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11 Temperature change as a driver of spatial patterns and long-term trends in chironomid

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48 ecosystems, insects

49

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51 **Abstract**

52 Anthropogenic activities have led to a global decline in biodiversity, and monitoring studies  
53 indicate that both insect communities and wetland ecosystems are particularly affected.  
54 However, there is a need for long-term data (over centennial- or millennial timescales) to  
55 better understand natural community dynamics and the processes that govern the observed  
56 trends. Chironomids (Insecta: Diptera: Chironomidae) are often the most abundant insects in  
57 lake ecosystems, sensitive to environmental change, and, because their larval exoskeleton  
58 head capsules preserve well in lake sediments, they provide a unique record of insect  
59 community dynamics through time. Here, we provide the results of a meta-data analysis of  
60 chironomid diversity across a range of spatial and temporal scales. First, we analyse spatial  
61 trends in chironomid diversity using Northern Hemispheric datasets overall consisting of 837  
62 lakes. Our results indicate that in most of our datasets summer temperature ( $T_{jul}$ ) is strongly  
63 associated with spatial trends in modern-day chironomid diversity. We observe a strong  
64 increase in chironomid alpha diversity with increasing  $T_{jul}$  in regions with present day  $T_{jul}$   
65 between 2.5-14 °C. In some areas with  $T_{jul} > 14$  °C chironomid diversity stabilises or declines.  
66 Second, we demonstrate that the direction and amplitude of change in alpha diversity in a  
67 compilation of subfossil chironomid records spanning the last glacial-interglacial transition  
68 (~15,000-11,000 years ago) are similar to those observed in our modern data. A compilation  
69 of Holocene records shows that during phases when the amplitude of temperature change was  
70 small, site-specific factors had a greater influence on the chironomid fauna obscuring the  
71 chironomid diversity-temperature relationship. Our results imply expected overall  
72 chironomid diversity increases in colder regions such as the Arctic under sustained global  
73 warming, but with complex and not necessarily predictable responses for individual sites.  
74

75 **Introduction**

76 Key environmental parameters such as greenhouse gas concentrations, ocean acidity, and  
77 erosion rates are now beyond their previous Holocene range of variability as a result of  
78 human activity (Corlett, 2015; Steffen et al., 2015). These environmental stressors are leading  
79 to dramatic changes in the structure and composition of biological communities across local  
80 to global spatial scales and to a decrease in global biodiversity (e.g. Ripple et al., 2017). For  
81 example, the invertebrate fauna of northwest Europe is showing signs of a dramatic decrease  
82 in abundance and diversity (Hallmann et al., 2017; Bidau, 2018; Jourdan et al., 2018; Leather  
83 2018; Rada et al., 2019) and freshwater ecosystems are showing a particularly high rate of  
84 biodiversity loss (Dudgeon et al., 2006).

85 Most records that are used to assess the effects of anthropogenic drivers (e.g. climate  
86 variability, eutrophication, toxins, impacts associated with invasive species) on biodiversity  
87 are based on decadal-scale ecological data (Vellend et al., 2013; Birks et al., 2016a; W.W.F.,  
88 2016). In many natural settings it has been difficult to disentangle natural variability from the  
89 effects of human-induced ecosystem change (Loreau et al., 2001; Willis & Birks, 2006) as a  
90 result of these short time-scales typically used. Datasets that cover much longer timescales,  
91 e.g. several centuries to millennia, can help to provide a broader temporal context for current  
92 and future trends in biodiversity and facilitate the development of effective conservation  
93 strategies (Willis & Birks, 2006; Gregory-Eaves & Beisner, 2011; Birks et al., 2016a). Willis  
94 & Birks (2006) and Birks et al. (2016a) provide examples of the role that palaeoecological  
95 datasets can play in providing such centennial- to millennial-scale time series, and how these  
96 data can provide new insights into the complex relationships that exist between biodiversity,  
97 ecosystem functioning, and environmental variability. Despite the fact that many natural  
98 archives are available for study by palaeo- and neo-ecologists, these sources of information  
99 have rarely been used to infer past changes in biodiversity within the context of human

100 impact and the ‘Anthropocene’ (Gregory-Eaves & Beisner, 2011; Corlett, 2015). We  
101 therefore have a limited understanding of long-term trends ( $10^2$ - $10^5$  years) in biodiversity,  
102 including insect diversity, and, as a result, it remains difficult to disentangle effects of  
103 anthropogenic disturbances from natural trends and internal variability.

104 Palaeoecological records describe the development of ecosystems over timescales  
105 ranging from a few decades to several hundreds of thousands of years (e.g. Smol et al., 2005).  
106 They are typically derived from lake deposits, peat bogs, marine sediments, or other natural  
107 archives. Fossils encountered in these materials can be used to reconstruct past ecological and  
108 environmental change and provide estimates of past biodiversity for different parts of the  
109 ecosystem (e.g. terrestrial vegetation, algal flora, invertebrate fauna) (e.g. Smol et al., 2005).

110 A method that has provided insights into ecological, environmental and climatic  
111 development across the last glacial/interglacial cycle is the analysis of subfossil chironomid  
112 remains preserved in lake sediments (e.g. Brooks, 2006; Walker & Cwynar, 2006).  
113 Chironomids (Insecta: Diptera: Chironomidae) are holometabolous insects, and the larval  
114 stage of most species is aquatic. In lakes, chironomids are usually the most abundant  
115 macroinvertebrate group, and they are a critical component of the benthic community,  
116 contributing to processes essential for lake ecosystem functioning (Hölker et al., 2015),  
117 including biogeochemical cycling of carbon and nutrients. Parts of their larval exoskeleton  
118 (the head capsules) are well-preserved in lake sediments (e.g. Brooks et al., 2007). Subfossil  
119 chironomid head capsules are abundant in lake sediments, often in concentrations of 50-100  
120 head capsules per gram of sediment, can be identified to genus, species morphotype, or  
121 species level, and provide a record of changes in the chironomid fauna of a lake through time.  
122 By comparing subfossil chironomid assemblages to their modern-day distribution patterns,  
123 quantitative reconstructions of changes in their past environment can be made. For instance,  
124 chironomids have been used to quantitatively reconstruct past changes in temperature

125 (Medeiros et al., 2012; Heiri et al., 2014; Brooks et al., 2016), water depth (Engels et al.,  
126 2012; Nazarova et al., 2017), salinity (Dickson et al., 2014), hypolimnetic oxygen (Quinlan &  
127 Smol, 2001), and several other environmental variables. Subfossil chironomids encountered  
128 in lake sediment records can additionally be used to track changes in past species richness or  
129 evenness of the fauna through time (e.g. Engels et al., 2010). However, palaeoecological  
130 datasets describing chironomid faunal dynamics on centennial to millennial timescales have  
131 not yet been compiled to produce systematic and super-regional studies of past diversity  
132 patterns.

133         While it is often assumed that the global decline in biodiversity is accompanied by  
134 declines at finer spatial scales, local biodiversity has been shown to have been stable in many  
135 regions even when global biodiversity trends show significant decreases (Cardinale et al.,  
136 2018; Primack et al., 2018). It therefore follows that biodiversity at large spatial scales is not  
137 necessarily an additive function of biodiversity at smaller scales (Vellend et al., 2013) and  
138 that investigating biodiversity at a range of spatial scales is necessary to understand the  
139 ongoing changes in biodiversity as a result of climatic and environmental change (Primack et  
140 al., 2018). While palynological records provide long-term trends of regional changes in  
141 vegetation (e.g. Birks et al., 2016a), there are currently no studies that assess long-term  
142 diversity change on finer spatial scales, such as individual aquatic ecosystems. Therefore, this  
143 study aims to contribute toward filling the gap in our understanding of long-term trends in  
144 local-scale biodiversity changes and to provide a long-term perspective to the recent decline  
145 in insect diversity. Specifically, we aim to assess long-term changes in chironomid diversity,  
146 a keystone member of freshwater ecosystems, by:

- 147         (1) Determining the relationship between diversity of (subfossil) chironomid  
148         assemblages in sediment samples and environmental parameters, with an emphasis on

149 the effects of summer temperature on chironomid assemblages across the mid- and  
150 high-latitudes of the northern hemisphere (reflecting the availability of datasets);  
151 (2) Analysing spatiotemporal changes in chironomid diversity across a range of  
152 timescales; and  
153 (3) Assessing the suitability of subfossil chironomid assemblages as an approach to  
154 reconstruct changes in diversity over longer timescales.

155

## 156 **Materials and methods**

### 157 Materials

158 We determine, for the first time, spatial trends in chironomid diversity in chironomid-climate  
159 calibration datasets from Norway (Brooks & Birks, 2001; Brooks, 2006), Russia (Nazarova et  
160 al., 2011; 2015; Self et al., 2011), Canada (Gajewski et al., 2005; Porinchu et al., 2009; Fortin  
161 & Gajewski, 2011; Medeiros & Quinlan, 2011), Switzerland (Lotter et al., 1997; Heiri &  
162 Lotter, 2010) and Finland (Luoto 2009a; 2009b) (Fig. 1; Supplementary Table S1). Samples  
163 presented here from the Canadian dataset have been re-identified where necessary and the  
164 taxonomy of the datasets analysed here follows Brooks et al. (2007).

165 Chironomid-climate calibration datasets document the relationship between  
166 chironomids and their contemporaneous environment (Brooks, 2006), often with a specific  
167 focus on the influence of summer air temperature on chironomid distribution patterns (e.g.  
168 Heiri et al., 2014). As such, these datasets capture a wide (summer) temperature range,  
169 whereas the impact of other environmental variables (e.g. lake water pH) is typically  
170 minimised. As a result of this sampling approach, the datasets provide excellent resources to  
171 study the temperature-chironomid diversity relationship. However, as the datasets cover a  
172 range of different secondary gradients (e.g. Medeiros et al., 2015) and include measurements  
173 of different environmental variables (see Supplementary Table S1), testing the influence of

174 environmental parameters other-than-temperature on chironomid diversity will be more  
175 empirical.

176

177 To determine temporal trends in chironomid diversity we selected northern hemisphere sites  
178 with clear information on the taxonomic resolution, and for which we had access to the  
179 original count data (Supplementary Table S2, S3). The sites presented in this study cover  
180 different timescales, ranging from records that date back as far as 200,000 cal yr BP to  
181 records that cover the last few centuries. We specifically focus on the last glacial-interglacial  
182 transition (LGIT; ca. 14,500-11,600 calendar years before the present (cal yr BP)), the current  
183 interglacial, i.e. the Holocene (ca. 11,600 cal yr BP to the present) and high-resolution  
184 records covering the last few centuries. For the selection of the Holocene and recent records  
185 used in this study (Supplementary Table S3) we focussed on sites that are relatively removed  
186 from local human impacts.

187         The LGIT was characterised by a number of climate events in the North Atlantic  
188 region. The general trend of climate warming was interrupted by a major cold phase (stadial)  
189 known as the Younger Dryas (YD), which occurred between ca. 12,650 and 11,600 cal yr BP  
190 (e.g. Litt et al., 2001). The relatively warm Bølling-Allerød interstadial (B/A; ca 14,500-  
191 12,650 cal yr BP) preceding the YD was punctuated by at least two decadal to centennial  
192 scale climate cooling events, the Gerzensee Oscillation (GZO or Greenland Interstadial event  
193 (GI)-1b) and the Older Dryas (or GI-1d; Lotter et al., 1992). The YD has been  
194 palynologically identified in each of the LGIT records presented in this paper and several of  
195 the records also identified the Gerzensee Oscillation and the Older Dryas (depending on  
196 location of the sites, temporal sampling resolution and proxy sensitivity). Supplementary  
197 Table S2 provides more details on the sites used in this study.

198

199 Numerical analyses

200 We focus on two biodiversity measures that are relevant to subfossil chironomid  
201 assemblages: (a) alpha diversity, here defined as the taxon richness of an assemblage at one  
202 point in time and space, and (b) compositional turnover, i.e. changes in assemblage  
203 composition across time (cf. McGill et al., 2015).

204

205 First, we analysed spatial trends in alpha diversity by calculating taxon richness using  
206 rarefaction analysis for each of our modern datasets. Rarefaction simulates a random  
207 selection without replacement, estimating the taxon richness for each sample using a fixed  
208 count size, which typically equals the smallest count sum recorded in a sequence of samples  
209 (e.g. Birks & Line, 1992). Results of rarefaction analyses can be quantitatively compared  
210 between samples and datasets with different counts. Prior to rarefaction analysis, we rounded  
211 the counts in our datasets to integers and set our cut-value to a count sum of 40 head capsules  
212 for all analyses. Whilst chironomid studies often report a minimum count sum of 50 head  
213 capsules per sample, we noted that some of our fossil sites had depth-intervals where this  
214 number was not consistently reached. Instead of amalgamating or removing these samples  
215 and thus losing information, we decided to set a cut-value of 40 head capsules in order to  
216 retain more samples. Test runs comparing results of changing cut-values from 50 to 40 head  
217 capsules showed no substantial differences in the results and did not change interpretations of  
218 patterns and trends. Sites that had count values below 40 head capsules were removed prior to  
219 analysis. Rarefaction analysis was implemented using the vegan package in R (Oksanen et  
220 al., 2015).

221         Visual inspection of scatterplots of selected environmental variables against alpha  
222 diversity revealed the existence of non-linear but monotonic relationships. We subsequently  
223 calculated Spearman rank-order correlation coefficients between the rarefaction values and

224 environmental observations for each modern dataset (Table 1). The results indicated that  
225 generally there was a significant positive association between July air temperature ( $T_{jul}$ ) and  
226 alpha diversity. We produced scatter plots of chironomid diversity (estimated using  
227 rarefaction analysis) as a function of July air temperature and used Generalized Additive  
228 Modelling (GAM) to summarise trends in the data (Simpson, 2018) (see Supplementary  
229 Information for R code).

230

231 Second, we reconstructed trends in alpha diversity as well as in compositional turnover (as an  
232 approximation for temporal beta diversity) for each of our fossil records. Prior to rarefaction  
233 analysis, samples with  $< 40$  head capsules were amalgamated with adjacent samples, making  
234 sure that samples were only combined within lithological units. If samples could not be  
235 combined with adjacent samples they were left out of the analysis.

236         While beta diversity is a commonly used component in (palaeoecological)  
237 biodiversity studies, there is no consensus on how to derive and interpret beta diversity (e.g.  
238 Jost 2007; Marcon et al., 2012; Birks et al., 2016b). Beta diversity, or the change in species  
239 composition per unit space or time (McGill et al., 2015), is often quantified as a rate-of-  
240 change or a turnover metric (Birks, 2012; Birks et al., 2016a). Even though estimating  
241 assemblage compositional turnover along a temporal gradient does not provide a true  
242 diversity component but rather a measure of compositional complexity (Tuomisto, 2010;  
243 Birks et al., 2016b), compositional turnover is commonly interpreted to approximate temporal  
244 changes in beta diversity, and compositional turnover techniques have become popular tools  
245 in palaeoecological studies (e.g. Smol et al., 2005; Birks & Birks, 2008; Colombaroli &  
246 Tinner, 2013; Feurdan et al., 2013; Stivrins et al., 2016). The difference in scores on a  
247 Detrended Canonical Correspondence Analysis (DCCA) axis between subsequent samples

248 can be used to highlight times of increased turnover, reflecting increased beta diversity  
249 between samples.

250 In this study we follow the examples of Smol et al. (2005) and Birks & Birks (2008)  
251 and estimate changes in beta diversity through calculating DCCA axis 1-scores on a temporal  
252 gradient. DCCA results are robust to differences in sample numbers for comparable time  
253 periods (Birks, 2007), as is the case for e.g. our LGIT records. Changes in compositional  
254 turnover were determined by running DCCAs for each of our fossil sites with time as the  
255 constraining variable, or, when no robust chronology was available, using sample depth as  
256 the constraining variable. In accordance with previously published results, the percent-  
257 abundance datasets were square-root transformed prior to DCCA, and we applied detrending  
258 by segments with no down-weighting of rare taxa and non-linear rescaling in our analyses.  
259 DCCAs were performed using CANOCO v4.5 (ter Braak and Šmilauer, 2002).

260

261 Finally, we quantitatively compare the rarefaction results for the Norwegian calibration  
262 dataset to the LGIT reconstructions to assess whether the effects of temperature on alpha  
263 diversity, as observed in modern-day chironomid assemblages, are comparable to those of the  
264 distant past. To do so, we assessed the change in rarefaction ( $\Delta RF$ ) with changing  $T_{jul}$  ( $\Delta T_{jul}$ )  
265 across the entire temperature interval included in the Norwegian calibration dataset. In a first  
266 step, we calculated the average RF ( $RF_{ave}$ ) value for each consecutive 1-°C bin (e.g. 3.00-  
267 3.99 °C ( $T_{3.5C}$ )) in the Norwegian calibration dataset. We then calculated changes in RF  
268 ( $\Delta RF$ ) for each possible combination of 1-°C bins across the 3-16 °C temperature interval  
269 covered by the Norwegian calibration dataset. This approach allows us to observe whether  
270 e.g. a change of 2 °C has the same effects on the taxonomic diversity of a lake situated e.g. at  
271 8 °C as for a lake situated at e.g. 14 °C, as well as to compare the effects an increase of 2 °C  
272 would have compared to the effects of an increase of 4 °C at the same site. We used the

273 geom\_raster function as included in the R ggplot2 package to produce a continuous plot of  
274 changes in RF ( $\Delta$ RF) for each absolute temperature (e.g.  $T = 3.5\text{ }^{\circ}\text{C}$ ) and each possible  
275 increase in temperature ( $\Delta T$ ).

276 We subsequently calculated the change in alpha diversity associated with the two  
277 major climate transitions in our LGIT records, the Allerød-YD and the YD-Holocene  
278 transitions. We assessed  $RF_{\text{ave}}$  for each climate zone in each LGIT record, avoiding periods  
279 of transition and the effects of short-scale oscillations such as the Older Dryas, and calculated  
280  $\Delta$ RF values by comparing  $RF_{\text{ave}}$  for subsequent climate zones (e.g. YD versus Holocene). We  
281 use published quantitative LGIT  $T_{\text{jul}}$  inferences (see Supplementary Table S2) to assess the  
282 average temperature during each interval (e.g.  $T_{\text{YD}}$ ) and calculated the change in temperature  
283 between subsequent intervals ( $\Delta T$ ) to be able to compare the LGIT results to the modern-day  
284 patterns in alpha diversity. Using this approach, we can assess what the change in alpha  
285 diversity was at a given starting temperature and under a particular climate forcing (i.e.  
286 temperature difference between consecutive time intervals). These inferences for the fossil  
287 records can be quantitatively compared to the inferences based on the modern dataset to  
288 assess whether fossil and present trends in the chironomid diversity-temperature relationship  
289 are of a similar magnitude. We refer to the supplementary information for more details on the  
290 procedure.

291 The  $T_{\text{jul}}$  records used in this calculation are chironomid-based temperature inferences  
292 and are based on the same datasets as the alpha diversity reconstructions, and as such are not  
293 independent. However, in the absence of independent temperature estimates this is currently  
294 the only method that allows the quantitative comparison of our modern data to our fossil  
295 reconstructions.

296

## 297 **Results and interpretation**

298 Spatial trends in chironomid diversity

299 All datasets show similar TR values ranging between minima of 1-5 to maximum values over  
300 20 (Fig. 2). Chironomid alpha diversity generally shows an increasing trend with increasing  
301  $T_{\text{jul}}$  for four out of the five regional datasets (Fig. 2). In the Norwegian and Canadian datasets  
302 the increase in alpha diversity is steepest in the coldest part of the temperature gradient (ca. 3-  
303 7 °C interval), after which a more moderate increase in diversity can be seen. For some of the  
304 datasets that cover temperatures exceeding ca. 14 °C (e.g. Russia, Switzerland) we observe a  
305 stabilising or decreasing trend in alpha diversity with higher temperatures. Three of the  
306 datasets show additional variation superimposed on the general trend of increasing diversity  
307 with increasing temperature, which might be the result of sampling density along the  
308 temperature gradient, site-specific factors resulting in a lower alpha diversity in individual  
309 lakes, or it might be a true reflection of decreasing alpha diversity for currently unidentified  
310 reasons. The Finnish dataset captures a smaller temperature gradient than the other datasets  
311 and GAM shows a highly variable but non-directional trend in alpha diversity. However, as  
312 in the other datasets, some of the lakes with mean July air temperature higher than 14 °C are  
313 characterized by relatively low alpha diversity. Explanations for the general increase in  
314 chironomid diversity with temperature in most of our datasets could include availability of  
315 more and higher-quality food sources with increasing temperatures. For instance, the  
316 lengthening of the ice-free period in Arctic lakes has been shown to lead to more diverse and  
317 ecologically complex algal communities (Griffiths et al., 2017). Additionally, lakes can  
318 support more complex and varied habitats with increasing temperatures as e.g. more complex  
319 aquatic macrophyte communities, a major structuring element in lake ecosystems, may occur  
320 in warmer lakes. Additionally, more pronounced thermal stratification under warmer climates  
321 may lead to the parallel occurrence of both summer warm and summer cold habitats in the  
322 same lake, whereas this may not be the case in colder climatic conditions. The stabilising or

323 even decreasing trends in alpha diversity at the warm end of the gradient could be explained  
324 by temperature-related effects such as seasonal stratification in combination with oxygen  
325 depletion, leading to the elimination of some chironomid species. Similarly, warmer lakes  
326 could experience a loss of aquatic macrophyte habitat due to phytoplankton blooms.

327

328 Comparisons of alpha diversity against environmental factors reveal that  $T_{jul}$  is the factor that  
329 is most strongly associated with chironomid diversity in four of our datasets (Table 1), with  
330 Spearman rank correlation coefficients between chironomid diversity and  $T_{jul}$  reaching a  
331 maximum value of  $\rho=0.79$ . Many of the chironomid datasets used in this study have been  
332 specifically designed to capture a large temperature gradient while aiming to minimise the  
333 influence of other environmental parameters, potentially partially explaining why water  
334 depth, pH or conductivity do not show strong relationships with chironomid diversity.

335         There is a positive association between TOC/DOC and chironomid diversity in the  
336 datasets for which TOC/DOC data is available ( $\rho$  ranges between 0.35 and 0.70). However,  
337 TOC/DOC is strongly correlated to  $T_{jul}$  in e.g. the Swiss and Norwegian datasets (Lotter et  
338 al., 1997; 1998; Brooks & Birks, 2001), and it is therefore unclear to what extent variations in  
339 temperature and variations in TOC/DOC independently drive spatial patterns in chironomid  
340 diversity. Similarly, there is a positive association between TP and chironomid diversity but it  
341 is unclear what the unique effects of TP are, independent of temperature. To further test the  
342 potential association between chironomid diversity and TP we applied rarefaction analysis to  
343 a lake dataset from Ontario (USA) by Quinlan & Smol (2001) which covers a gradient from  
344 ultraoligotrophic lakes to eutrophic lakes whilst covering a relatively short temperature  
345 gradient. The results indicate that there is no statistically significant association between  
346 chironomid diversity and TP ( $\rho = 0.072$ ,  $p = 0.573$ ) in this dataset.

347 Similarly, by running additional tests on a chironomid dataset from New England, US  
348 (Engels & Cwynar, 2011) as well as a dataset of lakes and reservoirs from New Jersey and  
349 New York states, US (Wazbinski & Quinlan, 2013) we further explored whether the absence  
350 of a strong correlation between water depth and chironomid diversity could be related to  
351 dataset design. The distribution of many individual chironomid taxa in the dataset by Engels  
352 & Cwynar (2011) is significantly correlated to water depth, likely attributable to factors like  
353 habitat differentiation, taphonomical processes, and oxygen availability. Analysis of both  
354 datasets shows only a weak positive association between chironomid diversity and water  
355 depth of  $\rho = 0.08$  ( $p=0.37$ ) for the Engels & Cwynar (2011) dataset, whereas the Wazbinski  
356 & Quinlan (2013) dataset shows a negative association of  $\rho = -0.38$  ( $p=0.01$ ) between water  
357 depth and chironomid diversity. The combined results suggest that unlike summer  
358 temperature, water depth is not a strong driver of chironomid diversity at the observed spatial  
359 scales, but that more research is needed to further explore the relationship between  
360 chironomid diversity and water depth.

361

### 362 Temporal trends in chironomid diversity

#### 363 *Last glacial–interglacial transition (LGIT)*

364 Four of the six UK LGIT records show a distinct change in diversity during the YD (Fig. 3a),  
365 either as a decrease in alpha diversity (e.g. Ashik; Fig. 3a) or as high compositional turnover  
366 (e.g. Sunbiggin Tarn; Fig. 3a). The records from Abernethy and Urswick Tarn furthermore  
367 show a decrease in both alpha diversity and increased compositional turnover during the  
368 multi-decadal cold interval associated with the Older Dryas (Fig. 3a). The records from Ashik  
369 and Whitrig Bog show high compositional turnover during the Older Dryas, but no variation  
370 in alpha diversity. The Older Dryas has not been identified in the Little Hawes Water and  
371 Sunbiggin Tarn records, and although there are oscillations in the compositional turnover

372 records of these sites, it is unclear whether these are associated with Older Dryas climate  
373 change or if they are the result of other factors.

374

375 The six LGIT sites from the European mainland (Fig. 3b) are located on a N-S transect (Fig.  
376 1). The southernmost two of these sites (Aubrac, Gerzensee) capture different parts of the  
377 LGIT interval, but neither site shows abrupt changes in diversity associated with the onset of  
378 the YD or the Holocene (Fig. 3). The records from Hijkermeer and Kråkenes show a decrease  
379 in alpha diversity as well as increased compositional turnover at the onset of the YD, whereas  
380 the diversity records for the sites from northern Europe (Lusvatnet, Jansvatnet) do not show  
381 any response to this large-scale climate cooling. A potential explanation for this discrepancy  
382 could lie in the fact that the amplitude of climate change showed regional differences across  
383 northwest Europe, with the most pronounced temperature change observed for the British  
384 Isles (e.g. Heiri et al., 2014), and that the change in temperature associated with the onset of  
385 the YD was not large enough to affect chironomid diversity across the European continent.  
386 All four central to northern European mainland sites show a distinct change in their alpha  
387 diversity and/or in compositional turnover records at the onset of the Holocene. The  
388 amplitude of climate change across this interval was large and occurred within a few decades  
389 (e.g. Brauer et al., 1999), and the direct effects of temperature most likely strongly influenced  
390 the composition of the freshwater invertebrate fauna across large parts of Europe (Heiri et al.,  
391 2014).

392 In summary, most of the LGIT records document decreasing chironomid diversity  
393 during colder periods, both during major climate oscillations (YD) as well as during shorter-  
394 lived climate oscillations (Older Dryas). The responses are not uniform across all sites, with  
395 some sites showing a decrease in alpha diversity and an increase in compositional turnover,  
396 but other sites only showing changes in one of the diversity parameters.

397

398 *Holocene*

399 The combined results for the Holocene records illustrate the complex relationship between  
400 chironomid diversity and the environment, where factors other than temperature override the  
401 diversity-temperature relationship that is apparent in the LGIT records. For instance, the  
402 chironomid diversity reconstructions for three Holocene chironomid records from the  
403 Kamchatka Peninsula show major differences between the sites (Fig. 4a). Lifebuoy Lake  
404 (Solovieva et al., 2015) shows changes in diversity and compositional turnover in the early  
405 Holocene, Pechora Lake (Andrén et al., 2015) shows increasing variability in the latter part of  
406 the record, and Olive-backed Lake (Self et al., 2015) shows a decreasing trend in alpha  
407 diversity throughout the entire Holocene. We suggest that for the Holocene, when  
408 temperature fluctuations for large parts of the Northern Hemisphere are generally assumed to  
409 have been smaller and more gradual than those of the LGIT (e.g. Bartlein et al., 2015),  
410 factors other than temperature (e.g. vegetation change, soil development) were more  
411 important drivers of changes in chironomid diversity at these sites.

412 Similarly, sites within relatively small regions like Norway and Finland show  
413 differences in both alpha diversity and compositional turnover trends during the Holocene,  
414 whereas climate change over these regions can be expected to be fairly homogeneous. Again,  
415 we attribute these differences in diversity trends to site-specific changes in the environment  
416 exerting a stronger influence on the chironomid fauna than climate change. For instance, the  
417 amplitude of temperature change during the Holocene across northern Europe was not as  
418 great as during the LGIT, and the chironomid fauna of some lakes, e.g. Giltjärnen, most  
419 likely responded most strongly to changes in the local environment (e.g. lake water pH, local  
420 peat development) rather than to temperature change (Antonsson et al., 2006).

421 From the North American sites, the Lake Hill record was retrieved from the remote  
422 St. Paul Island (Alaska, USA) and is assumed to have been primarily influenced by climate  
423 rather than anthropogenic factors (Wooller et al., 2018). It shows a decrease in alpha diversity  
424 around 6,000 cal yr BP (Fig. 4d). Similarly, while not reaching as far back in time as the Lake  
425 Hill record, the TK2 site from the Central Canadian Arctic shows high alpha diversity in the  
426 early part of the Holocene, with a decrease in alpha diversity and higher compositional  
427 turnover in the middle Holocene (ca 7,000 cal yr BP) (Porinchi et al., 2019). We suggest that  
428 these declines in diversity are related to regional climate cooling (Kaufman et al., 2004;  
429 Clegg et al., 2011).

430

#### 431 *Recent trends*

432 The complexity of the chironomid diversity-temperature relationship is also highlighted by  
433 recent records from northern North America (Fig. 5). While diversity increases with periods  
434 of recent anthropogenic warming in Baker Lake (BL01) and Lake T02, it decreases in Lake  
435 T15 (Fig. 5). The thermokarst basin of Lake T15 was shown to expand during a period that  
436 predated the warming trends for the southern Seward Peninsula in Alaska (Medeiros et al.,  
437 2014). The expansion of the thermokarst basin likely altered available habitat, including  
438 macrophyte growth and distribution, and as a result the chironomid assemblage shifted from a  
439 diverse fauna to a fauna dominated by a single taxon (Medeiros et al., 2014).

440

#### 441 *Deep-time ( $10^5$ years) records*

442 The lacustrine record from lake Billjakh (east Siberia, Russia; Diekmann et al., 2016) covers  
443 the time interval from the middle of the last glacial (MIS-3) to the present. The alpha  
444 diversity record of Billjakh shows highest diversity in the first part of MIS-3 and during the  
445 Holocene (Fig. 6a). This observation of higher chironomid diversity during warmer intervals

446 (early MIS-3, Holocene) across a large part of the last glacial cycle at Billjakh is in line with  
447 our results for the LGIT records (Fig. 3), which also showed increasing chironomid diversity  
448 with increasing temperature.

449 The sediment sequence of lake CF8, located in the northeastern Canadian Arctic,  
450 contains *in situ* preserved lake sediments that extend back from the present through the  
451 current interglacial (Holocene or Marine Isotope Stage (MIS)-1) to the two previous  
452 interglacials (MIS-5e and MIS-7). As such, it provides a unique record of past environmental  
453 change in the North American high Arctic (Axford et al., 2009). The MIS 7 part of the CF8  
454 record is relatively short, likely recording the waning, relatively cool part of this interglacial,  
455 and contains only a few chironomid samples with count sums that allow the calculation of  
456 changes in taxon richness (Fig. 6b). High taxon richness is recorded during the early and  
457 middle part of the MIS-5e record, when temperatures inferred from chironomid assemblages  
458 are significantly higher than today (Axford et al., 2009). Rarefaction results show increases  
459 from low values in the earliest part of the Holocene to maximum values in the cold late  
460 Holocene (Axford et al., 2009) with taxon richness values averaging around 10, similar to the  
461 maximum values reached during MIS-5e. The relatively low alpha diversity across the early  
462 and middle Holocene, when past temperatures likely were highest (e.g. Gajewski, 2015;  
463 Briner et al., 2016), is likely explained by the lower taxonomic resolution of this record.

464

#### 465 Quantitative comparison of modern-day and fossil trends in alpha diversity

466 This study provides, for the first time, a quantitative comparison between centennial- to  
467 multi-millennial-scale records and modern-day patterns in chironomid diversity. July air  
468 temperature shows a strong positive association to alpha diversity in our modern datasets  
469 (Fig. 2; Fig. 7), with particularly strong increases in diversity observed toward the colder end  
470 of the temperature gradient (ca. 2.5-14 °C). Similarly, most of the LGIT records presented in

471 this study document trends in chironomid alpha diversity that follow regional temperature  
472 variability, with higher diversity during the relatively warm Bølling/Allerød interstadial and  
473 during the early Holocene, and lower diversity during the YD and Older Dryas (Fig. 3). The  
474  $\Delta RF$  values for the modern Norwegian data and the fossil sites are mostly of a similar  
475 magnitude and show that there is a general trend of increasing  $\Delta RF$  with increasing  $\Delta T$  (Fig.  
476 7a). The increase in  $\Delta RF$  is limited when  $\Delta T$  is low (e.g.  $<2\text{ }^{\circ}\text{C}$ ). Between-site variation is  
477 high for the LGIT records and there is a relatively high number of fossil sites that show a  
478  $\Delta RF$  that is relatively small when compared to the  $\Delta RF$  observed in the Norwegian dataset  
479 for similar  $\Delta T$  and  $T_{jul}$  conditions. This low increase in  $\Delta RF$  for the fossil sites relative to the  
480  $\Delta RF$  observed in the modern sites might be related to the fact that in the modern dataset there  
481 are a number of environmental factors that differ between the individual sites (e.g. geology,  
482 soil development, microclimate), whereas the variations in environmental factors with time at  
483 one particular fossil site are likely to be lower, and mainly limited to climate change and its  
484 direct effects on catchment conditions.

485         The results for the YD-Holocene transition also show a general pattern of increasing  
486  $\Delta RF$  with increasing  $\Delta T$  in the fossil data (Fig. 7b), resembling both the pattern and  
487 magnitude of change in RF with increasing  $\Delta T$  as observed in the modern Norwegian dataset  
488 as well as the pattern observed for the B/A-YD transition. Results indicate that for this  
489 transition, which is characterised by abrupt climate warming, even small-scale warming (e.g.  
490  $<2\text{ }^{\circ}\text{C}$ ) led to a relatively high increase in  $\Delta RF$ . There are a few sites that show a  $\Delta RF$  in the  
491 fossil data that is larger than  $\Delta RF$  observed in the modern data (for similar  $\Delta T$  and  $T_{jul}$   
492 conditions), but again between-site variation is relatively large with some sites showing  
493 hardly any increase in  $\Delta RF$  even when e.g.  $\Delta T$  is  $4\text{ }^{\circ}\text{C}$  or higher. Concluding, the quantitative  
494 comparison between the Norwegian dataset and the LGIT records shows that the observed  
495 changes in alpha diversity are of similar direction and magnitude (Fig. 7). They furthermore

496 highlight that the positive association between alpha diversity and  $T_{jul}$  is especially well-  
497 expressed in colder or more Arctic sites, and, as expected, for larger changes in temperature  
498 (e.g.  $\Delta T > 4$  °C).

499

## 500 **Discussion**

### 501 Palaeoecological evidence for spatiotemporal trends in biodiversity

502 Our LGIT records generally show decreasing alpha diversity during colder periods such as  
503 the YD (Fig. 3). This confirms earlier, less comprehensive evidence on the relationship  
504 between temperature and lacustrine chironomid diversity patterns. Levesque et al. (1995)  
505 reconstructed chironomid diversity trends across the LGIT for four eastern Canadian records.  
506 Despite the low taxonomic resolution relative to later reconstructions, Levesque et al. (1995)  
507 documented decreasing alpha diversity during periods characterised by cold climate, similar  
508 to the results obtained in this study. Massaferro & Corley (1998) also reported decreasing  
509 chironomid diversity in response to climate cooling during the LGIT interval for sites in  
510 northern Patagonia. The amplitude of change in diversity in the records by Massaferro &  
511 Corley (1998) is relatively muted, which could be the result of the lower temperature  
512 amplitude associated with LGIT climate change in Northern Patagonia compared to the  
513 regions adjacent to the North Atlantic Ocean (Levesque et al., 1995; this study). However,  
514 there are major differences in the chironomid fauna adapted to cold environments in the  
515 southern hemisphere compared to the northern hemisphere (e.g. Brundin 1966), and  
516 Eggermont & Heiri (2012) show that globally different chironomid subfamilies have varying  
517 thermal optima. As chironomid-environment calibration datasets, as well as fossil datasets  
518 across a range of timescales, exist and are being developed for e.g. Australia (Rees et al.,  
519 2008), New Zealand (Van den Bos et al., 2018) or South America (Matthews-Bird et al.,  
520 2016), there is potential to apply our approach of comparing modern and fossil trends in

521 diversity to regions of the Southern Hemisphere as well as to the tropical regions presently  
522 under-represented in respect to fossil chironomid datasets. This will further improve our  
523 understanding of global drivers of chironomid diversity and will help to better predict future  
524 changes under projected global warming.

525         Stivrins et al. (2016) analysed lateglacial turnover rates in the Baltic region for a  
526 range of organisms, including higher plants, phytoplankton and animal communities. In  
527 general, all examined botanical and zoological groups show a similar trend, with lower  
528 turnover associated with the B/A-YD transition, and higher turnover associated with the YD-  
529 Holocene transition (Stivrins et al., 2016). This partially resembles our results, as we also  
530 observe abrupt and distinct changes in compositional turnover associated with Younger  
531 Dryas cooling and Holocene warming. We hypothesise that the relatively smaller impact of  
532 the cooling associated with the onset of the Younger Dryas on chironomid diversity, relative  
533 to the impact of the warming after the event, is related to the more gradual nature of this  
534 transition, whereas the onset of the Holocene in Europe was more abrupt (Brauer et al., 1999;  
535 Engels et al., 2016) and therefore had a stronger impact on freshwater ecosystems, including  
536 the chironomid fauna of our study sites.

537         The amplitude of temperature change during the Holocene was relatively small and  
538 occurred gradually at many of our sites, and we suggest that long term variations in site-  
539 specific factors such as soil development, vegetation change, nutrient availability and  
540 changes in the macrophyte community also influenced the development of the chironomid  
541 diversity in individual lakes. It could be argued that in the North Atlantic region the early  
542 Holocene (Walker et al., 2012) is the period with the highest environmental dynamics, as the  
543 catchments surrounding many sites were colonised by trees, soils stabilised and weathering  
544 dynamics and nutrient availability changed accordingly, potentially affecting the chironomid  
545 fauna at each of our study sites. However, our chironomid diversity records generally lack an

546 initial phase of instability during the early Holocene. Recent publications suggest that post-  
547 glacial ecosystem development in lakes has been much faster than previously thought  
548 (Helmens et al., 2018), and, combined with the potential for fast dispersal and colonisation by  
549 chironomids (Brooks et al., 2007), this might explain the relatively stability of our  
550 chironomid diversity records during the early Holocene.

551 Our results show a general trend of increasing chironomid diversity as a result of  
552 recent climate warming in two out of our three records (Fig. 5), which is in line with  
553 centennial-scale compositional turnover reconstructions for seven out of eight chironomid  
554 records from the Arctic (Smol et al., 2005). Ilyashuk et al. (2015) reconstructed trends in  
555 chironomid compositional turnover in three remote lakes in the Alps. While they show  
556 different trends for most of the past two millennia, major assemblage turnover was visible in  
557 all three sites in the interval between 1850 CE and the present (Ilyashuk et al., 2015). Finally,  
558 Nevalainen et al. (2015) studied chironomid diversity trends in four climate-sensitive treeline  
559 lakes in Austria. While their results show inter-site variability, chironomid diversity did  
560 increase in two of the studied lakes toward the twentieth and twenty-first centuries.

561

#### 562 Effects of projected global warming on chironomid diversity

563 Summer temperatures are predicted to increase across the 21<sup>st</sup> century as a result of enhanced  
564 atmospheric greenhouse gas concentrations, where polar amplification will result in higher  
565 temperature increases in high-latitude regions compared to the global average  
566 (Intergovernmental Panel on Climate Change, 2014). We speculate that cold-stenothermic  
567 taxa will go locally extinct from many shallow Arctic and subarctic lakes under sustained  
568 global warming (Armitage et al., 1995; Hamerlik et al., 2017). However, our results suggest  
569 that, as a result of this projected warming, lakes in the Arctic and subarctic are likely to  
570 experience an increase in chironomid diversity, as warm-stenothermic taxa disperse into

571 regions and habitats that currently experience temperatures that are too low for their  
572 development.

573         Our palaeoecological records show that for periods with relatively small temperature  
574 change, e.g. in the order of 2 °C or less, the response of chironomid diversity to temperature  
575 change is muted or even non-existent, and the influence of factors-other-than-temperature is  
576 relatively more important. Additionally, our results show stabilising or even decreasing alpha  
577 diversity with high summer temperatures (ca. >14 °C) which could at least partially be the  
578 result of indirect climate effects, where e.g. sufficiently high temperatures could result in  
579 algal blooms, longer growing seasons, lake water stratification and decreases in hypolimnetic  
580 oxygen availability, including greater winter under-ice oxygen depletion following warmer  
581 more productive summers, favouring chironomid taxa adapted to these environmental  
582 conditions. Combined, this means that for mid-latitude regions in the Northern Hemisphere,  
583 where projected warming is relatively small compared to high-latitude regions, a  
584 temperature-driven increase in chironomid diversity across the 21<sup>st</sup> century should not  
585 necessarily be expected.

586         The decreasing trend in chironomid diversity at higher temperatures as seen in some  
587 of our modern datasets could furthermore be explained by the greater human impact in  
588 catchments of warmer lakes, especially in Europe, where population density and human  
589 impact on the landscape are greater in the warmer parts of the regions covered by the  
590 respective datasets. Increased nutrient influx due to human land use has been known to lead  
591 to the disappearance of aquatic macrophytes (e.g. Bradshaw et al., 2005; Engels et al., 2018),  
592 as well as to a decrease in oxygen availability (Quinlan and Smol, 2001), thus decreasing  
593 habitat availability and variability, and, ultimately, the potential for a diverse chironomid  
594 community to develop or persist. With the ongoing anthropogenic impact on the landscape  
595 (Steffen et al., 2015) we will likely see further disturbances in freshwater ecosystems across

596 the globe (Doncaster et al., 2016). Our results imply expected overall chironomid diversity  
597 increases under sustained global warming, but with complex and not necessarily predictable  
598 responses for individual sites due to the effects of local disturbances such as eutrophication or  
599 land use change.

600 Chironomids are often among the most abundant invertebrates in a lake ecosystem  
601 and are a keystone taxon in freshwater ecosystems (Brooks et al., 2007). Their preservation in  
602 lake sediment records provides one of the very few means to reconstruct changes in insect  
603 diversity on timescales longer than e.g. the last 100 years. Recent studies that highlighted the  
604 ongoing declines in insect abundance and diversity were focussed on grasslands, heathlands  
605 and wastelands and did not include aquatic groups (e.g. Hallmann et al., 2017; Jourdan et al.,  
606 2018). As freshwater communities are threatened by high rates of biodiversity loss due to a  
607 range of different environmental factors (Dudgeon et al., 2006), a better understanding of  
608 natural variability and resilience in freshwater ecosystems is critical for effective wetland  
609 management and the conservation of freshwater biodiversity. Our results illustrate the  
610 potential of using chironomids as indicators of spatiotemporal changes in biodiversity and  
611 highlight the unique perspective that this source of data can provide in order to test ecological  
612 theory about diversity response to environmental change.

613

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625

626 The authors have no conflicts of interest.

627

### 628 **Supporting information**

629 Supplementary information consists of two files. First, a Word file containing three tables  
630 (Table S1: Modern chironomid datasets; Table S2: Lateglacial-interglacial transitions sites;  
631 Table S3: Holocene, recent and other chironomid records) and one figure (Figure S1a:  
632 Illustration of  $\Delta RF$  calculation for Norwegian dataset; Figure S1b: Illustration of  $\Delta RF$   
633 calculation for LGIT records), as well supporting text and the R code used to produce the  
634 results presented here. Second, the Supplementary Information contains an XLS-file with  
635 datasheets containing the results of this study.

636

### 637 **Data accessibility**

638 The data produced in this study can be found in the Supplementary information. The datafile  
639 includes all the diversity estimates produced as well as the information needed to produce the  
640 figures presented in this manuscript. Original chironomid count datasets can be requested  
641 from the original authors; see Supplementary Tables S1 (calibration datasets) and S2-S3  
642 (fossil records) for the original publication details.

643

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1017

1018 **Tables**

1019 *Table 1. Spearman’s rank-order coefficient of correlation for rarefaction values vs*  
 1020 *environmental variables for each of the individual calibration datasets. Due to the nature of*  
 1021 *designing and producing a chironomid-climate calibration dataset, not all environmental*  
 1022 *variables were measured at each site; if individual values were missing, these sites were left*  
 1023 *out of the calculation for that specific correlation coefficient. Typically, however, a large*  
 1024 *proportion of the sites (if not all) were included in the analysis. NA: Not Available; \**  
 1025 *statistically significant at  $p = 0.05$ , values corrected for multiple testing within a calibration*  
 1026 *dataset using False Discovery Rate (FDR) correction (Benjamini & Hochberg, 1995)*  
 1027 *following Garcia (2004)*

	Norwegian dataset	Russian dataset	Canadian dataset	Swiss dataset	Finnish dataset
T <sub>jul</sub>	0.79*	0.43*	0.61*	0.69*	0.07
Depth	0.30*	0.18*	-0.21	0.17*	-0.05
pH	-0.18	0.10	-0.02	0.08	0.22
Conductivity	0.00	-0.01	-0.06	0.52*	0.32*
TOC/DOC	0.70*	NA	0.35*	0.64*	NA
TP	NA	NA	0.17*	0.42*	NA

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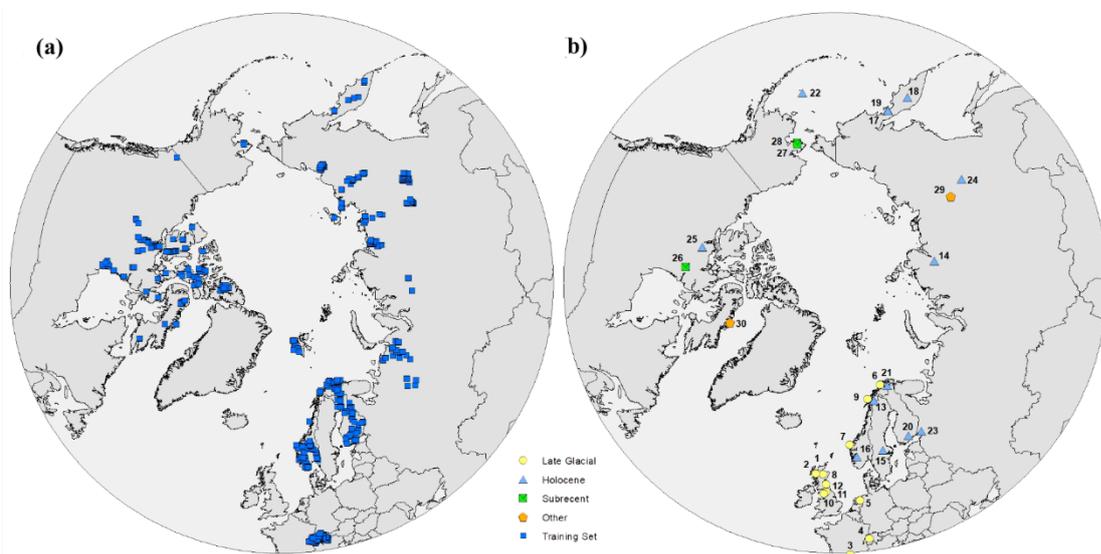
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1030 **Figure captions**

1031 *Fig. 1: Location of (a) the lakes included in the chironomid-climate calibration datasets (blue*  
1032 *squares) and (b) the downcore study sites (yellow circles = Lateglacial sites, blue triangles =*  
1033 *Holocene sites, green squares = subrecent sites, orange pentagons = other sites) presented in*  
1034 *this paper. Numbers in (b) correspond to lake numbers in Supplementary tables S2 and S3*  
1035 *where more details on the sites are provided.*

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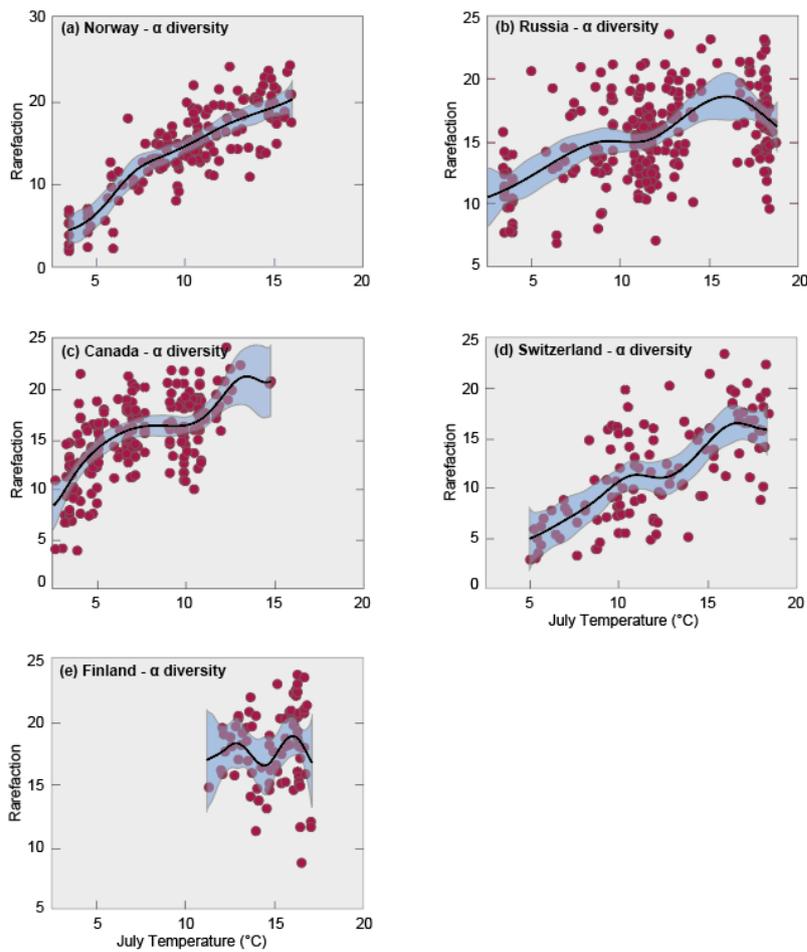
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1040 *Fig. 2: Modern-day subfossil chironomid diversity as estimated using rarefaction analysis*  
1041 *against July air temperatures (°C) for datasets from (a) Norway, (b) Russia, (c) Canada, (d)*  
1042 *Switzerland and (e) Finland (Supplementary Table S1). Solid black lines are GAM-based*  
1043 *trendlines for rarefaction values with uncertainty intervals in light blue.*

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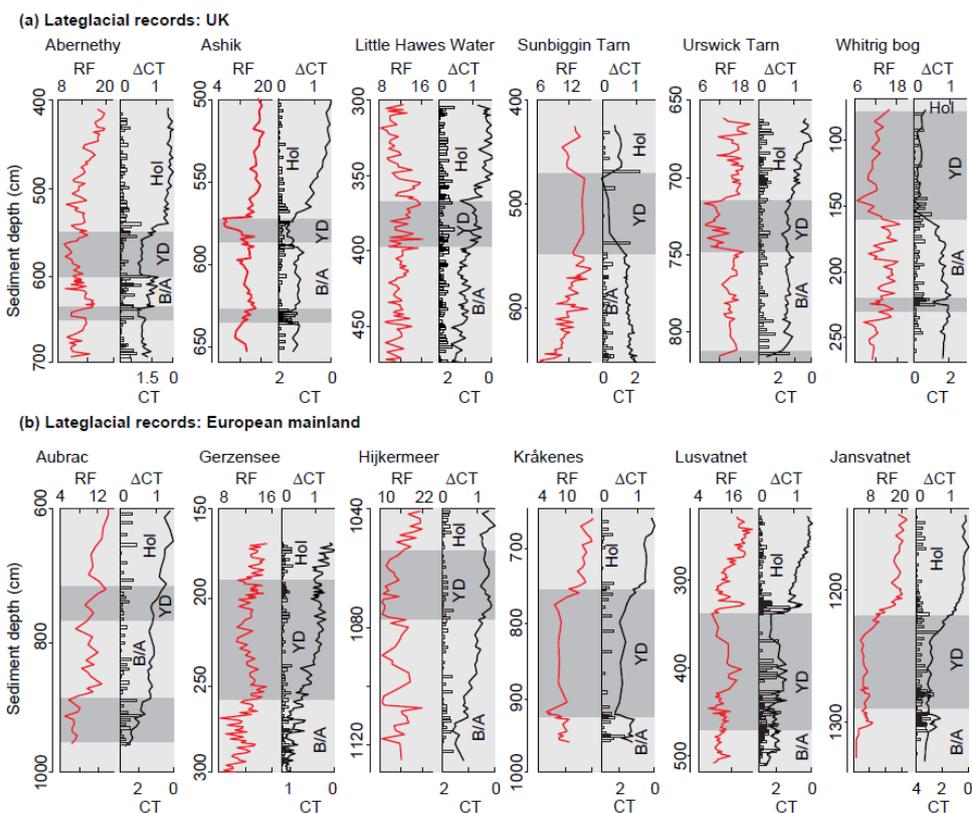
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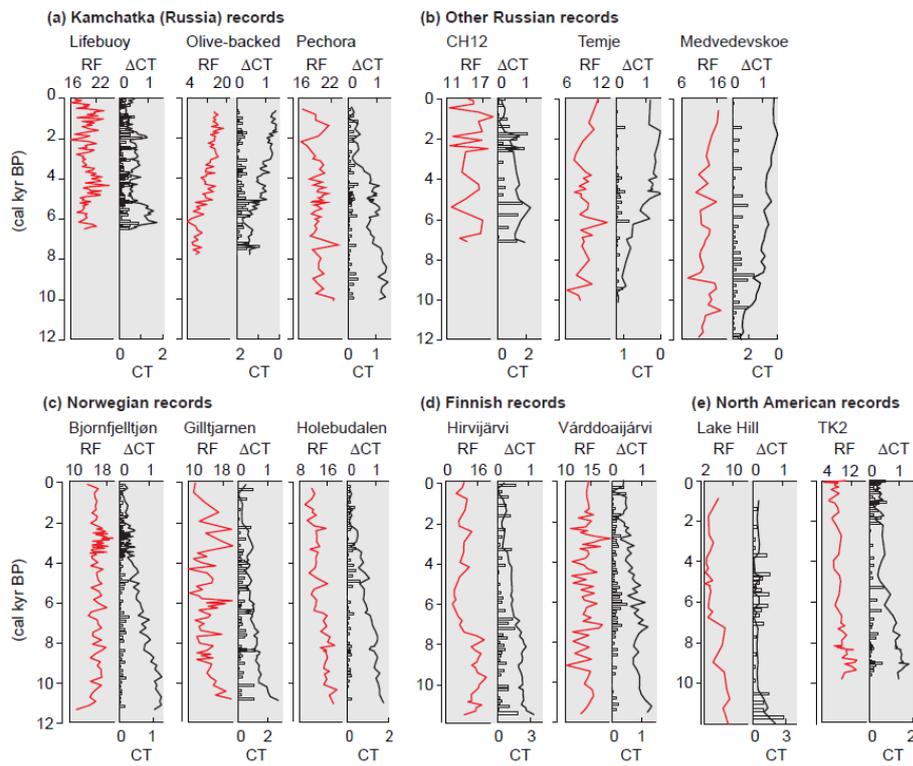
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1048 Fig. 3: Lateglacial-interglacial transition (LGIT) chironomid diversity records from  
 1049 northwest Europe: (a) UK sites and (b) sites from the European mainland, arranged on a S-N  
 1050 transect (see Fig. 1 for location of sites). Alpha diversity estimated through rarefaction  
 1051 analysis (RF; red solid line); compositional turnover (CT) as determined from Detrended  
 1052 Canonical Correspondence Analysis (DCCA) axis 1 (black solid line) in SD units (CT;  
 1053 bottom x-axis) and delta-CT for adjacent samples in open black bars ( $\Delta$ CT; SD units, top x-  
 1054 axis). Directions of CT plots differ between individual sites and are selected to enable  
 1055 comparison against the alpha diversity records. Dark (Younger Dryas; YD) and light shading  
 1056 (Bølling/Allerød (B/A) and Holocene (Hol)) indicate the Lateglacial biozones as determined  
 1057 for each site (see Supplementary Table S2 for more information on the sites).  
 1058  
 1059



1060

1061 Fig. 4: Chironomid diversity trends in Holocene records from (a) Kamchatka (Russia), (b)  
 1062 other Russian sites, (c) Norway, (d) Finland, and (e) North America. All records are plotted  
 1063 using the age-depth models as provided in the original publications (see Supplementary  
 1064 Table S3 for more details on the sites). See Fig. 3 for an explanation of the symbols.



1067

1068

1069 *Fig. 5: Recent chironomid diversity records from northern North America. Records are*  
1070 *plotted using the age-depth models provided in the original publications. See Supplementary*  
1071 *Table S3 for more details on the sites, and Fig. 3 for an explanation of the symbols. Note that*  
1072 *the x-axis for the CT plot for T15 has been reversed to better illustrate the similarity in trends*  
1073 *between alpha diversity and compositional turnover.*

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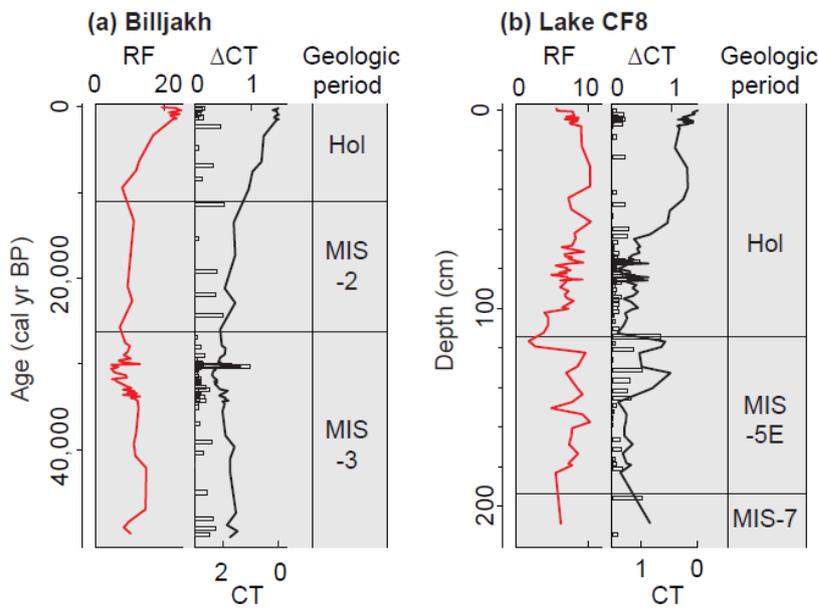
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1079 *Fig. 6: Chironomid diversity records from (a) Billjakh (East Siberia, Russia) and (b) CF8*  
 1080 *(Canada). The Billjakh record spans the period from the middle of Marine Isotope Stage*  
 1081 *(MIS) 3 to the present, whereas the CF8 record covers (parts of) the past three interglacials:*  
 1082 *MIS-7 (ca 245-186 kyr BP), MIS-5E (ca 129-116 kyr BP) and the Holocene (11.6 cal kyr BP-*  
 1083 *present). The geological periods are plotted next to the diversity records for reference. See*  
 1084 *Fig. 3 for an explanation of the symbols.*

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1089 *Fig. 7: Quantitative comparison of changes in alpha diversity ( $\Delta RF$ ) with changes in*  
1090 *temperature ( $\Delta T$ ) for the Norwegian dataset (continuous field in background) and the LGIT*  
1091 *records (circles) for (a) the Bølling/Allerød-Younger Dryas transition and (b) the Younger*  
1092 *Dryas- Holocene transition. X-axis indicates the lowest temperature of a couplet of*  
1093 *observations; y-axis represents the difference in absolute temperatures between the couplet*  
1094 *of observations ( $\Delta T$ ). Plotted values (represented by colour scale and, for fossil records,*  
1095 *symbol size) represent the change in alpha diversity as estimated through rarefaction*  
1096 *analysis ( $\Delta RF$ ) between any couplet of observations. For instance, the figure illustrates how*  
1097 *much, on average, RF increases in the Norwegian dataset between sites for a given lower*  
1098 *temperature (x-axis) and sites at temperatures  $\Delta T$  higher (y-axis). Similarly, the results show*  
1099 *by how much RF decreased between the B/A and the YD (Fig. 7a; results shown as absolute*  
1100 *values to enable comparison) and increased from the YD to the Holocene (Fig 7b) for each of*  
1101 *the LGIT sites by plotting the average temperature of the YD (x-axis), the change in*  
1102 *temperature across the climate transition (y-axis) and  $\Delta RF$  (symbol size and colour). See*  
1103 *main text and Supplementary Figure S1 for more information.*

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