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1 **Potential influence of birds on soil testate amoebae in the Arctic**

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14 **ABSTRACT**

15 Birds can be an important agent of environmental change in High Arctic ecosystems, particularly due  
16 to the role of seabirds as a vector transferring nutrients from the marine to terrestrial realms. The  
17 soils of bird nesting sites are known to host distinct plant communities but the consequences of bird  
18 modification for microorganisms are much less clear. Our focus here is testate amoebae: a widely-  
19 distributed group of protists with significant roles in many aspects of ecosystem functioning. We  
20 compared the testate amoeba assemblages of a site on Spitsbergen (Svalbard archipelago) affected  
21 by nesting birds, with nearby control sites. We found differences in assemblage between sites,  
22 typified by reduced relative abundance of *Phryganella acropodia* and *Centropyxis aerophila* in bird-  
23 modified soils. These changes may reflect a reduced availability of fungal food sources. We found no  
24 evidence for differences in assemblage diversity or test concentration between bird-modified and  
25 control soils. Our dataset is small but results provide the first evidence for the potential effect of bird  
26 modification of soils on testate amoebae in the Arctic. Results show only limited similarity to  
27 experimental studies of nutrient addition, implying that response mechanisms may be more  
28 complicated than simply additional nutrient supply through faeces.

29 **Keywords:** Birds; Testate amoebae; Protists; Protozoa; Svalbard

## 30 1. Introduction

31 High Arctic terrestrial ecosystems typically have very low rates primary production but adjacent  
32 seas can have relatively high productivity, at least during ice-free periods. Seabirds are an important  
33 vector transporting nutrients from the marine realm to terrestrial ecosystems, depositing them in  
34 the form of guano, eggshells, feathers, and carcasses (Zwolicki et al., 2013). This link may assume  
35 additional significance under climate change with retreating sea ice facilitating large phytoplankton  
36 blooms in Arctic seas (Arrigo et al., 2008; Yool et al., 2015). Other birds may have important roles in  
37 redistributing nutrients within and amongst Arctic terrestrial habitats. Bird colonies can form  
38 important nutrient 'hotspots' in nutrient-poor Arctic environments with bird-modified soils often  
39 enriched in key limiting nutrients including N, P, Mg and K (Ligeza and Smal, 2003; Wait et al., 2005;  
40 Zwolicki et al., 2013). This supply of nutrients may ultimately lead to the development of soils which  
41 are higher in moisture, more acidic and more saline than those of areas not affected by birds (García  
42 et al., 2002; Wait et al., 2005). Biological consequences of these changes include the tendency for  
43 bird-modified soils to host plants with more nutrient-rich tissues and plant communities with lower  
44 species richness, higher biomass, greater cover and domination by a smaller pool of ruderal, annual  
45 and cosmopolitan species (Anderson and Polis, 1999; Ellis, 2005). Bird-modified soils often host  
46 distinct micro-fauna assemblages with effects potentially extending some distance beyond nesting  
47 sites (Zawierucha et al., 2016; Zmudczyńska-Skarbek et al., 2017; Zmudczyńska-Skarbek et al., 2015).  
48 The combination of these varying impacts may ultimately have an important role in shaping long-  
49 term ecosystem development in High Arctic environments (Hodkinson et al., 2003; Sánchez-Piñero  
50 and Polis, 2000). With many direct and indirect anthropogenic factors currently acting on Arctic bird  
51 populations there is a need to understand how birds shape terrestrial ecosystems and how this may  
52 vary in the future (Moe et al., 2009; Stempniewicz et al., 2007; Wassmann et al., 2011).

53 While the consequences of bird-modification have been comparatively well-studied for plants,  
54 the consequences for the microorganisms which constitute the largest component of biodiversity  
55 are virtually unknown. Previous studies imply that birds increase total microbial biomass and,  
56 consequently soil respiration, and shift the competitive balance from fungi to bacteria, but other  
57 impacts are unclear (Smith, 2003, 2005; Wright et al., 2010). Birds may affect soil microbial groups  
58 through several pathways, both directly through the supply of nutrients and physical disturbance,  
59 and indirectly through impacts on prey, predators and competitors. Birds are also important agents  
60 in the movement of small organisms and given long ranging distances may be a vector for the  
61 transport of microorganisms to nesting sites (Wilkinson, 2009; Wilkinson et al., 2012). While there is  
62 basic knowledge about the effects of bird populations on overall microbial biomass and some

63 knowledge about changes in prokaryotes there is almost no knowledge about the response of  
64 microbial consumers despite their important role in shaping microbial food-web dynamics and  
65 ultimately many aspects of ecosystem function.

66 The particular focus of this paper is testate amoebae. Testate amoebae are an abundant group  
67 of protists in soils and can constitute a large proportion of total microbial biomass (Gilbert et al.,  
68 1998b). These microorganisms are amongst the larger protist groups (most taxa 20-200µm in length)  
69 and play important roles as consumers of smaller microorganisms and, in the case of some species, in  
70 primary production through endosymbiotic algae (Jassey et al., 2015; Wilkinson and Mitchell, 2010).  
71 While it is probable that general ecological studies of protozoa in high latitude environments have  
72 included samples from bird-modified soils (Smith, 1996; Vincke et al., 2004), to our knowledge the  
73 only study to directly address the impact of birds on soil testate amoebae is that of Vincke et al.  
74 (2007) from sub-Antarctic Île de la Possession (Crozet Archipelago). This study showed significant  
75 changes to testate amoeba assemblages but results are difficult to generalise to other sites because  
76 the study focused on the impact of wandering albatross which is restricted to the southern  
77 hemisphere and is an atypical bird species in terms of size and time spent on land. We are not aware  
78 of studies investigating the impacts of other bird species or any studies at all in the Arctic. However,  
79 numerous studies demonstrate impacts of various aspects of nutrient enrichment on soil testate  
80 amoebae (Mitchell, 2004; Payne et al., 2013; Payne et al., 2012) so it is reasonable to suppose that  
81 birds are affecting soil testate amoebae widely across the Polar regions. Here we address differences  
82 in testate amoebae between sites with differing extents of bird modification on the island of  
83 Spitsbergen in the Svalbard archipelago. We hypothesise that:

84 H1 Areas affected by birds sites host distinct assemblages of testate amoebae from adjacent  
85 sites.

86 H2. Areas affected by birds host exotic taxa not present in the wider environment due to avian  
87 transport.

88 H3 Areas affected by birds host a higher abundance of bacterivorous and lower abundance of  
89 fungivorous taxa relative to reference sites.

90 H4. Areas affected by birds have a lower alpha diversity of testate amoebae.

91

## 92 2. Material and methods

### 93 2.1. Study area

94 The Svalbard archipelago is located in the Arctic between 74° and 81° N and 10° and 35° E, at a  
95 distance of c.700 km from the nearest continental coast. The archipelago covers an area of about  
96 63,000 km<sup>2</sup>, 60% of which is covered with ice and snow (Hisdal, 1985). Our research was conducted  
97 in the Grønfjorden area of Western Spitsbergen, in the vicinity of the settlement of Barentsburg (78°  
98 02'N, 14° 12' E) in July 2012 (Fig. 1). The climate of Svalbard is atypically mild for the latitude because  
99 of northwards transfer of heat by the North Atlantic Drift. The nearest meteorological station with  
100 available data is located >50 km from our sampling area at Longyearbyen Airport. Here the average  
101 annual temperature is -4.6°C (1981-2010 average) with positive average temperatures recorded only  
102 in the summer months (June to September) (Førland et al., 2011). The monthly average air  
103 temperature in winter is often below -15°C, but the daily minimum temperatures can drop to -40°C.  
104 Precipitation, mostly as snow, varies from 210 to 525 mm per year (1981 – 2010). The study area is  
105 underlain by permafrost; monitoring data show active layer depths of 1-2m (Osokin and Sosnovsky,  
106 2008).

## 107 2.2. Fieldwork and sampling sites

108 Sampling was conducted in three different sites: one affected by birds ('bird site') and two  
109 nearby control sites without major bird influence ('control sites 1 & 2'). The bird site is a slope  
110 situated immediately below a nesting site for *Alle alle* (Little Auk), also with *Cephus grille* (Black  
111 guillemots), *Larus hyperboreus* (Glaucous Gull), and occasionally *Branta leucopsis* (Barnacle Goose).  
112 The colony is smaller than a typical Little Auk colony on Svalbard, containing no more than 500 pairs  
113 at the time of the sampling visit. In 2005 and 2008, bird numbers were quantified as around 200-250  
114 pairs of Little Auks, around 20-25 pairs of Black Guillemots, 2-6 pairs of Barnacle Geese and 14-17  
115 pairs of Glaucous Gulls (Ivanenko, 2006; Ivanenko, 2009). Although nest density is not particularly  
116 high, faeces and guano deposits were widely noted in the sampling site which occupies a slope  
117 between 53 and 134m above sea level, situated immediately below the main colony on the seaward  
118 side (Supplementary Fig. 1). Vegetation is discontinuous and includes a range of vascular plants and  
119 bryophytes with *Polytrichum* spp. and *Sanionia uncinata* particularly abundant (Fig. 1;  
120 Supplementary Fig. 1). Towards the base of the slope the vegetation includes shrubs such as *Salix*  
121 *polaris*, in the centre of the slope are forbs such as *Cerastium alpinum* and *Potentilla hyparctica*  
122 while the upper part of the slope vegetation is primarily of mosses. Control site 1 is located along the  
123 same coastline ca. 2km to the south on a slope between 66 and 88m asl. This site is less steeply  
124 sloping than the bird site with deeper humus-rich soils and more continuous mixed bryophyte-  
125 dominated vegetation typical of Arctic tundra. The vegetation was not surveyed in detail but  
126 contains no clear indication of nutrient enrichment and is distinct from the bird site. No nests or

127 guano were noted at this site although a small amount of geese faeces was noted. Control site 2 is  
128 located further south on flatter, lower elevation (6-44m) tundra at Cape Finneset. Vegetation  
129 includes more lichens than the other sites but in other respects the site is similar to control site 1  
130 with broadly-typical bryophyte-dominated tundra vegetation. A few nests of Snow Bunting  
131 (*Plectrophenax nivalis*) and Common Eider (*Somateria mollissima*) were noted but these were sparse  
132 and faecal deposits were much rarer than in the bird site. All three sites are beyond the boundaries  
133 of the settlement of Barentsburg and have not been significantly affected by anthropogenic  
134 disturbance through industrial or agricultural activity and are located well away from sites with  
135 imported soils (Coulson et al., 2013). It is however possible that bird distribution may have been  
136 different prior to the construction of Barentsburg (1920s) and that soils may exhibit legacy-effects  
137 from previous bird-derived nutrient addition. Five samples of topsoil and plants (5g each) were  
138 extracted from each sampling area spanning the range of variability in vegetation and  
139 microtopography. Sampling was conducted using a transect design with these transects  
140 perpendicular to the coastline in the bird site and control site 1 and parallel to the coastline in  
141 control site 2. Sampling locations were separated by distances of 10-200m and were 50-500m from  
142 the coast. Samples extracted were stored refrigerated until analysis (Mazei et al., 2015).

### 143 2.3. Laboratory work

144 Samples were prepared for microscopy following the method of Mazei and Chernyshov (2011)  
145 which comprises suspension in water, physical agitation and settling. All samples were inspected  
146 under light microscopy at 160× magnification. All testate amoeba tests in the samples were  
147 identified following Mazei and Tsyganov (2006). Live individuals were not differentiated from empty  
148 tests so the assemblage identified integrates communities living over a period of several years. Data  
149 are expressed as relative abundance; as a percentage of the total count of all tests. A second sample  
150 from the same location was weighed, oven dried and reweighed to calculate moisture content,  
151 which is known to be an important control on testate amoebae.

### 152 2.4. Data analysis

153 To address the adequacy of sampling in capturing the full amoeba community, at a sample level  
154 and overall, we used individual rarefaction to consider change in taxon richness with count and  
155 sample rarefaction of the entire dataset to assess how taxon richness changed with number of  
156 samples considered (Colwell et al., 2004). To assess the impact of bird presence we considered both  
157 the assemblage composition and measures of assemblage diversity. We conducted separate  
158 analyses of data based on both test concentration (ind. g<sup>-1</sup>) and relative abundance (%). To test for

159 differences in assemblage between bird and control sites we used one-way permutational analysis of  
160 variance (PERMANOVA) with 9999 permutations, based on Bray-Curtis dissimilarity matrices of raw  
161 data (Bray and Curtis, 1957). To visualise differences we used a detrended correspondence analysis  
162 (DCA) ordination (Hill and Gauch, 1980). We tested for differences in morphospecies richness, test  
163 concentration and moisture content between the sampling sites using Kruskal-Wallis tests with  
164 Bonferroni-corrected pairwise Mann-Whitney post-hoc tests. We also calculated Shannon diversity  
165  $H'$  based on the natural logarithm (DeJong, 1975). Data analysis was conducted in PAST vers. 3.04  
166 (Hammer et al., 2001).

167

### 168 3. Results

#### 169 3.1. Composition and taxon richness

170 Twenty six taxa were found in the fifteen samples (Table 1) with taxon richness by sample  
171 varying from 9 to 17 (mean=13). Shannon  $H'$  varied from 1.8-2.4. The most abundant identified taxa  
172 were *Trinema lineare* (19% of all tests counted), *Centropyxis aerophila* (15%), *Phryganella acropodia*  
173 (12%) and *Centropyxis sylvatica* (11%). Count totals for some samples were less than commonly-  
174 applied minima (mean=65 tests) (Payne and Mitchell, 2009) but individual rarefaction plots show  
175 that although an asymptote is not reached there is a marked reduction in rate of increase for most  
176 but not all samples (Fig. 2). At the level of the entire study area, the rarefaction curve similarly shows  
177 no asymptote but a strong reduction in gradient towards the maximum (Fig. 3). The sampling is likely  
178 to have captured most but not all testate amoeba taxa in this area.

#### 179 3.2. Differences with bird presence

180 PERMANOVA showed highly significant differences between sites (relative abundance:  
181  $F_{(1,1,1,8)}=4.1$ ,  $P<0.001$ ; concentration:  $F_{(1,6,2,4)}=2.6$ ,  $P<0.001$ ). Pairwise testing showed significant  
182 differences amongst all three sites with the most significant differences between the bird site and  
183 control site 1 ( $P=0.022$ ) and marginally significant differences with control site 2 ( $P=0.047$ ) and  
184 between the two control sites ( $P=0.049$ ). The DCA plots illustrate these differences (Fig. 4). In terms  
185 of concentration the bird samples are clearly separated from control sites along DCA2 (Fig. 4A) while  
186 in terms of relative abundance the samples are separated along DCA1 and, to a lesser extent, DCA2  
187 (Fig. 4B). The samples from both control sites are more tightly clustered in the ordination plots  
188 based on both relative abundance and concentration. Four taxa were only found in bird sites:  
189 *Cryptodifflugia oviformis*, *Cyclopyxis eurystoma*, *Nebela parvula*, and *Phryganella hemisphaerica*  
190 while three taxa were only found in control sites: *Euglypha simplex*, *Centropyxis cassis*, and

191 *Centropyxis elongata* (Table 1). The majority of these taxa were rare overall. Of the taxa with  
192 sufficient data for separate testing only two showed significant differences in relative abundance  
193 between sites: *Phryganella acropodia* (N=15, df=2, H=7.22, P=0.03) and *Centropyxis aerophila* (N=15,  
194 df=2, H=12.5, P=0.001). *C. aerophila* contributed a large proportion of all tests in the control sites (9-  
195 46%) but was rare in the bird sites (0-4%) (Fig. 5). *P. acropodia* relative abundance in the bird site  
196 was significantly lower than control site 2 (P<0.05) but not significantly lower than control site 1 (Fig.  
197 5). We found no significant difference in moisture between samples from the three sites (N=15,  
198 df=2, H=1.1, P=0.56)(Fig. 6). There was no significant difference between sites in terms of testate  
199 amoeba morphospecies richness (N=15, df=2, H=4.5, P=0.10) but the highest individual values were  
200 found in the bird site (Fig. 7). There was no significant difference between the sites for total test  
201 concentration (N=15, df=2, H=0.14, P=0.93) (Fig. 8).

202

#### 203 4. Discussion

204 With only fifteen samples our dataset is undeniably small but constitutes the first direct  
205 comparison of testate amoebae in bird-modified and control soils in the Arctic. The dataset is also  
206 one of comparatively few for testate amoebae from the region. Svalbard is one of the better-studied  
207 High Arctic regions for testate amoebae but protozoa are still clearly an under-recorded group  
208 (Coulson et al., 2014). Our dataset extends the geographic coverage and the known species pool. Of  
209 the taxa identified, most are well-known, widely found in soils and have been previously recorded in  
210 the Arctic (Beyens and Chardez, 1995). The most notable taxon identified is the single test (shell) of  
211 *Centropyxis elongata*. We believe this is the first record of this taxon on Svalbard and one of very  
212 few from the Arctic (Beyens and Chardez, 1995; Beyens et al., 1991), with most records from much  
213 more temperate environments (Lüftenegger et al., 1988; Ooms et al., 2015; Ying-zhi and Yun-fen,  
214 1996).

215 Our results show that there are significant differences in assemblage composition between the  
216 testate amoeba communities of sites with and without birds (Fig. 4). It is probable that these reflect  
217 the influence of birds on testate amoebae but it is also conceivable that our sampling sites also  
218 differed in other ways not related to birds. For instance, control site 2 was at a lower elevation and  
219 had flatter topography than the bird breeding site and both sites were less steeply sloping than the  
220 bird site. The comparison between the bird site and control site 1 is probably the more informative  
221 comparison given greater proximity and topographical situation. It is notable that we found some  
222 differences between the two control sites and these are unlikely to relate to bird use. We therefore

223 cannot rule out the possibility that the differences in testate amoebae we find are coincidental; this  
224 is a fundamental limitation of spatial comparisons of this nature. Birds do not select their nesting  
225 sites randomly; factors such as microclimate, proximity to food sources, accessibility to predators  
226 and human disturbance may determine choice of nesting site and some of these factors may also  
227 affect the soil biota (Anderson and Keith, 1980; Forbes and Kaiser, 1994). However, it appears  
228 probable that the birds have affected the testate amoeba assemblage in the soils at these sites.  
229 Thus, our data support hypothesis 1 and imply an impact of birds on soil testate amoebae.

230 One possibility which we anticipated at the outset is that bird nesting sites might host unusual  
231 testate amoebae including taxa translocated from other locations and other environments (H2). Of  
232 the bird populations present at our site, both Glaucous Gulls and Little Auks over-winter largely at  
233 sea in the North Atlantic but range widely across this region (Newton and Dale, 1996). There is a  
234 small possibility that these species might translocate amoebae from more southerly regions.  
235 Barnacle Geese from Svalbard appear to over-winter primarily in the Solway Firth area of Scotland  
236 (Butler et al., 1998; Owen and Black, 1989) and there is a somewhat higher possibility that they may  
237 transport amoebae to Svalbard. However, we found little unusual in the testate amoeba fauna of  
238 these samples. Across the entire Arctic region the most abundant testate amoeba taxa are *Trinema*  
239 *lineare*, *Assulina muscorum*, *Centropyxis aerophila* and *Corythion dubium* (Beyens and Bobrov, 2016).  
240 All of these taxa were located in our samples and they constituted the most abundant, 8<sup>th</sup>, 2<sup>nd</sup> and  
241 7<sup>th</sup> most abundant taxa respectively. None of the taxa we identify can be considered as a particular  
242 surprising presence in a habitat of this nature. The most notable occurrence was the single test of  
243 *Centropyxis elongata*. While this taxon has been more commonly recorded further south this test  
244 was identified at control site 1 where no birds were apparent so a bird vector seems unlikely. Given  
245 the recording of this species from Devon Island in the Canadian Arctic Archipelago (Beyens et al.,  
246 1991) it is more probable that this is an indigenous, albeit relatively rare, component of the Arctic  
247 testate amoeba fauna. Taxonomic grouping or inconsistency is also a possibility given the general  
248 morphological similarity of this taxon to other, more frequently recorded *Centropyxis* species such as  
249 *C. platystoma* (Mitchell et al., 2014; Payne et al., 2011). Our lack of evidence for unusual or exotic  
250 taxa associated with bird nesting on Svalbard parallels work on invertebrates which also found little  
251 evidence for species introductions in nesting sites (Coulson et al., 2009a), although bird transport of  
252 invertebrates has been demonstrated (Lebedeva and Krivolutsky, 2003). In the case of our study it is  
253 possible that the predominant presence of bird species which largely over-winter at sea may have  
254 reduced any species introduction and that this could have been greater in sites with other species.

255 Our data imply that birds have reduced the occurrence of taxa including *C. aerophila* and *P.*  
256 *acropodia* (the only two taxa to show significant differences in independent testing) and may have  
257 increased the abundance of *Centropyxis sylvatica*, *Assulina muscorum* and *Trinema enchelys*  
258 (although all were non-significantly different in independent testing). At the outset we anticipated  
259 that bird presence would increase the abundance of bacterivorous taxa and decrease the abundance  
260 of fungivorous taxa, based on previous findings of shifts in competitive balance from fungi towards  
261 bacteria most likely due to enhanced nutrient supply (Wright et al., 2010). Our data only partially  
262 support this expectation. *P. acropodia* is widely known as a taxon which is associated with fungi and  
263 this taxon was less abundant in bird-affected sites (Gilbert et al., 2000; Ogden and Pitta, 1990). *C.*  
264 *aerophila* has similarly been observed to feed on fungi (Gilbert et al., 2000) and was less abundant in  
265 soils from the bird site. These findings generally support the expectation of a reduction in  
266 fungivores, however our data only provide weak evidence for an increase in bacterivores. Although  
267 no taxa were significantly more abundant in soils with birds, the largest difference in overall relative  
268 abundance was in *Centropyxis sylvatica* which has a mean relative abundance more than three times  
269 greater in soils from the bird site than the control sites. We are not aware of any direct data on the  
270 feeding preference of this taxon but they can be expected to be similar to *C. aerophila* making it  
271 surprising to see opposing trends. Similarly, taxa which are both abundant and unambiguously  
272 bacterivores such as *Trinema lineare* do not differ between the sites (Gilbert et al., 2000). We do find  
273 a general trend towards higher abundance of *Trinema enchelys* and *Assulina muscorum* in the bird  
274 sites and these taxa are most likely bacterivorous. Overall, hypothesis 3 cannot be refuted but is only  
275 partially supported by the data.

276 Across a wide variety of groups of organisms it is a common finding that nutrient enrichment  
277 leads to a loss of diversity with increasing dominance by a small group of taxa (Stevens et al., 2004),  
278 we therefore anticipated that bird nesting sites would be less diverse (H4). However the data did not  
279 support our initial expectations. Our results show no significant difference between sites in terms of  
280 taxon richness. It may be the case that relatively modest nest density means that nutrient input is  
281 insufficient to facilitate dominance by a small group of taxa.

282 Our data show similarities and differences with previous datasets. The most directly  
283 comparable study is that of Vincke et al. (2007) from the sub-Antarctic. These authors found strong  
284 differences in testate amoebae with albatross influence, typified by increased abundance of  
285 *Diffugiella oviformis* and *Trinema lineare*. *D. oviformis* was not found in our samples whereas *T.*  
286 *lineare* was abundant but did not differ between sites. Vincke et al. (2007) found reduced diversity  
287 near albatross nests, again in contrast to our finding of no significant difference. The differences

288 between the two studies may partly reflect the intensity of disturbance involved. Vincke et al. (2007)  
289 found heavy deposition of guano leading to very large differences in nutrients, particularly  
290 phosphorous, combined with extensive physical disturbance. In our sites soil nutrients were not  
291 analysed but based on observations of the extent of faeces it is likely that nutrient input was much  
292 less than that in the sub-Antarctic sites of Vincke et al. (2007). Similarly, plant communities were not  
293 recorded in either study but disturbance appears to be more extensive in Vincke et al. (2007)'s sites  
294 than in our own.

295 Vincke et al. (2007) is the only study we are aware of to directly investigate the impact of birds  
296 on soil testate amoebae but other studies have addressed the impacts of nutrient enrichment.  
297 Comparison to these studies provides the possibility to evaluate the extent to which our results are  
298 concordant with a nutrient enrichment effect. In perhaps the most relevant study, Mitchell (2004)  
299 investigated the impact of N&P addition on an Alaskan tundra environment and found distinct  
300 changes in testate amoeba assemblage: *P. acropodia* and *C. aerophila* increased in relative  
301 abundance while *D. oviformis* declined. The increase in *P. acropodia* and *C. aerophila* is the opposite  
302 of what we find here while the decline in *D. oviformis* is the opposite of that found by Vincke et al.  
303 (2007). In a French peatland Gilbert et al. (1998b) found that nutrient input with both NPKCa and  
304 PKCa caused a loss of testate amoeba biomass relative to other microbial groups and Gilbert et al.  
305 (1998a) found similar results for N addition alone. In our study other microbial communities were  
306 not analysed but we found no significant difference in overall test concentrations. Payne et al.  
307 (2012) investigated the impact of N addition in a heathland soil and found a decline in relative  
308 abundance of *Corythion dubium* with N, a finding which is not paralleled in our data where this taxon  
309 was non-significantly more abundant in the bird sites. Payne et al. (2013) found that gaseous  
310 ammonia was associated with a non-significant trend towards greater testate amoeba biomass,  
311 primarily driven by increasing abundance of the largest taxa. This size-dependent response to  
312 nutrient addition was not paralleled in our data. From these comparisons it can be concluded that  
313 the response of testate amoebae to bird presence is unlikely to be a simple consequence of nutrient  
314 addition in faeces. We did not collect wider supporting data which would clearly have been helpful  
315 to fully understand the mechanisms at work. Direct data on soil nutrient composition would have  
316 allowed eutrophication effects to be more directly tested and data on other microbial groups would  
317 have allowed linkages to be explored across trophic levels. Further quantification of bird species,  
318 abundance and activity would also have been helpful given evidence for differing impacts of  
319 different bird species (Zmudczyńska-Skarbek et al., 2017). Larger and more holistic studies will be  
320 required to fully disentangle the mechanisms of impact. Nevertheless, our data provide the first

321 direct evidence for the effects of birds on soil testate amoebae in the Arctic and pave the way for  
322 future research.

323 It is clear that bird modification of soils is a significant issue in the Arctic, particularly given  
324 threats to birds from climate change, invasive species and pollutants (Coulson et al., 2009b;  
325 Gabrielsen et al., 1995). Bird influence is an important factor shaping high latitude ecosystems but  
326 current knowledge is fragmentary, particularly below-ground. Testate amoebae are just one  
327 component of the soil food-web but exemplify the limited knowledge of bird effects more widely.  
328 Our results go some way towards filling the knowledge gap but also demonstrate how little is  
329 known.

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### 340 **References**

- 341 Anderson, D.W., Keith, J.O., 1980. The human influence on seabird nesting success: Conservation  
342 implications. *Biological Conservation* 18, 65-80.
- 343 Anderson, W.B., Polis, G.A., 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient  
344 status on Gulf of California islands. *Oecologia* 118, 324-332.
- 345 Arrigo, K.R., van Dijken, G., Pabi, S., 2008. Impact of a shrinking Arctic ice cover on marine primary  
346 production. *Geophysical Research Letters* 35, n/a-n/a.
- 347 Beyens, L., Bobrov, A., 2016. Evidence supporting the concept of a regionalized distribution of  
348 testate amoebae in the Arctic. *Acta Protozoologica* 2016, 197-209.
- 349 Beyens, L., Chardez, D., 1995. An annotated list of testate amoebae observed in the Arctic between  
350 the longitudes 27E and 168W. *Archiv für Protistenkunde* 146, 219-233.
- 351 Beyens, L., Chardez, D., De Baere, D., 1991. Ecology of aquatic testate amoebae in coastal Lowlands  
352 of Devon Island (Canadian High Arctic). *Archiv für Protistenkunde* 140, 23-33.

353 Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin.  
354 Ecological Monographs 27, 325-349.

355 Butler, P.J., Woakes, A.J., Bishop, C.M., 1998. Behaviour and Physiology of Svalbard Barnacle Geese  
356 *Branta leucopsis* during Their Autumn Migration. *Journal of Avian Biology* 29, 536-545.

357 Colwell, R.K., Mao, C.X., Chang, J., 2004. Interpolating, extrapolating, and comparing incidence-based  
358 species accumulation curves. *Ecology* 85, 2717-2727.

359 Coulson, S., Convey, P., Aakra, K., Aarvik, L., Avila-Jimenez, M., Babenko, A., Biersma, E., Bostrom, S.,  
360 Brittain, J., Carlsson, A., Christoffersen, K., De Smet, W., Ekrem, T., Fjellberg, A., Fureder, L.,  
361 Gustafsson, D., Gwiazdowicz, D., Hansen, L., Holmstrup, M., Hulle, M., Kaczmarek, L., Kolicka,  
362 M., Kuklin, V., Lakka, H.-K., Lebedeva, N., Makarova, O., Maraldo, K., Melekhina, E., Odegaard,  
363 F., Pilskog, H., Simon, J., Sohlenius, B., Solhoy, T., Soli, G., Stur, G., Tanasevitch, A., Taskaeva, A.,  
364 Velle, G., Zawierucha, K., Zmudczynska-Skarbek, K., 2014. The terrestrial and freshwater  
365 invertebrate biodiversity of the archipelagoes of the Barents Sea; Svalbard, Franz Josef Land and  
366 Novaya Zemlya. *Soil Biology and Biochemistry* 68, 440-470.

367 Coulson, S., Fjellberg, A., Gwiazdowicz, D., Lebedeva, N., Melekhina, E., Solhoy, T., Erseus, C.,  
368 Maraldo, K., Miko, L., Schatz, H., Schmelz, R., Soli, G., Stur, E., 2013. Introduction of  
369 invertebrates into the High Arctic via imported soils: the case of Barentsburg in the Svalbard  
370 archipelago. *Biological Invasions* 15, 1-5.

371 Coulson, S., Moe, B., Monson, F., Gabrielsen, G., 2009a. The invertebrate fauna of High Arctic seabird  
372 nests: the microarthropod community inhabiting nests on Spitsbergen, Svalbard. *Polar Biology*  
373 32, 1041.

374 Coulson, S.J., Lorentzen, E., Strøm, H., Gabrielsen, G.W., 2009b. The parasitic tick *Ixodes uriae* (Acari:  
375 Ixodidae) on seabirds from Spitsbergen, Svalbard. *Polar Research* 28, 399-402.

376 DeJong, T., 1975. A comparison of three diversity indices based on their components of richness and  
377 evenness. *Oikos*, 222-227.

378 Ellis, J.C., 2005. Marine Birds on Land: A Review of Plant Biomass, Species Richness, and Community  
379 Composition in Seabird Colonies. *Plant Ecology* 181, 227-241.

380 Forbes, L.S., Kaiser, G.W., 1994. Habitat Choice in Breeding Seabirds: When to Cross the Information  
381 Barrier. *Oikos* 70, 377-384.

382 Førland, E., Benestad, R., Hanssen-Bauer, I., Haugen, J., Skaugen, T., 2011. Temperature and  
383 precipitation development at Svalbard 1900-2100. *Advances in Meteorology*, 893790.

384 Gabrielsen, G.W., Skaare, J.U., Polder, A., Bakken, V., 1995. Chlorinated hydrocarbons in glaucous  
385 gulls (*Larus hyperboreus*) in the southern part of Svalbard. *Science of the Total Environment*  
386 160, 337-346.

387 García, L.V., Marañón, T., Ojeda, F., Clemente, L., Redondo, R., 2002. Seagull influence on soil  
388 properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean  
389 islands. *Oikos* 98, 75-86.

390 Gilbert, D., Amblard, C., Bourdier, G., André-Jean, F., Mitchell, E.A., 2000. Le régime alimentaire des  
391 thécamoebiens (Protista, Sarcodina). *L'année Biologique* 39, 57-68.

392 Gilbert, D., Amblard, C., Bourdier, G., Francez, A.-J., 1998a. Short-term effect of nitrogen enrichment  
393 on the microbial communities of a peatland, in: Amiard, J.C., Le Rouzic, B., Berthet, B., Bertru, G.  
394 (Eds.), *Oceans, Rivers and Lakes: Energy and Substance Transfers at Interfaces: Proceedings of*  
395 *the Third International Joint Conference on Limnology and Oceanography held in Nantes,*  
396 *France, October 1996.* Springer Netherlands, Dordrecht, pp. 111-119.

397 Gilbert, D., Amblard, C., Bourdier, G., Francez, A.J., 1998b. The microbial loop at the surface of a  
398 peatland: structure, function, and impact of nutrient input. *Microbial ecology* 35, 83-93.

399 Hammer, Ø., Harper, D., Ryan, P., 2001. PAST-palaeontological statistics, ver. 1.89. *Palaeontologia*  
400 *electronica* 4.

401 Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis: an improved ordination  
402 technique, *Classification and ordination.* Springer, pp. 47-58.

403 Hisdal, V., 1985. *Geography of Svalbard.* Norwegian Polar Institutue, Oslo.

404 Hodkinson, I.D., Coulson, S.J., Webb, N.R., 2003. Community assembly along proglacial  
405 chronosequences in the high Arctic: vegetation and soil development in north-west Svalbard.  
406 *Journal of Ecology* 91, 651-663.

407 Ivanenko, N.Y., 2006. Bird observations in the vicinity of Barentsburg, Pyramid and Longyearbyen in  
408 Western Spitsbergen in summer 2005, in: Matishov, G.G., Tarasov, G.A. (Eds.), *Complex*  
409 *investigations of Spitsbergen nature.* . Kola Scientific Center Publications, pp. 305-321.

410 Ivanenko, N.Y., 2009. Breeding avifauna of the Grønfjord (Western Spitsbergen), in: Matishov, G.G.,  
411 Tarasov, G.A. (Eds.), *Problems of marine paleoecology and biogeography in the era of global*  
412 *changes. Complex studies of the nature of the Svalbard archipelago.* GEOS Moscow, pp. 272-  
413 283.

414 Jassey, V.E.J., Signarbieux, C., Hättenschwiler, S., Bragazza, L., Buttler, A., Delarue, F., Fournier, B.,  
415 Gilbert, D., Laggoun-Défarge, F., Lara, E., 2015. An unexpected role for mixotrophs in the  
416 response of peatland carbon cycling to climate warming. *Scientific reports* 5.

417 Lebedeva, N.V., Krivolutsky, D.A., 2003. Birds spread soil microarthropods to Arctic islands. *Doklady*  
418 *Biological Sciences* 391, 329-332.

419 Ligeza, S., Smal, H., 2003. Accumulation of nutrients in soils affected by perennial colonies of  
420 piscivorous birds with reference to biogeochemical cycles of elements. *Chemosphere* 52, 595-  
421 602.

422 Lüftenegger, G., Petz, W., Berger, H., Foissner, W., Adam, H., 1988. Morphologic and Biometric  
423 Characterization of Twenty-four Soil Testate Amoebae (Protozoa, Rhizopoda). *Archiv für*  
424 *Protistenkunde* 136, 153-189.

425 Mazei, Y., Chernyshov, V., Tsyganov, A.N., Payne, R.J., 2015. Testing the effect of refrigerated storage  
426 on testate amoeba samples. *Microbial ecology* 70, 861-864.

427 Mazei, Y., Tsyganov, A.N., 2006. *Freshwater testate amoebae*. KMK: Moscow.

428 Mazei, Y.A., Chernyshov, V., 2011. Testate amoebae communities in the southern tundra and forest-  
429 tundra of Western Siberia. *Biology Bulletin* 38, 789-796.

430 Mitchell, E.A.D., 2004. Response of testate amoebae (Protozoa) to N and P fertilization in an Arctic  
431 wet sedge tundra. *Arctic, Antarctic, and Alpine Research* 36, 78-83.

432 Mitchell, E.A.D., Lamentowicz, M., Payne, R.J., Mazei, Y., 2014. Effect of taxonomic resolution on  
433 ecological and palaeoecological inference—a test using testate amoeba water table depth  
434 transfer functions. *Quaternary Science Reviews* 91, 62-69.

435 Moe, B., Stempniewicz, L., Jakubas, D., Angelier, F., Chastel, O., Dinessen, F., Gabrielsen, G.W.,  
436 Hanssen, F., Karnovsky, N.J., Rønning, B., 2009. Climate change and phenological responses of  
437 two seabird species breeding in the high-Arctic. *Marine Ecology Progress Series* 393, 235-246.

438 Newton, I., Dale, L., 1996. Relationship between Migration and Latitude Among West European  
439 Birds. *Journal of Animal Ecology* 65, 137-146.

440 Ogden, C., Pitta, P., 1990. Biology and ultrastructure of the mycophagus, soil testate amoeba,  
441 *Phryganella acropodia* (Rhizopoda, Protozoa). *Biology and fertility of soils* 9, 101-109.

442 Ooms, M., Beyens, L., Temmerman, S., 2015. Testate amoebae as proxy for water level changes in a  
443 brackish tidal marsh. *Acta Protozoologica* 51, 271-289.

444 Osokin, N., Sosnovsky, A.V., 2008. Influence of climate on the thermal regime of permafrost on the  
445 Svalbard archipelago (in Russian), The nature of the shelves and archipelagoes of the European  
446 Arctic. *GEOS, Moscow*, pp. 280-284.

447 Owen, M., Black, J.M., 1989. Factors Affecting the Survival of Barnacle Geese on Migration from the  
448 Breeding Grounds. *Journal of Animal Ecology* 58, 603-617.

449 Payne, R.J., Jassey, V.E., Leith, I.D., Sheppard, L.J., Dise, N.B., Gilbert, D., 2013. Ammonia exposure  
450 promotes algal biomass in an ombrotrophic peatland. *Soil Biology and Biochemistry* 57, 936-  
451 938.

452 Payne, R.J., Lamentowicz, M., Mitchell, E.A.D., 2011. The perils of taxonomic inconsistency in  
453 quantitative palaeoecology: experiments with testate amoeba data. *Boreas* 40, 15-27.

454 Payne, R.J., Mitchell, E.A.D., 2009. How many is enough? Determining optimal count totals for  
455 ecological and palaeoecological studies of testate amoebae. *J Paleolimnol* 42, 483-495.

456 Payne, R.J., Thompson, A.M., Standen, V., Field, C.D., Caporn, S.J.M., 2012. Impact of simulated  
457 nitrogen pollution on heathland microfauna, mesofauna and plants. *European Journal of Soil*  
458 *Biology* 49, 73-79.

459 Sánchez-Piñero, F., Polis, G.A., 2000. Bottom-up dynamics of allochthonous input: direct and indirect  
460 effects of seabirds on islands. *Ecology* 81, 3117-3132.

461 Smith, H.G., 1996. Diversity of Antarctic terrestrial protozoa. *Biodiversity & Conservation* 5, 1379-  
462 1394.

463 Smith, V.R., 2003. Soil respiration and its determinants on a sub-Antarctic island. *Soil Biology and*  
464 *Biochemistry* 35, 77-91.

465 Smith, V.R., 2005. Moisture, carbon and inorganic nutrient controls of soil respiration at a sub-  
466 Antarctic island. *Soil Biology and Biochemistry* 37, 81-91.

467 Stempniewicz, L., Błachowiak-Samołyk, K., Węśławski, J.M., 2007. Impact of climate change on  
468 zooplankton communities, seabird populations and arctic terrestrial ecosystem—A scenario.  
469 *Deep Sea Research Part II: Topical Studies in Oceanography* 54, 2934-2945.

470 Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J., 2004. Impact of nitrogen deposition on the  
471 species richness of grasslands. *Science* 303, 1876-1879.

472 Vincke, S., Ledeganck, P., Beyens, L., Van De Vijver, B., 2004. Soil testate amoebae from sub-  
473 Antarctic Îles Crozet. *Antarctic Science* 16, 165-174.

474 Vincke, S., Van de Vijver, B., Ledeganck, P., Nijs, I., Beyens, L., 2007. Testacean communities in  
475 perturbed soils: the influence of the wandering albatross. *Polar Biology* 30, 395-406.

476 Wait, D.A., Aubrey, D.P., Anderson, W.B., 2005. Seabird guano influences on desert islands: soil  
477 chemistry and herbaceous species richness and productivity. *Journal of Arid Environments* 60,  
478 681-695.

479 Wassmann, P., Duarte, C.M., Agustí, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic  
480 marine ecosystem. *Global Change Biology* 17, 1235-1249.

481 Wilkinson, D., 2009. Have we underestimated the importance of humans in the biogeography of  
482 free-living microorganisms? *Journal of Biogeography* 37, 393-397.

483 Wilkinson, D.M., Koumoutsaris, S., Mitchell, E.A.D., Bey, I., 2012. Modelling the effect of size on the  
484 aerial dispersal of microorganisms. *Journal of Biogeography* 39, 89-97.

485 Wilkinson, D.M., Mitchell, E.A., 2010. Testate amoebae and nutrient cycling with particular reference  
486 to soils. *Geomicrobiology Journal* 27.

487 Wright, D.G., van der Wal, R., Wanless, S., Bardgett, R.D., 2010. The influence of seabird nutrient  
488 enrichment and grazing on the structure and function of island soil food webs. *Soil Biology and*  
489 *Biochemistry* 42, 592-600.

490 Ying-zhi, N., Yun-fen, S., 1996. Ecological studies on the forest soil protozoa of Mount Luojiashan and  
491 exploration of quantitative methods for soil protozoa. *Zoological Research* 17, 225-232.

492 Yool, A., Popova, E.E., Coward, A.C., 2015. Future change in ocean productivity: Is the Arctic the new  
493 Atlantic? *Journal of Geophysical Research: Oceans* 120, 7771-7790.

494 Zawierucha, K., Zmudczyńska-Skarbek, K., Kaczmarek, Ł., Wojczulanis-Jakubas, K., 2016. The  
495 influence of a seabird colony on abundance and species composition of water bears  
496 (Tardigrada) in Hornsund (Spitsbergen, Arctic). *Polar Biology* 39, 713-723.

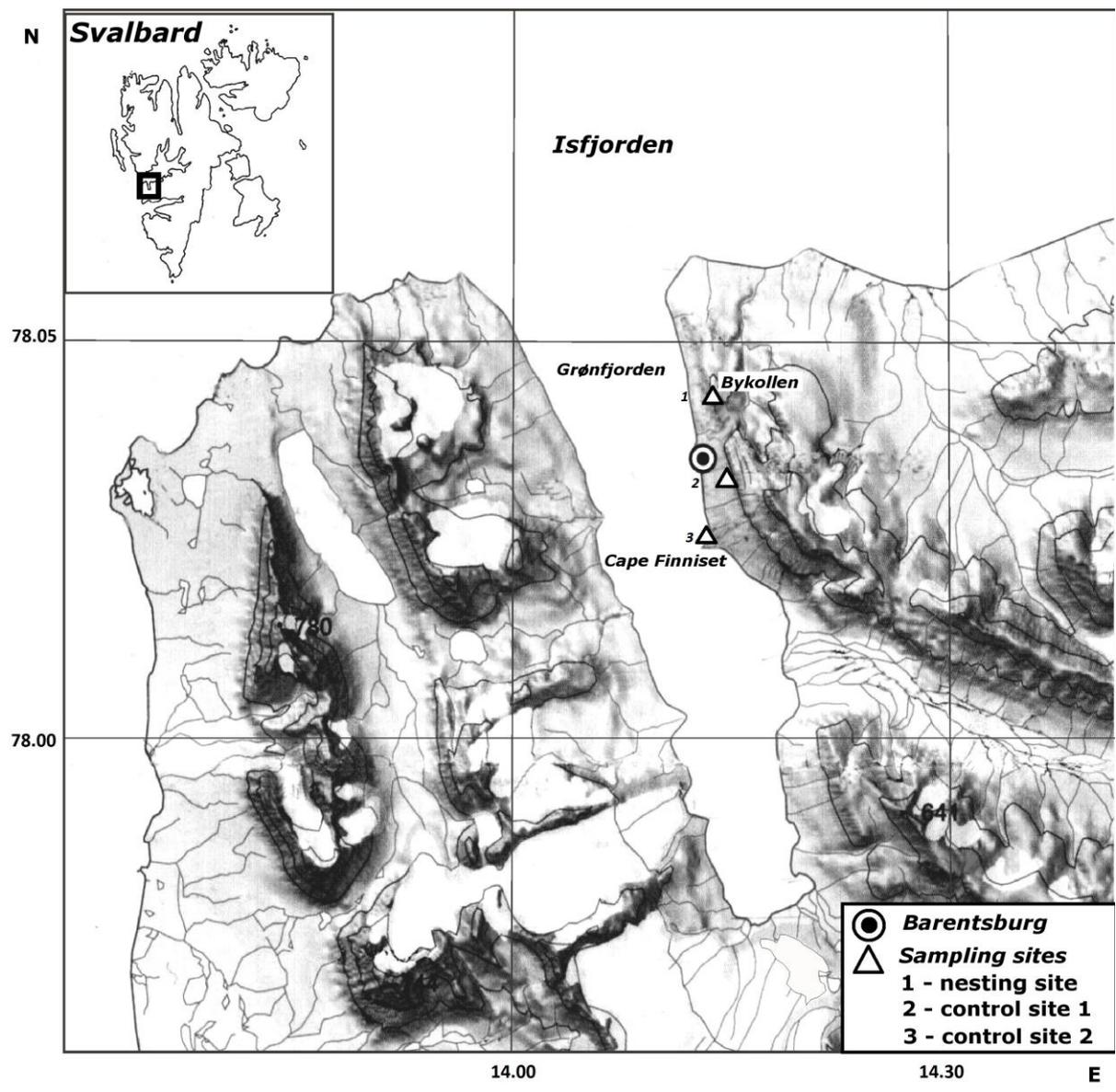
497 Zmudczyńska-Skarbek, K., Barcikowski, M., Drobnik, S.M., Gwiazdowicz, D.J., Richard, P., Skubała,  
498 P., Stempniewicz, L., 2017. Transfer of ornithogenic influence through different trophic levels of  
499 the Arctic terrestrial ecosystem of Bjørnøya (Bear Island), Svalbard. *Soil Biology and*  
500 *Biochemistry* 115, 475-489.

501 Zmudczyńska-Skarbek, K., Zwolicki, A., Convey, P., Barcikowski, M., Stempniewicz, L., 2015. Is  
502 ornithogenic fertilization important for collembolan communities in Arctic terrestrial  
503 ecosystems? *Polar Research* 34, 25629.

504 Zwolicki, A., Zmudczyńska-Skarbek, K.M., Iliszko, L., Stempniewicz, L., 2013. Guano deposition and  
505 nutrient enrichment in the vicinity of planktivorous and piscivorous seabird colonies in  
506 Spitsbergen. *Polar Biology* 36, 363-372.

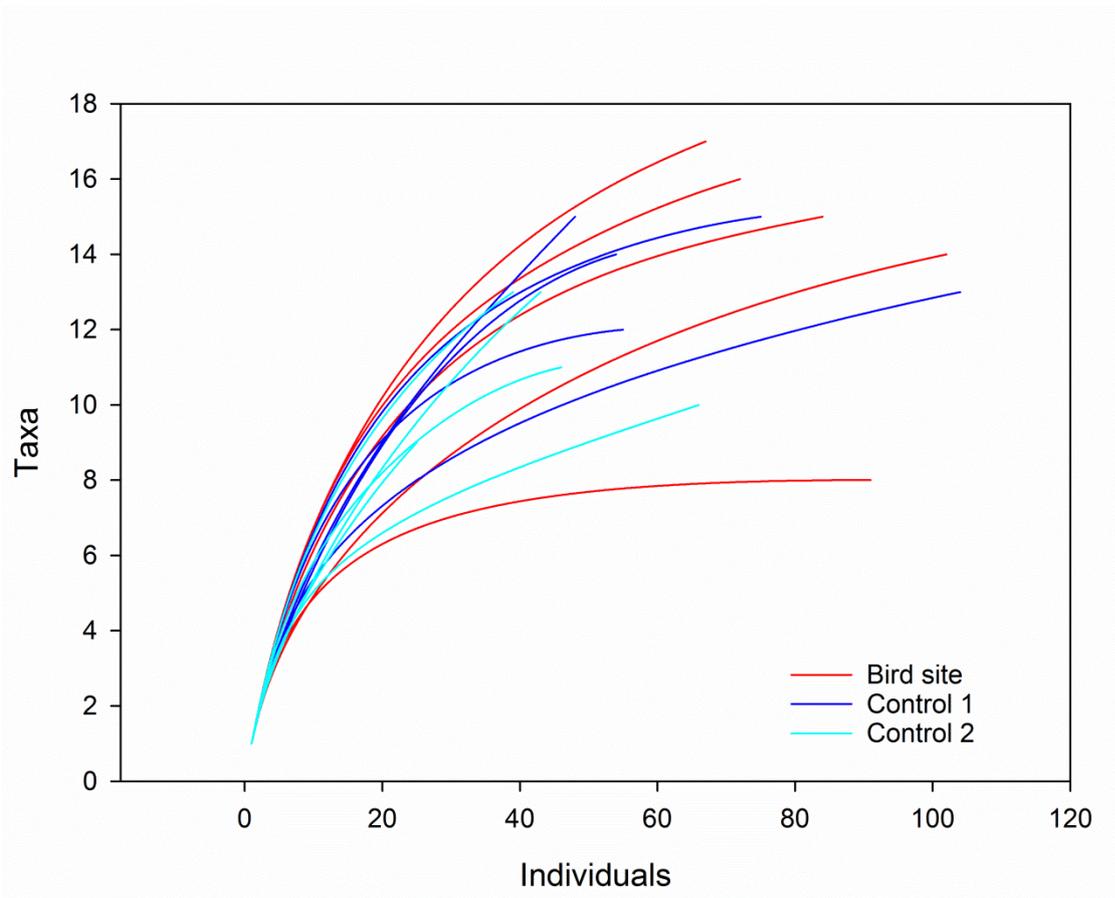
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508 **Figure 1.** Location of the three sampling sites and the settlement of Barentsburg.



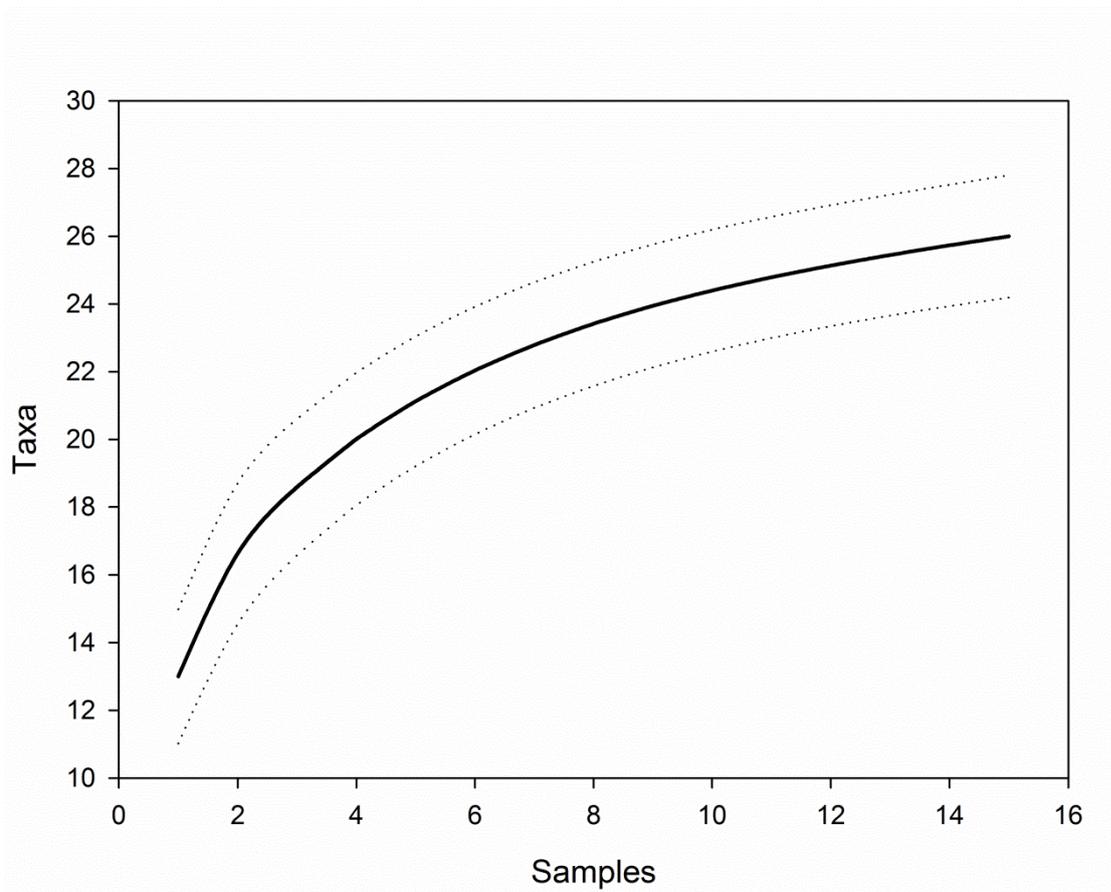
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510 **Figure 2.** Individual sample rarefaction curves of testate amoeba composition.



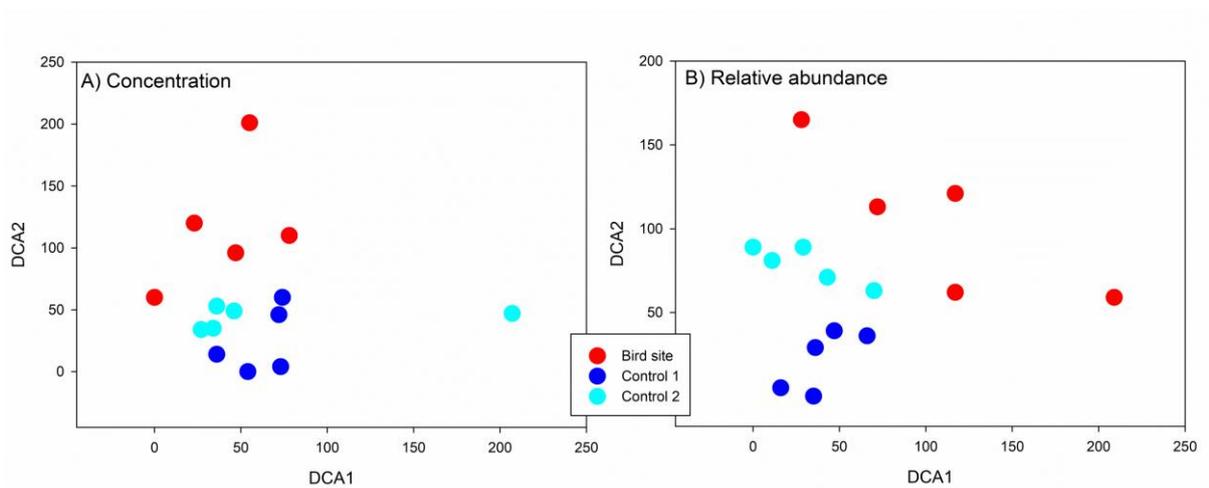
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512 **Figure 3.** Overall sample rarefaction curve for entire dataset based on Mao's Tau showing standard  
513 errors (dotted lines).



514

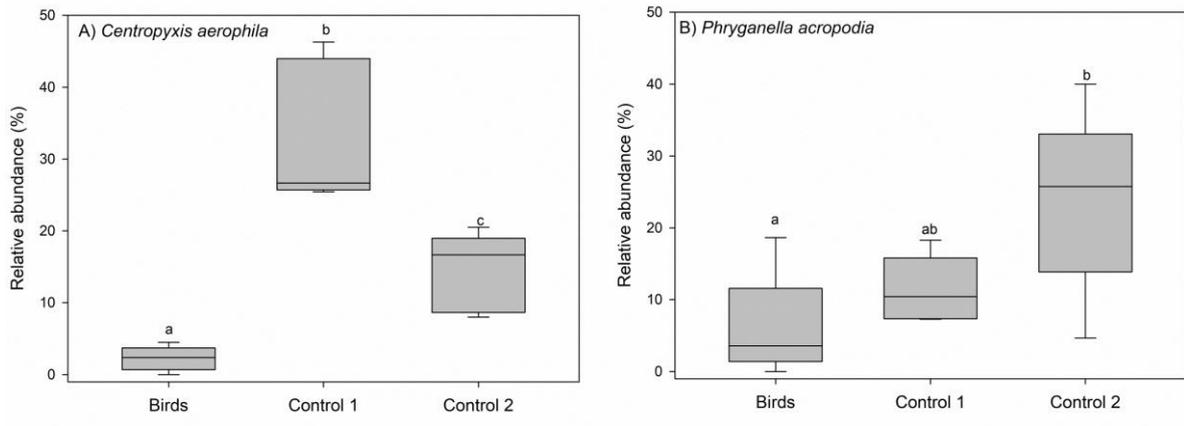
515 **Figure 4.** Detrended correspondence analysis ordination plots based on A) concentration and B)  
516 relative abundance of testate amoebae.



517

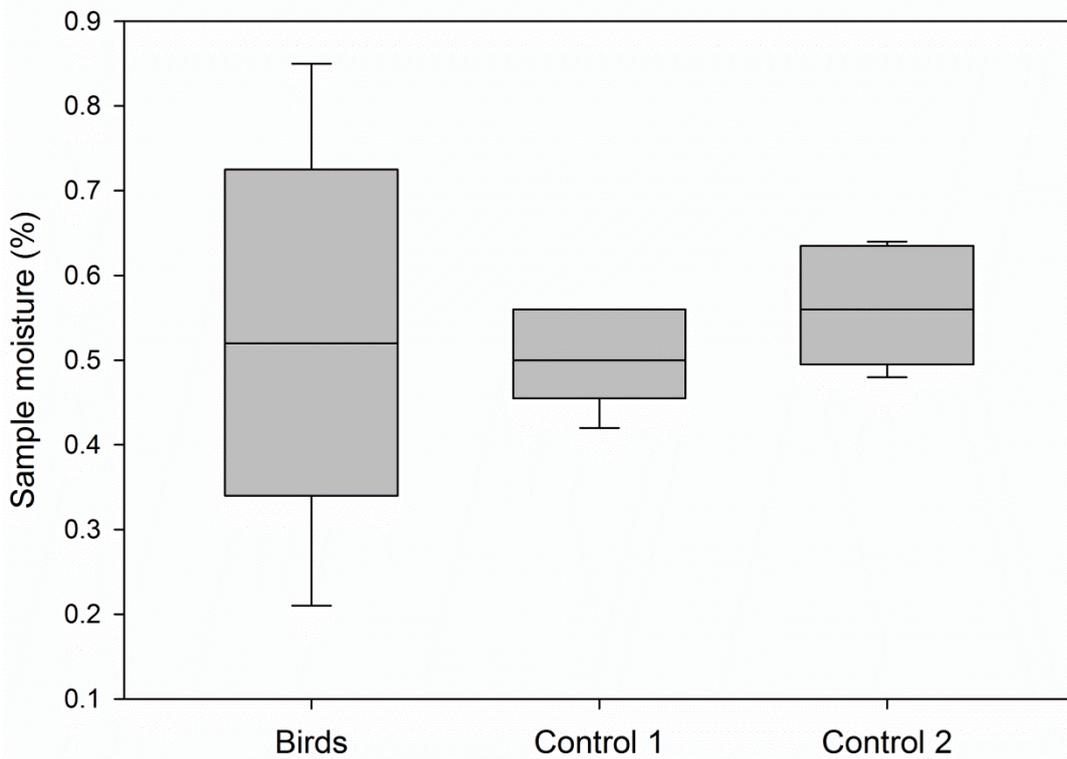
518 **Figure 5.** Relative abundance of *Centropyxis aerophila* (A) and *Phryganella acropodia* (B). Box-plots  
519 show median (central line), first and third quartiles (grey box) and tenth and ninetieth percentiles  
520 ('whiskers'). Bars marked with differing letters show significant difference in post-hoc testing, where

521 two letters are shown there is no significant difference from either other.



522

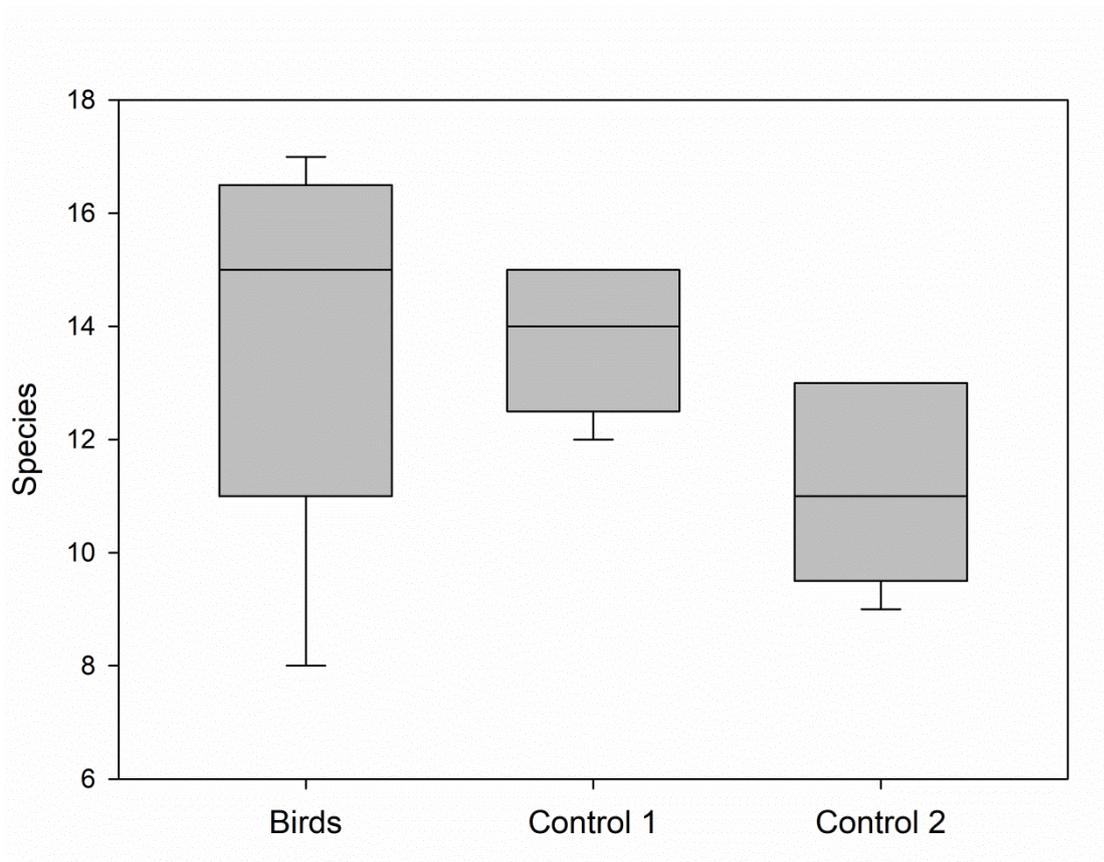
523 **Figure 6.** Sample moisture (proportion) in each of the sampling sites. Differences are non-significant  
524 ( $P>0.05$ ). Box-plots show median (central line), first and third quartiles (grey box) and tenth and  
525 ninetieth percentiles ('whiskers').



526

527 **Figure 7.** Morphospecies richness of testate amoebae in each of the sampling sites showing.  
528 Differences are non-significant ( $P>0.05$ ). Box-plots show median (central line), first and third

529    quartiles (grey box) and tenth and ninetieth percentiles ('whiskers').

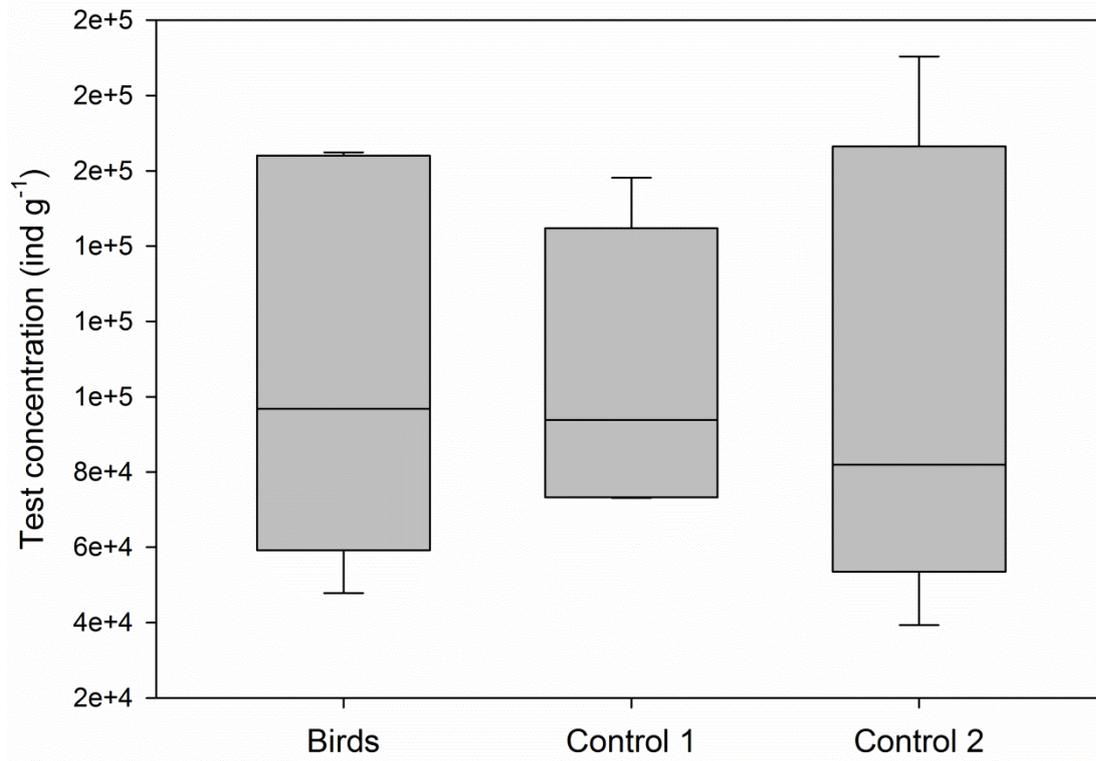


530

531    **Figure 8.** Test concentrations in each of the sampling sites. Differences are non-significant ( $P>0.05$ ).

532    Box-plots show median (central line), first and third quartiles (grey box) and tenth and ninetieth

533    percentiles ('whiskers').



534

535

536 **Table 1.** Relative abundance of all testate amoeba taxa in bird nesting site (n=5) and control sites  
537 (n=10). Figures rounded to one decimal place. Figures in bold show taxa with significant (P<0.05)  
538 difference between sites.

Taxon	Relative abundance (%)		
	Birds	Control 1	Control 2
<i>Arcella arenaria</i> var. <i>compressa</i> Chardez, 1974	1.2	1.2	2.3
<i>Assulina muscorum</i> Greeff, 1888	7.2	5.1	0.9
<i>Centropyxis aerophila</i> Deflandre, 1929	<b>2.2</b>	31.5	15.1
<i>Centropyxis cassis</i> (Wallich, 1864) Deflandre, 1929	0.0	0.0	0.5
<i>Centropyxis elongata</i> (Penard, 1890) Thomas, 1959	0.0	0.3	0.0
<i>Centropyxis platystoma</i> (Penard, 1890) Deflandre, 1929	0.2	0.6	0.9
<i>Centropyxis sylvatica</i> (Deflandre, 1929) Bonnet et Thomas, 1955	18.8	3.0	7.8
<i>Corythion dubium</i> Taránek, 1881	6.5	5.1	4.6
<i>Corythion orbicularis</i> (Penard, 1910) Iudina, 1996	9.6	4.8	3.2
<i>Cryptodiffugia oviformis</i> Penard, 1890	1.9	0.0	0.0
<i>Cyclopyxis eurystoma</i> Deflandre, 1929	0.7	0.0	0.0
<i>Euglypha laevis</i> (Ehrenberg, 1832) Perty, 1849	0.7	1.2	0.0
<i>Euglypha rotunda</i> Wailes, 1915	3.4	6.8	2.7
<i>Euglypha simplex</i> Decloitre, 1965	0.0	0.6	0.0
<i>Euglypha strigosa</i> var. <i>glabra</i> Wailes, 1898	3.1	3.0	3.7
<i>Euglypha tuberculata</i> Dujardin, 1841	1.7	0.3	1.8
<i>Nebela parvula</i> Cash, 1909	0.7	0.6	0.0
<i>Padaungiella lageniformis</i> (Penard, 1902) Lara et Todorov, 2012	0.2	0.0	0.0
<i>Phryganella acropodia</i> (Hertwig et Lesser, 1874) Hopkinson, 1909	<b>6.5</b>	12.5	22.8
<i>Phryganella hemisphaerica</i> Penard, 1902	1.4	0.0	0.0
<i>Plagiopixis callida</i> Penard, 1910	0.2	0.9	1.4
<i>Plagiopixis declivis</i> Thomas, 1958	1.2	0.6	0.0
<i>Tracheleuglypha dentata</i> Deflandre, 1928	0.2	0.0	0.9

<i>Trinema complanatum</i> Penard, 1890	4.3	3.3	1.4
<i>Trinema enchelys</i> (Ehrenberg, 1838) Leidy, 1878	8.7	4.8	2.7
<i>Trinema lineare</i> Penard, 1890	19.2	14.0	27.4

539