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

2 (Insecta: Diptera) diversity

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4 Running head: Temperature change and chironomid diversity

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39

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41 **Abstract**

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

65 **Introduction**

66 Key environmental parameters such as greenhouse gas concentrations, ocean acidity, and
67 erosion rates are now beyond their previous Holocene range of variability as a result of
68 human activity (Corlett, 2015; Steffen et al., 2015). These environmental stressors are leading
69 to dramatic changes in the structure and composition of biological communities across local
70 to global spatial scales and to a decrease in global biodiversity (e.g. Ripple et al., 2017). For
71 example, the invertebrate fauna of northwest Europe is showing signs of a dramatic decrease
72 in abundance and diversity (Hallmann et al., 2017; Bidau, 2018; Jourdan et al., 2018; Leather
73 2018; Rada et al., 2019) and freshwater ecosystems are showing a particularly high rate of
74 biodiversity loss (Dudgeon et al., 2006).

75 Most records that are used to assess the effects of anthropogenic drivers (e.g. climate
76 variability, eutrophication, toxins, impacts associated with invasive species) on biodiversity
77 are based on decadal-scale ecological data (Vellend et al., 2013; Birks et al., 2016a; W.W.F.,
78 2016). In many natural settings it has been difficult to disentangle natural variability from the
79 effects of human-induced ecosystem change (Loreau et al., 2001; Willis & Birks, 2006) as a
80 result of these short time-scales typically used. Datasets that cover much longer timescales,
81 e.g. several centuries to millennia, can help to provide a broader temporal context for current
82 and future trends in biodiversity and facilitate the development of effective conservation
83 strategies (Willis & Birks, 2006; Gregory-Eaves & Beisner, 2011; Birks et al., 2016a). Willis
84 & Birks (2006) and Birks et al. (2016a) provide examples of the role that palaeoecological
85 datasets can play in providing such centennial- to millennial-scale time series, and how these
86 data can provide new insights into the complex relationships that exist between biodiversity,
87 ecosystem functioning, and environmental variability. Despite the fact that many natural
88 archives are available for study by palaeo- and neo-ecologists, these sources of information
89 have rarely been used to infer past changes in biodiversity within the context of human

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

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

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

115 (Medeiros et al., 2012; Heiri et al., 2014; Brooks et al., 2016), water depth (Engels et al.,
116 2012; Nazarova et al., 2017), salinity (Dickson et al., 2014), hypolimnetic oxygen (Quinlan &
117 Smol, 2001), and several other environmental variables. Subfossil chironomids encountered
118 in lake sediment records can additionally be used to track changes in past species richness or
119 evenness of the fauna through time (e.g. Engels et al., 2010). However, palaeoecological
120 datasets describing chironomid faunal dynamics on centennial to millennial timescales have
121 not yet been compiled to produce systematic and super-regional studies of past diversity
122 patterns.

123 While it is often assumed that the global decline in biodiversity is accompanied by
124 declines at finer spatial scales, local biodiversity has been shown to have been stable in many
125 regions even when global biodiversity trends show significant decreases (Cardinale et al.,
126 2018; Primack et al., 2018). It therefore follows that biodiversity at large spatial scales is not
127 necessarily an additive function of biodiversity at smaller scales (Vellend et al., 2013) and
128 that investigating biodiversity at a range of spatial scales is necessary to understand the
129 ongoing changes in biodiversity as a result of climatic and environmental change (Primack et
130 al., 2018). While palynological records provide long-term trends of regional changes in
131 vegetation (e.g. Birks et al., 2016a), there are currently no studies that assess long-term
132 diversity change on finer spatial scales, such as individual aquatic ecosystems. Therefore, this
133 study aims to contribute toward filling the gap in our understanding of long-term trends in
134 local-scale biodiversity changes and to provide a long-term perspective to the recent decline
135 in insect diversity. Specifically, we aim to assess long-term changes in chironomid diversity,
136 a keystone member of freshwater ecosystems, by:

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

139 the effects of summer temperature on chironomid assemblages across the mid- and
140 high-latitudes of the northern hemisphere (reflecting the availability of datasets);
141 (2) Analysing spatiotemporal changes in chironomid diversity across a range of
142 timescales; and
143 (3) Assessing the suitability of subfossil chironomid assemblages as an approach to
144 reconstruct changes in diversity over longer timescales.

145

146 **Materials and methods**

147 Materials

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

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

164 environmental parameters other-than-temperature on chironomid diversity will be more
165 empirical.

166

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

177 The LGIT was characterised by a number of climate events in the North Atlantic
178 region. The general trend of climate warming was interrupted by a major cold phase (stadial)
179 known as the Younger Dryas (YD), which occurred between ca. 12,650 and 11,600 cal yr BP
180 (e.g. Litt et al., 2001). The relatively warm Bølling-Allerød interstadial (B/A; ca 14,500-
181 12,650 cal yr BP) preceding the YD was punctuated by at least two decadal to centennial
182 scale climate cooling events, the Gerzensee Oscillation (GZO or Greenland Interstadial event
183 (GI)-1b) and the Older Dryas (or GI-1d; Lotter et al., 1992). The YD has been
184 palynologically identified in each of the LGIT records presented in this paper and several of
185 the records also identified the Gerzensee Oscillation and the Older Dryas (depending on
186 location of the sites, temporal sampling resolution and proxy sensitivity). Supplementary
187 Table S2 provides more details on the sites used in this study.

188

189 Numerical analyses

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

194

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

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

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

220

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

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

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

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

250

251 Finally, we quantitatively compare the rarefaction results for the Norwegian calibration
252 dataset to the LGIT reconstructions to assess whether the effects of temperature on alpha
253 diversity, as observed in modern-day chironomid assemblages, are comparable to those of the
254 distant past. To do so, we assessed the change in rarefaction (ΔRF) with changing T_{jul} (ΔT_{jul})
255 across the entire temperature interval included in the Norwegian calibration dataset. In a first
256 step, we calculated the average RF (RF_{ave}) value for each consecutive 1-°C bin (e.g. 3.00-
257 3.99 °C ($T_{3.5C}$)) in the Norwegian calibration dataset. We then calculated changes in RF
258 (ΔRF) for each possible combination of 1-°C bins across the 3-16 °C temperature interval
259 covered by the Norwegian calibration dataset. This approach allows us to observe whether
260 e.g. a change of 2 °C has the same effects on the taxonomic diversity of a lake situated e.g. at
261 8 °C as for a lake situated at e.g. 14 °C, as well as to compare the effects an increase of 2 °C
262 would have compared to the effects of an increase of 4 °C at the same site. We used the

263 geom_raster function as included in the R ggplot2 package to produce a continuous plot of
264 changes in RF (Δ RF) for each absolute temperature (e.g. $T = 3.5\text{ }^{\circ}\text{C}$) and each possible
265 increase in temperature (ΔT).

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

281 The T_{jul} records used in this calculation are chironomid-based temperature inferences
282 and are based on the same datasets as the alpha diversity reconstructions, and as such are not
283 independent. However, in the absence of independent temperature estimates this is currently
284 the only method that allows the quantitative comparison of our modern data to our fossil
285 reconstructions.

286

287 **Results and interpretation**

288 Spatial trends in chironomid diversity

289 All datasets show similar TR values ranging between minima of 1-5 to maximum values over
290 20 (Fig. 2). Chironomid alpha diversity generally shows an increasing trend with increasing
291 T_{jul} for four out of the five regional datasets (Fig. 2). In the Norwegian and Canadian datasets
292 the increase in alpha diversity is steepest in the coldest part of the temperature gradient (ca. 3-
293 7 °C interval), after which a more moderate increase in diversity can be seen. For some of the
294 datasets that cover temperatures exceeding ca. 14 °C (e.g. Russia, Switzerland) we observe a
295 stabilising or decreasing trend in alpha diversity with higher temperatures. Three of the
296 datasets show additional variation superimposed on the general trend of increasing diversity
297 with increasing temperature, which might be the result of sampling density along the
298 temperature gradient, site-specific factors resulting in a lower alpha diversity in individual
299 lakes, or it might be a true reflection of decreasing alpha diversity for currently unidentified
300 reasons. The Finnish dataset captures a smaller temperature gradient than the other datasets
301 and GAM shows a highly variable but non-directional trend in alpha diversity. However, as
302 in the other datasets, some of the lakes with mean July air temperature higher than 14 °C are
303 characterized by relatively low alpha diversity. Explanations for the general increase in
304 chironomid diversity with temperature in most of our datasets could include availability of
305 more and higher-quality food sources with increasing temperatures. For instance, the
306 lengthening of the ice-free period in Arctic lakes has been shown to lead to more diverse and
307 ecologically complex algal communities (Griffiths et al., 2017). Additionally, lakes can
308 support more complex and varied habitats with increasing temperatures as e.g. more complex
309 aquatic macrophyte communities, a major structuring element in lake ecosystems, may occur
310 in warmer lakes. Additionally, more pronounced thermal stratification under warmer climates
311 may lead to the parallel occurrence of both summer warm and summer cold habitats in the
312 same lake, whereas this may not be the case in colder climatic conditions. The stabilising or

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

317

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

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

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

351

352 Temporal trends in chironomid diversity

353 *Last glacial–interglacial transition (LGIT)*

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

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

364

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

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

387

388 *Holocene*

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

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

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

420

421 *Recent trends*

422 The complexity of the chironomid diversity-temperature relationship is also highlighted by
423 recent records from northern North America (Fig. 5). While diversity increases with periods
424 of recent anthropogenic warming in Baker Lake (BL01) and Lake T02, it decreases in Lake
425 T15 (Fig. 5). The thermokarst basin of Lake T15 was shown to expand during a period that
426 predated the warming trends for the southern Seward Peninsula in Alaska (Medeiros et al.,
427 2014). The expansion of the thermokarst basin likely altered available habitat, including
428 macrophyte growth and distribution, and as a result the chironomid assemblage shifted from a
429 diverse fauna to a fauna dominated by a single taxon (Medeiros et al., 2014).

430

431 *Deep-time (10^5 years) records*

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

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

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

454

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

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

461 this study document trends in chironomid alpha diversity that follow regional temperature
462 variability, with higher diversity during the relatively warm Bølling/Allerød interstadial and
463 during the early Holocene, and lower diversity during the YD and Older Dryas (Fig. 3). The
464 ΔRF values for the modern Norwegian data and the fossil sites are mostly of a similar
465 magnitude and show that there is a general trend of increasing ΔRF with increasing ΔT (Fig.
466 7a). The increase in ΔRF is limited when ΔT is low (e.g. $<2\text{ }^{\circ}\text{C}$). Between-site variation is
467 high for the LGIT records and there is a relatively high number of fossil sites that show a
468 ΔRF that is relatively small when compared to the ΔRF observed in the Norwegian dataset
469 for similar ΔT and T_{Jul} conditions. This low increase in ΔRF for the fossil sites relative to the
470 ΔRF observed in the modern sites might be related to the fact that in the modern dataset there
471 are a number of environmental factors that differ between the individual sites (e.g. geology,
472 soil development, microclimate), whereas the variations in environmental factors with time at
473 one particular fossil site are likely to be lower, and mainly limited to climate change and its
474 direct effects on catchment conditions.

475 The results for the YD-Holocene transition also show a general pattern of increasing
476 ΔRF with increasing ΔT in the fossil data (Fig. 7b), resembling both the pattern and
477 magnitude of change in RF with increasing ΔT as observed in the modern Norwegian dataset
478 as well as the pattern observed for the B/A-YD transition. Results indicate that for this
479 transition, which is characterised by abrupt climate warming, even small-scale warming (e.g.
480 $<2\text{ }^{\circ}\text{C}$) led to a relatively high increase in ΔRF . There are a few sites that show a ΔRF in the
481 fossil data that is larger than ΔRF observed in the modern data (for similar ΔT and T_{Jul}
482 conditions), but again between-site variation is relatively large with some sites showing
483 hardly any increase in ΔRF even when e.g. ΔT is $4\text{ }^{\circ}\text{C}$ or higher. Concluding, the quantitative
484 comparison between the Norwegian dataset and the LGIT records shows that the observed
485 changes in alpha diversity are of similar direction and magnitude (Fig. 7). They furthermore

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

489

490 **Discussion**

491 Palaeoecological evidence for spatiotemporal trends in biodiversity

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

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

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

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

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

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

551

552 Effects of projected global warming on chironomid diversity

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

561 regions and habitats that currently experience temperatures that are too low for their
562 development.

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

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

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

590 Chironomids are often among the most abundant invertebrates in a lake ecosystem
591 and are a keystone taxon in freshwater ecosystems (Brooks et al., 2007). Their preservation in
592 lake sediment records provides one of the very few means to reconstruct changes in insect
593 diversity on timescales longer than e.g. the last 100 years. Recent studies that highlighted the
594 ongoing declines in insect abundance and diversity were focussed on grasslands, heathlands
595 and wastelands and did not include aquatic groups (e.g. Hallmann et al., 2017; Jourdan et al.,
596 2018). As freshwater communities are threatened by high rates of biodiversity loss due to a
597 range of different environmental factors (Dudgeon et al., 2006), a better understanding of
598 natural variability and resilience in freshwater ecosystems is critical for effective wetland
599 management and the conservation of freshwater biodiversity. Our results illustrate the
600 potential of using chironomids as indicators of spatiotemporal changes in biodiversity and
601 highlight the unique perspective that this source of data can provide in order to test ecological
602 theory about diversity response to environmental change.

603

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615

616 The authors have no conflicts of interest.

617

618 **Supporting information**

619 Supplementary information consists of two files. First, a Word file containing three tables
620 (Table S1: Modern chironomid datasets; Table S2: Lateglacial-interglacial transitions sites;
621 Table S3: Holocene, recent and other chironomid records) and one figure (Figure S1a:
622 Illustration of ΔRF calculation for Norwegian dataset; Figure S1b: Illustration of ΔRF
623 calculation for LGIT records), as well supporting text and the R code used to produce the
624 results presented here. Second, the Supplementary Information contains an XLS-file with
625 datasheets containing the results of this study.

626

627 **Data accessibility**

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

633

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1008 **Tables**

1009 *Table 1. Spearman's rank-order coefficient of correlation for rarefaction values vs*
 1010 *environmental variables for each of the individual calibration datasets. Due to the nature of*
 1011 *designing and producing a chironomid-climate calibration dataset, not all environmental*
 1012 *variables were measured at each site; if individual values were missing, these sites were left*
 1013 *out of the calculation for that specific correlation coefficient. Typically, however, a large*
 1014 *proportion of the sites (if not all) were included in the analysis. NA: Not Available; **
 1015 *statistically significant at $p = 0.05$, values corrected for multiple testing within a calibration*
 1016 *dataset using False Discovery Rate (FDR) correction (Benjamini & Hochberg, 1995)*
 1017 *following Garcia (2004)*

	Norwegian dataset	Russian dataset	Canadian dataset	Swiss dataset	Finnish dataset
T _{jul}	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

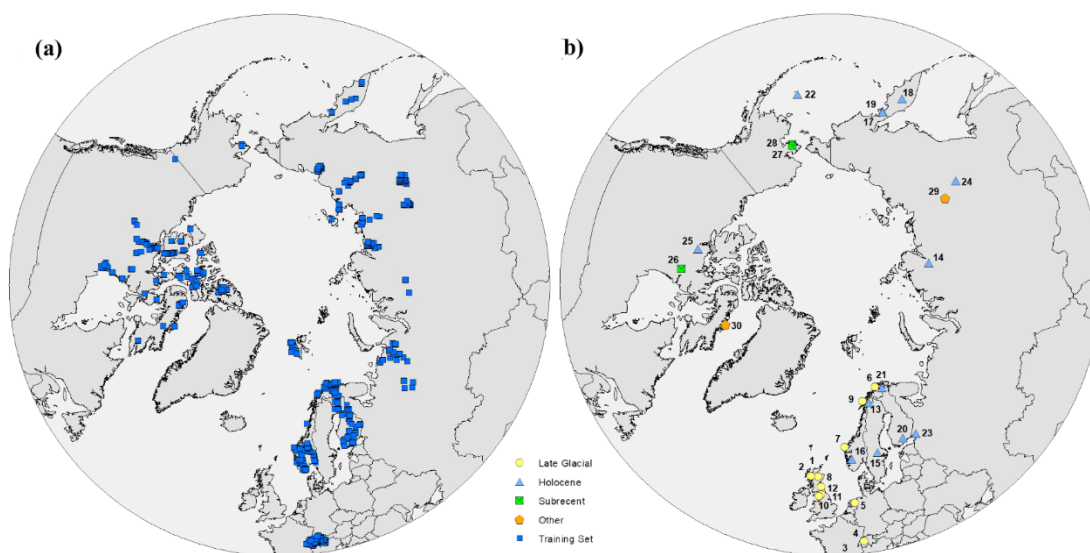
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1020 **Figure captions**

1021 *Fig. 1: Location of (a) the lakes included in the chironomid-climate calibration datasets (blue*
1022 *squares) and (b) the downcore study sites (yellow circles = Lateglacial sites, blue triangles =*
1023 *Holocene sites, green squares = subrecent sites, orange pentagons = other sites) presented in*
1024 *this paper. Numbers in (b) correspond to lake numbers in Supplementary tables S2 and S3*
1025 *where more details on the sites are provided.*

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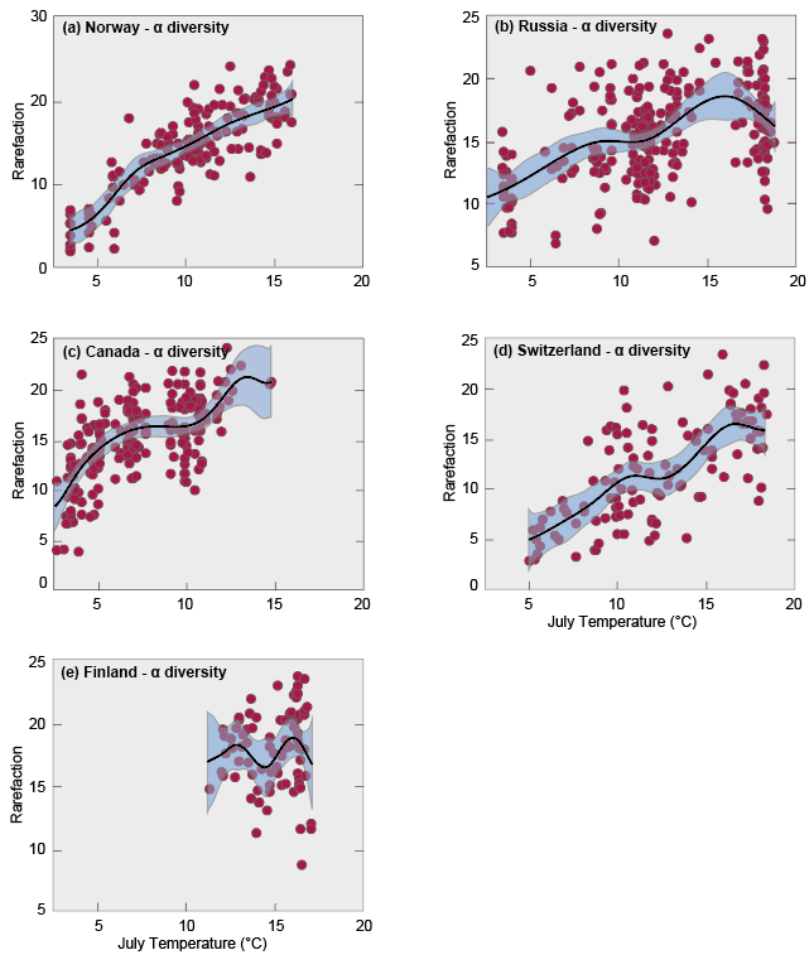


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1030 *Fig. 2: Modern-day subfossil chironomid diversity as estimated using rarefaction analysis*
1031 *against July air temperatures (°C) for datasets from (a) Norway, (b) Russia, (c) Canada, (d)*
1032 *Switzerland and (e) Finland (Supplementary Table S1). Solid black lines are GAM-based*
1033 *trendlines for rarefaction values with uncertainty intervals in light blue.*
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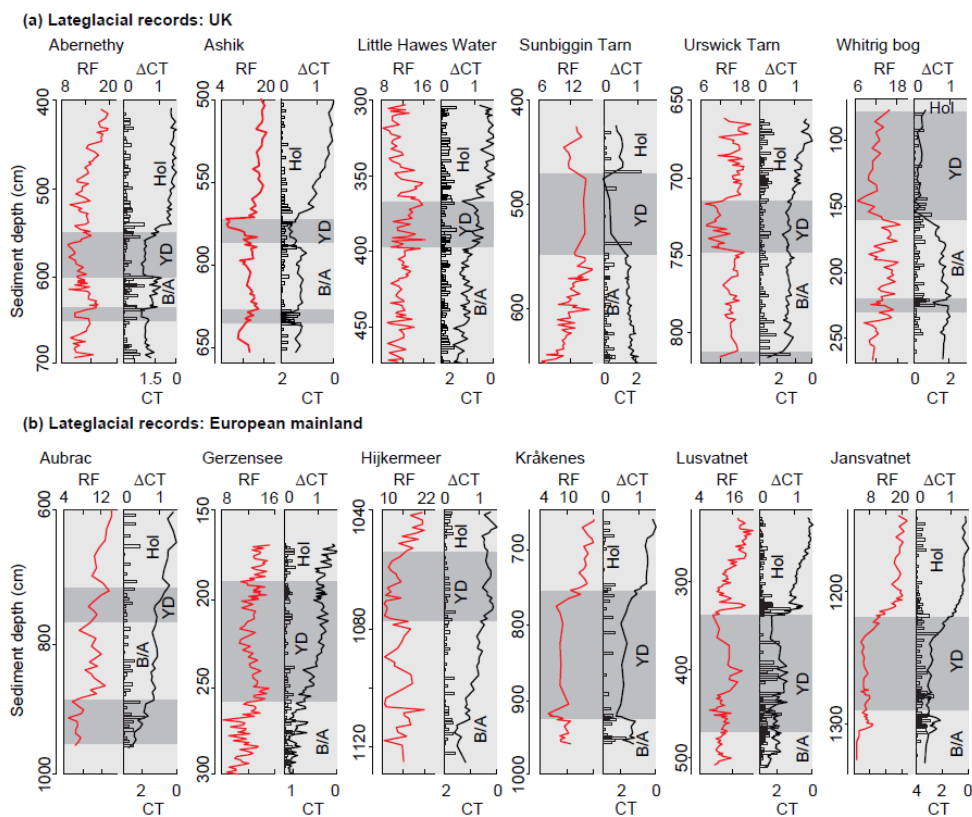


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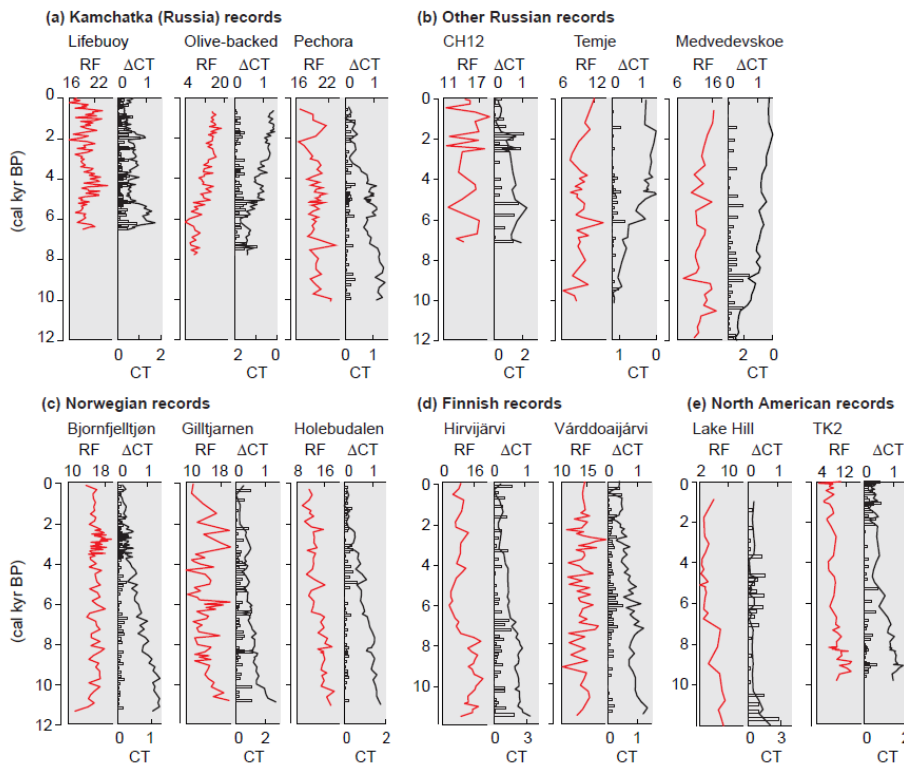
1038 Fig. 3: Lateglacial-interglacial transition (LGIT) chironomid diversity records from
 1039 northwest Europe: (a) UK sites and (b) sites from the European mainland, arranged on a S-N
 1040 transect (see Fig. 1 for location of sites). Alpha diversity estimated through rarefaction
 1041 analysis (RF; red solid line); compositional turnover (CT) as determined from Detrended
 1042 Canonical Correspondence Analysis (DCCA) axis 1 (black solid line) in SD units (CT;
 1043 bottom x-axis) and delta-CT for adjacent samples in open black bars (Δ CT; SD units, top x-
 1044 axis). Directions of CT plots differ between individual sites and are selected to enable
 1045 comparison against the alpha diversity records. Dark (Younger Dryas; YD) and light shading
 1046 (Bølling/Allerød (B/A) and Holocene (Hol)) indicate the Lateglacial biozones as determined
 1047 for each site (see Supplementary Table S2 for more information on the sites).
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1051 Fig. 4: Chironomid diversity trends in Holocene records from (a) Kamchatka (Russia), (b)
 1052 other Russian sites, (c) Norway, (d) Finland, and (e) North America. All records are plotted
 1053 using the age-depth models as provided in the original publications (see Supplementary
 1054 Table S3 for more details on the sites). See Fig. 3 for an explanation of the symbols.
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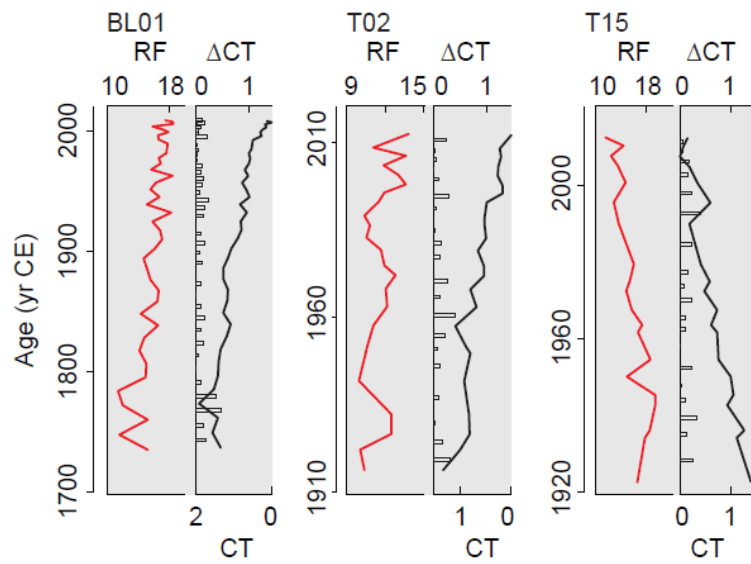
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1059 *Fig. 5: Recent chironomid diversity records from northern North America. Records are*
1060 *plotted using the age-depth models provided in the original publications. See Supplementary*
1061 *Table S3 for more details on the sites, and Fig. 3 for an explanation of the symbols. Note that*
1062 *the x-axis for the CT plot for T15 has been reversed to better illustrate the similarity in trends*
1063 *between alpha diversity and compositional turnover.*

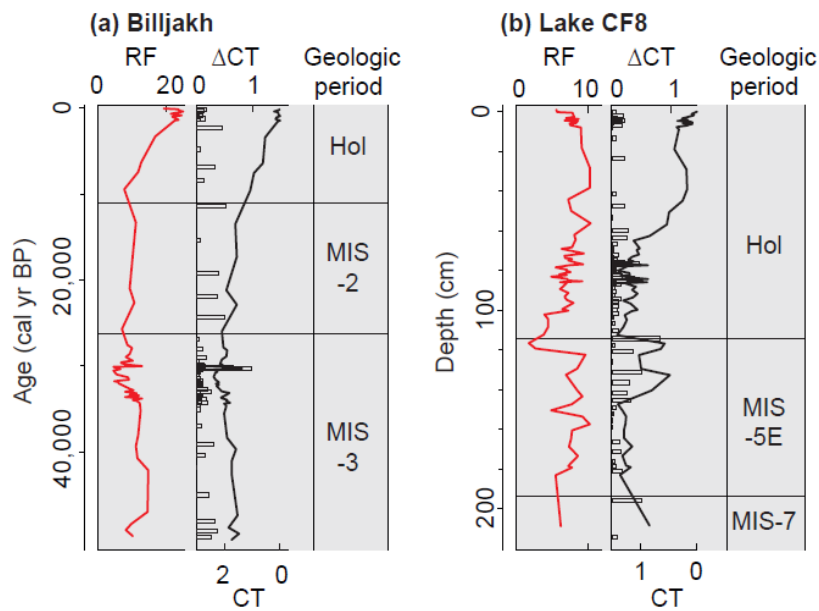
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1069 *Fig. 6: Chironomid diversity records from (a) Billjakh (East Siberia, Russia) and (b) CF8*
 1070 *(Canada). The Billjakh record spans the period from the middle of Marine Isotope Stage*
 1071 *(MIS) 3 to the present, whereas the CF8 record covers (parts of) the past three interglacials:*
 1072 *MIS-7 (ca 245-186 kyr BP), MIS-5E (ca 129-116 kyr BP) and the Holocene (11.6 cal kyr BP-*
 1073 *present). The geological periods are plotted next to the diversity records for reference. See*
 1074 *Fig. 3 for an explanation of the symbols.*

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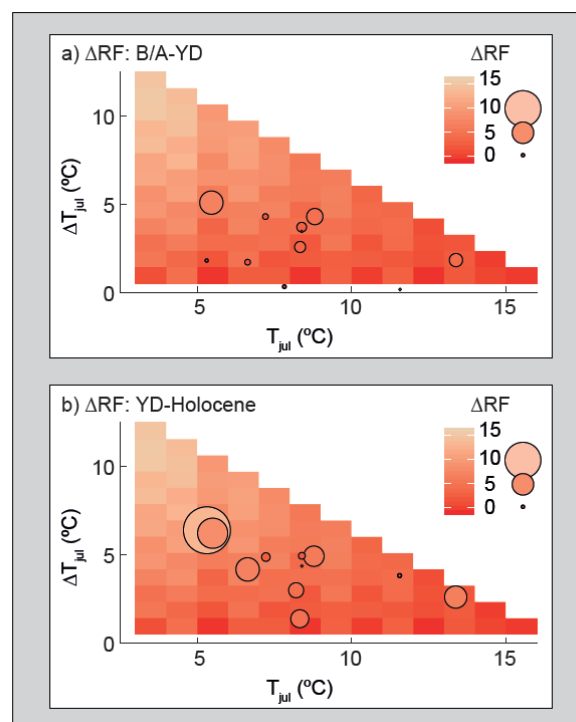


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1079 Fig. 7: Quantitative comparison of changes in alpha diversity (ΔRF) with changes in
1080 temperature (ΔT) for the Norwegian dataset (continuous field in background) and the LGIT
1081 records (circles) for (a) the Bølling/Allerød-Younger Dryas transition and (b) the Younger
1082 Dryas- Holocene transition. X-axis indicates the lowest temperature of a couplet of
1083 observations; y-axis represents the difference in absolute temperatures between the couplet
1084 of observations (ΔT). Plotted values (represented by colour scale and, for fossil records,
1085 symbol size) represent the change in alpha diversity as estimated through rarefaction
1086 analysis (ΔRF) between any couplet of observations. For instance, the figure illustrates how
1087 much, on average, RF increases in the Norwegian dataset between sites for a given lower
1088 temperature (x-axis) and sites at temperatures ΔT higher (y-axis). Similarly, the results show
1089 by how much RF decreased between the B/A and the YD (Fig. 7a; results shown as absolute
1090 values to enable comparison) and increased from the YD to the Holocene (Fig 7b) for each of
1091 the LGIT sites by plotting the average temperature of the YD (x-axis), the change in
1092 temperature across the climate transition (y-axis) and ΔRF (symbol size and colour). See



1093 *main text and Supplementary Figure S1 for more information.*

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