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)**

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Abstract

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

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

1 Introduction

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

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

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

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

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

2 Material and Methods

2.1 Study sites

The four study sites are located in southern (Hornsund fjord area, mean July air temperature 4.2 °C) and northeastern (Nordaustlandet, mean July air temperature 2 °C) Svalbard (Fig. 1). Svartvatnet (76º90'N, 15º68'E; 63 m a.s.l.) is an oligotrophic 80 ha lake located at the southern side of the

126 Hornsund fjord, whereas Fugledammen (77º00'N, 15º52'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).

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139 *2.2 Sediments and subfossil analyses*

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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 ^{14}C, paleomagnetic,

148 ^{137}Cs and ^{210}Pb 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 cm^3 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).

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160 *2.3 Numerical analyses*

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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.

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188   **3 Results**

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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

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

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

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

Excluding the first 1000 years, organic matter, subfossil abundance (benthic production), taxon richness, Shannon index and functional diversity were generally higher in the initial part of the Einstaken record (Fig. 6) and lower in the latter part from ~7000 cal yr BP onwards. However, a slight general increase in benthic production, DCA axis 1 scores and diversity parameters, concurrent with increases in magnetic susceptibility, was apparent during the past ~2000 years. In Svartvatnet (Fig. 7), magnetic susceptibility and organic matter showed no notable trends, except in the most recent centuries when magnetic susceptibility reached the lowest and organic matter highest values in the record. Subfossil abundance and the diversity parameters had higher values in the later part of the record (past ~2000 years), contrasting the DCA axis 1 scores, 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 ($P\leq0.05$) 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.

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250   **4 Discussion**

251 *4.1 Functional ecology*

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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 at 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

depth suggesting control of benthic and pelagic production, respectively. Hence, the present results

appear to confirm our previous findings where the presence of the collector-feeding lifestyle of

chironomids characterized a functionally diverse community and a healthy pre-disturbance aquatic

ecosystem state (Luoto and Ojala, 2014).

Although benthic functions are related to inlake factors that regulate habitat

characteristics and food availability (Vadeboncoeur et al., 2002), they are also related to external

processes, such as climate. It has been shown from Finnish lakes that at both spatial and long-term

temporal scales the relative importance of chironomid feeding guilds fluctuates alongside climate

characteristics (Luoto and Nevalainen, 2015). Under cold climate conditions and during cold

climate events of the Holocene, such as the early Holocene and the Little Ice Age, collector-filterers

tend to dominate, whereas under warm and intermediate climate conditions and similar climate

episodes of the past, collector-gatherers, shredders, scrapers and predators have more important

roles (Luoto and Nevalainen, 2015). In the current results, similar climate-driven temporal patterns

are not clear. Only in Einstaken which is the most oligotrophic site, collector-gatherers increase at

the expense of collector-filterers during the recent climate warming (Fig. 2). Whereas the temporal

changes in the bird-impacted sites have remained minute (Figs 4, 5), possibly partly related to

shorter chronological time span, a distinct shift has occurred in Svartvatnet, where collector-

gatherers gradually increased (Fig. 3). Instead of a response to climate, it is more likely that this is

related to catchment originated increase in nutrient inputs, which is demonstrated by the decreasing

magnetic susceptibility values (Fig. 7) suggesting physical catchment control (Royall, 2001).

4.2 Biodiversity

Changes in taxon richness and taxonomic and functional diversity appear site-specific in the studied

lakes. In the longest record, Einstaken, diversity peaks during the early Holocene following the

thermal maximum at ~10,000 cal yr BP (Fig. 6), a diversity trend also found in records from

continental Northern Europe (Shala et al., 2014). Similarly, concurrent with the present climate

warming, the diversity indices showed increases in the most recent sediment layers suggesting that

chironomid assemblages and functional behavior are most diverse during warmer climate

conditions (Levesque et al., 1996; Burgmer et al., 2007). In addition, the accumulation of

chironomid subfossil head capsules, indicating benthic production (Itkonen et al., 1999; Fortin and

Gajewski, 2010), has been high during the early Holocene and the most recent period. The

Svartvatnet record is less clear, but showed a similar increase in benthic production and taxonomic

richness and diversity during the most recent times. The results thus confirm previous evidence that

favorable climate conditions support habitat availability and diversity to a certain extent (Schindler

and Smol, 2006).

Benthic production, taxon richness and taxonomic and functional diversity decreased

in Fugledammen alongside climate warming since the Little Ice Age (Fig. 8) in contrast with the

oligotrophic sites. Although not as clear as in Fugledammen, taxon richness and diversity also

decreased in Kvalroslaguna. In all the records, although not synchronous, organic matter content

tended to follow air temperature dynamics, as biological production is known to be temperature

dependent (Meyers and Lallier-Verges, 1999). The diversity changes more or less tracked the

changes in organic matter in the study sites, so that in the oligotrophic sites organic matter and

diversity had positive relationship, and in the bird-impacted sites the relationship was negative. This

fits well with the general observations on invertebrate biodiversity patterns in freshwaters that

diversity increases along biological production until a limnological threshold, after which diversity

begins to decrease (Nyman et al., 2005; Luoto, 2011; Jensen et al., 2013). Variability in magnetic

susceptibility also reflects climate oscillations to some extent. The majority of magnetic minerals

found in these sediments are magnetite of different grain sizes that are delivered into lakes by

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

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

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

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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.

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378 *4.3 Environmental controls on communities*

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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

composition from chironomid head capsules, hence while being independent records, a fully

external record (Sundqvist et al., 2014) was selected for the temperature comparisons in this study.

In addition to temperature, limnological factors, such as biological productivity, are

known to have major influence on chironomids at the local scale (Brodersen and Quinlan, 2006).

Although temperature had a significant role determining the temporal variability in chironomid

communities of Einstaken and Kvalroslaguna, the influence of biological production explained a

larger part of the dynamics (Fig. 10). Whereas the functional differences in chironomids were

clearly related to biological catchment influences (bird impact), the reason behind the differences in

community changes between the different geographical locations may be climate-related. Since the

Hornsund sites Svartvatnet and Fugledammen are located in southern Svalbard and the

Nordaustlandet sites Einstaken and Kvalroslaguna in northernmost Svalbard, there is naturally a

significant climate difference (Børre Ørbæk et al., 1999). Therefore, it may be that since the climate

in Nordaustlandet has been constantly extremely cold for chironomids throughout the Holocene (i.e.

a continuous stable state for cold-adapted chironomids), the limnological effects (i.e., changes in

organic matter) explain a larger portion of variability in chironomid assemblages at these colder

sites.

Magnetic susceptibility significantly (P≤0.05) explained temporal chironomid

community variability only in Einstaken (Table 1) suggesting that physical changes in catchment

properties and the rate of erosion do not play a major role in the chironomid community dynamics

of the other three study sites. Aquatic communities in Arctic lakes, which are poorly buffered or

have barren catchments may, however, be especially susceptible to catchment greening and changes

in hydrology (Schindler and Smol, 2006; Rantala et al., 2017). This is well demonstrated in the

present results by the significance of organic matter in explaining the chironomid communities of

the extreme Nordaustlandet sites, which have an open-water season only of ~1 month and

catchments with simpler vegetation characteristics. The influence of extreme environmental

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

5 Conclusions

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

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

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453 **6 Acknowledgements**

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459 **7 References**

460

461 Arppe, L., Kurki, E., Wooller, M.J., Luoto, T.P., Zajączkowski, M., Ojala, A.E.K., 2017. A 5500-

462 year oxygen isotope record of high-arctic environmental change from southern Spitsbergen.

463 Holocene 27, 1948–1962.

464

465 Belle, S., Luoto, T.P., Kivilä, E.H., Nevalainen, L., 2017. Chironomid paleo diet as an indicator of

466 past carbon cycle in boreal lakes: Lake Kylmänlampi (Kainuu province; Eastern Finland) as a case

467 study. Hydrobiologia 785, 149–158.

468

469 Berg, M. B., 1995. Larval food and feeding behaviour. In Armitage, P.D., Cranston, P.S., Pinder,

470 L.C.V. (eds). The Chironomidae, 136-168. Springer, Dordrecht.

471

472 Brodersen, K.P., Quinlan, R., 2006. Midges as palaeoindicators of lake productivity, eutrophication

473 and hypolimnetic oxygen. Quat. Sci. Rev. 25, 1995–2012.

474

475 Brooks S.J., Birks, H.J.B., 2004. The dynamics of Chironomidae (Insecta: Diptera) assemblages in

476 response to environmental change during the past 700 years on Svalbard. J. Paleolimnol. 31, 483–

477 498.

478

479 Brooks, S.J., Langdon, P.G., Heiri, O., 2007. The identification and use of Palaeoarctic

480 Chironomidae larvae in palaeoecology. QRA Technical Guide No. 10, Quaternary Research

481 Association, London.

482

483 Burgmer, T., Hillebrand, H., Pfenninger, M., 2007. Effects of climate-driven temperature changes

484 on the diversity of freshwater macroinvertebrates. Oecologia 151, 93–103.

485

486 Børre Ørbæk, J., Hisdal, V., Edin Svaasand, L., 1999. Radiation climate variability in Svalbard:

487 surface and satellite observations. Polar Res. 18, 127–134.

488

489 Cadotte, M.V., Carscadden, K., Mirotchnik, N., 2011. Beyond species: functional diversity and the

490 maintenance of ecological processes and services. J. Appl. Ecol. 48, 1079–1087.

491

492 Correa-Metrio, A., Dechnik, Y., Lozano-García, S., Caballero, M., 2014. Detrended correspondence

493 analysis: A useful tool to quantify ecological changes from fossil data sets. Boletín de la Sociedad

494 Geológica Mexicana, 66.

495

496 Covich, A.P., Palmer M.A., Crowl, T.A., 1999. The role of benthic invertebrate species in

497 freshwater ecosystems. Bioscience 49, 119–127.

498

499 Cummins, K.W., 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. 2418, 183–206.

500

Dearing, J.A., 1999. Holocene environmental change from magnetic proxies in lake sediments. In

Maher, B.A., Thompson R. (eds.) Quaternary Climates, Environments and Magnetism. Cambridge

University Press, pp. 231–278.

Eggermont, H., Heiri, O., 2012. The chironomid-temperature relationship: expression in nature and

palaeoenvironmental implications. Biol. Rev. 87, 430–456.

Engels, S., Self, A.E., Luoto, T.P., Brooks, S.J., Helmens, K.F., 2014. A comparison of three

Eurasian chironomid-climate calibration datasets on a W-E continentality gradient and the

implications for quantitative temperature reconstructions. J. Paleolimnol. 51, 529–547.

Feld, C.K., de Bello F., Dolédec, S., 2014. Biodiversity of traits and species both show weak

response to hydromorphological alteration in lowland river macroinvertebrates. Freshw. Biol. 59,

233–248.

Fortin, M.C., Gajewski, K., 2010. Holocene climate change and its effect on lake ecosystem

production on Northern Victoria Island, Canadian Arctic. J. Paleolimnol. 43, 219–234.

Fournier, B., Lara, E., Jassey, V.E., Mitchell, E.A., 2015. Functional traits as a new approach for

interpreting testate amoeba palaeo-records in peatlands and assessing the causes and consequences

of past changes in species composition. Holocene 25, 1375–1383.

Frey, D.G., 1988. Littoral and offshore communities of diatoms, cladocerans and dipterous larvae,

and their interpretation in paleolimnology. J. Paleolimnol. 3, 179–191.

525

526   Gregory-Eaves, I., Beisner, B.E., 2011. Palaeolimnological insights for biodiversity science: an

527   emerging field. Freshw. Biol. 56, 2653–2661.

528

529   Grey, J., Kelly, A., Ward, S., Sommerwerk, N., Jones, R.I., 2004. Seasonal changes in the stable

530   isotope values of lake-dwelling chironomid larvae in relation to feeding and life cycle variability.

531   Freshw. Biol. 49, 681–689.

532

533   Heiri, O., Brooks, S.J., Birks, H.J.B., Lotter, A.F., 2011. A 274-lake calibration data-set and

534   inference model for chironomid-based summer air temperature reconstruction in Europe. Quat. Sci.

535   Rev. 30, 3445–3456.

536

537   Ilyashuk, E.A., Ilyashuk, B.P., Tylmann, W., Koinig, K.A, Psenner, R., 2015. Biodiversity

538   dynamics of chironomid midges in high-altitude lakes of the Alps over the past two millennia.

539   Insect Conserv. Diver. 8, 547–561.

540

541   Isaksen, K., Benestad, R.E., Harris, C., Sollid, J.L., 2007. Recent extreme near-surface permafrost

542   temperatures on Svalbard in relation to future climate scenarios. Geophys. Res. Lett. 34.

543

544   Itkonen, A., Marttila, V., Meriläinen, J., Salonen, V.-P., 1999. 8000-year history of

545   palaeoproductivity in a large boreal lake. J. Paleolimnol. 21, 271–294.

546

547   Jensen, T.C., Dimante-Deimantovica, I., Schartau, A.K., Walseng, B., 2013. Cladocerans respond to

548   differences in trophic state in deeper nutrient poor lakes from Southern Norway. Hydrobiologia,

549   715, 101–112.

550

Jeppesen, E., Leavitt, P., De Meester, L., Jensen, J. P., 2001. Functional ecology and

palaeolimnology: using cladoceran remains to reconstruct anthropogenic impact. Trends Ecol. Evol.

16, 191–198.

554

Keatley, B.E., Douglas, M.S., Blais, J.M., Mallory, M.L., Smol, J.P., 2009. Impacts of seabird-

derived nutrients on water quality and diatom assemblages from Cape Vera, Devon Island,

Canadian High Arctic. Hydrobiologia 621, 191–205.

558

Levesque, A.J., Cwynar, L.C., Walker, I.R., 1996. Richness, diversity and succession of late-glacial

chironomid assemblages in New Brunswick, Canada. J. Paleolimnol. 16, 257–274.

561

Linderholm, H.W., Nicolle, M., Francus, P., Gajewski, K., Helama, S., Korhola, A., Solomina, O.,

Yu, Z., Zhang, P., D'Andrea, W.J., Debret, M., Divine, D., Gunnarson, B.E., Loader, N.J., Massei,

N., Seftifgen, K., Thomas, E.K., Werner, J., Andersson, S., Berntsson, A., Luoto, T.P., Nevalainen,

L., Saarni, S. & Väliranta, M., 2018. Arctic hydroclimate variability during the last 2000 years:

current understanding and research challenges. Clim. Past 14, 473–514.

567

Liu, X.Q., Wang, H.Z., 2008. Food web of benthic macroinvertebrates in a large Yangtze River-

connected lake: the role of flood disturbance. Fundam. Appl. Limnol. 171, 297–309.

570

Luoto, T.P., 2011. The relationship between water quality and chironomid distribution in Finland –

A new assemblage-based tool for assessments of long-term nutrient dynamics. Ecol. Indic. 11, 255–

262.

574

575 Luoto, T.P., Ojala, A.E.K., Arppe, L., Brooks, S.J., Kurki, E., Oksman, M., Wooller, M.J.,

576 Zajączkowski, M., 2018. Synchronized proxy-based temperature reconstructions reveal mid- to late

577 Holocene climate oscillations in High Arctic Svalbard. J. Quat. Sci. 33, 93–99.

578

579 Luoto, T.P., Nevalainen, L., 2015. Climate-forced patterns in midge feeding guilds. Hydrobiologia

580 742, 141–152.

581

582 Luoto, T.P., Ojala, A.E.K., 2014. Paleolimnological assessment of ecological integrity and

583 eutrophication history for Lake Tiiläänjärvi (Askola, Finland). J. Paleolimnol. 51, 455–468.

584

585 Luoto, T.P., Oksman, M., Ojala, A.E.K., 2016. Invertebrate communities of the High Arctic ponds

586 in Hornsund. Pol. Polar Res. 37, 105–119.

587

588 Luoto, T.P., Oksman, M., Ojala A.E.K., 2015. Climate change and bird impact as drivers of High

589 Arctic pond deterioration. Polar Biol. 38, 357–368.

590

591 Luoto, T.P., Brooks, S.J., Salonen, V.-P., 2014. Ecological responses to climate change in a bird-

592 impacted High Arctic pond (Nordaustlandet, Svalbard). J. Paleolimnol. 51, 87–97.

593

594 Luoto, T.P., Nevalainen, L., Kubischta, F., Kultti, S., Knudsen, K.L., Salonen, V.-P., 2011. Late

595 Quaternary ecological turnover in high arctic Lake Einstaken, Nordaustlandet, Svalbard (80° N).

596 Geogr. Ann. A 93, 337–354.

597

598   Majewski, W., Szczuciński, W., Zajączkowski, M., 2009. Interactions of Arctic and Atlantic

599   water-masses and associated environmental changes during the last millennium, Hornsund (SW

600   Svalbard). Boreas 38, 529–544.

601

602   Mandaville, S.M., 2002. Benthic Macroinvertebrates in Freshwaters—Taxa Tolerance Values,

603   Metrics, and Protocols. Soil & Water Conservation Society of Metro Halifax.

604

605   Massaferro, J., Corley, J., 1998. Environmental disturbance and chironomid palaeodiversity: 15 kyr

606   BP of history at Lake Mascardi, Patagonia, Argentina. Aquat. Conserv. Mar. Freshw. Ecosyst. 8,

607   315–323.

608

609   McKay, N.P., Kaufman, D.S., 2014. An extended Arctic proxy temperature database for the past

610   2,000 years. Sci. Data 1, 140026.

611

612   Merritt, R.W., Cummins K.W. (eds), 1996. An Introduction to the Aquatic Insects of North

613   America. Kendall-Hunt, Dubuque.

614

615   Meyers, P.A., Lallier-Verges, E., 1999. Lacustrine sedimentary organic matter records of Late

616   Quaternary paleoclimates. J. Paleolimnol. 21, 345–372.

617

618   Meyers, P.A., Teranes, J.L., 2002. Sediment organic matter. Tracking environmental change using

619   lake sediments, pp. 239–269.

620

621   Nevalainen, L., Luoto, T.P., 2017. Relationship between cladoceran (Crustacea) functional diversity

622   and lake trophic gradients. Funct. Ecol. 31, 488–498.

623

624 Nevalainen, L., Brown, M., Manca, M., 2018. Sedimentary record of cladoceran functionality under

625 eutrophication and re-oligotrophication in Lake Maggiore, Northern Italy. Water 10, 86.

626

627 Nevalainen, L., Rantala, M.V., Luoto, T.P., 2015a. Sedimentary cladoceran assemblages and their

628 functional attributes record late Holocene climate variability in southern Finland. J. Paleolimnol. 54,

629 239–252.

630

631 Nevalainen, L., Luoto, T.P., Manca, M., Weisse, T., 2015b. A paleolimnological perspective on

632 aquatic biodiversity in Austrian mountain lakes. Aquat. Sci. 77, 59–69.

633

634 Nevalainen, L., Van Damme, K., Luoto, T.P., Salonen, V.-P., 2012. Fossil remains of an unknown

635 Alona species (Chydoridae, Aloninae) from a high arctic lake in Nordaustlandet (Svalbard) in

636 relation to glaciation and Holocene environmental history. Polar Biol. 35, 325–333.

637

638 Nyman, M., Korhola, A., Brooks, S.J., 2005. The distribution and diversity of Chironomidae

639 (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. Glob. Ecol.

640 Biogeogr. 14, 137–153.

641

642 Ojala, A.E.K., Arppe, L., Luoto, T.P., Wacker, L., Kurki, E., Zajączkowski, M., Pawłowska, J.,

643 Damrat, M., Oksman, M., 2016. Sedimentary environment, lithostratigraphy and dating of sediment

644 sequences from Arctic lakes Revvatnet and Svartvatnet in Hornsund, Svalbard. Pol. Polar Res. 37,

645 23–48.

646

Palmer, M.A., Covich, A.P., Finlay, P.J., et al., 1997. Biodiversity and ecosystem processes in freshwater sediments. Ambio 26, 571–577.

Paull, T.M., Finkelstein, S.A., Gajewski, K., 2017. Interactions between climate and landscape driven Holocene ecological change in a High Arctic lake on Somerset Island, Nunavut, Canada. Arctic Science 3, 17–38.

Pinder, L.C.V., 1986. Biology of freshwater Chironomidae. Annu. Rev. Entomol. 31, 1–23.

Pla-Rabes, S., Flower, R.J., Shilland, E.M., Kreiser, A.M., 2011. Assessing microbial diversity using recent lake sediments and estimations of spatio-temporal diversity. J. Biogeogr. 38, 2033–2040.

Quinlan, R., Douglas, M.S., Smol, J.P., 2005. Food web changes in arctic ecosystems related to climate warming. Global Change Biol. 11, 1381–1386.

Rantala, M.V., Luoto, T.P., Weckström, J., Rautio, M., Nevalainen, L., 2017. Climate drivers of diatom distribution in shallow subarctic lakes. Freshw. Biol. 62, 1971–1985.

Rautio, M., Dufresne, F., Laurion, I., Bonilla, S., Vincent, W.F., Christoffersen, K.S., 2011. Shallow freshwater ecosystems of the circumpolar Arctic. Ecoscience 18, 204–222.

Robroek, J.M., Jassey, V.E.J., Payne, R.J. et al., 2017. Taxonomic and functional turnover are decoupled in European peat bogs. Nat. Comm., DOI: 10.1038/s41467-017-01350-5.

672 Royall, D., 2001. Use of mineral magnetic measurements to investigate soil erosion and sediment

673 delivery in a small agricultural catchment in limestone terrain. Catena 46, 15–34.

674

675 Sandgren, P., Snowball, I., 2002. Application of mineral magnetic techniques to paleolimnology. In

676 Tracking environmental change using lake sediments, pp. 217-237. Springer Netherlands.

677

678 Schilder, J., van Hardenbroek, M., Bodelier, P., Kirilova, E.P., Leuenberger, M., Lotter, A.F., Heiri,

679 O., 2017. Trophic state changes can affect the importance of methane-derived carbon in aquatic

680 food webs. Proceedings of the Royal Society B 284, 20170278.

681

682 Schindler, D.W., Smol, J.P., 2006. Cumulative effects of climate warming and other human

683 activities on freshwaters of Arctic and subarctic North America. Ambio 35, 160–168.

684

685 Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity

686 indices. Ecol. Monogr. 80, 469–484.

687

688 Schmera, D., Heino, J., Podani, J., Erős, T., Dolédec, S., 2017. Functional diversity: a review of

689 methodology and current knowledge in freshwater macroinvertebrate research. Hydrobiologia 787,

690 27–44.

691

692 Serreze, M.C., Barry, R.G., 2011. Processes and impacts of Arctic amplification: A research

693 synthesis. Glob. Planet. Change 77, 85–96.

694

695   Shala, S., Helmens, K.F., Luoto, T.P., Väliranta, M., Weckström, J., Salonen, J.S., Kuhry, P., 2014.

696   Evaluating environmental drivers of Holocene changes in water chemistry and aquatic biota

697   composition at Lake Loitsana, NE Finland. J. Paleolimnol. 52, 311–329.

698

699   Shannon, C.E., 1948. A mathematical theory of communication. The Bell System Technical Journal

700   27, 379–423, 623–656.

701

702   Šmilauer, P., Lepš, J., 2014. Multivariate analysis of ecological data using CANOCO 5. Cambridge

703   University Press.

704

705   Smol, J.P., 2010. The power of the past: using sediments to track the effects of multiple stressors on

706   lake ecosystems. Freshw. Biol. 55, 43–59.

707

708   Smol, J.P., Douglas, M.S., 2007. From controversy to consensus: making the case for recent climate

709   change in the Arctic using lake sediments. Front. Ecol. Environ. 5, 466–474.

710

711   Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future

712   challenges. J N Amer. Benthol. Soc. 29, 344–358.

713

714   Sundqvist, H.S., Kaufman, D.S., McKay, N.P. et al., 2014. Arctic Holocene proxy climate database

715   - new approaches to assessing geochronological accuracy and encoding climate variables. Clim.

716   Past 10, 1605–1631.

717

718   Vadeboncoeur, Y., Vander Zanden, M.J., Lodge, D.M., 2002. Putting the Lake Back Together:

719   Reintegrating Benthic Pathways into Lake Food Web Models: Lake ecologists tend to focus their

720   research on pelagic energy pathways, but, from algae to fish, benthic organisms form an integral

721   part of lake food webs. AIBS Bulletin 52, 44–54.

722

723   van Hardenbroek, M., Lotter, A.F., Bastviken, D., Andersen, T.J., Heiri, O., 2014. Taxon-specific

724    $\delta^{13}C$ analysis of chitinous invertebrate remains in sediments from Strandsjön, Sweden. Journal of

725   Paleolimnology 52, 95–105.

726

727   Velle, G., Kongshavn, K., Birks, H.J.B., 2011. Minimizing the edge-effect in environmental

728   reconstructions by trimming the calibration set: chironomid-inferred temperatures from Spitsbergen.

729   Holocene 21, 417–430.

730

731   Wrona, F.J., Johansson, M., Culp, J.M. et al., 2016. Transitions in Arctic ecosystems: Ecological

732   implications of a changing hydrological regime. J. Geophys. Res. Biogeosci. 121, 650–674.

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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≤0.05) are marked in bold type.

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	Variable	Contribution (%)	*F*	*P*
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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9 Figure captions

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

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

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

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

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

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

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Fig. 7 Svartvatnet record. North Atlantic temperature variability (Sundqvist et al., 2014), magnetic

susceptibility and organic matter content (measured as loss on ignition) of the sediment compared

with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes

scores, taxon richness, taxonomic diversity (Shannon index, H') and functional diversity of

chironomids in the Svartvatnet sediment record.

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Fig. 8 Fugledammen record. Arctic temperature variability (McKay and Kaufman, 2014), magnetic

susceptibility and organic matter content (measured as loss on ignition) of the sediment compared

with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes

scores, taxon richness, taxonomic diversity (Shannon index, H') and functional diversity of

chironomids in the Fugledammen sediment record.

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Fig. 9 Kvalroslaguna record Arctic temperature variability (McKay and Kaufman, 2014), magnetic

susceptibility and organic matter content (measured as loss on ignition) of the sediment compared

with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes

scores, taxon richness, taxonomic diversity (Shannon index, H') and functional diversity of

chironomids in the Kvalroslaguna sediment record.

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Fig. 10 Linear relationships between taxonomic and functional diversity. Data points are unlabeled

core intervals. The oligotrophic sites include Einstaken and Svartvatnet, whereas the bird-impacted

sites consist of Fugledammen and Kvalroslaguna.