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Temperature change as a driver of spatial patterns and long-term trends in chironomid (Insecta: Diptera) diversity

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Abstract

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

KEYWORDS

Arctic, biodiversity, climate warming, freshwater ecosystems, insects, palaeoecology, Quaternary

1 | INTRODUCTION

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

Most records that are used to assess the effects of anthropogenic drivers (e.g. climate variability, eutrophication, toxins, impacts associated with invasive species) on biodiversity are based on decadal-scale ecological data (Birks, Felde, & Seddon, 2016; Vellend et al., 2013; W.W.F., 2016). In many natural settings, it has been difficult to disentangle natural variability from the effects of human-induced ecosystem change (Loreau et al., 2001; Willis & Birks, 2006) as a result of these short timescales typically used. Data sets that cover much longer timescales, for example, several centuries to millennia, can help to provide a broader temporal context for current and future trends in biodiversity and facilitate the development of effective conservation strategies (Birks, Felde, & Seddon, 2016; Gregory-Eaves & Beisner, 2011; Willis & Birks, 2006). Willis and Birks (2006) and Birks, Felde, and Seddon (2016) provide examples of the role that palaeoecological data sets can play in providing such centennial to millennial scale time series, and how these data can provide new insights into the complex relationships that exist between biodiversity, ecosystem functioning and environmental variability. Despite the fact that many natural archives are available for study by palaeo- and neo-ecologists, these sources of information have rarely been used to infer past changes in biodiversity within the context of human impact and the 'Anthropocene' (Corlett, 2015; Gregory-Eaves & Beisner, 2011). We therefore have a limited understanding of long-term trends (10^2–10^5 years) in biodiversity, including insect diversity, and, as a result, it remains difficult to disentangle effects of anthropogenic disturbances from natural trends and internal variability.

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

A method that has provided insights into ecological, environmental and climatic development across the last glacial/interglacial cycle is the analysis of subfossil chironomid remains preserved in lake sediments (e.g. Brooks, 2006; Walker & Cwynar, 2006). Chironomids (Insecta: Diptera: Chironomidae) are holometabolous insects, and the larval stage of most species is aquatic. In lakes, chironomids are usually the most abundant macroinvertebrate group, and they are a critical component of the benthic community, contributing to processes essential for lake ecosystem functioning (Hölker et al., 2015), including biogeochemical cycling of carbon and nutrients. Parts of their larval exoskeleton (the head capsules) are well preserved in lake sediments (e.g. Brooks, Langdon, & Heiri, 2007). Subfossil chironomid head capsules are abundant in lake sediments, often in concentrations of 50–100 head capsules per gram of sediment, can be identified to genus, species morphotype or species level and provide a record of changes in the chironomid fauna of a lake through time. By comparing subfossil chironomid assemblages to their modern-day distribution patterns, quantitative reconstructions of changes in their past environment can be made. For instance, chironomids have been used to quantitatively reconstruct past changes in temperature (Brooks, Davies, Mather, Matthews, & Lowe, 2016; Heiri et al., 2014; Medeiros, Friel, Finkelstein, & Quinlan, 2012), water depth (Engels, Cwynar, Shuman, & Rees, 2012; Nazarova, Bleibtreu, Hoff, Dirksen, & Diekmann, 2017), salinity (Dickson, Bos, Pellatt, & Walker, 2014), hypolimnetic oxygen (Quinlan & Smol, 2001) and several other environmental variables. Subfossil chironomids encountered in lake sediment records can additionally be used to track changes in past species richness or evenness of the fauna through time (e.g. Engels, Helmens, Väliranta, Brooks, & Birks, 2010). However, palaeoecological data sets describing chironomid faunal dynamics on centennial to millennial timescales have not yet been compiled to produce systematic and super-regional studies of past diversity patterns.

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

1. Determining the relationship between diversity of (subfossil) chironomid assemblages in sediment samples and environmental parameters, with an emphasis on the effects of summer

temperature on chironomid assemblages across the mid- and high latitudes of the northern hemisphere (reflecting the availability of data sets);

2. Analysing spatiotemporal changes in chironomid diversity across a range of timescales; and

3. Assessing the suitability of subfossil chironomid assemblages as an approach to reconstruct changes in diversity over longer timescales.

2 | MATERIALS AND METHODS

2.1 | Materials

We determine, for the first time, spatial trends in chironomid diversity in chironomid–climate calibration data sets from Norway (Brooks, 2006; Brooks & Birks, 2001), Russia (Nazarova, Herzschuh, Wetterich, Kumke, & Pestjakova, 2011; Nazarova et al., 2015; Self et al., 2011), Canada (Fortin & Gajewski, 2011; Gajewski, Bouchard, Wilson, Kurek, & Cwynar, 2005; Medeiros & Quinlan, 2011; Porinchu, Rolland, & Moser, 2009), Switzerland (Heiri & Lotter, 2010; Lotter, Birks, Hofmann, & Marchetto, 1997) and Finland (Luoto, 2009a, 2009b; Figure 1; Table S1). Samples presented here from the Canadian data set have been re-identified where necessary and the taxonomy of the data sets analysed here follows Brooks et al. (2007).

Chironomid–climate calibration data sets document the relationship between chironomids and their contemporaneous environment (Brooks, 2006), often with a specific focus on the influence of summer air temperature on chironomid distribution patterns (e.g. Heiri et al., 2014). As such, these data sets capture a wide (summer) temperature range, whereas the impact of other environmental variables (e.g. lake water pH) is typically minimized. As a result of this sampling approach, the data sets provide excellent resources to study the temperature–chironomid diversity relationship. However, as the data sets cover a range of different secondary gradients (e.g. Medeiros, Gajewski, Porinchu, Vermaire, & Wolfe, 2015) and include measurements of different environmental variables (see Table S1), testing the influence of environmental parameters other than temperature on chironomid diversity will be more empirical.

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

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

2.2 | Numerical analyses

We focus on two biodiversity measures that are relevant to subfossil chironomid assemblages: (a) alpha diversity, here defined as the taxon richness of an assemblage at one point in time and space; and (b) compositional turnover (CT), that is, changes in assemblage composition across time (cf. McGill, Dornelas, Gotelli, & Magurran, 2015).

First, we analysed spatial trends in alpha diversity by calculating taxon richness using rarefaction analysis for each of our modern data sets. Rarefaction simulates a random selection

FIGURE 1 Location of (a) the lakes included in the chironomid–climate calibration data sets (blue squares) and (b) the downcore study sites (yellow circles = Lateglacial sites, blue triangles = Holocene sites, green squares = subrecent sites, orange pentagons = other sites) presented in this paper. Numbers in (b) correspond to lake numbers in Tables S2 and S3 where more details on the sites are provided
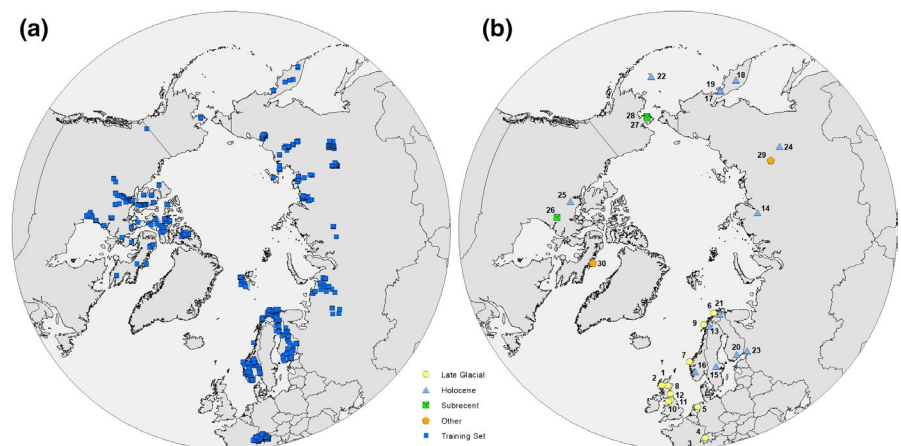
without replacement, estimating the taxon richness for each sample using a fixed count size, which typically equals the smallest count sum recorded in a sequence of samples (e.g. Birks & Line, 1992). Results of rarefaction analyses can be quantitatively compared between samples and data sets with different counts. Prior to rarefaction analysis, we rounded the counts in our data sets to integers and set our cut-value to a count sum of 40 head capsules for all analyses. While chironomid studies often report a minimum count sum of 50 head capsules per sample, we noted that some of our fossil sites had depth intervals where this number was not consistently reached. Instead of amalgamating or removing these samples and thus losing information, we decided to set a cut-value of 40 head capsules in order to retain more samples. Test runs comparing results of changing cut-values from 50 to 40 head capsules showed no substantial differences in the results and did not change interpretations of patterns and trends. Sites that had count values below 40 head capsules were removed prior to analysis. Rarefaction analysis was implemented using the vegan package in R (Oksanen et al., 2019).

Visual inspection of scatterplots of selected environmental variables against alpha diversity revealed the existence of non-linear but monotonic relationships. We subsequently calculated Spearman rank-order correlation coefficients between the rarefaction values and environmental observations for each modern data set (Table 1). The results indicated that generally there was a significant positive association between July air temperature (T_{jul}) and alpha diversity. We produced scatter plots of chironomid diversity (estimated using rarefaction analysis) as a function of July air temperature and used Generalized Additive Modelling (GAM) to summarize trends in the data (Simpson, 2018; see Supporting Information for R code).

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

While beta diversity is a commonly used component in (palaeoecological) biodiversity studies, there is no consensus on how to derive and interpret beta diversity (e.g. Birks, Felde, Bjune, et al., 2016; Jost, 2007; Marcon, Hérault, Baraloto, & Lang, 2012). Beta diversity, or the change in species composition per unit space or time (McGill et al., 2015), is often quantified as a rate-of-change or a turnover metric (Birks, 2012; Birks, Felde, & Seddon, 2016). Even though estimating assemblage CT along a temporal gradient does not provide a true diversity component but rather a measure of compositional complexity (Birks, Felde, Bjune, et al., 2016; Tuomisto, 2010), CT is commonly interpreted to approximate temporal changes in beta diversity, and CT techniques have become popular tools in palaeoecological studies (e.g. Birks & Birks, 2008; Colombaroli & Tinner, 2013; Feurdan et al., 2013; Smol et al., 2005; Stivrins et al., 2016). The difference in scores on a Detrended Canonical Correspondence Analysis (DCCA) axis between subsequent samples can be used to highlight times of increased turnover, reflecting increased beta diversity between samples.

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

Finally, we quantitatively compare the rarefaction results for the Norwegian calibration data set to the LGIT reconstructions to assess whether the effects of temperature on alpha diversity, as observed in modern-day chironomid assemblages, are comparable to those of the distant past. To do so, we assessed the change in

TABLE 1 Spearman's rank-order coefficient of correlation for rarefaction values versus environmental variables for each of the individual calibration data sets

	Norwegian data set	Russian data set	Canadian data set	Swiss data set	Finnish data set
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

Note: Due to the nature of designing and producing a chironomid–climate calibration data set, not all environmental variables were measured at each site; if individual values were missing, these sites were left out of the calculation for that specific correlation coefficient. Typically, however, a large proportion of the sites (if not all) were included in the analysis.

Abbreviation: NA, not available; TOC/DOC, total organic carbon/dissolved organic carbon.

*Statistically significant at $p = .05$, values corrected for multiple testing within a calibration data set using false discovery rate (FDR) correction (Benjamini & Hochberg, 1995) following Garcia (2004).

rarefaction (ΔRF) with changing T_{jul} (ΔT_{jul}) across the entire temperature interval included in the Norwegian calibration data set. In a first step, we calculated the average RF (RF$_{ave}$) value for each consecutive 1°C bin (e.g. 3.00–3.99°C [$T_{3.5C}$]) in the Norwegian calibration data set. We then calculated changes in RF (ΔRF) for each possible combination of 1°C bins across the 3–16°C temperature interval covered by the Norwegian calibration data set. This approach allows us to observe whether, for example, a change of 2°C has the same effects on the taxonomic diversity of a lake situated, for example, at 8°C as for a lake situated at, for example, 14°C, as well as to compare the effects an increase of 2°C would have compared to the effects of an increase of 4°C at the same site. We used the geom_raster function as included in the R ggplot2 package to produce a continuous plot of changes in RF (ΔRF) for each absolute temperature (e.g. T = 3.5°C) and each possible increase in temperature (ΔT).

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

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

3 | RESULTS AND INTERPRETATION

3.1 | Spatial trends in chironomid diversity

All data sets show similar TR values ranging between minima of 1–5 and maximum values over 20 (Figure 2). Chironomid alpha diversity generally shows an increasing trend with increasing T_{jul} for four out of the five regional data sets (Figure 2). In the Norwegian and Canadian data sets, the increase in alpha diversity is steepest in the coldest part of the temperature gradient (ca. 3–7°C interval), after which a more moderate increase in diversity can be seen. For some of the data sets that cover temperatures exceeding ca. 14°C (e.g. Russia, Switzerland), we observe a stabilizing or decreasing trend in alpha diversity with higher temperatures. Three of the data sets show additional variation superimposed on the general trend of increasing diversity with increasing temperature, which might be the result of sampling density along the temperature gradient, site-specific factors resulting in a lower alpha diversity in individual lakes, or it might be a true reflection of decreasing alpha diversity for currently unidentified reasons. The Finnish data set captures a smaller temperature gradient than the other data sets and GAM shows a highly variable but non-directional trend in alpha diversity. However, as in the other data sets, some of the lakes with mean July air temperature higher than 14°C are characterized by relatively low alpha diversity. Explanations for the general increase in chironomid diversity with temperature in most of our data sets could include availability of more and higher quality food sources with increasing temperatures. For instance, the lengthening of the ice-free period in Arctic lakes has been shown to lead to more diverse and ecologically complex algal communities (Griffiths, Michelutti, Sugar, Douglas, & Smol, 2017). Additionally, lakes can support more complex and varied habitats with increasing temperatures as, for example, more complex aquatic macrophyte communities, a major structuring element in lake ecosystems, may occur in warmer lakes. Additionally, more pronounced thermal stratification under warmer climates may lead to the parallel occurrence of both summer warm and summer cold habitats in the same lake, whereas this may not be the case in colder climatic conditions. The stabilizing or even decreasing trends in alpha diversity at the warm end of the gradient could be explained by temperature-related effects such as seasonal stratification in combination with oxygen depletion, leading to the elimination of some chironomid species. Similarly, warmer lakes could experience a loss of aquatic macrophyte habitat due to phytoplankton blooms.

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

There is a positive association between total organic carbon/dissolved organic carbon (TOC/DOC) and chironomid diversity in the data sets for which TOC/DOC data are available (ρ ranges between 0.35 and 0.70). However, TOC/DOC is strongly correlated with T_{jul} in, for example, the Swiss and Norwegian data sets (Brooks & Birks, 2001; Lotter et al., 1997; Lotter, Birks, Hofmann, & Marchetto, 1998), and it is therefore unclear to what extent variations in temperature and variations in TOC/DOC independently drive spatial patterns in chironomid diversity. Similarly, there is a positive association between TP and chironomid diversity but it is unclear what
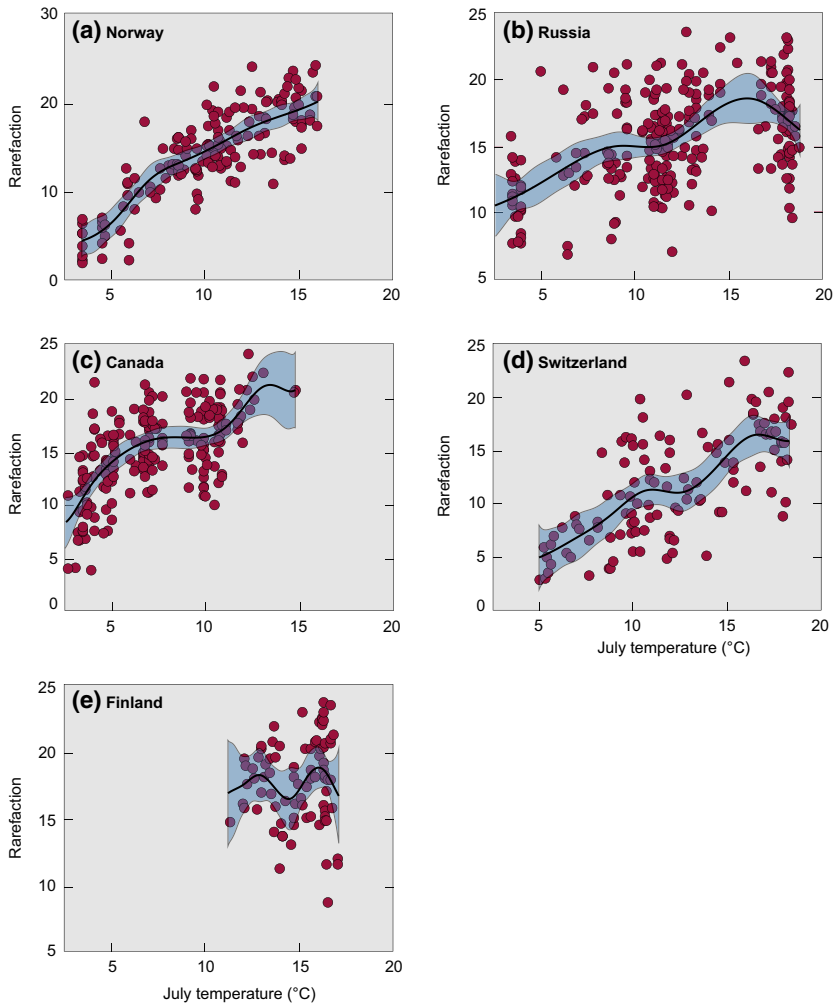
FIGURE 2 Modern-day subfossil chironomid diversity as estimated using rarefaction analysis against July air temperatures (°C) for data sets from (a) Norway, (b) Russia, (c) Canada, (d) Switzerland and (e) Finland (Table S1). Solid black lines are GAM-based trendlines for rarefaction values with uncertainty intervals in light blue

the unique effects of TP are, independent of temperature. To further test the potential association between chironomid diversity and TP, we applied rarefaction analysis to a lake data set from Ontario (Canada) by Quinlan and Smol (2001) which covers a gradient from ultraoligotrophic lakes to eutrophic lakes while covering a relatively short temperature gradient. The results indicate that there is no statistically significant association between chironomid diversity and TP (ρ = 0.072; p = .573) in this data set.

Similarly, by running additional tests on a chironomid data set from New England, United States (Engels & Cwynar, 2011) as well as a data set of lakes and reservoirs from New Jersey and New York states, United States (Wazbinski & Quinlan, 2013), we further explored whether the absence of a strong correlation between water depth and chironomid diversity could be related to data set design. The distribution of many individual chironomid taxa in the data set by Engels and Cwynar (2011) is significantly correlated with water depth, likely attributable to factors like habitat differentiation, taphonomical processes and oxygen availability. Analysis of both data sets shows only a weak positive association between chironomid diversity and water depth of ρ = 0.08 (p = .37) for the Engels and Cwynar (2011) data set, whereas the Wazbinski and Quinlan (2013) data set shows a negative association of ρ = −0.38 (p = .01) between water depth and

chironomid diversity. The combined results suggest that unlike summer temperature, water depth is not a strong driver of chironomid diversity at the observed spatial scales, but that more research is needed to further explore the relationship between chironomid diversity and water depth.

3.2 | Temporal trends in chironomid diversity

3.2.1 | Last glacial–interglacial transition

Four of the six UK LGIT records show a distinct change in diversity during the YD (Figure 3a), either as a decrease in alpha diversity (e.g. Ashik; Figure 3a) or as high CT (e.g. Sunbiggin Tarn; Figure 3a). The records from Abernethy and Urswick Tarn furthermore show a decrease in both alpha diversity and increased CT during the multidecadal cold interval associated with the Older Dryas (Figure 3a). The records from Ashik and Whitrig Bog show high CT during the Older Dryas, but no variation in alpha diversity. The Older Dryas has not been identified in the Little Hawes Water and Sunbiggin Tarn records, and although there are oscillations in the CT records of these sites, it is unclear whether these are associated with Older Dryas climate change or if they are the result of other factors.

FIGURE 3 Last glacial–interglacial transition (LGIT) chironomid diversity records from northwest Europe: (a) UK sites and (b) sites from the European mainland, arranged on a S–N transect (see Figure 1 for location of sites). Alpha diversity estimated through rarefaction analysis (RF; red solid line); compositional turnover (CT) as determined from Detrended Canonical Correspondence Analysis axis 1 (black solid line) in *SD* units (CT; bottom *x*-axis) and delta-CT for adjacent samples in open black bars (ΔCT; *SD* units, top *x*-axis). Directions of CT plots differ between individual sites and are selected to enable comparison against the alpha diversity records. Dark (Younger Dryas [YD]) and light shading (Bølling/Allerød [B/A] and Holocene [Hol]) indicate the Lateglacial biozones as determined for each site (see Table S2 for more information on the sites)
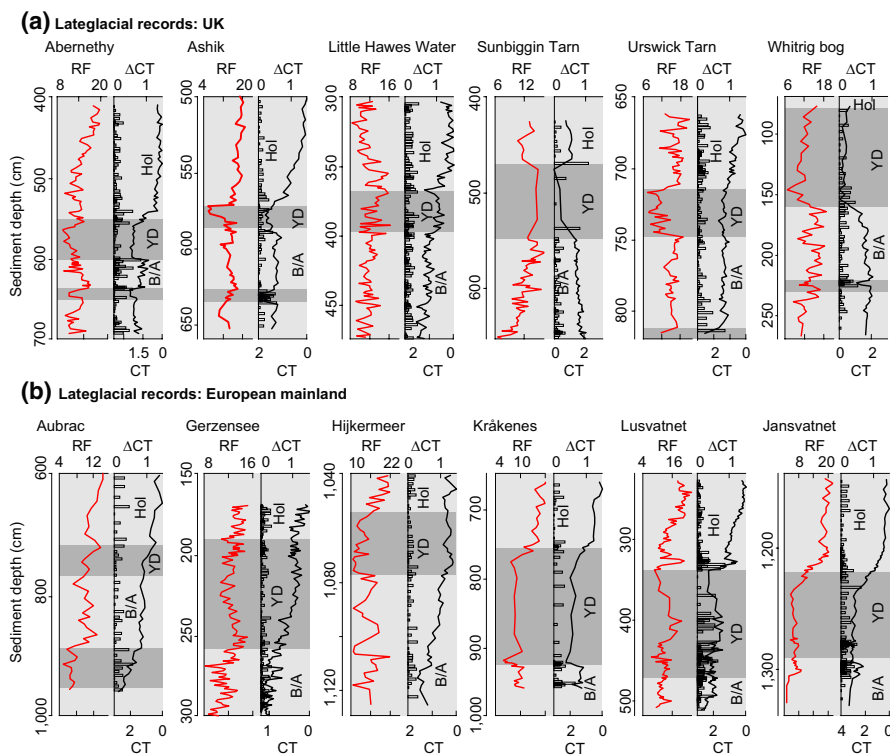

The six LGIT sites from the European mainland (Figure 3b) are located on an N–S transect (Figure 1). The southernmost two of these sites (Aubrac, Gerzensee) capture different parts of the LGIT interval, but neither site shows abrupt changes in diversity associated with the onset of the YD or the Holocene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

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

3.2.2 | Holocene

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

Similarly, sites within relatively small regions like Norway and Finland show differences in both alpha diversity and CT trends during the Holocene, whereas climate change over these regions can be expected to be fairly homogeneous. Again, we attribute these differences in diversity trends to site-specific changes in the environment exerting a stronger influence on the chironomid fauna than climate change. For instance, the amplitude of temperature change during the Holocene across northern Europe was not as great as during the LGIT, and the chironomid fauna of some lakes, for example, Gilltjarnen, most likely responded most strongly to changes in the local environment (e.g. lake water pH, local peat development)
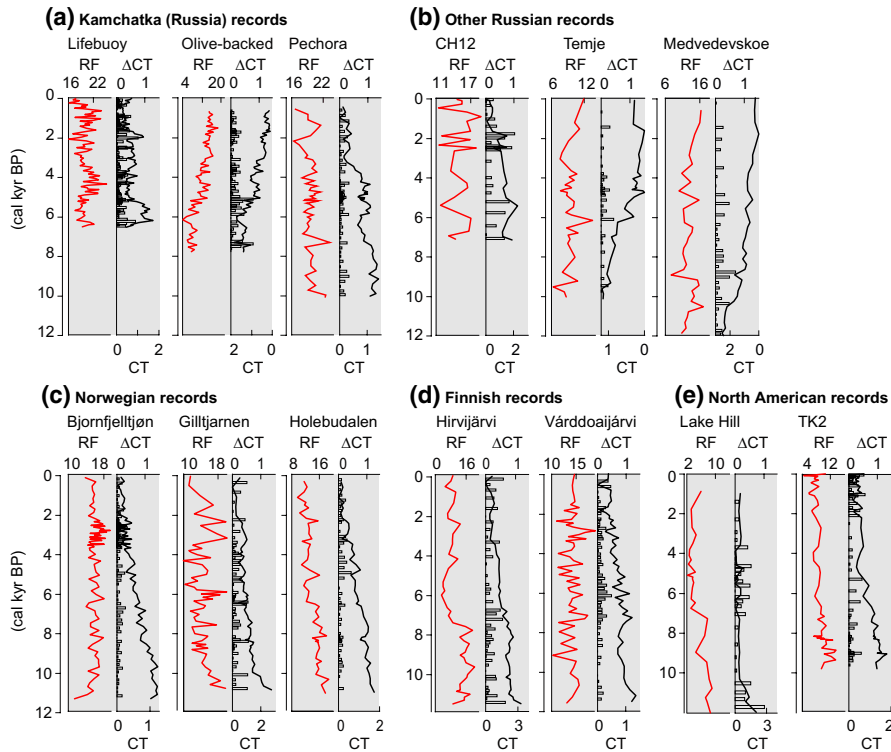
FIGURE 4 Chironomid diversity trends in Holocene records from (a) Kamchatka (Russia), (b) other Russian sites, (c) Norway, (d) Finland and (e) North America. All records are plotted using the age-depth models as provided in the original publications (see Table S3 for more details on the sites). See Figure 3 for an explanation of the symbols. CT, compositional turnover; RF, rarefaction

rather than to temperature change (Antonsson, Brooks, Seppä, Telford, & Birks, 2006).

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

3.2.3 | Recent trends

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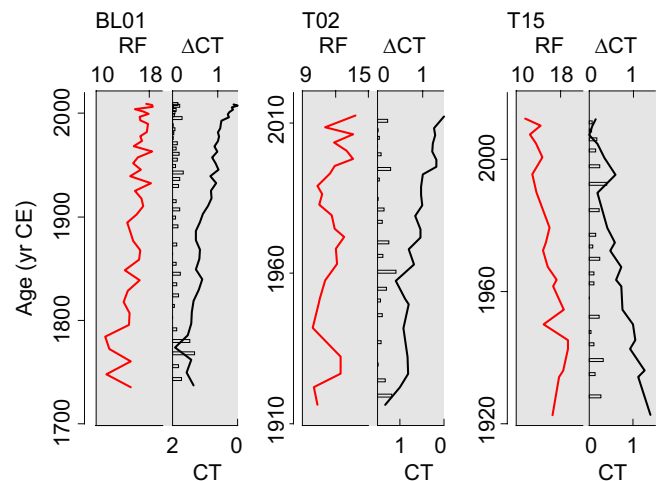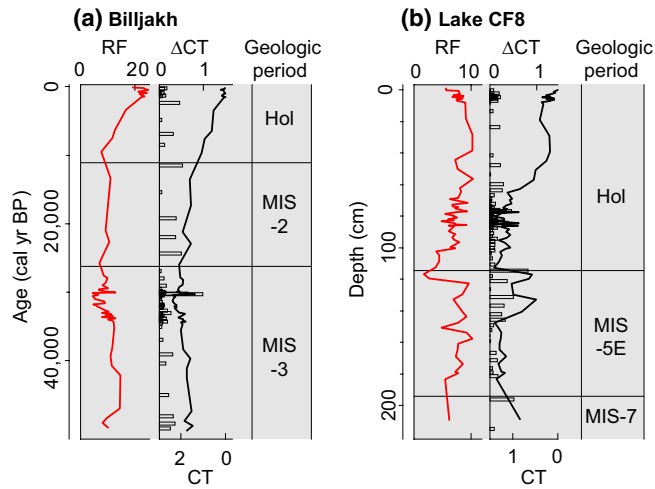

FIGURE 5 Recent chironomid diversity records from northern North America. Records are plotted using the age-depth models provided in the original publications. See Table S3 for more details on the sites, and Figure 3 for an explanation of the symbols. Note that the x-axis for the compositional turnover (CT) plot for T15 has been reversed to better illustrate the similarity in trends between alpha diversity and compositional turnover. RF, rarefaction

3.2.4 | Deep-time (10^5 years) records

The lacustrine record from lake Billjakh (east Siberia, Russia; Diekmann et al., 2016) covers the time interval from the middle of the last glacial (MIS-3) to the present. The alpha diversity record of Billjakh shows highest diversity in the first part of MIS-3 and during the Holocene (Figure 6a). This observation of higher chironomid
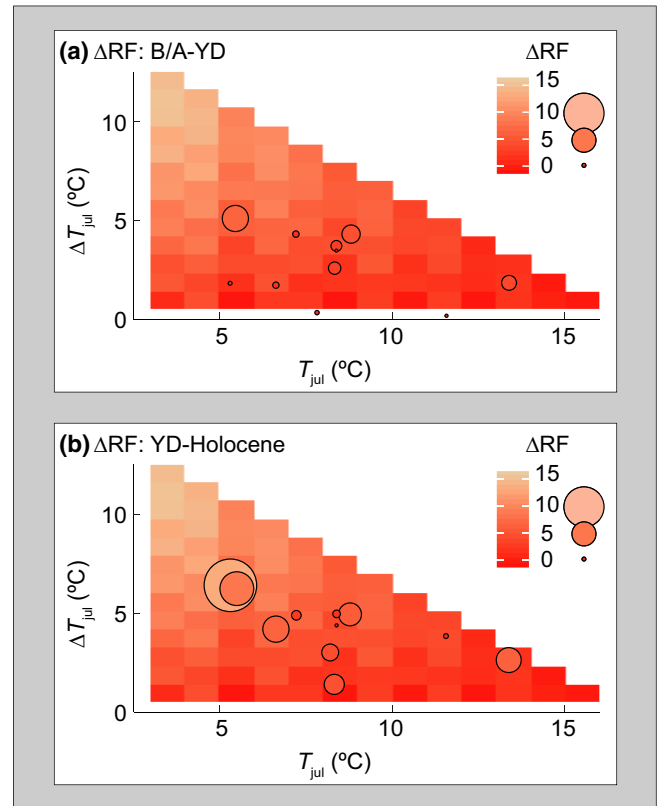
FIGURE 6 Chironomid diversity records from (a) Billjakh (East Siberia, Russia) and (b) CF8 (Canada). The Billjakh record spans the period from the middle of Marine Isotope Stage (MIS) 3 to the present, whereas the CF8 record covers (parts of) the past three interglacials: MIS-7 (ca. 245–186 kyr BP), MIS-5E (ca. 129–116 kyr BP) and the Holocene (11.6 cal kyr BP–present). The geological periods are plotted next to the diversity records for reference. See Figure 3 for an explanation of the symbols. CT, compositional turnover; RF, rarefaction

FIGURE 7 Quantitative comparison of changes in alpha diversity (ΔRF) with changes in temperature (ΔT) for the Norwegian data set (continuous field in background) and the last glacial–interglacial transition (LGIT) records (circles) for (a) the Bølling/Allerød (B/A)-Younger Dryas (YD) transition and (b) the YD-Holocene transition. *X*-axis indicates the lowest temperature of a couplet of observations; *y*-axis represents the difference in absolute temperatures between the couplet of observations (ΔT). Plotted values (represented by colour scale and, for fossil records, symbol size) represent the change in alpha diversity as estimated through rarefaction analysis (ΔRF) between any couplet of observations. For instance, the figure illustrates how much, on average, RF increases in the Norwegian data set between sites for a given lower temperature (*x*-axis) and sites at temperatures ΔT higher (*y*-axis). Similarly, the results show by how much RF decreased between the B/A and the YD (Figure 7a; results shown as absolute values to enable comparison) and increased from the YD to the Holocene (Figure 7b) for each of the LGIT sites by plotting the average temperature of the YD (*x*-axis), the change in temperature across the climate transition (*y*-axis) and ΔRF (symbol size and colour). See main text and Figure S1 for more information

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

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

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

This study provides, for the first time, a quantitative comparison between centennial to multi-millennial scale records and modern-day

patterns in chironomid diversity. July air temperature shows a strong positive association with alpha diversity in our modern data sets (Figures 2 and 7), with particularly strong increases in diversity observed towards the colder end of the temperature gradient (ca. 2.5–14°C). Similarly, most of the LGIT records presented in this study document trends in chironomid alpha diversity that follow regional temperature variability, with higher diversity during the relatively warm B/A interstadial and during the early Holocene, and lower diversity during the YD and Older Dryas (Figure 3). The ΔRF values for the modern Norwegian data and the fossil sites are

mostly of a similar magnitude and show that there is a general trend of increasing ΔRF with increasing ΔT (Figure 7a). The increase in ΔRF is limited when ΔT is low (e.g. <2°C). Between-site variation is high for the LGIT records and there is a relatively high number of fossil sites that show a ΔRF that is relatively small when compared to the ΔRF observed in the Norwegian data set for similar ΔT and T_{jul} conditions. This low increase in ΔRF for the fossil sites relative to the ΔRF observed in the modern sites might be related to the fact that in the modern data set, there are a number of environmental factors that differ between the individual sites (e.g. geology, soil development, microclimate), whereas the variations in environmental factors with time at one particular fossil site are likely to be lower, and mainly limited to climate change and its direct effects on catchment conditions.

The results for the YD-Holocene transition also show a general pattern of increasing ΔRF with increasing ΔT in the fossil data (Figure 7b), resembling both the pattern and magnitude of change in RF with increasing ΔT as observed in the modern Norwegian data set as well as the pattern observed for the B/A-YD transition. Results indicate that for this transition, which is characterized by abrupt climate warming, even small-scale warming (e.g. <2°C) led to a relatively high increase in ΔRF. There are a few sites that show a ΔRF in the fossil data that is larger than ΔRF observed in the modern data (for similar ΔT and T_{jul} conditions), but again between-site variation is relatively large with some sites showing hardly any increase in ΔRF even when, for example, ΔT is 4°C or higher. Concluding, the quantitative comparison between the Norwegian data set and the LGIT records shows that the observed changes in alpha diversity are of similar direction and magnitude (Figure 7). They furthermore highlight that the positive association between alpha diversity and T_{jul} is especially well expressed in colder or more Arctic sites, and, as expected, for larger changes in temperature (e.g. ΔT > 4°C).

4 | DISCUSSION

4.1 | Palaeoecological evidence for spatiotemporal trends in biodiversity

Our LGIT records generally show decreasing alpha diversity during colder periods such as the YD (Figure 3). This confirms earlier, less comprehensive evidence on the relationship between temperature and lacustrine chironomid diversity patterns. Levesque, Cwynar, and Walker (1995) reconstructed chironomid diversity trends across the LGIT for four eastern Canadian records. Despite the low taxonomic resolution relative to later reconstructions, Levesque et al. (1995) documented decreasing alpha diversity during periods characterized by cold climate, similar to the results obtained in this study. Massaferro and Corley (1998) also reported decreasing chironomid diversity in response to climate cooling during the LGIT interval for sites in northern Patagonia. The amplitude of change in diversity in the records by Massaferro and Corley (1998) is relatively muted, which could be the result of the lower temperature amplitude associated with LGIT climate change in Northern Patagonia compared to the regions

adjacent to the North Atlantic Ocean (Levesque et al., 1995; this study). Additionally, there are major differences in the chironomid fauna adapted to cold environments in the southern hemisphere compared to the northern hemisphere (e.g. Brundin, 1966), and Eggermont and Heiri (2012) show that globally different chironomid subfamilies have varying thermal optima. As chironomid–environment calibration data sets, as well as fossil data sets across a range of timescales, exist and are being developed, for example, Australia (Rees, Cwynar, & Cranston, 2008), New Zealand (Van den Bos et al., 2018) or South America (Matthews-Bird, Brooks, Holden, Montoya, & Gosling, 2016), there is potential to apply our approach of comparing modern and fossil trends in diversity to regions of the Southern Hemisphere as well as to the tropical regions presently under-represented in respect to fossil chironomid data sets. This will further improve our understanding of global drivers of chironomid diversity and will help to better predict future changes under projected global warming.

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

The amplitude of temperature change during the Holocene was relatively small and occurred gradually at many of our sites, and we suggest that long-term variations in site-specific factors such as soil development, vegetation change, nutrient availability and changes in the macrophyte community also influenced the development of the chironomid diversity in individual lakes. It could be argued that in the North Atlantic region, the early Holocene (Walker et al., 2012) is the period with the highest environmental dynamics, as the catchments surrounding many sites were colonized by trees, soils stabilized and weathering dynamics and nutrient availability changed accordingly, potentially affecting the chironomid fauna at each of our study sites. However, our chironomid diversity records generally lack an initial phase of instability during the early Holocene. Recent publications suggest that postglacial ecosystem development in lakes has been much faster than previously thought (Helmens et al., 2018), and, combined with the potential for fast dispersal and colonization by chironomids (Brooks et al., 2007), this might explain the relatively stability of our chironomid diversity records during the early Holocene.

Our results show a general trend of increasing chironomid diversity as a result of recent climate warming in two out of our three records (Figure 5), which is in line with centennial-scale CT reconstructions for seven out of eight chironomid records from the Arctic

(Smol et al., 2005). Ilyashuk, Ilyashuk, Tylmann, Koinig, and Psenner (2015) reconstructed trends in chironomid CT in three remote lakes in the Alps. While they show different trends for most of the past two millennia, major assemblage turnover was visible in all three sites in the interval between 1850 CE and the present (Ilyashuk et al., 2015). Finally, Nevalainen, Luoto, Manca, and Weisse (2015) studied chironomid diversity trends in four climate-sensitive treeline lakes in Austria. While their results show inter-site variability, chironomid diversity did increase in two of the studied lakes towards the 20th and 21st centuries.

4.2 | Effects of projected global warming on chironomid diversity

Summer temperatures are predicted to increase across the 21st century as a result of enhanced atmospheric greenhouse gas concentrations, where polar amplification will result in higher temperature increases in high-latitude regions compared to the global average (Intergovernmental Panel on Climate Change, 2014). We speculate that cold-stenothermic taxa will go locally extinct from many shallow Arctic and subarctic lakes under sustained global warming (Armitage, Cranston, & Pinder, 1995; Hamerlik, Svitok, Novikmec, Veslská, & Bitušik, 2017). However, our results suggest that, as a result of this projected warming, lakes in the Arctic and subarctic are likely to experience an increase in chironomid diversity, as warm-stenothermic taxa disperse into regions and habitats that currently experience temperatures that are too low for their development.

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

The decreasing trend in chironomid diversity at higher temperatures as seen in some of our modern data sets could furthermore be explained by the greater human impact in catchments of warmer lakes, especially in Europe, where population density and human impact on the landscape are greater in the warmer parts of the regions covered by the respective data sets. Increased nutrient influx due to human land use has been known to lead to the disappearance of aquatic macrophytes (e.g. Bradshaw, Rasmussen, & Odgaard, 2005; Engels et al.,

2018), as well as to a decrease in oxygen availability (Quinlan & Smol, 2001), thus decreasing habitat availability and variability, and, ultimately, the potential for a diverse chironomid community to develop or persist. With the ongoing anthropogenic impact on the landscape (Steffen et al., 2015), we will likely see further disturbances in freshwater ecosystems across the globe (Doncaster et al., 2016). Our results imply expected overall chironomid diversity increases under sustained global warming, but with complex and not necessarily predictable responses for individual sites due to the effects of local disturbances such as eutrophication or land use change.

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

CONFLICT OF INTEREST

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data produced in this study can be found in the Supplementary Information. The datafile includes all the diversity estimates

produced as well as the information needed to produce the figures presented in this manuscript. Original chironomid count data sets can be requested from the original authors; see Table S1 (calibration data sets) and Tables S2 and S3 (fossil records) for the original publication details.

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