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A continental-scale chironomid training set for reconstructing Arctic temperatures

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ABSTRACT

We present chironomid species assemblage data from 402 lakes across northern North America, Greenland, Iceland, and Svalbard to inform interpretations of Holocene subfossil chironomid assemblages used in paleolimnological reconstruction. This calibration-set was developed by re-identifying and taxonomically harmonizing chironomids in previously described surface sediment samples, with identifications made at finer taxonomic resolution than in original publications. The large geographic coverage of this dataset is intended to provide climatic analogues for a wide range of Holocene climates in the northwest North Atlantic region and North American Arctic, including Greenland. For many of these regions, modern calibration data are sparse despite keen interest in paleoclimate reconstructions from high latitudes. A suite of chironomid-based temperature models based upon this training set are evaluated here and the best statistical model is used to reconstruct late glacial (Allerød and Younger Dryas) and Holocene paleotemperatures at five non-glacial lakes representing a wide range of climate zones across Greenland. The new continent-scale training set offers more analogues for the majority of Greenland subfossil assemblages than existing smaller training sets, with many in Iceland and northern Canada. We find strong agreement between chironomid-based reconstructions derived from the new model and independent glacier-based evidence for multi-millennial Holocene temperature trends. Some of the new Holocene reconstructions are very similar to published data, but at a subset of sites and time periods we find improved paleotemperature reconstructions attributable both to the new model's finer taxonomic resolution and to its expanded geographic/climatic coverage, which resulted in improved characterization of species optima. In the late glacial, the new model's finer taxonomic resolution yields a unique ability to resolve temperatures of the Allerød from colder temperatures of the Younger Dryas, although the magnitude of that temperature difference may be underestimated. This study demonstrates the value of geographically and climatically broad paleoecological training sets. The large, taxonomically harmonized dataset presented here should be useful for a wide range of future investigations, including but not limited to paleotemperature reconstructions across the Arctic.

1. Introduction

Understanding environmental change in the past can facilitate a

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better understanding of current and future climate, but reliable proxies for the past are needed in order to achieve this goal. Subfossil assemblages of chironomids (Diptera: Chironomidae) have well-demonstrated utility for reconstructing paleotemperatures (Hofmann, 1988; Walker et al., 1991; Walker, 1995; Engels et al., 2020). Insects are known to be especially responsive to temperature-dependent processes that govern growth, reproduction, feeding behavior, and emergence (Danks, 2007; Lee and Denlinger, 2012). The indirect effect of temperature on the physical and chemical characteristics of lakes is known to be a principle mechanism for determining the distribution chironomid larvae (Eggermont and Heiri, 2011). For Arctic regions, a dominance of cold-stenothermal taxa that lack a plurimodal response (Rossaro, 1991) strengthen the temperature-assemblage relationship. Spatial surveys of surface sediments across multiple bioregions in adjacent northern Canada and Alaska (e.g. Walker, 1990; Gajewski et al., 2005; Barley et al., 2006; Francis et al., 2006; Medeiros and Quinlan, 2011) and Iceland (Langdon et al., 2008) have identified temperature as the primary control on modern chironomid species distributions, facilitating a calibration approach to paleotemperature reconstructions (Smol, 1992). Accordingly, chironomid assemblages now provide a large fraction of the quantitative Holocene paleotemperature reconstructions available from the Arctic (e.g., Kaufman et al., 2016, 2020), although large spatial gaps remain.

In recent years chironomid records have added substantially to the sparse database of summer paleotemperature reconstructions from Greenland, where ice cores provide high-resolution but annually integrated temperature reconstructions (e.g., see review by Axford et al., 2021). Past summer temperatures are a key factor in understanding the Greenland Ice Sheet's past sensitivity to temperature change, thus a high priority for paleoclimate reconstruction. While some studies have shown that chironomid assemblages from Greenland are primarily responsive to temperature (Millet et al., 2014), published chironomid-based paleoclimate inferences from Greenland have either taken a qualitative approach or have relied upon calibration data (training sets) from adjacent regions of Canada and Iceland due to very limited availability of data from across most of Greenland's climate zones (Brodersen and Bennike, 2003; Wooller et al., 2004; Schmidt et al., 2011; Axford et al., 2013, 2017, 2019; Millet et al., 2014; McFarlin et al., 2018). Dense networks of training set collections from Greenland have only been accomplished in two logistically accessible regions near Kangerlussuaq and Nuuk (Brodersen and Anderson, 2002; Medeiros et al., 2021; Fig. 1). These two study sites are separated by < 300 km and experience relatively warm summer temperatures compared with most of Greenland, which spans ~1500 km north to south and a wide range of climates from the high Arctic to the subarctic. Published reconstructions from chironomids agree well with a broad range of independent evidence for Holocene climate (e.g., from ice core proxies and glacier extents; Axford et al., 2021), but reliance on training sets and models developed outside Greenland adds uncertainty to those reconstructions as these are principally different biogeographic regions that are known to have unique assemblages (Medeiros et al., 2021). In addition, Fortin et al. (2015) demonstrated that increasing the number of modern analogues in the calibration approach using chironomid assemblages allowed for improved interpretation of past climate. Thus, there is strong incentive to develop training sets that include as many analogous modern assemblages and comparable climate zones as possible.

Here, we assemble taxonomically harmonized chironomid assemblage data from the surface sediments of 402 lakes spanning northern North America, parts of Greenland, Svalbard, and Iceland, creating a climatically and geographically broad calibration set. We evaluate the applicability of a broad-based regional chironomid transfer function for reconstructing quantitative temperatures in Greenland, an assessment that may be relevant to other under-sampled regions as well. Furthermore, we aim to present a climatically and geographically broad, taxonomically harmonized training set that may be useful to paleoecologists for reconstructions across the Arctic.

2. Materials and methods

2.1. Training set sites and data sources

We present a large dataset of chironomid assemblages collected from the surficial sediments of 402 lakes from northern North America, southwest and east Greenland, Iceland, and Svalbard (Fig. 1; Supplemental Table S1). Most of these samples (except 12 new sites from east Greenland and Svalbard, see the paragraph below) have been previously used in local and regional training sets and studies of chironomid distributions (Walker et al., 1991; Brodersen and Anderson, 2002; Gajewski et al., 2005; Francis et al., 2006; Langdon et al., 2008; Porinchu et al., 2009; Medeiros and Quinlan, 2011; Medeiros et al. 2014, 2021; Fortin et al., 2015). We re-identified the chironomids used in these studies in order to harmonize taxonomy across this broad region and among our international collaborations. We note that not all samples from previously published datasets were available for renumeration due to loss of the original sample since the time of publication (Supplementary Table S1). The re-identified samples from northeast Canada, southwest Greenland, and Iceland were previously combined in an investigation of biogeography, which found that within each region air temperature explained the largest amount of variation in chironomid assemblages, but spatial (i.e., biogeographic) controls were also important between regions (Medeiros et al., 2021). Since existing published chironomid training sets offer few climatic and biogeographic analogues for the sparsely populated, under-sampled, Mid to High Arctic regions of Greenland, and especially for eastern Greenland, we also publish here for the first time surface assemblages collected from 6 additional lakes in eastern Greenland, and 6 lakes from Svalbard (Fig. 1). For these new sites, the uppermost 0–1 cm of sediment was collected from the deepest part of the lakes in the summer of 2010.

The calibration set (Fig. 1) includes sites that span from ~51.4 to 80.8 °N and ~16 to −165° W, covering a gradient in annual mean temperatures from 4.4 to −22.9 °C, summer (mean of the warmest quarter) temperatures from −1.2 to 12.8 °C, and altitude from 0 to 855 m a.s.l., and spanning from boreal forest to High Arctic tundra. Each of the original regional training sets were collected as part of their own separate study (Supplemental Table S1) with associated field collection protocols. As the original study design of each dataset differed slightly in the manner in which environmental data were collected, we used a standardized estimate of mean annual temperature and mean summer temperature of the warmest quarter, extracted for each lake across all training sets using the WorldClim 2.1 gridded bioclimatic dataset at 2.5 min resolution (Fick and Hijmans, 2017). This provides a uniform estimate of temperature (based on an average temperature from 1970 to 2000 CE) for all sites in our study despite the paucity of weather stations across most of the study area. The WorldClim gridded climate dataset does not provide single-month inferences, so instead of using July air temperature (the variable mostly used for reconstructions in chironomid-based transfer function models) in our model, we used the bioclimatic variable ‘mean annual air temperature of the warmest quarter’ (June, July, and August [JJA] for northern North America) to represent summer air temperatures. The WorldClim dataset uses an elevation model to generate

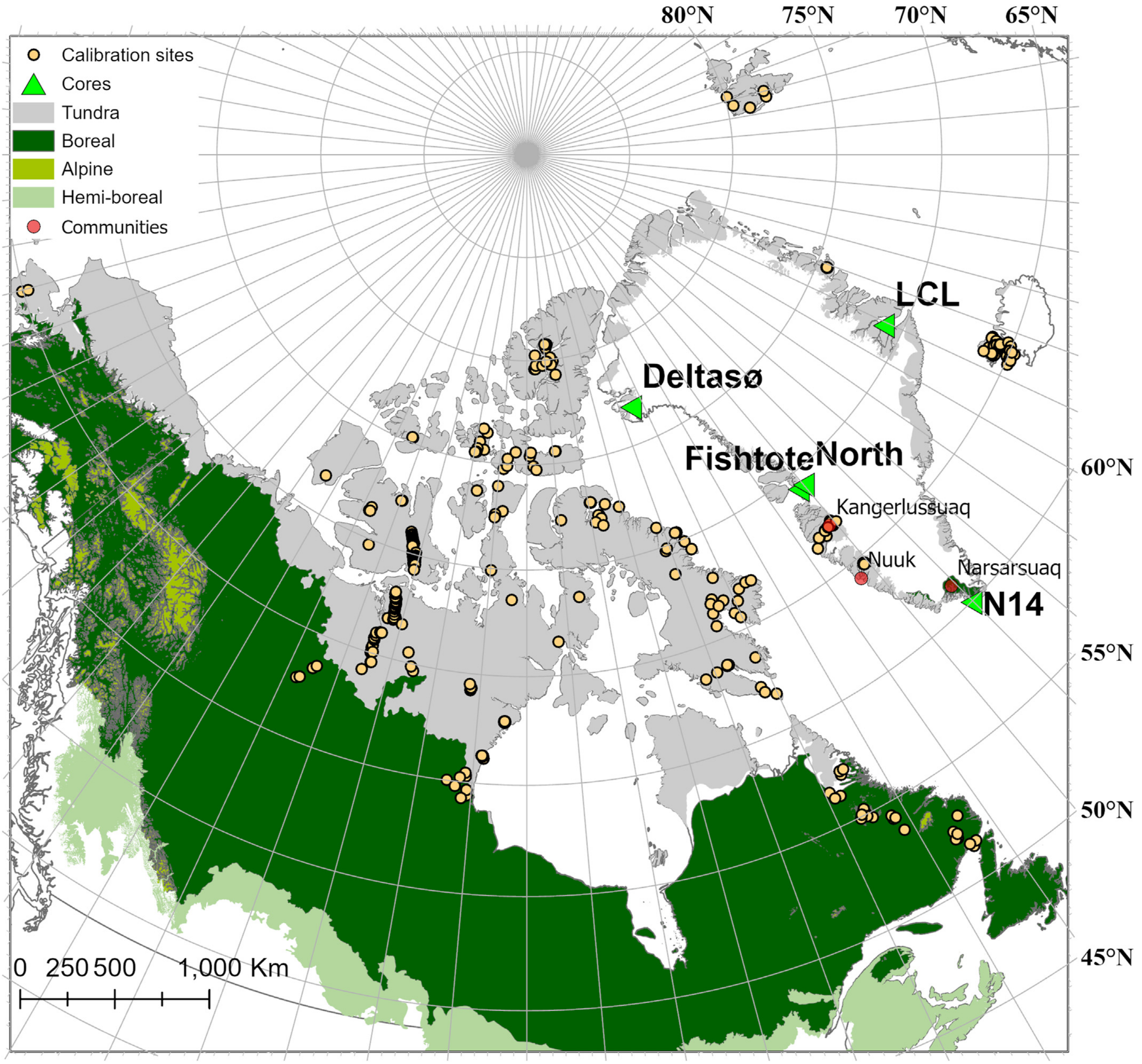

Fig. 1. The 402 sites in the full calibration-set (●) for North America, Greenland, Svalbard and Iceland. Locations of downcore records from Greenland (Last Chance Lake [LCL], Fishtote Lake, North Lake, Lake N14, and Deltasø), to which the temperature-inference model presented here is applied, are shown as triangles (▲). The extent of the North American Boreal Zone is outlined (Brandt, 2009) and the settlements of Narsarsuaq, Nuuk, and Kangerlussuaq are shown (●).

temperature normals and does not fully account for small-scale local topography, so conceivably WorldClim-estimated site temperatures in high-relief or coastal areas could be less accurate. However, temperature gradients within the high-relief Iceland and southwest Greenland training sets in the WorldClim temperature estimates are not notably smaller than in the original estimates, suggesting that local topography is quite well represented in WorldClim modeling. Overall, the WorldClim temperature estimates for the training set sites are in good agreement with the previously published temperature estimates for the sites (which utilized differing, locally determined best-available methods for estimating temperatures; see Supplemental Fig. S1). The WorldClim JJA mean temperature estimates are, as expected, overall slightly lower than the published July mean temperature estimates, with a mean difference of 1.1 °C (±0.9 °C). Our high-resolution chironomid assemblage data and summer temperatures used to generate inference models used in this study from all sites are archived at the US NSF Arctic Data Center https://doi.org/10.18739/A27H1DN9Q.

2.2. Downcore subfossil data

To assess analogues for late Pleistocene and Holocene subfossil assemblages in Greenland, and to evaluate temperature reconstructions based upon the new calibration dataset, we utilized new late glacial and Holocene subfossil assemblage data from Lake N14 in southernmost Greenland (Fig. 1) and published Holocene subfossil assemblage data from four lakes representing three additional geographically and climatically distinct regions of Greenland: Fishtote Lake and North Lake in the west near Disko Bugt (Fig. 1; Axford et al., 2013), Deltasø in the northwest near Qaanaaq and Pituffik/Thule Air Base (Axford et al., 2019), and Last Chance Lake in the east inboard of Scoresby Sund (Axford et al., 2017). For the four published sites, detailed site geography and sediment chronologies are presented in the respective original publications. The original publications report the following modern (late 20th/early 21st century instrumental) mean July temperature estimates for each of the sites or nearest weather stations: 7.7 °C at North and Fishtote lakes, 6.1 °C at Deltasø, and 7.1 °C at Last Chance Lake (the latter likely being an overestimate, from a weather station 600 m lower in elevation and 140 km away). All four lakes are small (<0.5 km^2 and <20 m deep) and three have been isolated from glacier meltwater since regional deglaciation in the early Holocene. Deltasø has been influenced by meltwater since a local glacier advance ~1850 CE.

Lake N14 is a small lake (<0.1 km^2, $Z_{max} = 8$ m) on Angissoq Island off the coast of southernmost Greenland (Fig. 1; 59°58.85′N, 45°10.80′W; 33 m a.s.l.). Lake N14 is an isolation basin that was among the earliest in Greenland to deglaciate and isolate from the sea after the last glacial maximum, and is known to contain a lacustrine record of the late Allerød, the Younger Dryas and the entire Holocene (Björck et al., 2002). Modern (1981–2010 CE) mean JJA air temperature is 7.1 °C (and 7.6 °C for July) recorded at the Qaqortoq coastal weather station ~85 km northwest of Lake N14. WorldClim 2.1 estimates of the mean temperature of the warmest quarter (JJA, 1970–2000 CE) is 7.8 °C at this site. Bedrock throughout and surrounding the watershed is Paleoproterozoic granite and granodioritic gneiss (Steenfelt et al., 2016). The sediment core used here (19-N14-N7) was collected in summer 2019 from the central region of the lake at 4.2 m water depth using a percussion piston corer. Surface sediments (from 0 to 1 and 1–2 cm depths combined) were collected nearby with an Ekman sampler to assess modern chironomid assemblages. The core is ~380 cm long and contains 345.5 cm of laminated, banded or very moss-rich lacustrine sediment underlain by a basal unit of glaciomarine clay. We examine subfossil chironomid assemblages from the bottom lacustrine section to reconstruct the relatively large temperature changes that occurred over Greenland in the late glacial period and earliest Holocene, especially across the Allerød-Younger Dryas and Younger Dryas-early Holocene transitions at 12,900 and 11,700 cal yr BP respectively (Björck et al., 2002; Rasmussen et al., 2006; Buizert et al., 2014, 2018).

The age model for Lake N14 sediments is based upon AMS ^{14}C ages of aquatic mosses (n = 18) supplemented with ages of organic matter in 1-cm-thick bulk sediment samples for intervals where plant macrofossils were absent (n = 6; see Supplementary Table S2). Ages were calibrated using Calib version 8.2 (Stuiver et al., 2022) and the IntCal20 calibration curve (Reimer et al., 2020). Age modeling utilized the R package Bacon (Blaauw and Christen, 2011; see Supplemental Fig. S2). Lacustrine sedimentation began prior to the oldest ^{14}C age of 13,605 (13,480–13770 2σ; Table S2), at ~13,700 cal yr BP according to our age model.

2.3. Data analysis

All statistical analyses were performed using R v4.0.2 (R Core Team, 2013). The gradient lengths of chironomid assemblages from the 402-lake dataset were determined through a Detrended Correspondence Analysis (DCA) using the *vegan* package (Oksanen et al., 2013). As distinct clusters of sites were observed in DCA, we tested for overlap between sediment core samples and the modern samples using multivariate homogeneity of group dispersions (Fig. 2; Supplemental Fig. S3). In order to compare the sediment cores to the modern dataset, chironomid assemblages were coded by region and statistically compared using 9999 permutations of an ANOVA of Bray-Curtis distances between samples using the *betadisper* function of the vegan package, which is a multivariate analogue of Levene's test for homogeneity of variance (Anderson, 2006).

Summer air temperature inference models were developed using partial least squares (PLS), weighted average (WA), and weighted average partial least squares regressions (WAPLS). Models were developed using identifications merged to the taxonomic resolution that aligns to the downcore datasets. The downcore record from Lake N14 was identified with relatively high taxonomic resolution using the new training set, whereas models used with the published downcore records required merging of training set taxa to match the lower taxonomic resolution of older published data. Most notably, to harmonize with published downcore data *Heterotrissocladius, Micropsectra,* and *Oliveridia/Hydrobaenus* morphotypes were each lumped as groups in the model rather than split into their respective species-level morphotypes (see complete harmonization in Supplemental Table S3). Thus, the new reconstructions from published data did not leverage the full taxonomic resolution of the new training set. See Supplemental Information for full details.

Species data were square-root transformed, and models were cross-validated with a 9999 bootstrap process. Model selection followed the criteria outlined in Fortin et al. (2015), where r^2_{jack} was maximized and the maximum bias and root mean squared error of prediction (RMSEP) were minimized. To apply the new model to published downcore chironomid records from each core, we merged taxa as needed to match the taxonomic resolution of the downcore assemblage data and calculated anomalies versus the uppermost sample in each record. The new chironomid-based calibration-set was used to reconstruct Holocene summer air temperatures based upon published assemblage data from Last Chance Lake, Deltasø, Fishtote Lake, and North Lake (using a taxonomically "coarse model") and late glacial and early Holocene temperatures based upon new assemblage data from Lake N14 (using a "high resolution model"). In both cases, the WA-PLS2 model was found to be significant, and had a higher r^2_{jack} and lower bias and RMSEP than other models (Supplementary Table 4). We applied the WA-PLS2 models to the assemblage data for each core. For the previously published downcore records, we also compared the new reconstructions to published temperature anomalies for each lake. We analyzed goodness-of-fit of reconstructions of each core, as well as the squared chord distance of analogues between the downcore intervals and training set (see supplemental information). To further assess how late Pleistocene and Holocene downcore samples from Greenland compare with the calibration-set, the trajectory of subfossil data from each core was passively plotted within the modern calibration space constrained to summer air temperature using timetrack analysis within the package '*analogue*' (Simpson, 2007; Supplemental Fig. S6).

3. Results

A DCA of all sampling locations indicated strong regional spatial gradients, with some regions appearing highly dissimilar to lakes in Greenland (Fig. 2a). An analysis of multivariate homogeneity of variances conducted on a Bray-Curtis distance matrix (Anderson, 2006) showed that modern chironomid assemblages from Greenland (the majority of which were from low Arctic sites in southwest Greenland) were most similar to those of Iceland;

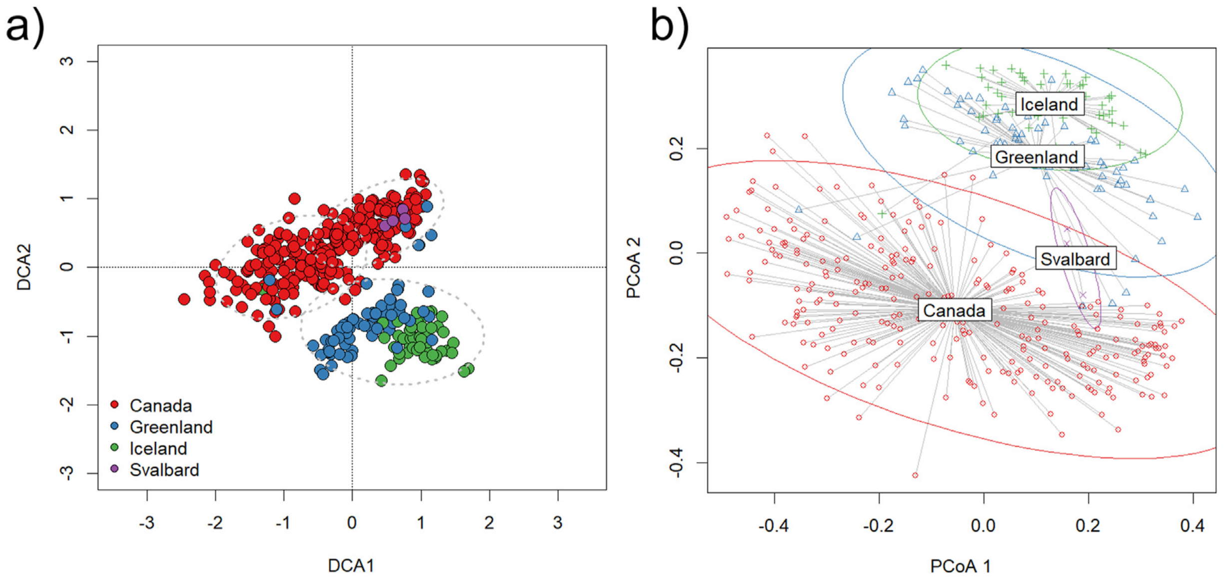

Fig. 2. Analysis of applicability of regions covered in the 402 calibration-set for reconstructions of lakes in Greenland demonstrated by **a)** Detrended Correspondence Analysis (DCA) of chironomid assemblages, and b) multivariate homogeneity of variances with non-euclidean distances between sites. Group centroids shown as ellipsoids based on 95% confidence intervals where original distances to principal coordinates are calculated (Anderson, 2006).

however, some sites were more similar to regions of northern Canada. Samples from Svalbard were more similar to both northern North America and Greenland (Fig. 2b).

Based on the results shown in Fig. 2, we included Icelandic sites in our analysis due to the high probability of assemblage analogues for Greenland lakes. This is supported by reported similarities between aquatic invertebrate faunas (e.g., Gislason, 2021). Ultimately, several samples in our downcore reconstructions had good analogues in Iceland (Supplementary Fig. S3).

For northwest and east Greenland, the new Holocene temperature reconstructions are similar to the original published reconstructions that used smaller training sets from North America (Francis et al., 2006; Fortin et al., 2015; Fig. 4b and c). In west Greenland, Axford et al. (2013) reported somewhat divergent temperature reconstructions utilizing two different training sets, one from Iceland and one from northeast North America. For those sites, situated ~250 km north of the nearest Greenland calibration sites in our training set, the strongest analogues in the new training set were found in Iceland (Supplemental Fig. S3). Accordingly, the new reconstructions more closely resemble the published reconstructions that were based on the Icelandic training set, although the new reconstructions diverge significantly from the Iceland-based reconstructions in the early Holocene at Fishtote Lake and from 6000 to 4000 cal yr BP at North Lake (Fig. 4d). Downcore assemblages from all four lakes and three regions of Greenland had good analogues within the training-set (Supplemental Fig. S4); however, Last Chance Lake had a number of intervals that showed a poor fit to the model (Supplemental

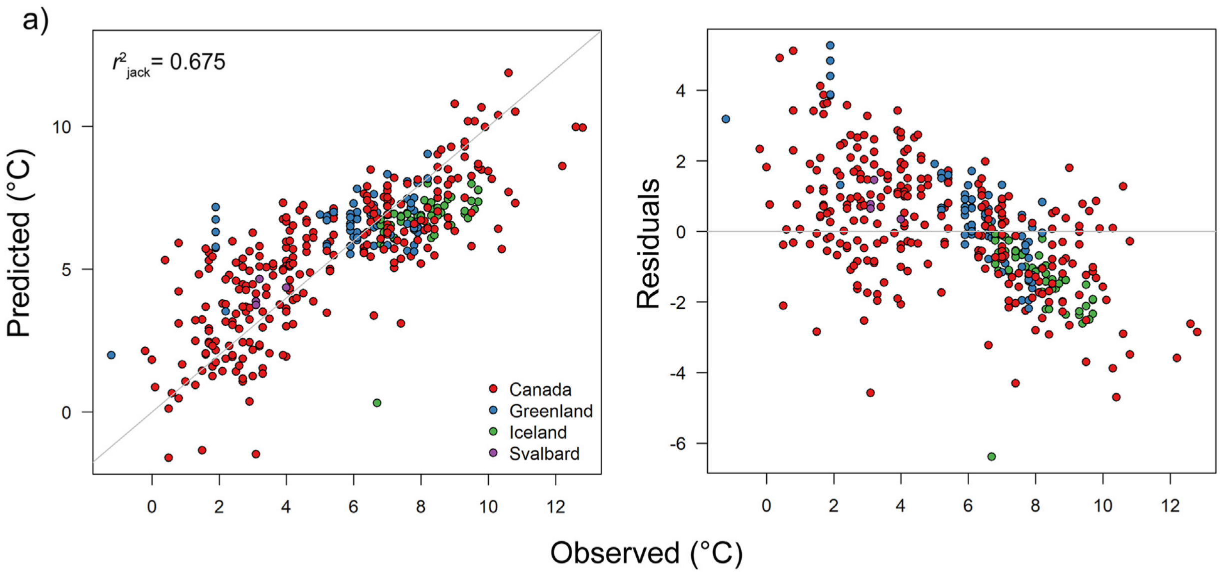

Fig. 3. Chironomid-based paleotemperature model using 402 lakes in northern Canada and Alaska, southwest and east Greenland, Iceland and Svalbard. a) Modeled mean summer temperatures versus observed (WorldClim climate mean of the three warmest months), b) residuals from the model.

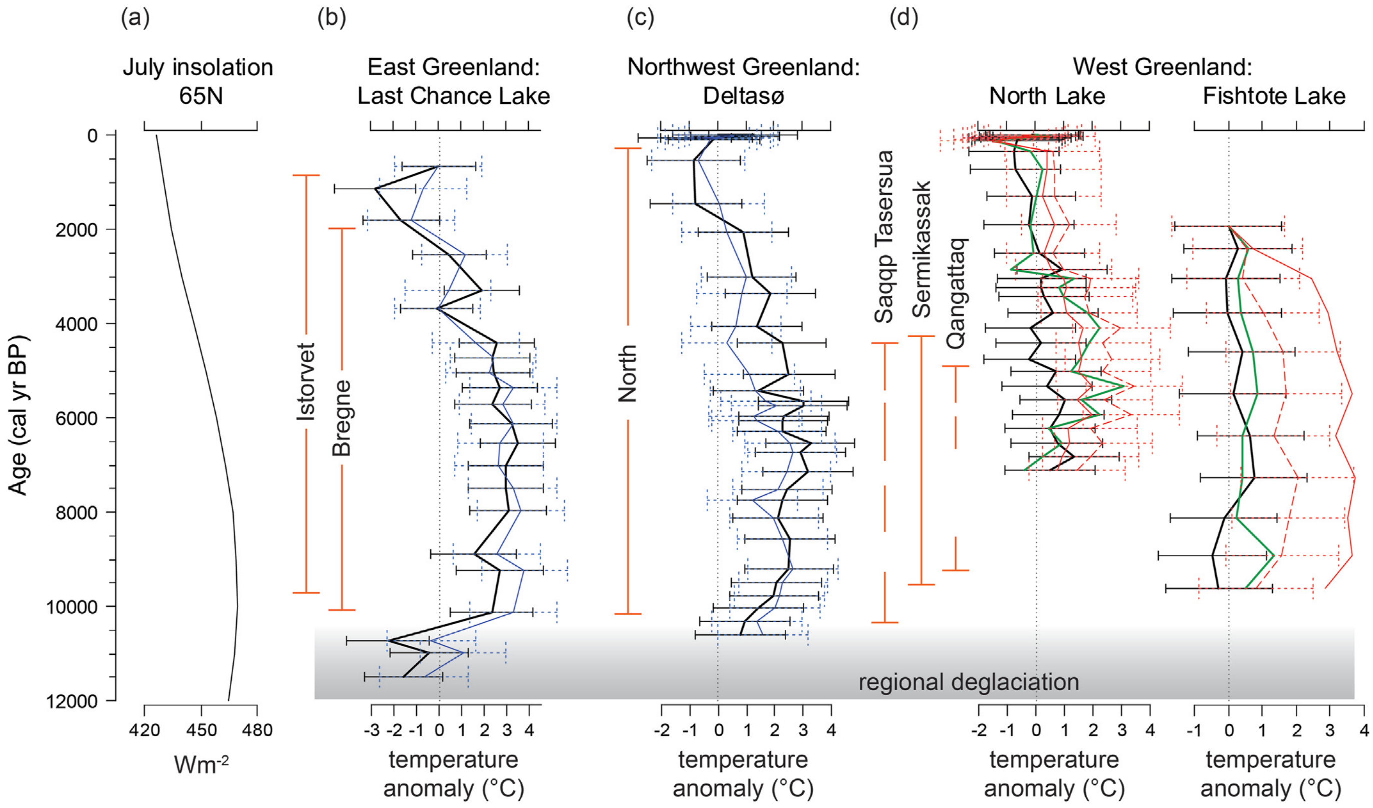

Fig. 4. New chironomid-based reconstructions of mean summer temperatures in three regions of Greenland compared with published chironomid-based July temperature reconstructions and independent evidence for summer climate. (a) July insolation forcing at 65 °N (Berger and Loutre, 1991); (b, c, d) summer paleotemperature records from east, northwest and west Greenland, respectively. New reconstructions (in black) use the region-wide WAPLS model presented here. Anomalies were calculated versus the uppermost sample in each record. Original published July air temperature reconstructions (from Axford et al., 2013, 2017, 2019) are shown in colors (blue lines are reconstructions based upon the northern North American WAPLS model of Fortin et al. (2015) with RMSEP 1.9 °C; solid (dashed) red lines are based upon the northeast North American WA model with (without) tolerance down-weighting of Francis et al. (2006) with RMSEP 1.5 °C (1.6 °C); green lines are based upon the Icelandic WAPLS model of Langdon et al. (2008) with RMSEP 1.1 °C). Where the original publication indicated a preferred reconstruction model, only that model is shown here. For each site, sample-specific errors are shown for the new model and one older model for comparison. Vertical orange bars mark periods when ice caps near each lake were smaller than their current extents, suggesting summer temperatures warmer than those of the mid-20th century (ice cap/glacier names are given in the figure; results from Lowell et al., 2013; Levy et al., 2014; Schweinsberg et al., 2017, 2019; Axford et al., 2019). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Fig. S5). This was primarily due to the large number of *Psectrocladius* nr. *barbimanus*-type, a taxon that is primarily represented in the mid-late Holocene and thus far rarely found in modern sediments.

Subfossil species assemblages from Lake N14 in southernmost Greenland reflect major climate changes of the Allerød, Younger Dryas, and early Holocene, as do the corresponding temperature reconstructions (Fig. 5; Supplemental Fig. S7). Assemblages in the lowest part of the core, i.e., the early Allerød, were dominated by several morphotypes of the cold stenotherm *Hydrobaenus* (Supplemental Fig. S7). The extreme cold stenotherm *Oliveridia* rose to >50% abundance in the later part of the Allerød and dominated Younger Dryas assemblages at abundances up to 92%. Overall head capsule concentrations dropped within the Younger Dryas. In the uppermost Younger Dryas sample and bottom two Holocene samples, concentrations were so low that statistically representative count sums (≥50) could not be obtained, even after combining adjacent samples (Supplemental Fig. S7). Allerød and Younger Dryas samples had closest analogues in Arctic Canada, but the goodness-of-fit to the WAPLS2 model was poor (Supplemental Fig. S8).

Oliveridia and *Hydrobaenus* declined abruptly at the start of the Holocene 11,700 cal yr BP. These cold stenotherms remained but in low abundances and were largely replaced by morphotypes of *Micropsectra* and *Psectrocladius*, plus low abundances of *Einfeldia pagana*-type and *Corynocera oliveri*-type (Supplemental Fig. S4), yielding an inferred rapid warming to interglacial temperatures at the start of the Holocene (Fig. 5). Head capsule concentrations were extremely low in the first few centuries of the Holocene, due to high concentrations of aquatic moss remains, but chironomid assemblages were nonetheless clearly distinct from those of the Younger Dryas. Overall head capsule abundances rose at ~11,100 cal yr BP, and for several hundred years chironomids shifted back to Allerød-like assemblages dominated by *Hydrobaenus* and to a lesser extent *Oliveridia*. By 10,600 cal yr BP, *Einfeldia* and *C. oliveri-type* returned to the lake. At ~10,500 cal yr BP, *Hydrobaenus* and *Oliveridia* completely disappeared and assemblages were dominated by *Psectrocladius* and *C. oliveri-type*. Holocene assemblages since 10,500 cal yr BP were represented by analogues from Greenland; only these most recent intervals had a ‘good’ goodness-of-fit to the WAPLS2 model (Supplemental Fig. S5). The new transfer function modeled an accurate estimate of modern temperatures based upon recent assemblages at Lake N14; chironomids in a surface sediment sample (0–2 cm depth) collected in 2019 yielded a modeled JJA temperature of 7.0 °C, compared with meteorological JJA temperature of 7.1 °C at nearby Qaqortoq. Sample-specific errors of downcore reconstructions were slightly smaller using the new temperature-inference model (Fig. 5).

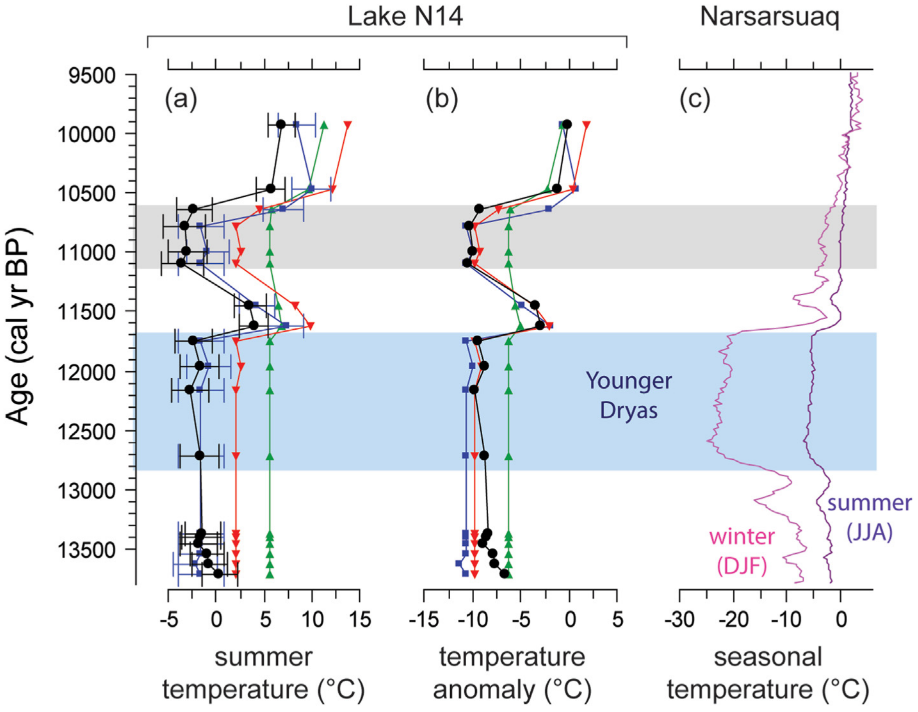

Fig. 5. Late glacial and early Holocene air temperature reconstructions from southernmost Greenland. Chironomid-based (a) absolute summer air temperature reconstructions and (b) air temperature anomalies at Lake N14 compared with summer and winter temperature reconstructions for the nearby town of Narsarsuaq, Greenland (c). New reconstructions of JJA temperatures (in black) use the region-wide WAPLS model presented here. Anomalies in panel (b) were calculated versus a reconstruction from modern Lake N14 surface sediments. July air temperature reconstructions shown in blue are based upon the northern North American WAPLS model of Fortin et al. (2015) and in green and red are based upon the northeast North American WA model of Francis et al. (2006) (with and without tolerance down-weighting, respectively). Sample-specific errors are shown for both WAPLS models (but for figure clarity, not for all models). Estimates of winter (pink) and summer (violet) temperatures at Narsarsuaq are from Buizert et al. (2018) and are based upon Summit ice core δ^{15}N combined with estimates of past seasonality and spatial patterns in climate derived from climate model simulations. The Younger Dryas is shaded light blue and a cryptic interval of cold indicator taxa and low chironomid-inferred early Holocene temperatures is shaded light gray. See Fig. 1 for site locations. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

4.1. Greenland analogues in the continent-scale training set

Our results show that modern chironomid assemblages from non-glacial lakes in multiple climate zones of Greenland, enumerated with relatively detailed taxonomic resolution, are well represented by analogues in Arctic Canada and Iceland (Supplemental Fig. S3). A basic premise of models built from calibration data of chironomid-temperature relationships is that the primary relationship is significant and comparable between different regions and in different temporal settings (Juggins, 2013). Although there are known differences in within-region chironomid-environment relationships between Iceland and Greenland (Medeiros et al., 2021), the overlap between chironomid assemblages of these two regions (Fig. 2b) in our analysis strongly suggests analogues from Iceland could improve interpretations of downcore assemblage shifts. Some assemblages in Greenland, especially those dominated by morphotypes of *Hydrobaenus* and *Oliveridia,* were also similar to Arctic Canada. Calibration data from Greenland itself remain limited to a few small areas, albeit with the substantial altitudinal differences among sites in southwest Greenland providing a more extensive climate gradient than implied by the narrow geographic spatial coverage. Given the challenges of acquiring an extensive calibration dataset from sparsely settled mid to high Arctic parts of Greenland, it is encouraging that analogues for both current and past assemblages across Greenland's broad climate footprint are reasonably well-represented by available data elsewhere.

4.2. Species optima in the continent-scale vs. regional training sets

Chironomids have a non-linear response to temperature (Rossaro, 1991; Danks, 2007), and if we know this relationship we can accurately predict the underlying optima and tolerance of temperature estimated from the mode and standard deviation of the Gaussian curve (Battarbee, 2000). The expansion of calibration space, as well as increased precision in the chironomid-temperature relationship, should increase the ability of models to accurately reflect the Gaussian distribution of a taxon relative to environmental variables. This, in turn, should improve the accuracy of paleoenvironmental reconstructions.

In our dataset, we differentiate taxa commonly merged, including morphotypes of *Psectrocladius*, *Cricotopus/Orthocladius,* Tanytarsini, and several taxa from the Tribe Pentaneurini. In particular, lakes in Greenland have chironomid assemblages with several different *Psectrocladius* morphotypes and/or Tanytarsini taxa, which Axford et al. (2013, 2017) noted had notable shifts throughout the early-mid Holocene. For example, the optima of different *Psectrocladius* morphotypes were found to be up to 4 °C different from one another in our new model, consistent with the merged group's broad tolerance in older datasets (e.g., tolerance of 3.6 °C in Francis et al., 2006). Whereas the broad, lumped subfamily Tanytarsini had an air temperature optimum of 9.9 °C and tolerance of 4.3 °C in the North American training set of Francis et al. (2006), the new training set distinguishes between different morphotypes within the subfamily, which have optima ranging from 6.1 to 9.5 °C. The optimum of *Dicrotendipes*, important in Holocene assemblages from North Lake, was found to be lower in our high-resolution dataset (Supplemental Table S3; 6.9 °C vs. 11.3 °C in Fortin et al., 2015 and 15.1 °C in Francis et al., 2006). This most likely reflects different species (formerly lumped at the genus level) being represented in the various training sets. In our high-resolution dataset, we differentiate *Dicrotendipes notatus*-type (optima 8.1 °C in our high-resolution model) from *Dicrotendipes nervosus*-type (optima 6.9 °C). Previous work has documented *Dicrotendipes* in shallow littoral areas of high-Arctic lakes associated with macrophytes (Brooks et al., 2007; Medeiros and Quinlan, 2011). Since the new model includes additional shallow cold lakes hosting abundant *Dicrotendipes nervosus*-type, our larger dataset likely captures a better representation of this taxon's true temperature optimum (Supplemental Table S3).

4.3. Evaluating paleotemperature reconstructions in Greenland

Downcore chironomid assemblages from Lake N14 provide a unique opportunity to test how the continent-scale midge training set performs compared with previously published training sets/transfer functions, throughout major climate shifts of the latest Pleistocene (Allerød, Younger Dryas) and early Holocene (Fig. 5). Unlike for the previously published sites discussed below, subfossil chironomids from Lake N14 in south Greenland were identified here at the same fine taxonomic resolution as the training set, allowing us to explore the effects of finer taxonomic resolution in the new model. We compared Lake N14 reconstructions using the high-resolution new model versus the more coarsely resolved published models (the Fortin et al. (2015) WA-PLS model, and the Francis et al. (2006) WA model with and without tolerance downweighting). We also compared chironomid-based temperature reconstructions with independent estimates of annual and summer temperature shifts in nearby Narsarsuaq (135 km north of Lake N14). Buizert et al. (2018) derived their Narsarsuaq estimates from a combination of ice core-based temperature inferences at Summit on the central Greenland Ice Sheet, and climate model-derived estimates of past spatial patterns and seasonality of temperatures. The Narsarsuaq temperature estimates have the advantage of being fully independent of our chironomid-based inferences, but the disadvantage of presuming that climate shifts on Greenland's south coast paralleled those at Summit ~1300 km away and far inland. That assumption means large uncertainty in the Narsarsuaq temperature estimates.

A structure in the residuals reveals model overestimation of the lowest summer temperatures and underestimation of highest summer temperatures in our dataset (Fig. 3). This is common for large calibration datasets as the samples encompass both a large geographic/climate gradient and a wide range of correlating and orthogonal environmental factors (e.g., differences in lake depth and morphology between sites). Medeiros et al. (2015) note that the weighted averaging process reduces these secondary-gradient effects, and for cores that reside within the primary temperature gradient it may not be a large factor for Arctic datasets. However, users should assume larger uncertainties near both ends of the calibrated temperature gradient. Furthermore, locations that are warmer than most of our training set because of lower latitude will have different biogeographic effects on assemblages (Medeiros et al., 2021). For the colder end of the gradient, < about 2 °C, there is also a biophysical limitation to take into consideration when extrapolating from models due to the extensive ice coverage on lakes below this temperature; the ecology of Chironomidae in perennially ice-covered lakes is poorly known. Likewise, while there are a number of typically ice-covered lakes in the dataset (which may or may not be perennially ice-covered in recent years due to warming), these are also some of the most extreme northerly sites, which can have biogeographic limits on the taxa that can both distribute in a single year as well as persist (Medeiros et al., 2021). The model may therefore assume a colder than expected assemblage, as well as a poor analogue, if core intervals have high abundances of taxa similar to modern analogues at these locations. As one outcome of these limitations of the model, we note below that our temperature reconstructions for the Younger Dryas in South Greenland are likely over-estimations.

The new transfer function performed somewhat better than older chironomid models at resolving temperature changes within the cool Allerød and very cold Younger Dryas. The less taxonomically resolved older models lump *Oliveridia* and *Hydrobaenus* and reconstructed flat-lined temperatures throughout the late glacial period. In contrast, the new model, which distinguishes *Oliveridia* from *Hydrobaenus* and resolves several morphotypes of *Hydrobaenus*, inferred summer temperatures up to 3 °C warmer during the Allerød than during the Younger Dryas. Although that amplitude of temperature change is still small compared with estimates from the Summit, Greenland, ice cores (and thus also the estimates for Narsarsuaq), its general pattern agrees with other records of climate in the North Atlantic region (Buizert et al., 2018; Fig. 5). Allerød temperature reconstructions could be overestimates if relatively thermophilous taxa had not yet migrated to what would have been a pioneering first outcropping of ice-free land in Greenland during regional deglaciation. Given that reconstructed temperatures of the Younger Dryas fall below the calibration range of all available training sets, Younger Dryas temperatures may be over-estimated. However, to support chironomids the lake must have had at least an ice-free moat during some weeks of summer; thus, JJA temperatures were likely not much below the reconstructed values. The new model estimated that Younger Dryas JJA temperatures at Lake N14 were ~9–9.5 °C lower than modern (i.e., than temperatures modeled from the surface sample, which were 0.1 °C lower than 1981–2010 instrumental measurements at Qaqortoq). That estimate is intermediate between summer and annual temperature anomalies modeled for Narsarsuaq based upon ice cores and climate modeling (~3–4 °C larger than the Narsarsuaq summer anomaly and ~12–13 °C smaller than the Narsarsuaq annual temperature anomaly, with anomalies calculated relative to results for 1981–2010 CE; Buizert et al., 2018).

All models except the tolerance-downweighted WA model reconstructed an abrupt increase in summer temperatures at Lake N14 at the onset of the Holocene. The tolerance-downweighted WA model was very strongly influenced by the narrow tolerance of the *Oliveridia/Hydrobaenus* group in the corresponding training set (Francis et al., 2006). Our new chironomid-based paleotemperature model estimated a Holocene onset warming of ~6.5 °C, which is similar to the estimated summer warming at Narsarsuaq of ~5 °C (Buizert et al., 2018). The biggest divergence between the chironomid-based reconstructions for Lake N14 and the ice core- and climate model-based reconstructions for Narsarsuaq occurred between ~11,100 and 10,600 cal yr BP. During this period, the cold stenotherms *Oliveridia* and *Hydrobaenus* again dominated chironomid assemblages and *Psectrocladius* disappeared – clear qualitative evidence for strong cooling. Appropriately, all models inferred very cold summer temperatures during this period. Inferred temperatures at Lake N14 returned to interglacial values shortly after ~10,600 cal yr BP. The centuries of very cold temperatures at this time, clearly indicated by qualitative assessment of the insect assemblages, contrast with the gradual warming inferred at Summit in central Greenland (and at Narsarsuaq in south Greenland based on Summit data; Buizert et al., 2018) over the same time. It appears that temperatures at Lake N14 diverged from those at Summit for several centuries, though the spatial extent and cause of the early Holocene cooling are unknown. Glacial geologic studies in the region indicate that the Greenland Ice Sheet margin had retreated far inland of Angissoq Island and Lake N14's watershed by this time (e.g., Larsen et al., 2011; Levy et al., 2020), and the island's low-relief landscape would not have hosted local mountain glaciers. Therefore, glacier meltwater influx to the lake itself cannot explain the dominance of cold taxa during this time. However, outlet glaciers still fed into fjords in the broader region, and the reconstructed early Holocene cold period at Lake N14 is consistent with some local evidence for conditions offshore of southwest Greenland, where meltwater from the waning Greenland Ice Sheet had profound effects on sea surface conditions in the early Holocene. For example, Allan et al. (2021) reported suppression of sea-surface temperatures off southwest Greenland by meltwater until the "onset of interglacial conditions at a regional scale" at ~10,000 cal yr BP. It is increasingly recognized that both Laurentide and Greenland Ice Sheet meltwaters protractedly and repeatedly influenced sea-surface conditions in the Labrador Sea throughout the early Holocene, probably suppressing temperatures over land in south and southwest Greenland (Jennings et al., 2015; Larocca et al., 2020; Young et al., 2020; Allan et al., 2021; Axford et al., 2021). Angissoq Island's position offshore may have made it especially susceptible to this effect, but more research in the region is needed to establish how widespread any early Holocene cooling was.

To further test the performance of the new model for reconstructing climate across a wide range of Greenland's climate zones, we compared chironomid-inferred Holocene temperatures from four lakes with independent Holocene paleotemperature evidence from the extents of local ice caps near each lake. As such, chironomid-based temperature reconstructions from the four sites using our new model were compared with the glacier-based summer temperature constraints to assess which model(s) performed best. Summer insolation forcing (Berger and Loutre, 1991) is known to have strongly influenced Holocene summer temperatures in Greenland, leading to generally the warmest Holocene climate in many parts of Greenland from ~10,000 to 6000 cal yr BP and gradually declining summer temperatures throughout the late Holocene (Axford et al., 2021; Fig. 4a). Despite this overall broad pattern, there were distinct regional differences in Holocene temperature trends across Greenland, most notably from north to south/southwest (Briner et al., 2016; Larocca et al., 2020; Axford et al., 2021), so local-scale independent information was also needed for comparison. Prior research has established that major local ice caps near each of the lakes were smaller than their present sizes for parts of the early to middle Holocene, attributed to summer temperatures elevated above those of the 20th Century (Lowell et al., 2013; Levy et al., 2014; Schweinsberg et al., 2017, 2019; Axford et al., 2019).

To model temperatures at each of the four lakes using our new training set required merging some taxa in the new training set because it utilized finer taxonomic resolution than the published downcore identifications. However, unlike the training sets used to model previously published temperature reconstructions for these sites, our new training set utilizes the full taxonomic resolution of the subfossil data that were collected at the four sites. Thus, this exercise also assessed the value of increased taxonomic resolution, albeit lower than the high taxonomic resolution of the new model.

At the mid to high arctic sites Last Chance Lake (Fig. 4b) and Deltasø (Fig. 4c), the new model successfully reconstructed peak temperatures during the early to middle Holocene periods of smaller ice cap size and higher summer insolation forcing. The new reconstructions at these sites also mirrored the amplitudes and patterns of published midge-based reconstructions that utilized a training set from North America only (the training set of Fortin et al., 2015), reflecting the importance of North American analogues to modern and past climates in the very cold climates of east/northeast and northwest Greenland. No samples yielded differences between published and new reconstructions that exceeded model RMSEP or sample-specific uncertainties between both models. Reconstruction uncertainties were slightly improved using the new model.

In west Greenland, the original publication noted significant differences between reconstructions using Icelandic vs. North American training sets, and our new reconstructions differed yet again (Fig. 4d). Axford et al. (2013) argued that because the models used to infer past temperature from Fishtote Lake's chironomid assemblages did not adequately differentiate Tanytarsini (which comprised up to 94% of the core's assemblage, including up to 78% *Micropsectra* spp.), the original temperature reconstructions from the lake were less precise. This was especially true when applying the North American model of Francis et al. (2006), which lumped all Tanytarsini, whereas the Icelandic model differentiated several Tanytarsini morphotypes following the same taxonomic scheme as the subfossil data. When the dominant taxa of a calibration set are merged together such that they become generalists, they effectively become eurythermic in the temperature models utilized. The new model leverages the full taxonomic resolution of the subfossil data, as did the Iceland model in the published reconstructions. The new model improves upon the Iceland model by employing a training set with much broader climatic and spatial coverage and thus more thoroughly characterizing the temperature optima of genus- and species-level morphotypes. At Fishtote Lake *Psectrocladius* and Tanytarsini, especially, exerted strong influences on the major trends in the original reconstructions; the optima and taxonomic resolution of these taxa were significantly updated in the new model (Supplemental Fig. S5, Supplemental Table S3).

The original temperature reconstructions from North Lake, which contained a more diverse assemblages than Fishtote Lake, were considered more reliable, and indicated warmer-than-present summer temperatures until ~3000 cal yr BP, with peak warmth occurring from 6000 to 4000 cal yr BP. Our new reconstruction from North Lake also indicates temperatures warmer-than-present until ~3000 cal yr BP, but with peak temperatures from the onset of the record ~7700 cal yr BP until ~5000 cal yr BP (Fig. 4d). At North Lake, *Dicrotendipes* was important in driving inferred warmth from 6000 to 4000 cal yr BP in the original reconstructions. The lower optimum estimated for this taxon in the new training set contributed to lower modeled temperatures during this warmest interval compared with previous models.

The new reconstructions from North and Fishtote lakes agreed better than published reconstructions with the independent summer temperature evidence from west Greenland ice caps, which were retracted beginning in the early Holocene and expanded to their current extents between 5000 and 4000 cal yr BP (Fig. 4d; Schweinsberg et al., 2017, 2019). Compared with the published reconstructions using subregional training sets, the decline to Little Ice Age minimum temperatures was more gradual through the late Holocene in the new North Lake reconstruction, and the overall amplitude of multi-millennial Holocene climate change was smaller (~2 °C). This amplitude of Holocene cooling was also smaller than reconstructed in north and northwest Greenland. The implied spatial difference remains speculative due to the paucity of quantitative temperature records from the region, but is consistent with an emerging view that overall Holocene cooling may have been smaller in west and south Greenland than in the north (Axford et al., 2021), likely due to differing effects of meltwater-influenced sea-surface conditions and ocean surface currents. Encouragingly, the new reconstructions from Fishtote Lake were very similar to those from nearby North Lake throughout the period of overlap between the two records. The Fishtote Lake core extends earlier than at North Lake and suggests that temperatures prior to ~8000 cal yr BP were suppressed relative to the middle Holocene. A qualitative summer temperature reconstruction based upon sedimentary leaf wax δ^2H supports elevated temperatures and subarctic climate conditions in west Greenland ~8000-5000 cal yr BP (Thomas et al., 2016), in good agreement with both new chironomid-based reconstructions. The leaf wax record does not extend into the early Holocene. Additional proxy-based reconstructions are needed to confirm temperatures of the early Holocene (i.e., prior to 8200 cal yr BP) in west Greenland.

In summary, at a wide range of Greenland sites we found strong agreement between chironomid-based reconstructions using the new model and independent evidence (from ice sheet proxies or ice cap extent) for temperature trends. In northwest and central east (mid to high Arctic) Greenland, new reconstructions were very similar to published reconstructions but reduced the uncertainty of those reconstructions. At the other sites, reconstructions using the new training set appeared to be substantially improved relative to reconstructions using less taxonomically resolved, regional-scale training sets. Specifically, the new model applied to two lakes in central west Greenland yielded Holocene temperature reconstructions that were newly consistent with independent temperature evidence. At Lake N14 in southernmost Greenland, the new model had the unique ability to distinguish temperatures of the Allerød from those of the Younger Dryas, despite very low species diversity in the late glacial period, because it distinguished between several morphologically similar taxa. The new model may underestimate the magnitude of the Allerød-Younger Dryas cooling, however; and the cause and extent of a surprising early Holocene cold period recorded by chironomid assemblages at Lake N14 is unknown, but not a function of model performance. The new, more taxonomically resolved model confirmed the large warming at the onset of the Holocene at Lake N14, in agreement with two of three existing models applied there. These improvements to paleoclimate reconstructions were attributable both to the new model's finer taxonomic resolution and to its expanded geographic/climatic coverage, which resulted in more thorough characterization of species optima.

5. Conclusion

We present taxonomically harmonized chironomid assemblage data from the surficial sediments of 402 lakes in northern North America, Greenland, Iceland, and Svalbard. The chironomid-temperature transfer function generated with this new training set is comparable in terms of model statistics to published models covering smaller sub-regions, but this larger dataset offers a much broader range of climate and assemblage analogues and thus more thoroughly characterizes the temperature optima of individual taxa. This new continent-scale training set, which offers increased taxonomic resolution compared to the previously published regional training sets, contains good analogues for modern and subfossil chironomid assemblages of Greenland, including from sites in Iceland and northern Canada.

Downcore summer temperature reconstructions based upon new and published Greenland subfossil assemblages using the new model agree well with independent summer temperature evidence. Late-glacial temperature shifts of the Allerød and Younger Dryas in south Greenland are registered only by the new, more taxonomically resolved model presented here, although the new model may underestimate their magnitude. In contrast, published models that merge morphologically similar taxa yield flat-lined temperature reconstructions through the late glacial. The new model, and the majority of published models, agree with independent evidence for the magnitude of warming at the end of the Younger Dryas (i.e., onset of the Holocene) in south Greenland. Elsewhere, Holocene temperature reconstructions generated by applying the new model to published subfossil assemblages from Greenland lakes in a wide range of climate zones also appear successful, judging by agreement with independent temperature evidence from ice cap extents. Differences with previously published Holocene reconstructions in east and northwest Greenland are small, but there are some changes in reconstructions from west Greenland. There, the improved taxonomic resolution and more thorough characterization of species optima in the new training set yielded temperature reconstructions that agree better among sites and with the independent glacier evidence.

The large, taxonomically harmonized dataset presented here should be useful for a range of other investigations, including but not limited to paleotemperature reconstructions on the northwest North Atlantic islands and in the North American Arctic and subarctic. Notably, the increased geographic and climatic coverage and higher taxonomic resolution of our dataset relative to the original publications allows for more precise characterization of chironomid-temperature relationships. One outcome should be more accurate and precise paleotemperature reconstructions, especially in regions where local calibration data are limited and/or key shifts occur between morphologically similar taxa that are newly distinguished in this dataset. While we demonstrate the utility of the broad calibration space and higher taxonomic resolution of our dataset, future high-resolution identifications of subfossil chironomid assemblages at new sites in the studied regions will likely glean additional information from our model.

Author contributions

A.S.M and Y.A. conceived the ideas and led the writing; A.S.M. analyzed the data; D.R.F., I.R.W., L.H., P.L., S.W., and M.C. contributed to the collection of training set data, collaborated on taxonomic harmonization, and contributed to discussions and writing; P.J.K.P., G.S., and R.S. collected data from Lake N14 and contributed to discussions and writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Chironomid assemblage data and site temperatures from the training set are publicly archived with the U.S. National Science Foundation’s Arctic Data Center, https://doi.org/10.18739/A27H1DN9Q. The datafiles used in this study, and associated R scripts, are publicly available in the corresponding author’s github repository; https://github.com/arcticecology/Greenland_TS.

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Appendix A. Supplementary data

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