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Controls of climate, catchment erosion and biological production on long-term community and functional changes of chironomids in High Arctic lakes (Svalbard)

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1 **Controls of climate, catchment erosion and biological production on long-term**
2 **community and functional changes of chironomids in High Arctic lakes**
3 **(Svalbard)**

4

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26 **Abstract**

27

28 Arctic freshwater basins are diversity hotspots and sentinels of climate change, but their long-term
29 variability and the environmental variables controlling them are not well defined. We examined
30 four available lake sediment sequences from High Arctic Svalbard for their subfossil Chironomidae
31 communities, biodiversity and functional traits and assessed the influence of climatic and
32 limnological variability on the long-term ecological dynamics. Our results indicated that collector-
33 filterers had an important role in the oligotrophic sites, whereas collector-gatherers dominated the
34 nutrient-enriched sites with significant bird guano inputs. In the oligotrophic sites, benthic
35 production, taxon richness and taxonomic and functional diversity were highest during the early
36 Holocene, when temperatures showed a rapid increase. An increase in subfossil abundance and
37 diversity metrics was also found in recent samples of the oligotrophic sites, but not in the bird-
38 impacted sites, where the trends were decreasing. When partitioning out the environmental forcing
39 on chironomid communities, the influence of climate was significant in all the sites, whereas in-lake
40 production (organic matter) was significant in two of the sites and catchment erosion (magnetic
41 susceptibility) had only minor influence. The findings suggest that major changes in Arctic
42 chironomid assemblages were driven by climate warming with increasing diversity in oligotrophic
43 sites, but deteriorating ecological functions in environmentally stressed sites. We found that
44 although taxonomic and functional diversity were always coupled, taxonomical and functional
45 turnovers were coupled only in the oligotrophic sites suggesting that the ecological functions
46 operated by chironomids in these low-productivity sites may not be as resilient to future
47 environmental change.

48

49 *Keywords:* Biodiversity; Chironomids; Climate change; Functional traits; Paleoecology; Polar lakes

50

51 **1 Introduction**

52

53 A significant portion of inland biodiversity in the Arctic is found in freshwater lakes (Rautio et al.,
54 2011). However, ongoing climate warming, which has amplified impacts in the Arctic (Serreze and
55 Barry, 2011; Linderholm et al., 2018) is altering the balance of aquatic communities by rates
56 already exceeding natural variability (Smol and Douglas, 2007). Although it is well-documented
57 that aquatic communities have been increasingly changing in the Arctic (Wrona et al., 2016), less is
58 known about the variability between different types of freshwater systems or limnoecological
59 functioning, especially at long temporal scales. In addition, understanding long-term climate
60 impacts on Arctic lake ecosystems requires separating the effects of climate from within-lake and
61 catchment changes over a long time span (Paull et al., 2017). The paleolimnological approach to
62 studying long-term limnoecological changes provides powerful means of examining ecological
63 shifts and the environmental history of lakes, giving insights into past and present dynamics, but
64 also offering an opportunity to forecast future changes in aquatic environments (Smol, 2010; Pla-
65 Rabes et al., 2011). However, only few quantitative palaeolimnological studies have addressed
66 biodiversity questions, defining the drivers of change in species richness or identifying functional
67 traits that best capture ecosystem processes (Gregory-Eaves and Beisner, 2011; Nevalainen et al.,
68 2018).

69 Paleoecological research has traditionally focused on using communities as the main
70 unit, since many aquatic organism groups that are well preserved as subfossils, such as diatom
71 algae, Cladocera zooplankton and Chironomidae macrobenthos, respond sensitively to
72 environmental perturbation through community changes (Frey, 1988). Although the potential of
73 using functional traits to characterize long-term aquatic ecosystem changes has been known
74 (Jeppesen et al., 2001) it has gained more interest only recently (Fournier et al., 2015; Nevalainen et
75 al., 2015a, b; Nevalainen and Luoto, 2017). Since ecosystem functions rely more on the living

76 habits of organisms than taxonomic categories, the use of functional traits may enable the
77 assessment of ecosystem functioning and stability more comprehensively than traditional taxonomic
78 identification (Cadotte et al., 2011). Benthic invertebrates, including chironomids, have vital
79 functions in lakes operating crucial biogeochemical cycles behind food-web structure by taking part
80 in processes related to detrital decomposition, nutrient release and transfer, prey control and food
81 supply (Palmer, 1997; Covich et al., 1999), for example. While being invaluable for lake functions,
82 benthic insect larvae can be the most threatened organisms in lakes (Strayer and Dudgeon, 2013).

83 For chironomids, the most useful functional traits for ecological studies are related to
84 their feeding habits (Pinder, 1986; Schmera et al., 2017). Although chironomids tend to vary in their
85 modes of feeding depending on their life cycle stage (Grey et al., 2004), their primary feeding
86 preferences can be divided into eight guilds: collector-filterers, collector-gatherers, predators,
87 scrapers, shredders, parasites, omnivores and piercers (Merritt and Cummins, 1996). Collector-
88 gatherers (deposit-feeders) are the most common feeding guild that depends on fine particulate
89 organic matter of sediments. Another common guild, collector-filterers, which often live in tubes,
90 are suspension feeders filtering food particles from the water column, epiphytic algae being the
91 most common food item (Berg et al., 1995). Among the less dominant guilds, scrapers shear food
92 material from the sediment and submerged rocks, vegetation and wood, whereas shredders feed on
93 coarse particulate organic matter, such as living vascular plants, submerged wood, macro- or
94 colonial algae, or leaf litter (Berg, 1995). Predators on the other hand attack other invertebrates and
95 ingest all part of the prey (engulfers) or pierce the tissues and withdraw the fluids of the prey
96 (piercers) (Cummins, 1973). In paleolimnology, the thus far rarely used chironomid functional
97 feeding characteristics or their paleo-diets estimated through stable isotopic compositions from head
98 capsules (van Hardenbroek et al., 2014; Belle et al., 2017; Schilder et al. 2017) can be used to
99 provide valuable information on past food web structures, biogeochemical cycling or environmental
100 controls.

101 Previous studies (Brooks and Birks, 2004; Nevalainen et al. 2012) have revealed
102 significant ecological changes in High Arctic lakes in Svalbard, which is located in an intersection
103 of major oceanic currents and is a focal point for the development of the Polar Front (Majewski et
104 al., 2009). Hence, Svalbard represents a climatically and oceanographically sensitive region
105 (Isaksen et al., 2007). Building from previous studies with available chironomid taxonomic
106 biostratigraphies, in this study, we analyze chironomid functional traits (feeding guilds) and
107 compare the findings against independent air temperature reconstructions, sediment organic matter
108 content and magnetic susceptibility measurements. Our analysis has the potential to provide new
109 knowledge on the influence of climate and limnology on High Arctic ecosystem changes at long
110 temporal scales (decades to millennia). More particularly, we test chironomid paleobiodiversity
111 changes in relation to natural variability caused by sudden short-term catchment originated “pulse
112 events” and in relation to long-term climatic “press events” (Massaferro and Corley, 1998).
113 Furthermore, in wetland ecosystems species turnover across environmental gradients is restricted to
114 functionally similar species, i.e. taxonomic and functional turnover are decoupled, which may allow
115 maintaining ecosystem functioning when subject to future environmental change (Robroek et al.,
116 2017). Here, we test this general theory in four High Arctic aquatic ecosystems with different
117 environmental characteristics including typical low-nutrient tundra sites and nutrient-enriched bird-
118 impacted sites with densely vegetated catchments.

119

120 **2 Material and Methods**

121 *2.1 Study sites*

122

123 The four study sites are located in southern (Hornsund fjord area, mean July air temperature 4.2 °C)
124 and northeastern (Nordaustlandet, mean July air temperature 2 °C) Svalbard (Fig. 1). Svartvatnet
125 (76°90'N, 15°68'E; 63 m a.s.l.) is an oligotrophic 80 ha lake located at the southern side of the

126 Hornsund fjord, whereas Fugledammen (77°00'N, 15°52'E; 15 m a.s.l.), located at the northern side
127 of the fjord, is a shallow (2 m) nutrient-rich pond (2 ha). Einstaken (79°58'N; 18°42'E, 54 m a.s.l.)
128 is situated in the Murchisonfjorden area at the southern side of the Isvika bay in Nordaustlandet.
129 The 5 ha lake is currently oligotrophic and has a depth of 8 m. The fourth study site, Kvalroslaguna
130 (79°58'N, 18°34'E; 12 m a.s.l.), is a shallow (1 m) nutrient-rich pond (0.5 ha), located at the
131 northern side of the Isvika bay. Einstaken and Svartvatnet are pristine periglacial basins, whereas
132 Fugledammen and Kvalroslaguna have significant grazing and nesting bird-influence in their
133 catchments. At both sites, birds are present in high numbers and produce a large amount of guano,
134 which is high in nutrients, resulting in thick moss growth in the catchment and giving a murky
135 eutrophic appearance to the ponds. Detailed description of catchment and limnological
136 characteristics can be found from previous publications (Luoto et al., 2011, 2014, 2015, 2016,
137 2018).

138

139 *2.2 Sediments and subfossil analyses*

140

141 Samples consist of two long sediment cores (sampled with a Livingstone piston corer) from
142 Einstaken (134 cm, past ~13,000 years) and Svartvatnet (164 cm, past ~5500 years) and two short
143 cores (sampled with a Russian peat corer) from Fugledammen (100 cm, past ~150 years) and
144 Kvalroslaguna (28 cm, past ~400 years). The cores from Einstaken and Kvalroslaguna were
145 collected during the 2009 field campaign in Nordaustlandet (Kinnvika project) and the Svartvatnet
146 and Fugledammen cores during the 2013 field campaign in Hornsund (QUAL project). The
147 chronologies of the sediment profiles have been previously published (AMS ¹⁴C, paleomagnetic,
148 ¹³⁷Cs and ²¹⁰Pb dating), alongside analyses of organic matter content (measured as loss on ignition,
149 LOI), measurements of magnetic susceptibility and the original chironomid stratigraphies for
150 Einstaken (Luoto et al., 2011), Svartvatnet (Luoto et al., 2018), Fugledammen (Luoto et al., 2015)

151 and Kvalroslaguna (Luoto et al., 2014). The Svartvatnet chronology was originally published in
152 Ojala et al. (2016). Subfossil chironomid analyses were performed from 1 cm³ subsamples using
153 standard methods using the same taxonomy between the cores (Brooks et al., 2007). For this study,
154 the chironomid subfossils handpicked from a Bogorov counting tray were further analyzed for their
155 feeding habits characterizing functional attributes (Schmera et al., 2017). The feeding guilds were
156 based on classifications by Merritt and Cummins (1996) and Mandaville (2002). Chironomid
157 abundance, measured as head capsules per 1 g dry sediment weight, was used as a measure for
158 benthic production (Itkonen et al., 1999; Fortin and Gajewski, 2010).

159

160 *2.3 Numerical analyses*

161

162 Taxonomic diversity (mostly species type level) was assessed using number of taxa (taxon richness,
163 S) and Shannon index (H') (Shannon, 1948) based on a consistent number of examined specimens
164 (50-60) per sample. Functional diversity (FD) was based on the Shannon index of the relative
165 abundances of feeding guilds (Schleuter et al., 2010). Detrended correspondence analysis (DCA)
166 was used to indicate beta diversity (turnover) of chironomid taxa assemblages (Correa-Metrio et al.,
167 2014). The DCAs were run using square-root transformed species data with rare species
168 downweighted. Redundancy analysis (RDA) was used to partial out the contribution of forward
169 selected environmental variables (air temperature, organic matter, magnetic susceptibility) on
170 chironomid taxa assemblages in the four study sites. The RDAs were run with square-root
171 transformed species data, downweighing of rare species and 999 permutations. Air temperature was
172 considered as a proxy for climate influence, organic matter for lake productivity (Meyers and
173 Teranes, 2001) and magnetic susceptibility for physical changes related to catchment erosion and
174 sediment delivery into the basins (Dearing, 1999). The statistical analyses were carried out using the
175 program Canoco 5 (Šmilauer and Lepš, 2014).

176 The temperature timeseries for the long profiles was the diatom-inferred (weighted
177 averaging-partial least squares technique) North Atlantic August temperature variability (Icelandic
178 core MD99-2269, Sundqvist et al., 2014) and for the short profiles the 2000-year synoptic Arctic air
179 temperature variability (PAGES Arctic 2k, McKay and Kaufman, 2014). The prediction error of the
180 North Atlantic temperature reconstruction is ± 0.9 °C (95% confidence level), whereas the Arctic
181 temperature variability (no prediction error estimate available) is averaged from a standardized
182 database of several proxy temperature records including tree ring, marine and lake sediment, glacier
183 ice, historical and speleothem data archives. The temperature records were fitted to the chronologies
184 (samples) of this study to match the time resolution using record mean surface air temperature
185 anomalies. However, it should be noted that due to local features in climate variability and inherent
186 uncertainties in chronological matching, the temperature records should be considered tentative.

187

188 **3 Results**

189

190 Collector-filterers dominated the chironomid compositions in Einstaken (Fig. 2), *Micropsectra*
191 *radialis*-type being the most abundant between ~13,000 and 2000 cal yr BP and *Micropsectra*
192 *insignilobus*-type during the past ~2000 years. Also *Paratanytarus austriacus*-type was common
193 throughout the sequence. Collector-gatherers, such as *Oliveridia* and *Orthocladius* (*P.*)
194 *consobrinus*-type, were common from 13,000 to 7000 cal yr BP and during the last ~2000 years.
195 Also predators, including *Procladius* and *Thienemannimyia*-type, occurred in the record between
196 ~12,000 and 2000 cal yr BP.

197 In Svartvatnet (Fig. 3), collector-filterers, such as *M. radialis*-type and *Micropsectra*
198 *contracta*-type dominated from the beginning of the record at ~5500 cal yr BP until 1000 cal yr BP.
199 In the most recent sediment layer, yet another *Micropsectra* species, *M. junci*-type, became
200 abundant. Collector-gatherers, mostly *Orthocladius trigonolabis*-type, *Hydrobaenus lugubris*-type

201 and *Oliveridia*, had an increasing trend in their relative proportion from ~5500 cal yr BP reaching
202 maximum abundances between ~3000 and 500 cal yr BP. Predators (*Procladius*) occurred in the
203 record between ~5500 and 3500 cal yr BP and shredders (*Cricotopus cylidraceus*-type) occasionally
204 from 2000 cal yr BP onwards.

205 The chironomid compositions in Fugledammen (Fig. 4) were almost monotonously
206 dominated by collector-gatherers, with *Psectrocladius sordidellus*-type being the most abundant
207 between ~1840 and 1870 AD and *O. consobrinus*-type from ~1880 AD until the present, when it
208 reached total dominance. The only non-collector-gatherer in the record was the shredder *Cricotopus*
209 (*I. intersectus*-type) that occurred in the two lowermost samples between ~1840 and 1850 AD.

210 Collector-gatherers were also the dominant feeding guild throughout the record in
211 Kvalroslaguna (Fig. 5) with *P. sordidellus*-type and *Metriocnemus eurynotus*-type as the most
212 abundant taxa. *Hydrobaenus conformis*-type was abundant in the initial part of the record between
213 ~1620 and 1660 AD, whereas *Chironomus anthracinus*-type increased from ~1880 AD onwards.
214 Predators (mostly *Procladius*) appeared in the record at ~1700 AD and shredders at ~1880 AD
215 (*Cricotopus*), although with low abundances.

216 Excluding the first 1000 years, organic matter, subfossil abundance (benthic
217 production), taxon richness, Shannon index and functional diversity were generally higher in the
218 initial part of the Einstaken record (Fig. 6) and lower in the latter part from ~7000 cal yr BP
219 onwards. However, a slight general increase in benthic production, DCA axis 1 scores and diversity
220 parameters, concurrent with increases in magnetic susceptibility, was apparent during the past
221 ~2000 years. In Svartvatnet (Fig. 7), magnetic susceptibility and organic matter showed no notable
222 trends, except in the most recent centuries when magnetic susceptibility reached the lowest and
223 organic matter highest values in the record. Subfossil abundance and the diversity parameters had
224 higher values in the later part of the record (past ~2000 years), contrasting the DCA axis 1 scores,
225 however with lower values around 500 cal yr BP. The organic matter content showed a progressive

226 increase throughout the record in Fugledammen (Fig. 8). In contrast, magnetic susceptibility,
227 subfossil abundance and diversity parameters showed a progressively decreasing trend towards the
228 present that was also apparent in the DCA axis 1 scores. The patterns in Kvalroslaguna (Fig. 9)
229 were similar to Fugledammen, however, the patterns in taxon richness and functional diversity
230 remained less clear.

231 Taxonomic diversity correlated significantly with functional diversity in all the study
232 sites (Fig. 10) with the combined data having an R^2 of 0.32 ($P < 0.001$). The oligotrophic sites
233 (Einstaken and Svartvatnet) had a stronger correlation ($R^2 = 0.54$, $P < 0.001$) than the bird-impacted
234 sites (Fugledammen and Kvalroslaguna), which nonetheless also had significant relationship ($R^2 =$
235 0.20 , $P < 0.001$).

236 In the DCAs, the variance explained by the first and second axes in Einstaken were
237 29.4% and 16.6%, in Svartvatnet 31.5% and 21.3%, in Fugledammen 36.4% and 23.3% and in
238 Kvalroslaguna 28.3% and 17.7%, respectively. The DCA axis 1 and 2 scores are shown in Figs 6-9.
239 Due to intermediate gradient lengths in the initial DCAs (2.4-2.6 SD), RDA was selected to partial
240 out variance of forward selected environmental variables on chironomids. Temperature, organic
241 matter and magnetic susceptibility explained 30.8% of all variance in Einstaken, 10.1% in
242 Svartvatnet, 31.8% in Fugledammen and 27.4% in Kvalroslaguna. Temperature was a significant
243 explanatory factor ($P \leq 0.05$) on chironomid community dynamics in all the study lakes, whereas
244 organic matter had significant influence in Einstaken and Kvalroslaguna and magnetic susceptibility
245 only in Einstaken (Table 1). In all, although the examined variables explained a relatively small
246 portion of the total variance, the RDA results generally suggest that the influence of climate and
247 biological production on chironomids has been significant in the study lakes, whereas the influence
248 of catchment erosion has been less important.

249

250 **4 Discussion**

251 *4.1 Functional ecology*

252

253 The transparent oligotrophic study sites Einstaken (Fig. 2) and Svartvatnet (Fig. 3) with no
254 significant catchment vegetation were dominated by collector-filterers. On contrast, collector-
255 filterers were completely absent in the nutrient-rich bird-impacted sites Fugledammen (Fig. 4) and
256 Kvalroslaguna (Fig. 5), which were dominated by collector-gatherers. Arctic birds that feed in the
257 Ocean and nest on lake catchments transport nutrients (P, N) from the marine to the terrestrial realm
258 (Keatley et al., 2009). These nutrients stored in bird guano are delivered directly or by surface
259 runoff to coastal lakes and ponds (Keatley et al., 2009). Potentially, bird-driven nutrient enrichment
260 of Arctic lakes will alter the limnoecological functions, which are reflected through, for example,
261 chironomid feeding habits. According to multiproxy results, the oxygen conditions in Fugledammen
262 deteriorated at the end of the 19th century (Luoto et al., 2015) causing for example a decrease in
263 chironomid diversity. In Kvalroslaguna, the bird-induced increase in nutrients appears to have
264 begun already during the 18th century based on the oxygen preferences of chironomids (Luoto et al.,
265 2014). Comparison of the study sites show that the relative significance of collector-gatherers fully
266 corresponds with the level of bird-impact. This is most likely related to the benthic requirements of
267 collector-filterers (Liu and Wang, 2008) that cannot succeed in the murky low-oxygen bird-
268 impacted sites. This is not a phenomenon related only to the Arctic, since collector-gathers
269 (detritivores) appear to dominate eutrophic sites also in boreal areas, while collector-filterers are
270 absent or rare at these sites (Luoto and Ojala, 2014).

271 If organic inputs to the sediment are not in balance with the decomposition capacity,
272 the functioning and biodiversity of lake ecosystems will be radically altered resulting in degradation
273 of water quality (Palmer et al., 1997). In general, the current results are logical in the sense that
274 collector-gatherers prefer high organic matter contents and shallow nutrient-rich waters, whereas
275 collector-filterers favor lower organic matter content and oligotrophic waters with intermediate

276 depth suggesting control of benthic and pelagic production, respectively. Hence, the present results
277 appear to confirm our previous findings where the presence of the collector-feeding lifestyle of
278 chironomids characterized a functionally diverse community and a healthy pre-disturbance aquatic
279 ecosystem state (Luoto and Ojala, 2014).

280 Although benthic functions are related to inlake factors that regulate habitat
281 characteristics and food availability (Vadeboncoeur et al., 2002), they are also related to external
282 processes, such as climate. It has been shown from Finnish lakes that at both spatial and long-term
283 temporal scales the relative importance of chironomid feeding guilds fluctuates alongside climate
284 characteristics (Luoto and Nevalainen, 2015). Under cold climate conditions and during cold
285 climate events of the Holocene, such as the early Holocene and the Little Ice Age, collector-filterers
286 tend to dominate, whereas under warm and intermediate climate conditions and similar climate
287 episodes of the past, collector-gatherers, shredders, scrapers and predators have more important
288 roles (Luoto and Nevalainen, 2015). In the current results, similar climate-driven temporal patterns
289 are not clear. Only in Einstaken which is the most oligotrophic site, collector-gatherers increase at
290 the expense of collector-filterers during the recent climate warming (Fig. 2). Whereas the temporal
291 changes in the bird-impacted sites have remained minute (Figs 4, 5), possibly partly related to
292 shorter chronological time span, a distinct shift has occurred in Svartvatnet, where collector-
293 gatherers gradually increased (Fig. 3). Instead of a response to climate, it is more likely that this is
294 related to catchment originated increase in nutrient inputs, which is demonstrated by the decreasing
295 magnetic susceptibility values (Fig. 7) suggesting physical catchment control (Royall, 2001).

296

297 *4.2 Biodiversity*

298

299 Changes in taxon richness and taxonomic and functional diversity appear site-specific in the studied
300 lakes. In the longest record, Einstaken, diversity peaks during the early Holocene following the

301 thermal maximum at ~10,000 cal yr BP (Fig. 6), a diversity trend also found in records from
302 continental Northern Europe (Shala et al., 2014). Similarly, concurrent with the present climate
303 warming, the diversity indices showed increases in the most recent sediment layers suggesting that
304 chironomid assemblages and functional behavior are most diverse during warmer climate
305 conditions (Levesque et al., 1996; Burgmer et al., 2007). In addition, the accumulation of
306 chironomid subfossil head capsules, indicating benthic production (Itkonen et al., 1999; Fortin and
307 Gajewski, 2010), has been high during the early Holocene and the most recent period. The
308 Svartvatnet record is less clear, but showed a similar increase in benthic production and taxonomic
309 richness and diversity during the most recent times. The results thus confirm previous evidence that
310 favorable climate conditions support habitat availability and diversity to a certain extent (Schindler
311 and Smol, 2006).

312 Benthic production, taxon richness and taxonomic and functional diversity decreased
313 in Fugledammen alongside climate warming since the Little Ice Age (Fig. 8) in contrast with the
314 oligotrophic sites. Although not as clear as in Fugledammen, taxon richness and diversity also
315 decreased in Kvalroslaguna. In all the records, although not synchronous, organic matter content
316 tended to follow air temperature dynamics, as biological production is known to be temperature
317 dependent (Meyers and Lallier-Verges, 1999). The diversity changes more or less tracked the
318 changes in organic matter in the study sites, so that in the oligotrophic sites organic matter and
319 diversity had positive relationship, and in the bird-impacted sites the relationship was negative. This
320 fits well with the general observations on invertebrate biodiversity patterns in freshwaters that
321 diversity increases along biological production until a limnological threshold, after which diversity
322 begins to decrease (Nyman et al., 2005; Luoto, 2011; Jensen et al., 2013). Variability in magnetic
323 susceptibility also reflects climate oscillations to some extent. The majority of magnetic minerals
324 found in these sediments are magnetite of different grain sizes that are delivered into lakes by
325 catchment erosion and originate from bedrock, subsoil, and topsoil in the lake's drainage. This

326 process is enhanced by climatic factors including temperature and precipitation (Sandgren and
327 Snowball, 2002). The changes in magnetic susceptibility are not easily connected with changes in
328 chironomid taxonomic or functional diversity in the oligotrophic sites, but in the impacted sites
329 there were increases in the diversity indices with decreasing magnetic susceptibility towards the
330 present day.

331 Reductions in chironomid paleobiodiversity have been shown to be related to natural
332 variability caused by sudden short-term catchment “pulse events” in water turbidity and long-term
333 climatic “press events” (Massaferro and Corley, 1998). During pulse disturbances (e.g. hydrological
334 events), diversity has a tendency to fall, but recover rapidly after the environmental stress is
335 released, whereas during press events (e.g. climatic shifts) diversity remains more constant. In the
336 present records, pulse events reflected by magnetic susceptibility do not appear to have distinct
337 influence on the taxonomic or functional diversity of chironomids (Figs 6-9). The reason for the low
338 influence of pulse disturbances may be that the periglacial catchments have simple characteristics
339 and the lakes are not subjected to direct human impacts or other major pulse event factors, such as
340 volcanic ash deposition (Massaferro and Corley, 1998). However, the climatic press impact on
341 chironomid diversity is clearer as the diversity indices have similar features with climate
342 oscillations.

343 In the examined temporal records, taxonomic and functional diversity correlate
344 significantly (Fig. 10). In agreement with the present results, long-term taxonomic and functional
345 diversity of aquatic invertebrate communities in the European Alps are closely linked, especially in
346 the case of chironomids (Nevalainen et al., 2015b). The positive relationship between taxon
347 diversity and functional diversity in macroinvertebrates has also been evidenced in contemporary
348 surveys (Feld et al., 2014). Nonetheless, it has also been recently shown that taxonomic and
349 functional turnovers of plants are decoupled in European peat bog ecosystems (Robroek et al.,
350 2017), which partly agrees with our findings from High Arctic lakes. In the oligotrophic sites, the

351 taxonomic and functional changes were concurrent (Figs 2, 3) but clearly differing in the bird-
352 impacted sites (Figs 4, 5). In case of peatland plant communities, when species turnover across
353 environmental gradients is restricted to functionally similar species and taxonomic and functional
354 turnovers are decoupled, it allows maintaining ecosystem functioning under environmental change
355 (Robroek et al., 2017). Hence, when turning this general ecological theory around, our results
356 would indicate that when losing chironomid biodiversity, the oligotrophic sites where the
357 taxonomical and functional turnovers are coupled are at greater risk under the ongoing climate
358 change and its future impacts. When benthic functions are reduced, it affects the entire lake
359 ecosystem negatively through simplified food web and inefficient biogeochemical cycling, for
360 example (Jeppesen et al., 2001). This is well illustrated by the bird-impacted sites, where nutrients
361 are recycled from the sediments also due to reduced benthic functions causing internal nutrient
362 enrichment, oxygen depletion in the bottom water, and ecological deterioration (Luoto et al., 2014,
363 2015).

364 While using paleoecological data in biodiversity assessments has its benefits (Ilyashuk
365 et al., 2015), the varying level of taxonomic identification of subfossil chironomids should be taken
366 into critical consideration. Although most taxa in the current records were identified to species-type
367 level, there were several taxa that could only be identified at genus level (Figs 2-5). Therefore,
368 owing to the potential of a genus consisting of more than one species, the biodiversity information
369 may be partly biased, this problem becoming especially important when compared with
370 contemporary datasets using species data. Consequently, the use of functional characterization
371 instead of taxonomic identification may be a more recommendable approach when using subfossil
372 chironomids as a biodiversity measure. This is because the general chironomid feeding preferences
373 do not show notable variability within any genus, with the exception of *Cricotopus*, which includes
374 collector-gatherers, shredders and scrapers (Merritt and Cummins, 1996; Mandaville, 2002).

375 Nonetheless, it should also be noted that most chironomids are omnivorous at some extent and not
376 fully restricted to a single feeding guild.

377

378 *4.3 Environmental controls on communities*

379

380 The most important environmental factor controlling chironomid species distribution at the regional
381 scale is air temperature (Heiri et al., 2011; Engels et al., 2014). The effects of climate are also
382 reflected in chironomids via the influence of water temperature, which usually correlate with air
383 temperature (Eggermont and Heiri, 2012). Therefore, the effects of climate are mediated by habitat
384 differences, as well as the physiological effects of water temperature. In our study, despite that the
385 portion of explained variance was relative low, the chironomid assemblage dynamics had
386 significant relationship with temperature in all four sites (Table 1), climate explaining the most
387 significant part of the examined environmental factors in Svartvatnet and Fugledammen. However,
388 detailed comparison with the temperature records probably suffers from chronological biases
389 (chronological matching errors between independent timeseries) compared to the other examined
390 factors (organic matter and magnetic susceptibility), which were analyzed from the sediment
391 profiles and even the same subsamples. Therefore, the correlation between temperature and
392 chironomid communities would most likely be stronger without these chronological issues. In fact,
393 the original study from Svartvatnet (Luoto et al., 2018) showed close correlation between the
394 chironomid dynamics and a temperature reconstruction using a Norwegian (including lakes from
395 Svalbard) chironomid-temperature dataset (Velle et al., 2011). In addition, the chironomid-inferred
396 temperatures were synchronous with an oxygen isotope-based temperature reconstruction from
397 Svartvatnet (Arppe et al., 2017), providing well-built evidence for the close link between
398 chironomids and climate at the study site. The reason why the temperature reconstruction based on
399 the oxygen isotope record was not used in this study was that it was derived from the isotope

400 composition from chironomid head capsules, hence while being independent records, a fully
401 external record (Sundqvist et al., 2014) was selected for the temperature comparisons in this study.

402 In addition to temperature, limnological factors, such as biological productivity, are
403 known to have major influence on chironomids at the local scale (Brodersen and Quinlan, 2006).
404 Although temperature had a significant role determining the temporal variability in chironomid
405 communities of Einstaken and Kvalroslaguna, the influence of biological production explained a
406 larger part of the dynamics (Fig. 10). Whereas the functional differences in chironomids were
407 clearly related to biological catchment influences (bird impact), the reason behind the differences in
408 community changes between the different geographical locations may be climate-related. Since the
409 Hornsund sites Svartvatnet and Fugledammen are located in southern Svalbard and the
410 Nordaustlandet sites Einstaken and Kvalroslaguna in northernmost Svalbard, there is naturally a
411 significant climate difference (Børre Ørbæk et al., 1999). Therefore, it may be that since the climate
412 in Nordaustlandet has been constantly extremely cold for chironomids throughout the Holocene (i.e.
413 a continuous stable state for cold-adapted chironomids), the limnological effects (i.e., changes in
414 organic matter) explain a larger portion of variability in chironomid assemblages at these colder
415 sites.

416 Magnetic susceptibility significantly ($P \leq 0.05$) explained temporal chironomid
417 community variability only in Einstaken (Table 1) suggesting that physical changes in catchment
418 properties and the rate of erosion do not play a major role in the chironomid community dynamics
419 of the other three study sites. Aquatic communities in Arctic lakes, which are poorly buffered or
420 have barren catchments may, however, be especially susceptible to catchment greening and changes
421 in hydrology (Schindler and Smol, 2006; Rantala et al., 2017). This is well demonstrated in the
422 present results by the significance of organic matter in explaining the chironomid communities of
423 the extreme Nordaustlandet sites, which have an open-water season only of ~1 month and
424 catchments with simpler vegetation characteristics. The influence of extreme environmental

425 conditions on chironomids has been well demonstrated also from the European Alps, where major
426 changes in long-term chironomid communities coincided with shifts between different climate
427 regimes and were mainly associated with taxonomic shifts indicating the crossing of ecological
428 thresholds related to ice-cover duration (Ilyashuk et al., 2011). Therefore, ice phenology that also
429 controls the lakes' limnology via the length of biological production and food web development
430 (Quinlan et al., 2005) is probably among the most important environment variables affecting the
431 chironomid assemblages in the High Arctic lakes of Svalbard.

432

433 **5 Conclusions**

434

435 The results indicated major ecological turnovers in High Arctic lakes of Svalbard over different
436 temporal scales and clear differences in taxonomic and functional ecology between sites were
437 observed. Taxonomic and functional diversity of chironomids were highest during the early
438 Holocene, when temperatures showed a rapid increase, and in the most recent samples of the
439 oligotrophic sites (Einstaken and Svartvatnet) but not in the bird-impacted sites (Kvalroslaguna and
440 Fugledammen). Climate was a significant explanatory factor in all the sites, whereas biological
441 production (measured as organic matter) was significant in two of the most climatically extreme
442 sites, suggesting that the continuous harsh climate conditions throughout the Holocene and
443 associated short ice-free period and simple catchment characteristics may play a major role in these
444 coldest sites.

445 The results showed that although taxonomical and functional diversity are always
446 coupled, taxonomic and functional turnovers may be decoupled in certain lakes suggesting that the
447 resilience to future environmental change is site-specific, especially if functional redundancy is lost.
448 In particular, the oligotrophic sites appear to be at greater risk under the ongoing climate change. It
449 also appears that functional diversity in sediment records well-explained environmental conditions

450 in lakes, and consequently has great potential in environmental change paleoreconstructions, which
451 can be used also to understand future changes.

452

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454

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458

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745 **8 Tables**

746 **Table 1** Variance partitioning. Variance explained by forward selected variables (organic matter =
 747 loss on ignition, susceptibility = magnetic susceptibility, temperature = surface air temperature
 748 anomaly) from the total variance in lakes in Svalbard assessed using constrained redundancy
 749 analysis (RDA). Statistically significant variables ($P \leq 0.05$) are marked in bold type.

750

	Variable	Contribution (%)	<i>F</i>	<i>P</i>
Einstaken	Organic matter	18.9	13.3	0.002
	Susceptibility	6.5	4.9	0.004
	Temperature	5.3	4.2	0.002
Svartvatnet	Temperature	5.6	2.3	0.050
	Susceptibility	2.8	1.2	0.308
	Organic matter	1.8	0.7	0.604
Fugledammen	Temperature	25.2	7.4	0.002
	Susceptibility	3.3	1.0	0.376
	Organic matter	3.3	1.0	0.392
Kvalroslaguna	Organic matter	17.5	5.5	0.002
	Temperature	5.5	1.8	0.050
	Susceptibility	4.3	1.5	0.176

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757 **9 Figure captions**

758 **Fig. 1** Study sites. Lakes 1) Svartvatnet, 2) Fugledammen, 3) Einstaken and 4) Kvalroslaguna in
759 Hornsund and Nordaustlandet, High Arctic Svalbard.

760

761 **Fig. 2** Einstaken biostratigraphy. Relative taxa abundances (originally published in Luoto et al.,
762 2011) and feeding guilds of chironomids in the Einstaken sediment record. The shading of the taxa
763 refers to the shading of the associated feeding guild.

764

765 **Fig. 3** Svartvatnet biostratigraphy. Relative taxa abundances (originally published in Luoto et al.,
766 2018) and feeding guilds of chironomids in the Svartvatnet sediment record. The shading of the taxa
767 refers to the shading of the associated feeding guild.

768

769 **Fig. 4** Fugledammen biostratigraphy. Relative taxa abundances (originally published in Luoto et al.,
770 2015) and feeding guilds of chironomids in the Fugledammen sediment record. The shading of the
771 taxa refers to the shading of the associated feeding guild.

772

773 **Fig. 5** Kvalroslaguna biostratigraphy. Relative taxa abundances (originally published in Luoto et al.,
774 2014) and feeding guilds of chironomids in the Kvalroslaguna sediment record. The shading of the
775 taxa refers to the shading of the associated feeding guild.

776

777 **Fig. 6** Einstaken record. North Atlantic temperature variability (Sundqvist et al., 2014), magnetic
778 susceptibility and organic matter content (measured as loss on ignition) of the sediment compared
779 with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes
780 scores, taxon richness, taxonomic diversity (Shannon index, H') and functional diversity of
781 chironomids in the Einstaken sediment record.

782

783 **Fig. 7** Svartvatnet record. North Atlantic temperature variability (Sundqvist et al., 2014), magnetic
784 susceptibility and organic matter content (measured as loss on ignition) of the sediment compared
785 with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes
786 scores, taxon richness, taxonomic diversity (Shannon index, H') and functional diversity of
787 chironomids in the Svartvatnet sediment record.

788

789 **Fig. 8** Fugledammen record. Arctic temperature variability (McKay and Kaufman, 2014), magnetic
790 susceptibility and organic matter content (measured as loss on ignition) of the sediment compared
791 with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes
792 scores, taxon richness, taxonomic diversity (Shannon index, H') and functional diversity of
793 chironomids in the Fugledammen sediment record.

794

795 **Fig. 9** Kvalroslaguna record Arctic temperature variability (McKay and Kaufman, 2014), magnetic
796 susceptibility and organic matter content (measured as loss on ignition) of the sediment compared
797 with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes
798 scores, taxon richness, taxonomic diversity (Shannon index, H') and functional diversity of
799 chironomids in the Kvalroslaguna sediment record.

800

801 **Fig. 10** Linear relationships between taxonomic and functional diversity. Data points are unlabeled
802 core intervals. The oligotrophic sites include Einstaken and Svartvatnet, whereas the bird-impacted
803 sites consist of Fugledammen and Kvalroslaguna.