, flushing and mixing of water (Tang et al. 1997). Although not all Cyanobacteria
399 may fix nitrogen directly from the atmosphere, open holes could also experience nitrogen
400 deposition (e.g., via snow and rain precipitation) stimulating algal growth, but inhibiting

401 cyanobacterial activities (Telling et al. 2011), especially in dynamic cryoconite holes on a small
402 glacier. None of those mechanisms, however, have been well studied indicating the scope of
403 work that lays ahead.

404

405 *4.4. Animals*

406 The rotifers and mites found in our samples are filter- and liquid- or suspension-feeders, feeding
407 on bacteria, algae and perhaps detritus. For the first time on Ecology Glacier, a species of a mite
408 (*Nanorchestes nivalis*) is fully confirmed (as a new metazoan group in cryoconite) and
409 identified. The species have been previously reported from the Maritime Antarctic (Petermann
410 I., Anvers I., Deception I. (South Shetland), Monroe I. (South Orkney)) and the Subantarctic
411 (Candlemas I. (South Sandwich), South Georgia I. - Trouessart 1914, Strandtmann 1982).

412 Antarctic nanorchestid mites have been observed in soil and mosses (e.g., Marshall & Pugh
413 1996, Convey & Smith 1997, Hogg & Stevens 2002, Niemi et al. 2002), but never fully
414 confirmed in cryoconite holes (Zawierucha et al. 2015, 2019). According to Rounsevell &
415 Greenslade (1988), *Nanorchestes* spp. are characterised by granulations in the cuticle, an
416 adaptation to life in very humid or water habitats, where the roughness of the surface by trapping
417 layers of air allows for respiration and protects against freezing. The ability to survive freezing
418 up to -41°C was demonstrated by Fitzsimons (1971). *Nanorchestes antarcticus* Strandtmann,
419 1963 was observed to maintain normal motoric activity between -23°C to +31 °C (Fitzsimons
420 1971). More importantly, *Nanorchestes* spp. can feed on algae (Schuster & Schuster 1977)
421 indicating preadaptations for living in icy ecosystems such as cryoconite holes, especially those
422 on Ecology Glacier dominated by diatoms. Therefore, the presence of *N. nivalis* on Ecology
423 Glacier, does not appear merely accidental, especially that more recently (2018) sediments
424 retrieved from the same glacier contained the same mite (Zawierucha, Buda, Magowski -
425 personal observation, Zawierucha et al. 2019). Taking into account that representatives of *N.*

426 *nivalis* are relatively small in comparison with other Antarctic mites and under
427 stereomicroscope resemble organic granules it is easy to overlooked these animals (Figure 3 A,
428 B). Most probably, the lack of aforementioned physiological adaptations in a vast majority of
429 mites prevents them from colonising glaciers, and single individual findings elsewhere are
430 rather fortuitous in cryoconite holes. A good example is a single individual of the oribatid
431 tritonymph, *Platynothrus punctatus* (C.L. Koch, 1879) (Acari: Oribatida), which was detected
432 only on one (Hansbreen) among six glaciers on Svalbard, indicating an accidental windblown
433 faunal element (Olszanowski - personal observation). We confirmed presence of various instars
434 of mites in cryoconite holes on Ecology Glacier during two seasons. Definitely, our results shows
435 that *N. nivalis* on Ecology Glacier can be persistent resident in cryoconite holes.

436 Invertebrates like tardigrades and rotifers are common in cryoconite holes in polar regions
437 acting as top consumers (Zawierucha et al. 2015, 2018, 2019). Rotifer diversity found on
438 Ecology Glacier is lower than in other reports on cryoconite holes in the Arctic, and higher than
439 in the Continental Antarctic. Porazinska et al. (2004) observed 2 rotifer species on glaciers in
440 the McMurdo Dry Valleys, while De Smet and Van Rompu (1994) found 7 species of rotifers
441 on a glacier on Svalbard. Densities of rotifers on Ecology Glacier are greater than in the
442 McMurdo Dry Valleys (Porazinska et al. 2004) and comparable with those in the Arctic
443 (Zawierucha et al. 2018).

444 *Acutuncus antarcticus* (Richters, 1904) is a common Antarctic tardigrade found previously in
445 cryoconite holes (Cesari et al. 2016, Porazinska et al. 2004), however, not a single specimen of
446 any tardigrade species was found in our study, nor in samples collected in 2018 (personal
447 observation, Zawierucha et al. 2019). On Ecology Glacier, a single specimen of *A. antarcticus*
448 was detected in a cryoconite hole material collected by J. Grzesiak in 2009. Their absence
449 remains unclear.

450

451 *4.5. Radionuclides*

452 The main sources of plutonium in the Southern Hemisphere were French and British nuclear
453 tests in the Southern Pacific (Mururoa), Australia (Woomera) and Indian Ocean (Monte Bello)
454 areas. Another and most significant source of ^{238}Pu (90%) in the Antarctic is accidental burn-
455 up of the SNAP-9A satellite in the atmosphere over Madagascar in 1964. In addition, the
456 $^{238}\text{Pu}/^{239+240}\text{Pu}$ ratios in few samples suggest contributions from local or perhaps more recent
457 trace of Pu of a different origin.

458 Occurrence of ^{241}Am is related to directly by nuclear explosions, and its
459 environmental activity is increasing, because of the decay product of the fallout beta emitter
460 ^{241}Pu ($T_{1/2} = 14.4$ yr). Therefore the $^{241}\text{Am}/^{239+240}\text{Pu}$ ratio can rise to the range of 0.32 - 0.42.
461 The ratio can be also as high in the Southern Hemisphere as 0.80 (2017) based on the high-
462 yield US nuclear tests in 1953 at Bikini Atoll, Marshal Island and Enewetak Atoll (Jia et al.
463 1999). It was calculated from the $^{241}\text{Pu}/^{239+240}\text{Pu}$ activity ratio in 1953. To what extent these
464 pollutants affect cryoconite communities is still unknown, but warrants further research.

465 There is ongoing interest in radioactivity of Antarctic terrestrial and marine
466 ecosystems (Roos et al. 1994, Jia et al. 1999, 2000, Desideri et al. 2003, Giuliani et al. 2003,
467 Mietelski et al. 2000, 2008, Szufa et al. 2018), including ice shelves (Koide et al. 1979).
468 Radionuclide activity concentrations in cryoconite holes may reach much higher values than in
469 surrounding glacier habitats including mosses and lichens. Recently cryoconite was suggested
470 as efficient accumulator of radionuclides in the high mountain regions due to being significantly
471 more radioactive than the matrices usually adopted for the environmental monitoring of
472 radioactivity (Łokas et al. 2018, Baccolo et al. 2020). Indeed, our results of radioactivity of
473 cryoconite from Ecology Glacier indicate the same phenomenon for Antarctic region.
474 Prolonged exposure of cryoconite to atmospheric dust and the presence of cryophilic organisms
475 and organic matter may lead to a build-up of radionuclide levels (Figure 5). Comparing our data

476 with the maximum activity concentrations of ^{137}Cs in mosses (50 Bq kg^{-1}), lichens (162 Bq kg^{-1}) (Jia et al. 1999) and soils (30 Bq kg^{-1}) (Schuller et al. 1993), values from cryoconite holes are
477 1) (Jia et al. 1999) and soils (30 Bq kg^{-1}) (Schuller et al. 1993), values from cryoconite holes are
478 2 to 3 times higher. A similar trend was observed in activity concentrations of ^{238}Pu , $^{239+240}\text{Pu}$
479 and ^{241}Am in mosses (0.21 Bq kg^{-1} , 0.91 Bq kg^{-1} , 0.61 Bq kg^{-1}), lichens (0.75 Bq kg^{-1} , 4.6 Bq
480 kg^{-1} , 1.9 Bq kg^{-1}) and soils (0.003 Bq kg^{-1} , 0.019 Bq kg^{-1} , 0.010 Bq kg^{-1}) (Jia et al. 1999).

481 Studies around the world indicate that radionuclides are actively trapped in cryoconite and ice.
482 First studies on artificial radionuclides content on glaciers were conducted by Jaworowski et al.
483 (1978) who showed that artificial radioactive isotopes are stored in ice. Cryoconite is a kind of
484 biogenic sediment formed when combination of the processes acting in the supraglacial zone
485 leads to mixing and interaction of mineral particulate matter of local and remote origin with
486 organic compounds, bacteria and algae (Takeuchi et al. 2010, 2011 a, b). We suspect that
487 anthropogenic (artificial) radionuclides stored in ice, during melting are released and
488 accumulate in microbes and fungi and up the food chain in microinvertebrates. When viruses
489 lyse cells, they release radionuclides into the cryoconite again. We found that the highest
490 contents of lead, cesium and plutonium were observed in samples with highest organic matter
491 that may effectively accumulate and recycle artificial radionuclides (Łokas et al. 2016). Values
492 of activity ratios (Łokas et al. 2018, Baccolo et al. 2017) in cryoconite collected from holes
493 suggest their yearly biogeochemical recycling, also on Ecology Glacier for more than 70 years
494 when first artificial radionuclides appeared (Figure 6 5). Presence of artificial radionuclides on
495 Ecology Glacier is indicator that mineral material in cryoconite cannot be old englacial origin
496 and most probably derived within last 70 years (windblown from mountains and forefields).
497 High level of radionuclides could be related to algae and cyanobacteria, but effects of such
498 bioaccumulation on glaciers needs closer attention.

499

500 **5. Summary**

- 501
- 502 - We observed variation of cryoconite holes depth, organic matter content, Rotifera counts as
503 well as lead-210 concentration. Such heterogeneity may result from the specific
504 morphology of the glacier surface, distance from terminus (potential transport of
505 aerosols) as well as altitude.
- 506 - Depth of cryoconite holes on Ecology Glacier in January 2017 was related to elevation and
507 increased towards the glacier margin.
- 508 - Distribution of organic matter content was homogenous and unrelated to hole morphology.
- 509 - Seventeen taxa of algae and cyanobacteria, three taxa of rotifers, and one of acari were found.
- 510 - Cryoconite holes on Ecology Glacier were dominated by Bacillariophyceae. This
511 predominance most probably prevents formation of glacier cryoconite granules.
- 512 -, A suspension-feeding mite species was observed for the first time in cryoconite holes.
- 513 - Densities of animals were more similar to Arctic than to continental Antarctic cryoconite
514 holes.
- 515 - Radionuclides have been likely stored on Ecology Glacier since 1950s and these radionuclides
516 are most probably recycled in cryoconite each season by microbial communities.
- 517 - Taking into account all the literature and recently presented data, Ecology Glacier may
518 constitute robust glacier model for comparison of glacial biodiversity between South
519 America and Continental Antarctic.
- 520 - All biotic characteristics of cryoconite holes on Ecology glacier presented in this study are
521 specific functions of time and space (locality) of sampling in Maritime Antarctic.

522

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536

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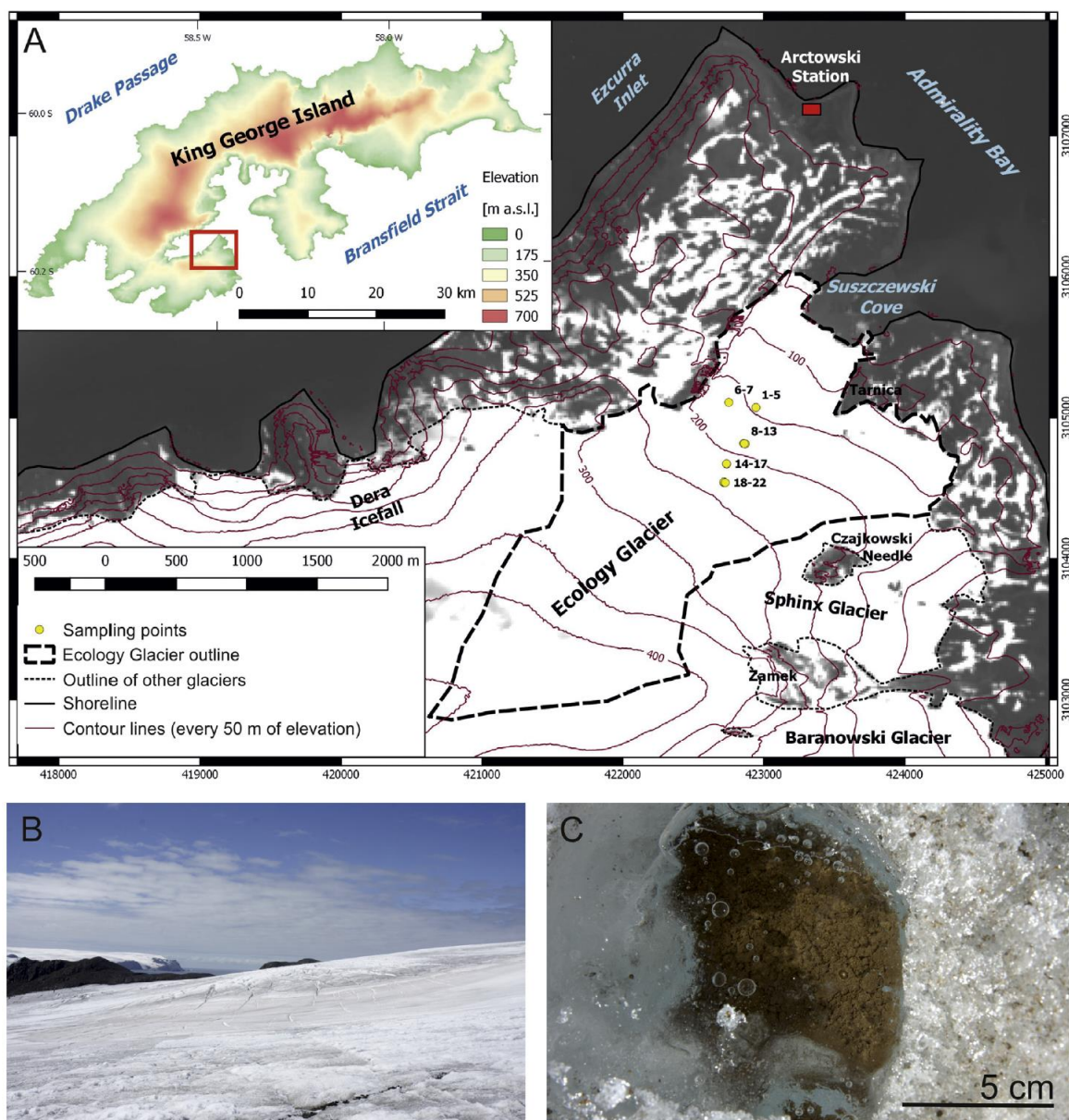
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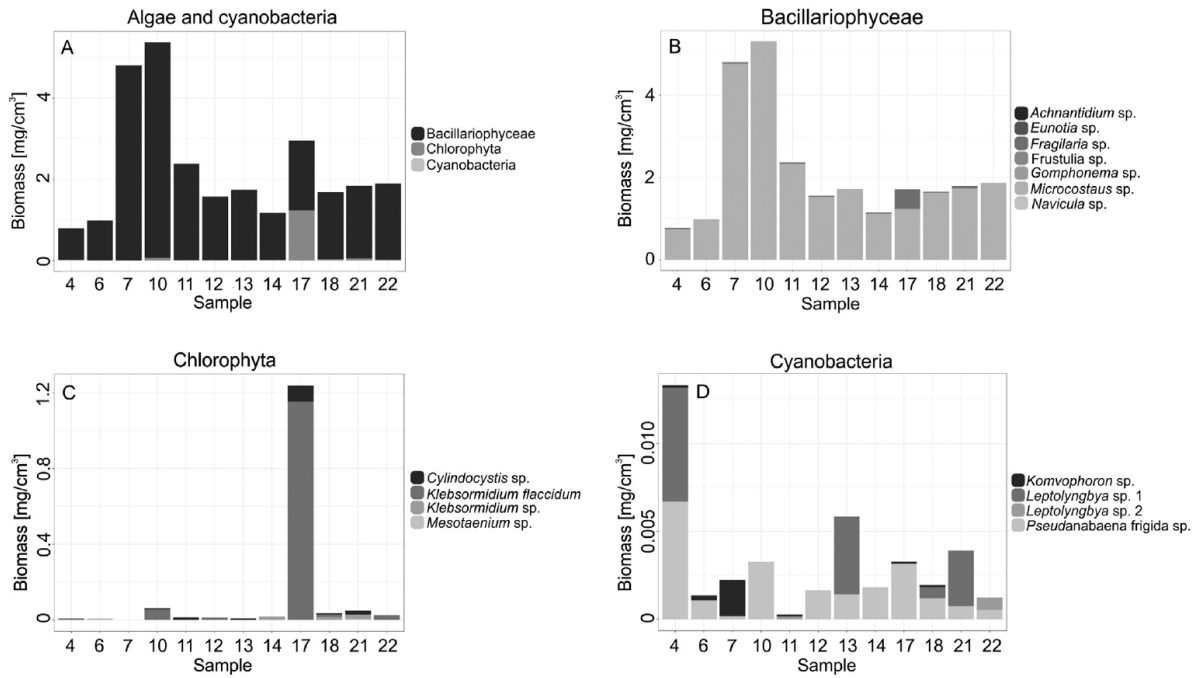
894 **Figure captions**



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896 **Figure 1.** A: Map of study area, B: surface of Ecology Glacier in midsummer 2017, C:
897 cryoconite hole on Ecology Glacier.

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900 **Figure 2.** Biomass of cyanobacteria and algae in cryoconite holes from Ecology Glacier in mid
 901 Austral Summer 2017. A: Comparison of biomass between Bacillariophyceae, Chlorophyta and
 902 Cyanobacteria, B: Biomass of particular taxa among Bacillariophyceae, C: Biomass of
 903 particular taxa among Chlorophyta, D: Biomass of particular taxa among Cyanobacteria.

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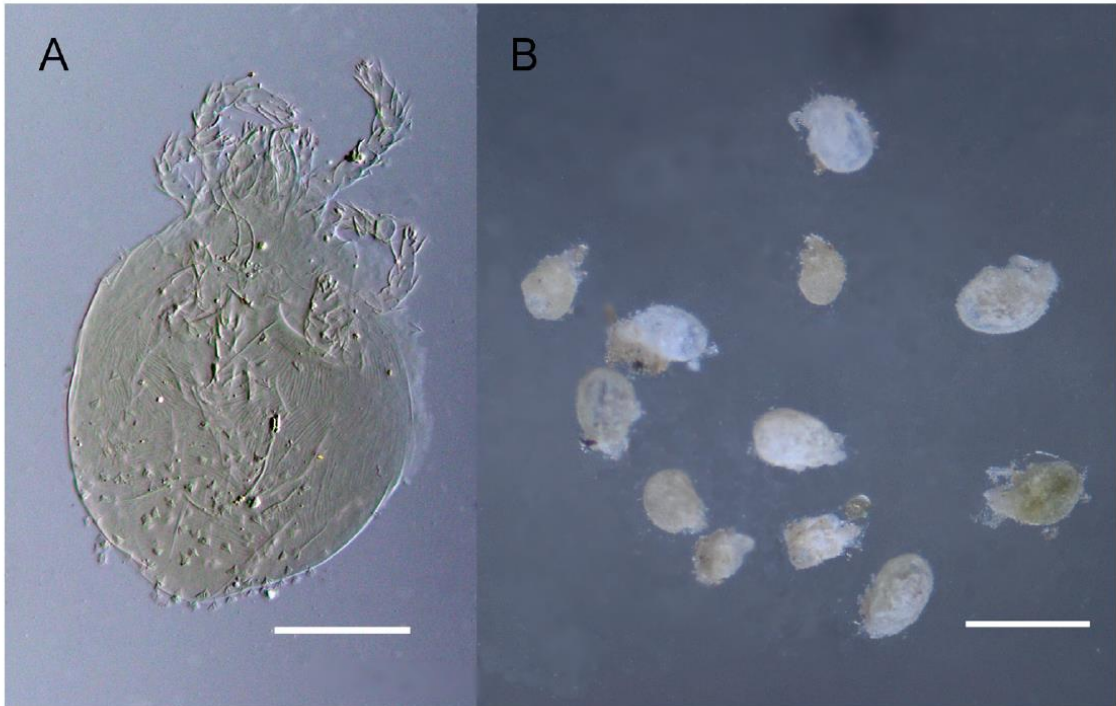
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914 **Figure 3.** *Nanorchestes nivalis* (Trouessart, 1914) from cryoocnite holes: A- tritonymph

915 mounted on slide (scalebar 100 µm), B- nymphs and few adults (scalebar 500 µm).

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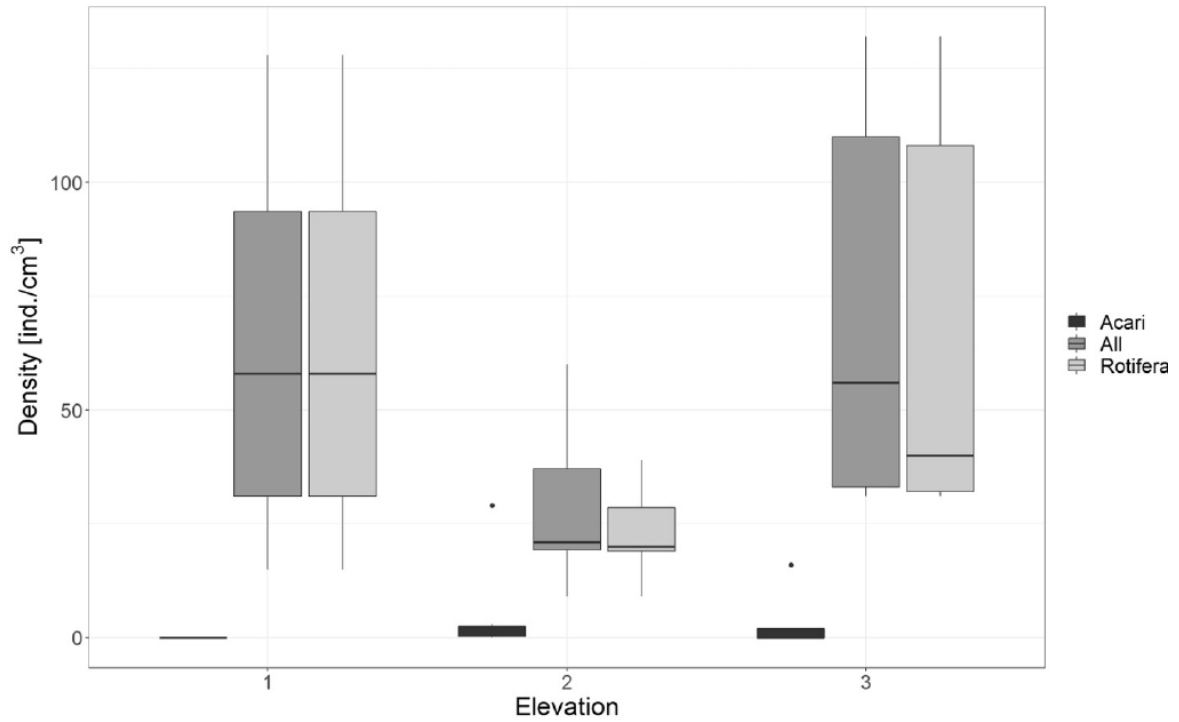
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926 **Figure 4.** Densities of Acari, Rotifera and both in cryoconite holes from Ecology Glacier in
 927 mid Austral Summer 2017. Boxes denote 25th, 50th, and 75th percentiles; whiskers represent the
 928 lowest and highest datum within the 1.5 interquartile ranges of the lower and upper quartiles.

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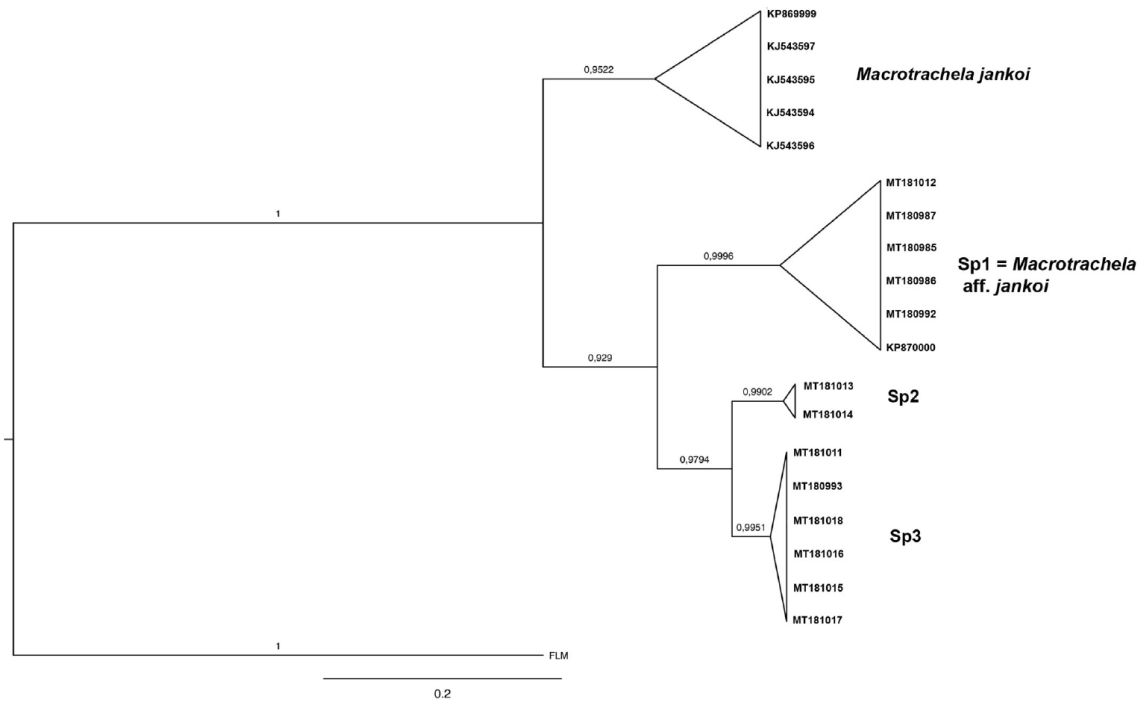
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939 **Figure 5.** Species delimitation of rotifers found in cryoconite from Ecology Glacier (sp. 1, sp.
 940 2, sp. 3), and their phylogenetic relationships to some Antarctic rotifer species (*Macrotrachela*
 941 *jankoi* s. str., *M. aff. jankoi*). Each clade represents a unique species (Independent Evolutionary
 942 Entity, IEE).

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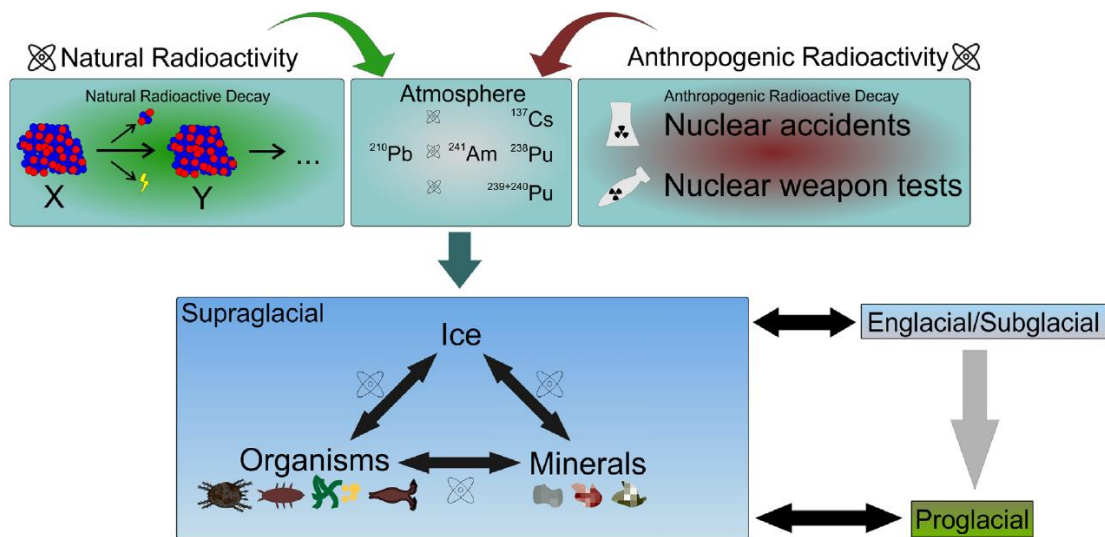
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952 **Figure 6.** Scheme presents sources of radionuclides and their connections with ice, organisms
 953 and minerals.

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