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

12 (Insecta: Diptera) diversity

13

14 Running head: Temperature change and chironomid diversity

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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 (ΔRF) with changing T_{jul} (ΔT_{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 (ΔRF) 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 (Δ RF) for each absolute temperature (e.g. $T = 3.5\text{ }^{\circ}\text{C}$) and each possible
275 increase in temperature (ΔT).

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_{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 Δ RF values by comparing RF_{ave} for subsequent climate zones (e.g. YD versus Holocene). We
281 use published quantitative LGIT T_{jul} inferences (see Supplementary Table S2) to assess the
282 average temperature during each interval (e.g. T_{YD}) and calculated the change in temperature
283 between subsequent intervals (ΔT) 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_{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_{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 (ρ 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) (Porinchu 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 Δ 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 Δ RF with increasing Δ T (Fig.
476 7a). The increase in Δ RF is limited when Δ T is low (e.g. <2 °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 Δ RF that is relatively small when compared to the Δ RF observed in the Norwegian dataset
479 for similar Δ T and T_{jul} conditions. This low increase in Δ RF for the fossil sites relative to the
480 Δ 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 Δ RF with increasing Δ T in the fossil data (Fig. 7b), resembling both the pattern and
487 magnitude of change in RF with increasing Δ 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 °C) led to a relatively high increase in Δ RF. There are a few sites that show a Δ RF in the
491 fossil data that is larger than Δ RF observed in the modern data (for similar Δ T and T_{jul}
492 conditions), but again between-site variation is relatively large with some sites showing
493 hardly any increase in Δ RF even when e.g. Δ T is 4 °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 21st 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 21st 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 ΔRF calculation for Norwegian dataset; Figure S1b: Illustration of ΔRF
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 _{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 |

1028

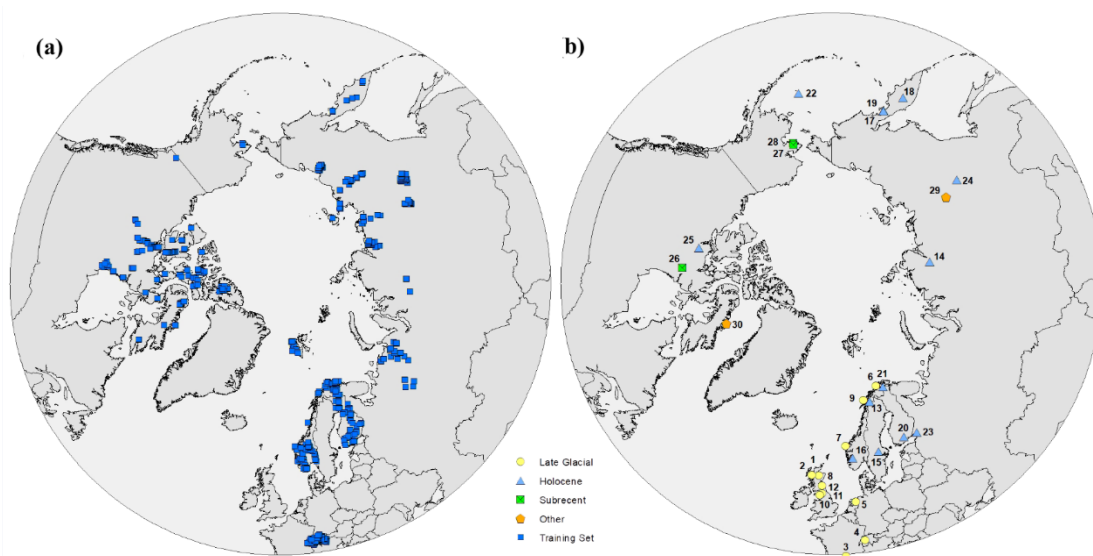
1029

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.*

1036

1037



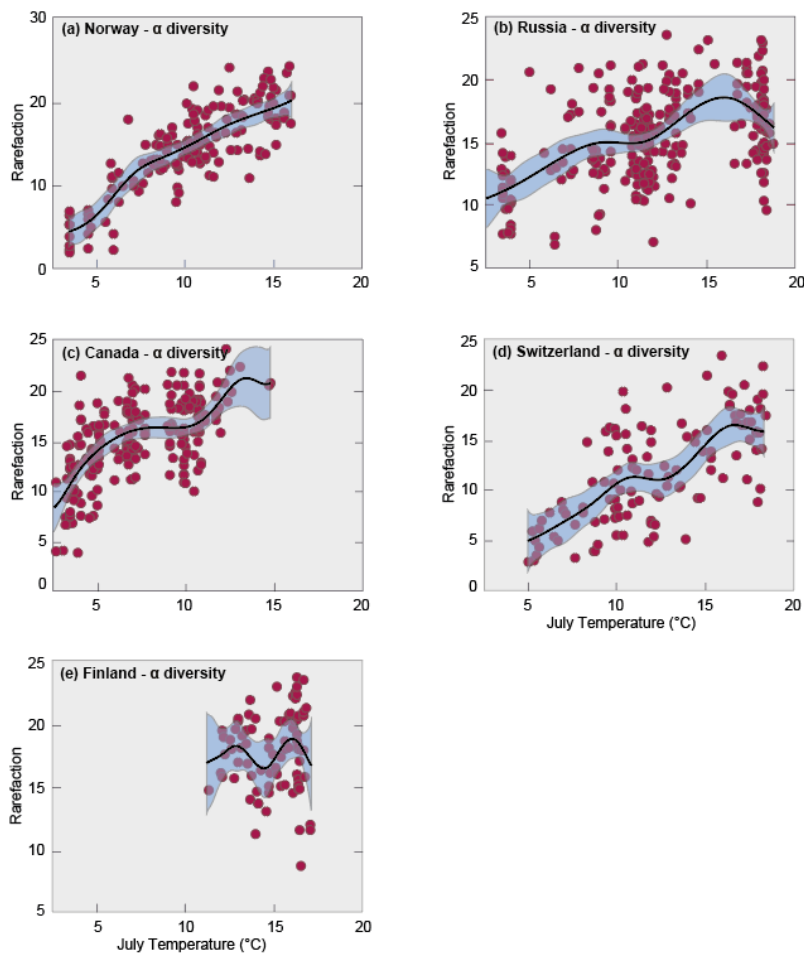
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1040 *Fig. 2: Modern-day subfossil chironomid diversity as estimated using rarefaction analysis*
1041 *against July air temperatures (°C) for datasets from (a) Norway, (b) Russia, (c) Canada, (d)*
1042 *Switzerland and (e) Finland (Supplementary Table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

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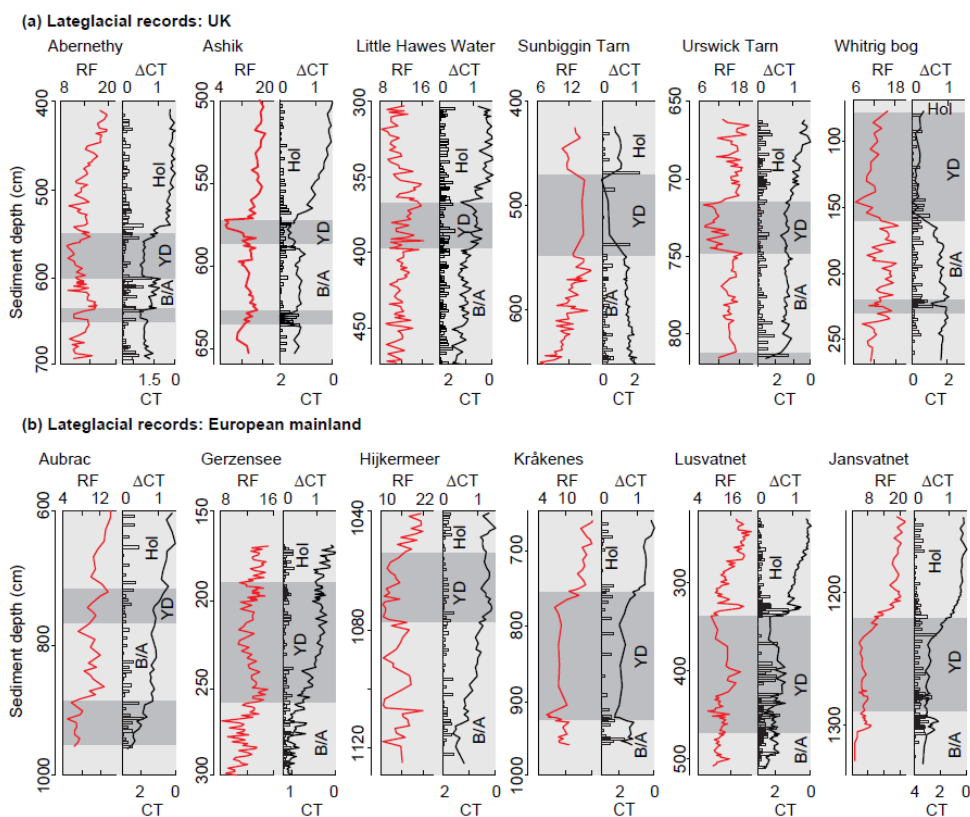
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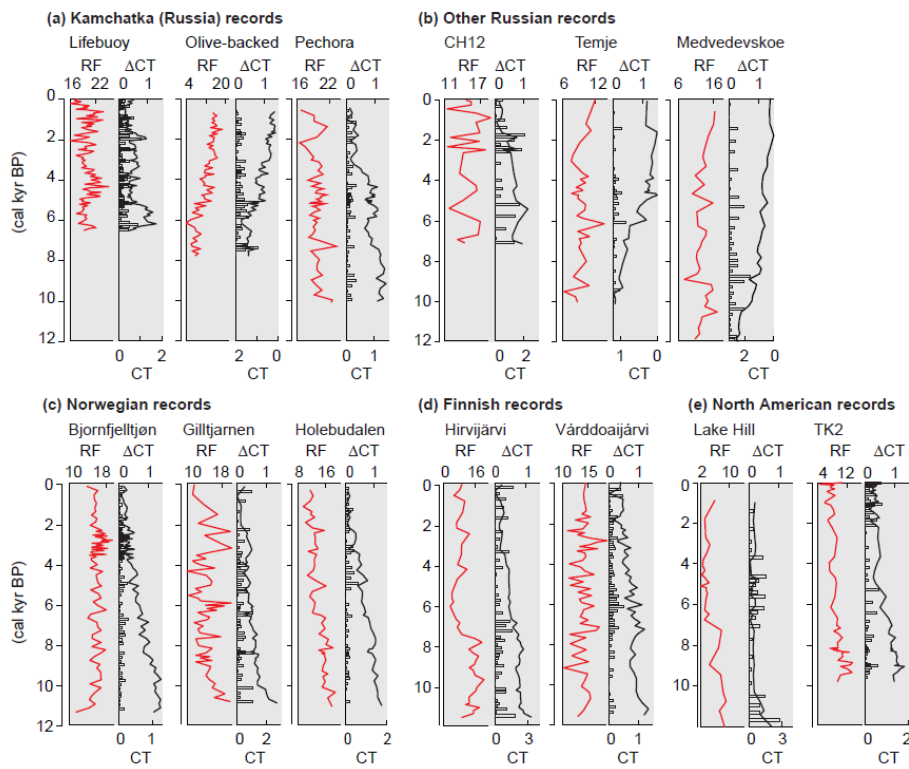
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1048 Fig. 3: Lateglacial-interglacial transition (LGIT) chironomid diversity records from
 1049 northwest Europe: (a) UK sites and (b) sites from the European mainland, arranged on a S-N
 1050 transect (see Fig. 1 for location of sites). Alpha diversity 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 (Δ 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).
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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.*



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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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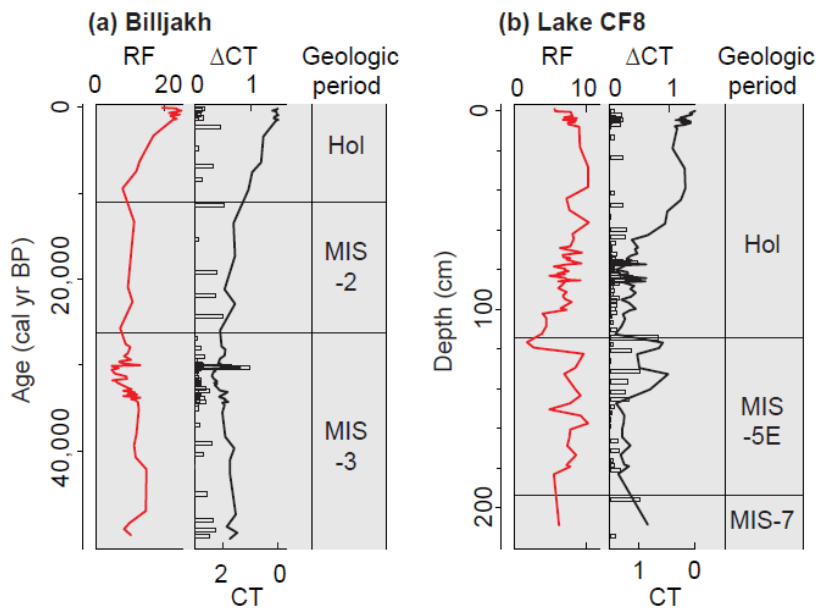
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1079 *Fig. 6: Chironomid diversity records from (a) Billjakh (East Siberia, Russia) and (b) CF8*
 1080 *(Canada). The Billjakh record spans the period from the middle of Marine Isotope Stage*
 1081 *(MIS) 3 to the present, whereas the CF8 record covers (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 (ΔRF) with changes in*
1090 *temperature (ΔT) 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 (ΔT). 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 (ΔRF) 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 ΔT 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 ΔRF (symbol size and colour). See*
1103 *main text and Supplementary Figure S1 for more information.*

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