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East European chironomid-based calibration model for past summer temperature reconstructions

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ABSTRACT: Understanding local patterns and large-scale processes in past climate necessitates a detailed network of temperature reconstructions. In this study, a merged temperature inference model using fossil chironomid (Diptera: Chironomidae) datasets from Finland and Poland was constructed to fill the lack of an applicable training set for East European sites. The developed weighted averaging partial least squares (WA-PLS) inference model showed favorable performance statistics, suggesting that the model can be useful for downcore reconstructions. The combined calibration model includes 212 sites, 142 taxa, and a temperature gradient of 11.3–20.1°C. The 2-component WA-PLS model has a cross-validated coefficient of determination of 0.88 and a root mean squared prediction error of 0.88°C. We tested the new East European temperature transfer function in chironomid stratigraphies from a Finnish high-resolution short-core sediment record and a Polish paleolake (Żabieniec) covering the past ~20 000 yr. In the Finnish site, the chironomid-inferred temperatures correlated closely with the observed instrumental temperatures, showing improved accuracy compared to estimates by the original Finnish calibration model. In addition, the long-core reconstruction from the Polish site showed logical results in its general trends compared to existing knowledge on the past regional climate trends; however, it had distinct differences when compared with hemispheric climate oscillations. Hence, based on these findings, the new temperature model will enable more detailed examination of long-term temperature variability in Eastern Europe, and consequently, reliable identification of local and regional climate variability of the past.

KEY WORDS: Chironomidae · Climate reconstruction · Finland · Holocene · Late Glacial · Paleoclimate · Poland · Training set · Transfer function

1. INTRODUCTION

Advances in paleoclimatology have enabled the building of comprehensive outlines of climate changes of the recent past, the Holocene epoch and the last glacial cycle (McCarroll 2015, Wanner et al. 2015, Linderholm et al. 2018). However, local differences and small-scale variation are still poorly established in several geographic areas. In addition to high-fidelity sediment archives, the paleoclimatological toolpack needs to be refined to reliably tackle the climate variability of the past. Non-biting midges (Insecta: Diptera: Chironomidae) have been recognized as one of the most powerful proxies to reconstruct past summer air temperature dynamics (Brooks 2006). Utilizing the fossil community compositions of the temperature-

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*Corresponding author: tomi.luoto@helsinki.fi sensitive chironomid taxa and applying the calibration set approach via a transfer function, quantitative climate inferences have become available from sites where other paleoclimate proxies have failed or are not possible to use (Ilyashuk et al. 2011, Luoto et al. 2018). In addition to confounding environmental variables, such as nutrients (Brodersen & Quinlan 2006, Eggermont & Heiri 2012, Medeiros et al. 2015), a potential downside of chironomids as a paleotemperature proxy lies in the suitability of the calibration set to the downcore site (Engels et al. 2014). In an ideal situation, the downcore site should be within the geographical area of the training set, the study site characteristics (such as lake size and depth) should be similar, and the calibration sites should constitute a temperature gradient that covers the expected range of past temperature changes. When applying inference models to cores outside the training set's geographical or environmental range, problems related to taxa occurrences (poor modern analogues) and unrealistic taxon-specific temperature optima arise. Moreover, continental-scale calibration sets (Heiri et al. 2011) may not be able to detect small-magnitude variation in temperatures, although they can be very useful in reconstructing the large-scale climate patterns.

Previously, it has been challenging to produce reliable chironomid-based temperature inferences at the ends of the temperature gradient in Eastern Europe. In downcore sites located in southern Finland, temperatures of warm climate events, such as the recent warming, Medieval Climate Anomaly and Holocene Thermal Maximum, may have been underestimated due to lack of equally warm calibration sites (Rantala et al. 2016, Shala et al. 2017). Similarly, the lack of warm calibration sites in the available chironomid-based temperature inference models have thus far caused problems in downcore studies of Polish sites due to a deficiency of warm analogues (Pawłowski et al. 2015, 2016a). Here, we combine the Finnish calibration sets (Luoto 2009, Luoto et al. 2016) with a dataset collected from Poland (previously unpublished) to create a more applicable temperature inference model for East European sites than has previously been available. In addition to standard numerical testing of the model performance, we validate the model using a chironomid stratigraphy from an annually laminated lake sediment record from Finland and compare the reconstruction against instrumentally measured temperatures. In addition, we apply the East European calibration model on a chironomid record from a Polish paleolake covering the past ~20 000 yr and compare the output against previous reconstructions. We aim to produce a new quantitative tool for more reliable reconstructions of past climate patterns in the East European sector to better describe local climate variability.

2. MATERIALS AND METHODS

2. 1. Study sites and sediments

The training set study sites comprise 212 lakes located in Finland and Poland (Fig. 1). The 114 Finnish sites, collected with a Limnos gravity corer between 2005 and 2014, originate from 2 previously published datasets located at a treeline transect in northeastern Lapland (32 lakes, 68° 47′ N–69° 55′ N) (Luoto et al. 2016) and along the latitudinal gradient of Finland (82 lakes, 60° 13′ N–69° 53′ N) (Luoto 2009). The mean July air temperature in the Finnish sites varies between 11.3 and 17.1°C (mean: 14.4°C, median: 14.1°C) within an altitudinal gradient of 4–405 m above sea level (a.s.l.). All sites are small and shallow (0.5–7.0 m) with pH between 4.6 and 8.4. The 98 Polish lakes, sampled in summer 2014 using a Kajak corer, are located between 49° 19′ N and 54° 68′ N and constitute an altitudinal gradient of 4–1624 m a.s.l. The mean July air temperature in the Polish sites varies between 11.6 and 20.1°C (mean: 18.6°C, median: 18.9°C), whereas the depth range is 0.3–15.0 m. The lake water pH fluctuates between 5.1 and 9.8. The Polish dataset is previously unpublished. A comparison between the combined training sets is given in Table 1.

The short-core test site Lake Nurmijärvi (61° 35′ N, 25° 55′ E; 87.7 m a.s.l.) is located in south-central Finland (Fig. 1). The lake with annually laminated sediments is currently circumneutral (pH = 7.0) and mesotrophic. The mean July air temperature at the study site is 16.9°C (climate normals for 1981–2010, Finnish Meteorological Institute). The sediment sequence was cored in winter 2016 using an HTH corer and subsampled at 1 cm intervals. The average sample interval in the verified varve chronology (Ojala et al. 2017, 2018) is 4 yr and the available meteorological data begins from the 1830s. The full chironomid stratigraphy of Nurmijärvi is published in Luoto & Ojala (2017).

The long-core sediment site Żabieniec (51° 51′ N, 19° 46′ E; 180 m a.s.l.) is currently a bog located in central Poland (Fig. 1). The present-day mean July air temperature at the study site is 18°C. Detailed descriptions of the study site and the paleolake sediments together with the full chironomid stratigraphy and chronology are given elsewhere (Płóciennik et

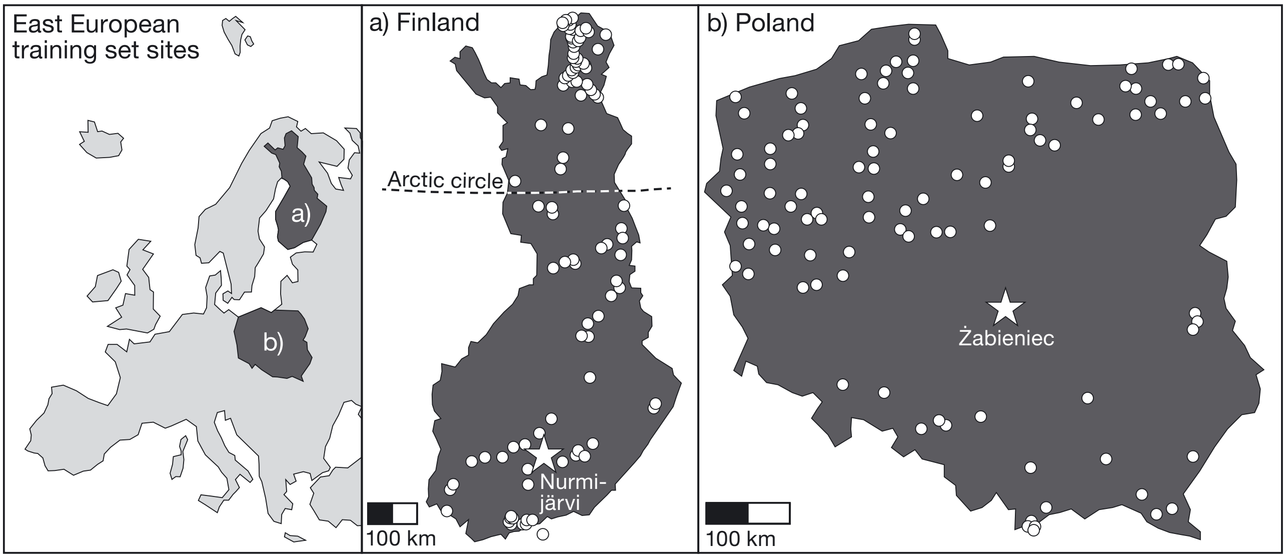

Fig. 1. Calibration sites (white dots) of the East European chironomid-based temperature training set. (a) The Finnish dataset (60° 13′ N–69° 55′ N) includes 114 lakes and (b) the Polish dataset (49° 19′ N–54° 68′ N) 98 lakes. Downcore study sites Żabieniec (Poland) and Nurmijärvi (Finland) are marked with stars

Table 1. Characteristics of study sites in Finnish, Polish and combined East European chironomid-based temperature datasets. Mean values are given in brackets. a.s.l. = above sea level

	Finnish	Polish	Combined
Number of sites (N)	114	98	212
Number of taxa (n)	111	100	142
Latitude (°N)	60.13–69.55 (65.91)	49.19–54.68 (52.60)	49.19–69.55 (59.60)
Longitude (°E)	22.00–30.13 (26.55)	14.51–23.42 (18.42)	14.51–30.13 (22.69)
Elevation (m a.s.l.)	4–405 (157)	4–1624 (196)	4–1624 (174)
Temperature gradient (°C)	11.3–17.1 (14.4)	11.6–20.1 (18.6)	11.3–20.1 (16.4)
Sampling depth (m)	0.5–7.0 (2.3)	0.3–15.0 (8.8)	0.3–15.0 (5.7)
pH	4.6–8.4 (6.5)	5.1–9.8 (8.3)	4.6–9.8 (7.5)

al. 2011). In brief, the paleolake sediments were sampled using a piston corer and the subsampling was performed at varying intervals. The stratigraphy represents roughly the past 20 000 yr. The chronology of the core is based on 13 radiocarbon dates and the age-depth model was originally presented in Lamentowicz et al. (2009).

2.2. Chironomid analysis

Fossil chironomid analysis was performed using standard methods in all the datasets and cores applying provided guidelines (Brooks et al. 2007). In short, a 100 µm mesh was used for sieving at least 50 chironomid head capsules per sample. Similar to unidentified remains, midges other than chironomids were ignored. Taxonomic harmonization of the training sets and the 2 sediment downcores was achieved through close collaboration between the chironomid analysts. The morphologically similar taxa *Thienemanniola* and *Constempellina* were separated in the combined training set according to their contemporary occurrence described in species checklists (Sæther & Spies 2013, Paasivirta 2014). In some cases (including *Ablabesmyia*, *Dicrotendipes* and *Microtendipes*), species type-level identification was scaled to genus level.

2.3. Statistical analyses

Taxon-specific mean July temperature optima in the merged dataset were estimated using weighted averaging (WA) with $\log_{10}$-transformed species data in the program C2 version 1.7.2 (Juggins 2007). Generalized linear modeling (GLM) was used to assess taxa that significantly ($p \leq 0.05$) respond to mean July air temperature. The GLMs were run using Poisson distribution in the program Past3 (Hammer et al. 2001). Detrended correspondence analysis (DCA) was used to assess the gradient lengths of the first 2 DCA axes for selection of the most suitable methods for further analyses. For linearly distributed data with short gradient lengths, principal component analysis (PCA) and redundancy analysis (RDA) are the most suitable methods (Šmilauer & Lepš 2014). The primary PCA axis scores were compared with site-specific temperatures using Pearson product-moment correlation coefficient (R), coefficient of determination (R^2) and the level of statistical significance ($p < 0.05$) to verify that the communities are responding to temperature. In addition, RDA with forward-selected environmental variables and 999 unrestricted permutations was used to partial out the significance of temperature, depth and pH (variables available from all datasets) on the chironomid assemblages in the joint dataset. The DCA, PCA and RDA were performed with $\log_{10}$-transformed species data using the CANOCO 5 program (Šmilauer & Lepš 2014).

The combined East European chironomid-based calibration model of mean July air temperature was developed using the weighted averaging partial least squares technique (WA-PLS), also with $\log_{10}$-transformed species data. The number of useful regression calibration components was assessed using *t*-test ($\alpha = 0.05$). Model performance was evaluated using jackknife cross-validation and subsequent coefficient of determination (R^2_{jack}), root mean squared error of prediction (RMSEP) and mean and maximum biases. The model was constructed using the program C2 version 1.7.2 (Juggins 2007), in which other common model types were also initially tested.

The model was verified against instrumentally measured (meteorological) temperatures available since the 1830s in the short-core sediment record from Nurmijärvi. The chironomid-inferred temperatures were tested against the observational data by applying R, R^2 and $p < 0.05$. Sample-specific modeling errors (estimated standard error of prediction = eSEP) were determined using bootstrapping cross-validation with 999 iterations. The model was also run to reconstruct temperatures in the Żabieniec long-core sediment record. LOESS smoothing was used to depict general trends using a span of 0.2. To test whether the Żabieniec reconstruction corresponded to the primary chironomid community variability, the temperatures were compared against the PCA axis 1 scores using the Pearson product-moment correlation coefficient and the associated level of statistical significance. Using the modern analogue technique (MAT), the cut-level of the 5th percentile of all squared-chord distances in the modern calibration data was determined. These distances were then compared to the distance between each fossil assemblage and its most similar assemblage in the modern dataset and used to define 'no close' analogues. The reconstruction was compared with previous chironomid-based reconstructions from the focal core using Norwegian (Brooks & Birks 2001, unpubl.), Russian (Self et al. 2011) and Swiss (Heiri & Lotter 2005, Bigler et al. 2006, von Gunten et al. 2008) calibration models. In addition, the reconstructed general local trends in temperature were compared with an ice-core temperature record (site-specific calibrations using ice-isotopic ratios, borehole temperatures and gas-isotopic ratios) from Greenland (GISP2; Cuffey & Clow 1997, Alley 2000) representing hemispheric climate development.

3. RESULTS

After merging the Finnish and Polish chironomid training sets, 142 taxa were encountered from the 212 calibration sites (Fig. 2). *Psectrocladius sordidellus*-type occurred in 86 sites, *Polypedilum nubeculosum*-type in 80 sites and *Dicrotendipes* and *Procladius* in 79 sites. *Limnophyes* reached the maximum relative abundance (75%) in a single site. *Lauterborniella agrayloides* (6.7%), *Ablabesmyia* (6.5%) and *Paratendipes nudisquama*-type (5.4%) had the highest mean abundances in the combined dataset.

The taxa with the coldest temperature optima (12.5–13.1°C) included *Heterotrissocladius maeaeri*-type, *Psectrocladius calcaratus*-type and *Zalutschia* type B, whereas the taxa with the warmest optima included *Polypedilum sordens*-type, *Glyptotendipes barbipes*-type and *Labrundinia longipalpis* (18.8–18.9°C) (Fig. 3). Taxa with intermediate temperature optima (16–17°C) and wide tolerances included *Paratanytarsus penicillatus*-type, *Dicrotendipes*, *Procladius* and *Chironomus anthracinus*-type. Of the most common taxa ($n > 5$), only *Dicrotendipes* did not respond statistically significantly to the temperature gradient (Fig. 3). For most taxa, the GLMs showed significant linear fit; however, significant nonlinear distribution was found in some taxa with intermediate temperature optima, including *Tanytarsus chinyensis*-type 1, *Natarsia punctata*-type, *Corynoneura lobata*-type, *Smittia* and *Endochironomus impar*-type.

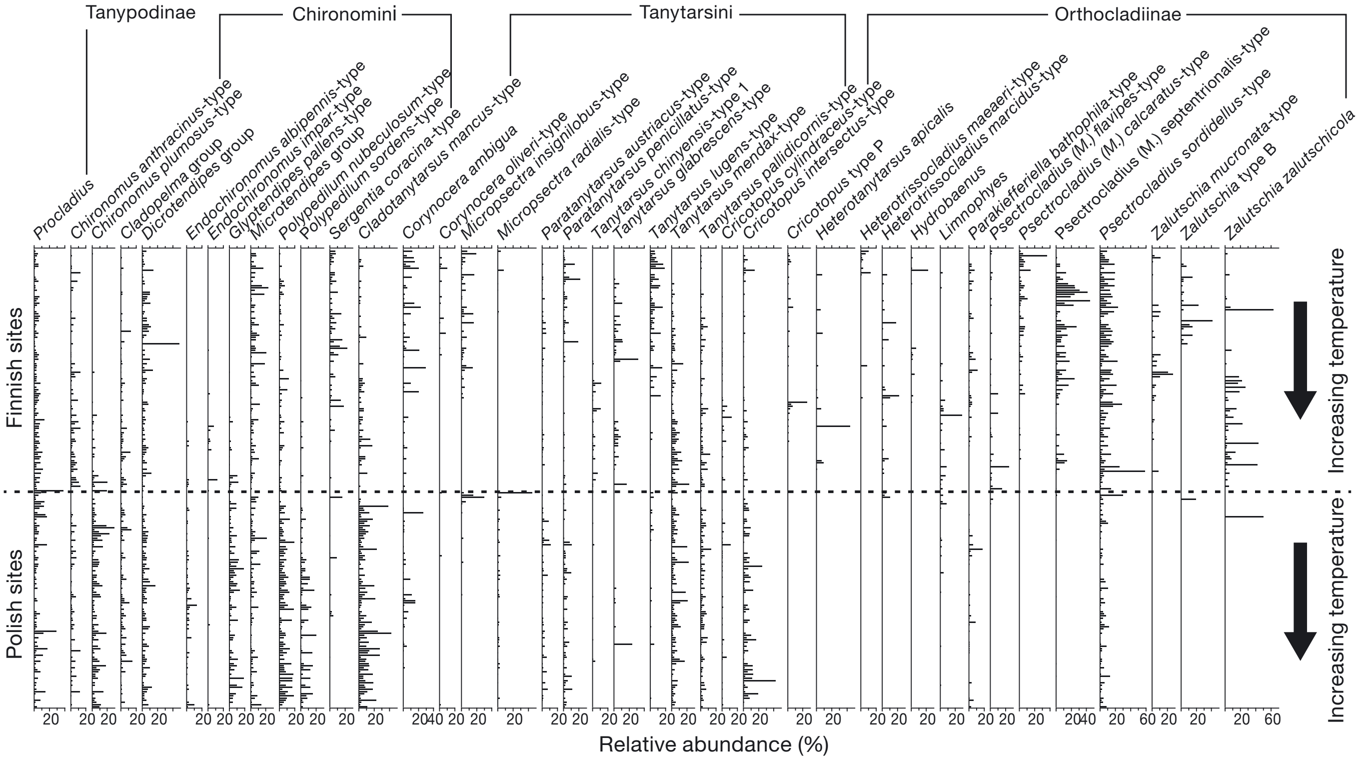

Fig. 2. Most common chironomid taxa (>10 occurrences and maximum abundance >10%) in the combined East European chironomid-temperature training set

Paratanytarsus penicillatus-type was the only taxon with bimodal distribution, with highest abundances at both ends of the temperature gradient.

The initial DCA indicated a gradient length of 2.8 SD for the surface sediment chironomid assemblages. Hence, owing to the linear nature of the data, PCA was recommended for ordination analysis (Šmilauer & Lepš 2014). Subsequently, PCA axis 1 showed an eigenvalue of 0.1974, and axis 2 an eigenvalue of 0.0659. The first axis explained 19.7% and the second 6.6% of the total variance. The first 4 axes explained 36.1% of the variance in total. In the ordination (Fig. 4), the samples along the primary PCA axis were arranged according to the site-specific mean July air temperatures, with Polish sites (warm) having negative scores and Finnish sites (cold) positive scores (Fig. 4a). The warm and cold indicator taxa identified with the PCA ordination (Fig. 4b) were the same as indicated with the WA optima and GLMs (Fig. 3). The PCA axis 1 scores of the samples were strongly correlated with the site-specific temperatures ($R = 0.91$, $R^2 = 0.82$, $p < 0.001$). RDA results showed that temperature was the most important variable in explaining chironomid distribution of the examined variables. Of variation explained by the examined variables (15.4%), temperature explained 78.8%, pH 13.7% and depth 7.5% (Table 2). Consequently, temperature clearly had the highest eigenvalue ratio (λ_1:λ_2; 1.061) that justified the construction of the chironomid-based temperature model.

Compared to other model types, WA-PLS had the best performance statistics with respect to its R^2_{jack} and RMSEP (Table 3). The developed WA-PLS model for mean July air temperature had an R^2_{jack} of 0.88, RMSEP of 0.88°C and mean and maximum biases of –0.02 and 0.79°C, respectively (Table 4). Addition of the second regression calibration component reduced the RMSEP by 8.8% (randomization *t*-test significance: 0.004). The 1:1 relationship between the inferred and observed temperatures in the model illustrated that the combined calibration set has a well-structured continuum in its temperature range, with relatively even distribution of samples (Fig. 6a). Slight distortions at both ends of the temperature gradient were observed (Fig. 5b).

The test of the developed model on the clastic-biogenic varve record from Lake Nurmijärvi showed similar trends between the chironomid-inferred and meteorologically observed temperatures over the instrumental period. In both inferred and observed records (Fig. 6a), the temperatures remained low during the 19th century, with increased temperatures in the 1930s. Following intermediate summer temperatures, the climate began to warm in the 1990s

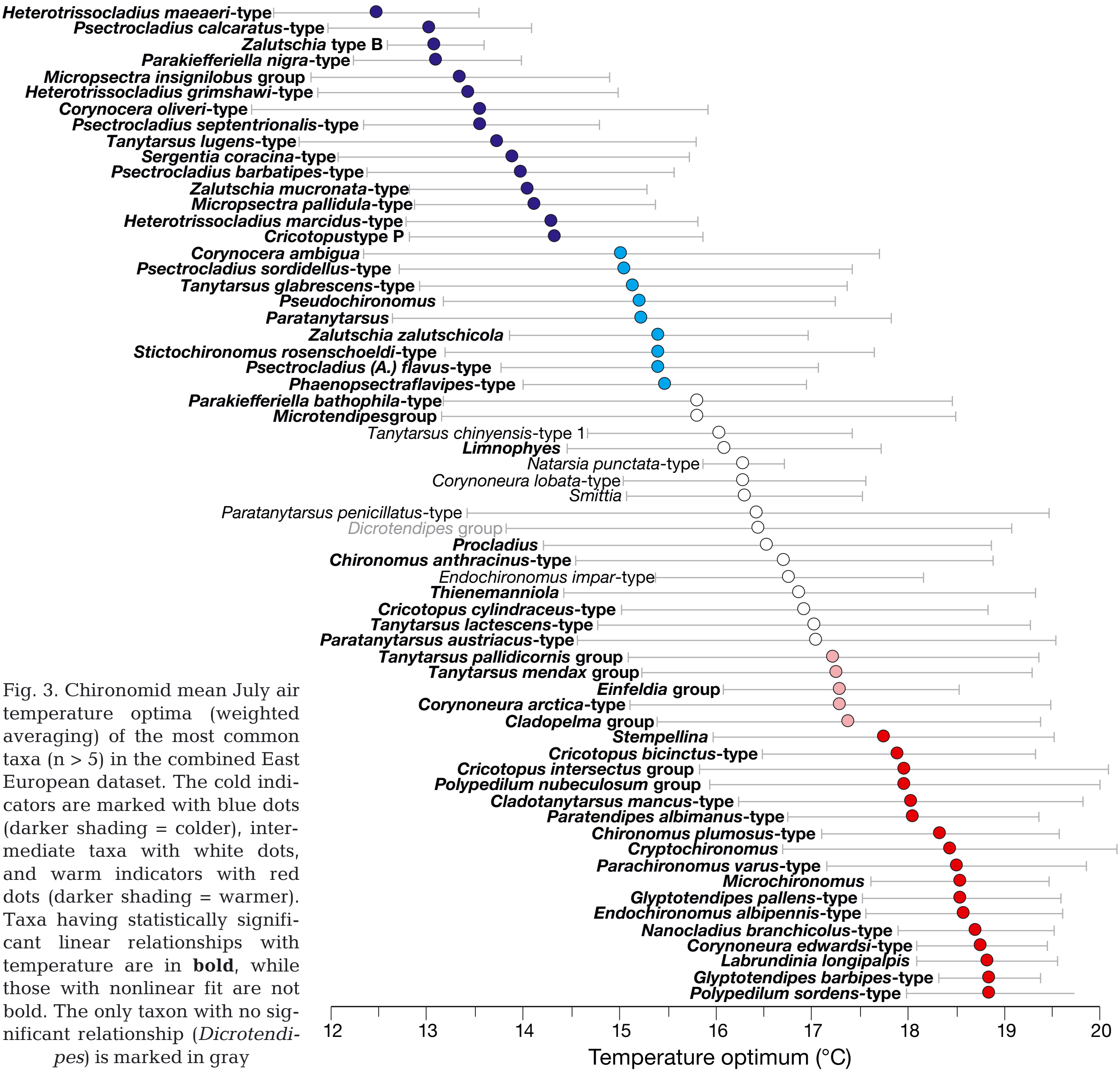

Fig. 3. Chironomid mean July air temperature optima (weighted averaging) of the most common taxa (n > 5) in the combined East European dataset. The cold indicators are marked with blue dots (darker shading = colder), intermediate taxa with white dots, and warm indicators with red dots (darker shading = warmer). Taxa having statistically significant linear relationships with temperature are in **bold**, while those with nonlinear fit are not bold. The only taxon with no significant relationship (*Dicrotendipes*) is marked in gray

and the record highest temperatures synchronously occurred during the 21st century. The correlation between the observed and inferred temperatures at the test site was statistically significant ($R = 0.72$, $R^2 = 0.52$, $R_{corrected} = 0.51$, $p < 0.001$), although in several samples the temperature difference was larger than the sample-specific error estimate (Fig. 6b).

In the long-core reconstruction, samples 1608–1181 cm (older than 15 000 calibrated [cal] yr BP) had poor modern analogues according to the MAT, suggesting that the early part of the sequence may not be reliably reconstructed. Nonetheless, the reconstructed values correlated with the primary PCA axis scores ($R = 0.50$, $p < 0.001$), indicating that chironomids do respond to the reconstructed variable in the sediment profile. The chironomid-inferred temperature trends using the East European model were rather similar to those reconstructed using the Norwegian, Russian and Swiss models (Fig. 7). However, the new model reconstructed higher temperatures for the initial part of the sediment record (1600–1500 cm, no age estimate), where poor modern analogues occurred. In all, the East European model was most similar to the reconstruction derived using the Russian model, whereas larger differences existed when compared with the results using the Norwegian and Swiss models. In ad-

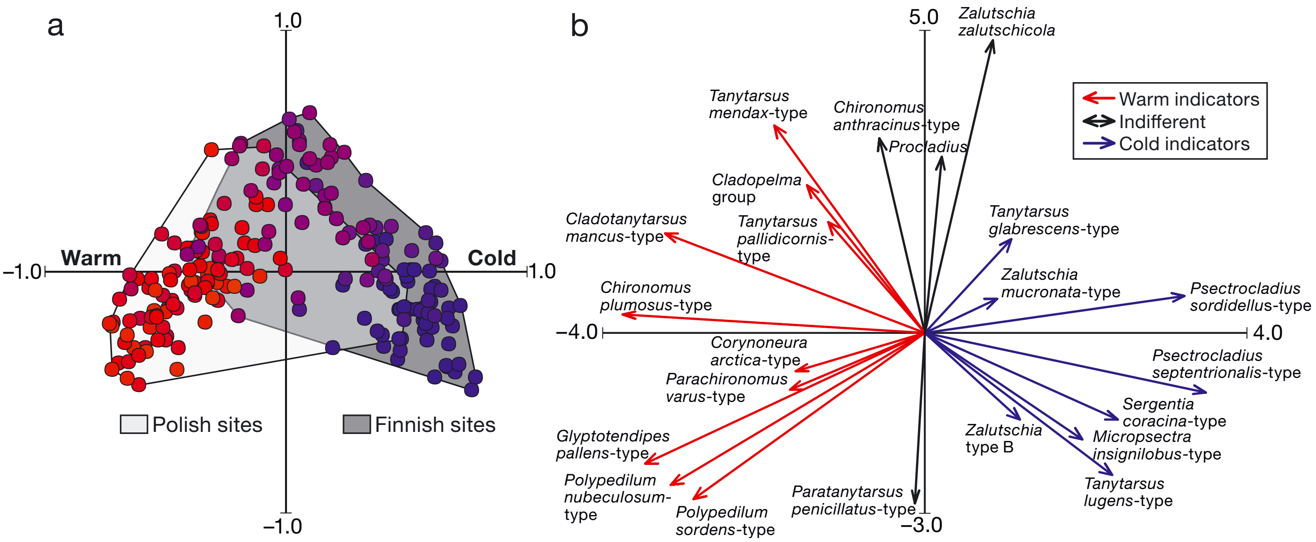

Fig. 4. Principal component analysis (PCA) ordination plots for (a) samples and (b) selected taxa based on surface sediment chironomid assemblages from lakes in Poland and Finland. The first (horizontal) PCA axis (eigenvalue = 0.20) explains 19.7 % and the second (vertical) PCA axis (eigenvalue = 0.07) 6.6 % of the total variance. Samples and sites are colored according to their temperature, from warm (red) to cold (blue), with purple dots indicating transitional temperatures, and the envelopes represent the different geographical regions

Table 2. Redundancy analysis (RDA) results for the combined East European chironomid dataset. All examined variables together explain 15.4 % of the total variance

Variable	λ_1:λ_2	Contribution (%)	*F*	p ($p_{\text{Bonferroni adjusted}}$)
Mean July air temperature	1.061	78.8	26.0	0.001 (0.003)
pH	0.563	13.7	4.6	0.001 (0.003)
Water depth	0.398	2.5	2.5	0.002 (0.006)

Table 3. Comparison of performance statistics using different model types (WA = weighted averaging, PLS = partial least squares) in the development of the East European chironomid-based calibration model. The model deemed most suitable for downcore reconstructions is in **bold**. R^2_{jack} = jackknife cross-validated correlation coefficient, RMSEP = root mean squared error of prediction

Calibration model type	R^2_{jack}	RMSEP (°C)	Maximum bias (°C)	Reduction in RMSEP (%)
$\text{WA}_{\text{inverse deshrinking}}$	0.86	0.96	1.22	
$\text{WA}_{\text{classical deshrinking}}$	0.86	1.01	0.76	
$\text{PLS}_{\text{component1}}$	0.84	1.04	1.51	
$\text{PLS}_{\text{component2}}$	0.86	0.96	0.93	7.99
$\text{WA-PLS}_{\text{component1}}$	0.86	0.97	1.24	
$\text{WA-PLS}_{\text{component2}}$	**0.88**	**0.88**	**0.79**	**8.78**

dition to the early part of the record, the East European model reconstructed high temperatures between 16 000 and 12 000 cal yr BP and during the past ~1000 yr. Based on the new model, the most distinct cold events occurred between 1400 and 1300 cm (ending at ~17 000–16 000 cal yr BP) and 2000–1000 cal yr BP. However, the latter cold event occurs in samples with low chironomid count sums and presence of semiterrestrial taxa (see Płóciennik et al. 2011 for details). When compared with the GISP2 record, the warm period at 15 000 cal yr BP and the following cooling is well represented. The rapid temperature rise during the early Holocene suggested by the GISP data and the late Holocene cooling trend in the current record suggest differences between the regional and global records.

4. DISCUSSION

4. 1. Training set

Combination of the Finnish and Polish chironomid datasets yielded a training set with a temperature gradient of 8.8°C (11.3–20.1°C), enabling wider usability with respect to paleoclimate reconstructions. The cold indicators (Figs. 2, 3 & 4b) in the combined dataset, such as *Heterotrissocladius maeaeri*-type, *H. grimshawi*-type, *Psectrocladius calcaratus*-type, *Sergentia coracina*-type, *Micropsectra insignilobus*-type and *Tanytarsus lugens*-type, are also commonly found in the cold lakes

Table 4. Performance statistics of the developed East European chironomid-based temperature calibration model compared with the original Finnish model (Luoto 2009). R^2_{jack} = jackknife cross-validated correlation coefficient, RMSEP = root mean squared error of prediction, WA-PLS = weighted averaging partial least squares

	East European model	Finnish model
Number of sites (N)	212	82
Number of taxa (n)	142	110
Model type	WA-PLS, component 2	WA-PLS, component 2
R^2_{jack}	0.88	0.78
RMSEP (°C)	0.88	0.72
Maximum bias (°C)	0.79	0.79

of other training sets from Eurasia (Heiri et al. 2011, Self et al. 2011). Similarly, the warm-preferring chironomids, such as *Polypedilum sordens*-type, *Glyptotendipes barbipes*-type, *G. pallens*-type and *Endochironomus albipennis*-type, are typical warm indicators in various other datasets (Heiri et al. 2003, Self et al. 2011). These warm taxa also appear to be more common in meso-eutrophic lakes, whereas the cold taxa are more often found in oligotrophic sites (Brooks et al. 2001, Brodersen & Quinlan 2006, Luoto 2011). This occurrence pattern has been previously documented (Eggermont & Heiri 2012) and is for a large part related to the fact that warm lakes are often more productive and human-influenced compared to the naturally oligotrophic cold lakes. In addition, the results showed that *Paratanytarsus penicillatus*-type, *Dicrotendipes*, *Procladius* and *Chironomus anthracinus*-type are eurythermic taxa with large temperature tolerances (Figs. 3 & 4b), which has also been described in various other datasets (Larocque et al. 2006, Fortin et al. 2015, Nazarova et al. 2015). These taxa aggregate several species and that is probably one of the reasons for their broad tolerance values. Of the most common taxa (Figs. 2 & 3), only *Dicrotendipes* did not have a statistically significant relationship with temperature and *Paratanytarsus penicillatus*-type was the only one having a bimodal distribution. These factors inevitably influence their use as temperature indicators. Although the general temperature indication of the taxa is in most part similar to the other training sets, there are significant differences in the values of the taxa-specific temperature optima that are related to the temperature gradients of the respective datasets. These regional differences in optima will become significant when selecting the training set to be used in a downcore, seriously affecting the reconstructed quantitative values (Engels et al. 2014, Fortin et al. 2015).

The PCA indicated a humped distribution of the samples in the ordination space (Fig. 4). The samples were clearly distributed along the primary PCA axis according to their site-specific temperatures, which

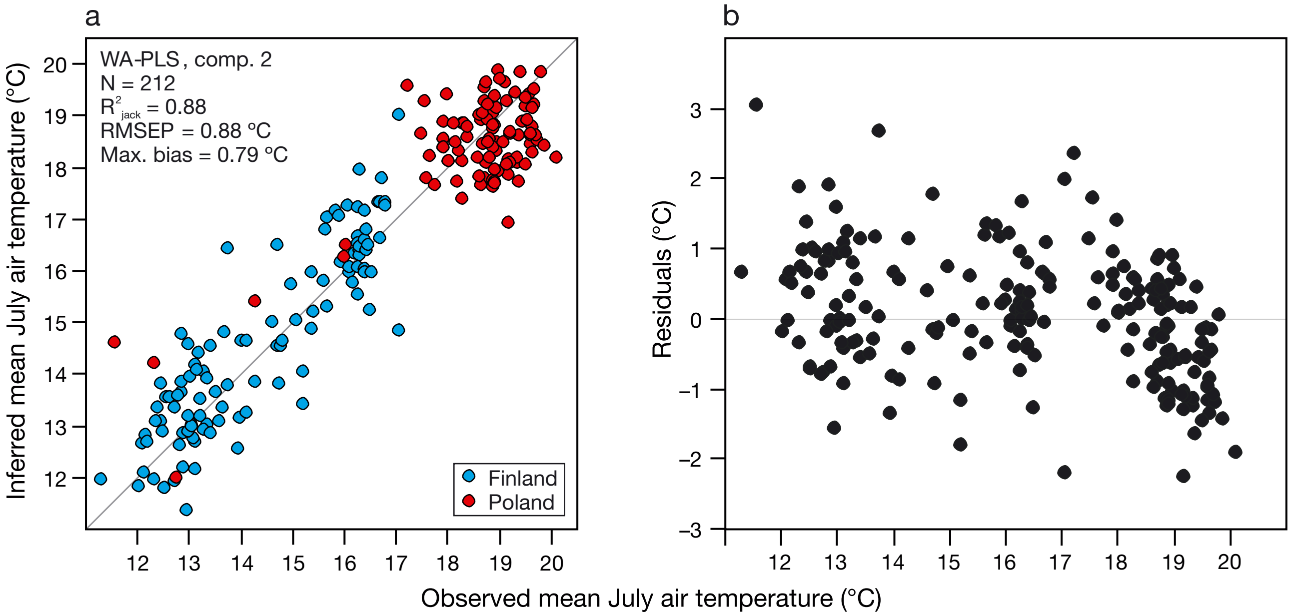

Fig. 5. (a) Relationship (1:1) between observed and chironomid-inferred mean July air temperatures in the East European calibration model using the weighted averaging partial least squares (WA-PLS) technique with 2 regression calibration components. N = number of calibration sites, R^2_{jack} = jackknife cross-validated correlation coefficient, RMSEP = root mean squared error of prediction. (b) Residuals versus observed temperatures

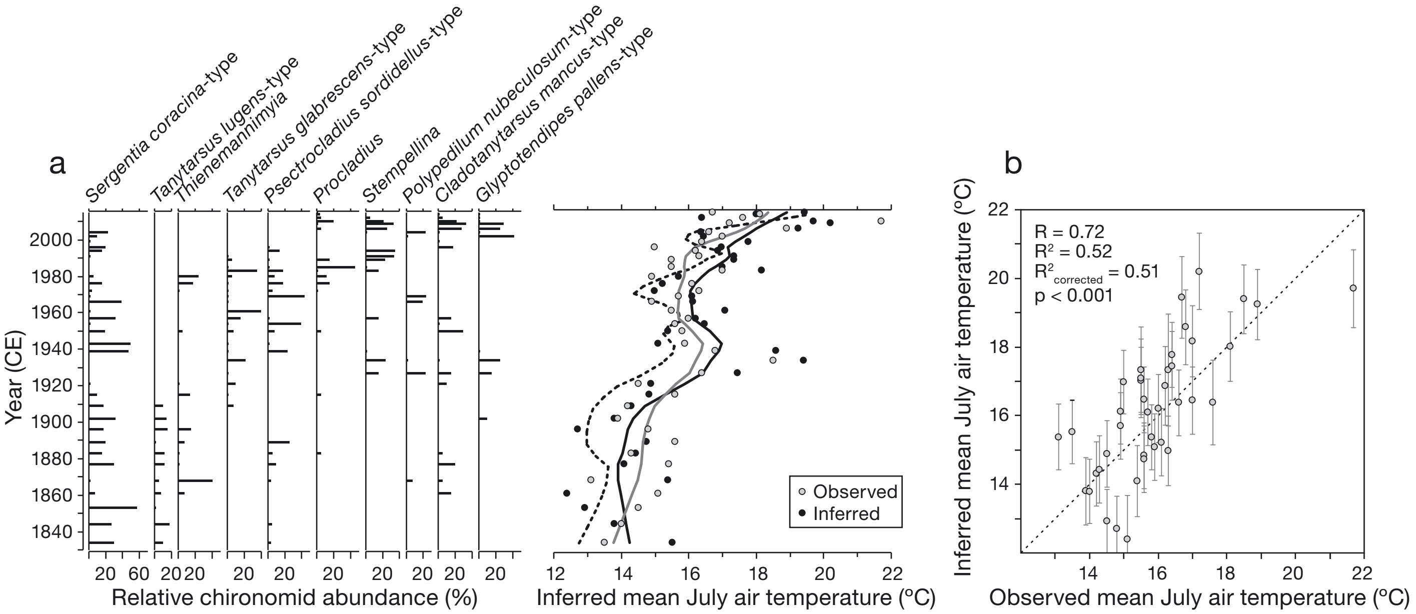

Fig. 6. (a) Ten most common chironomids (Luoto & Ojala 2017) and chironomid-inferred mean July air temperature reconstruction from Lake Nurmijärvi (southern Finland) using the East European calibration model compared with instrumentally measured temperatures and (b) their 1:1 relationship with sample-specific error estimates using bootstrapping cross-validation. Dashed curve is the smoothed (LOESS span: 0.2) original reconstruction using the Finnish model (Luoto & Ojala 2017). Taxa are ordered according to their temperature optima in the calibration set from the coldest to warmest

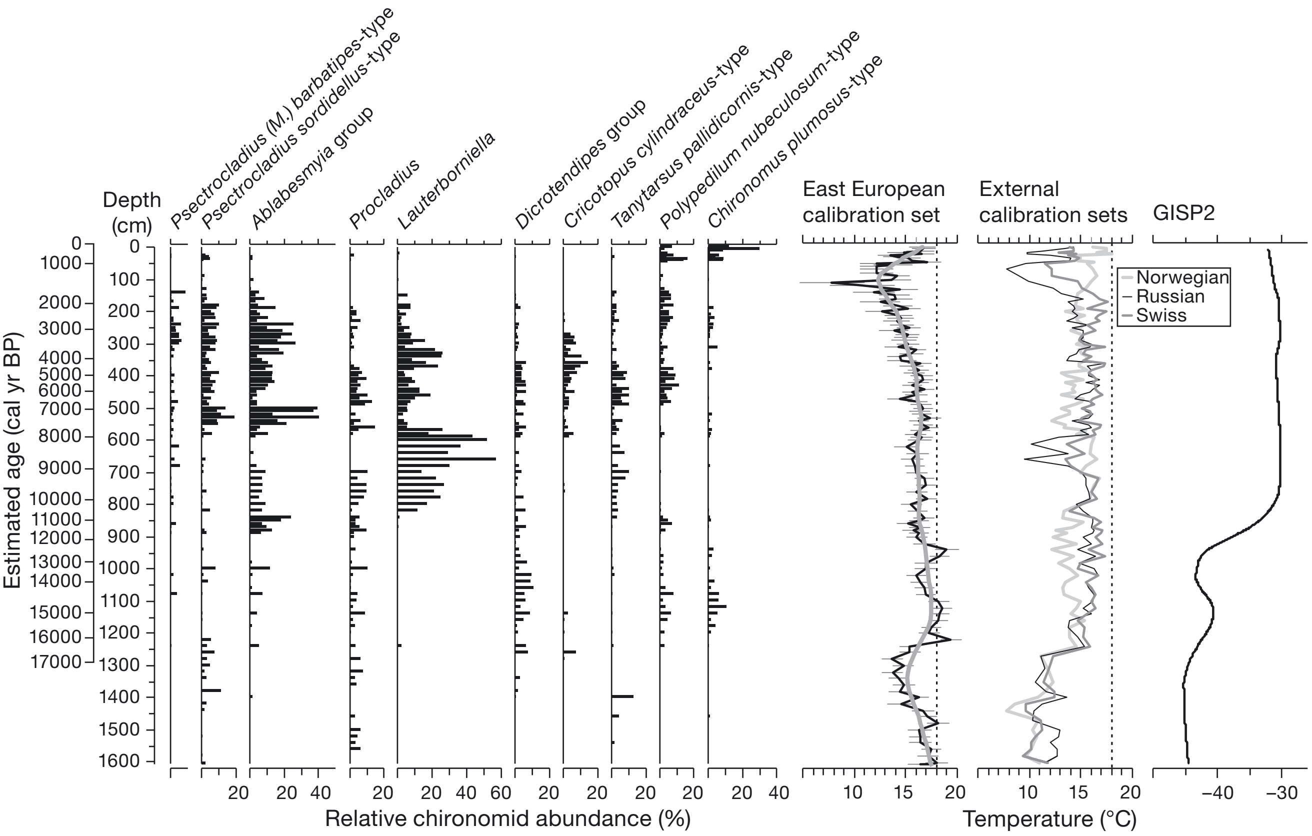

Fig. 7. Ten most common chironomids (Płóciennik et al. 2011) and chironomid-inferred mean July air temperature reconstruction from Żabieniec paleolake (Poland) using the East European calibration model compared with reconstructions (Płóciennik et al. 2011) using the Norwegian, Swiss and Russian calibration datasets. Taxa are ordered according to their temperature optima in the calibration set from the coldest to warmest. Gray line in the new reconstruction represents LOESS smoothing (span: 0.2), and error bars represent the bootstrap-estimated sample-specific errors. Modern temperature at the study site is drawn as dashed lines. Smoothed (0.2) Greenland ice core data (GISP2, Cuffey & Clow 1997, Alley 2000) is provided to illustrate hemispheric temperature development (note that the timescale is only tentative due to chronological uncertainties)

was also verified by the high correlation (R = 0.91, R^2 = 0.82, $p < 0.001$) between the PCA 1 scores and observed temperatures at the sites. Although the ordination plot illustrates that the secondary gradient also has influence on the assemblages, the PCA axis 2 explained only 6.6% of the total variance. In addition, the RDA results (Table 2) clearly indicated that temperature is the most significant variable explaining chironomid distribution among the mutually measured variables in the Finnish and Polish datasets. Importantly, water depth, which has been found to be significant in explaining intralake chironomid distributions in Finland (Luoto 2010) and elsewhere (Kurek & Cwynar 2009, Engels et al. 2012, Luoto 2012a,b), explained only a minor share of the chironomid community compositions. Therefore, these results demonstrate that the chironomid assemblages closely respond to mean July air temperature in the combined dataset, and consequently justify the development of the East European chironomid-based temperature model. The primary response of chironomids to temperature has been clearly evidenced in a bulk of distributional studies (Larocque & Hall 2003, Nyman et al. 2005, Brooks et al. 2012) and their biological response to temperature is also evident (Rossaro 1991, Eggermont & Heiri 2012). Nonetheless, detecting the potential influence of secondary environmental gradients, such as water depth, nutrients and dissolved organic carbon (DOC), on chironomid-based paleotemperature reconstructions remains important, especially since their significance may vary over time (Nyman et al. 2008, Shala et al. 2014, Medeiros et al. 2015).

4.2. Calibration model

The developed temperature calibration model used the WA-PLS technique, which outperformed the other tested model types (Table 3). Typical for chironomid-temperature calibration models (Heiri et al. 2011), the use of 2 WA-PLS components was statistically justified. The model's statistical performance (Fig. 5), measured in R^2_{jack}, was comparable with other chironomid-based temperature models (Heiri et al. 2011, Holmes et al. 2011) but in its RMSEP (0.88°C, 10% of calibration set gradient), it outperformed several of the other models, many of them having RMSEPs >1°C (Barley et al. 2006, Porinchu et al. 2009, Nazarova et al. 2011). Compared to the new East European model, the original latitudinal Finnish temperature model had lower R^2_{jack} (0.78) but also lower RMSEP (0.72°C, 12.4% of calibration set gradient) (Table 4). However, since RMSEP is inherently influenced by the gradient length of the examined variable, it may be more useful to compare the RMSEPs in relation to the temperature gradients. In this sense, the RMSEP is more favorable in the combined model.

The combination of the Finnish and Polish datasets resulted in a consistent continuum in the model's predictive abilities, as the Polish sites increased the temperature gradient of the model towards warmer temperatures (Fig. 5a). Longer environmental gradients will help in situations where past climate conditions approach the specific dataset's temperature limits (Birks et al. 2003). Slight distortions at both ends of the temperature gradient were observed (Fig. 5b), which is inherent in WA-PLS models (Heiri & Lotter 2010). This distortion, i.e. the edge effect, causes underestimation of warm temperatures and overestimation of cold temperatures, and hence potentially smoothens reconstructions.

4.3. Reconstructions

The best means to verify environmental reconstructions is to compare them with instrumentally measured data (Larocque et al. 2009, Larocque-Tobler et al. 2015). Our test site, Lake Nurmijärvi, with sediments constituting of clastic biogenic varves, is located in south-central Finland, close to the warm end of the temperature gradient of the original Finnish training set (Fig. 1). The reconstruction results showed that the East European model has the ability to accurately predict downcore temperatures, as it depicted well the cold temperatures of the 19th century, the increased temperatures of the 1930s and the rapid warming that began in the 1980s (Fig. 6). The mean difference in the inferred values compared to the observed was only 0.3°C, but the largest overestimation was 3.0°C and underestimation 2.7°C. The biased values are most likely related to lags in chironomid response times, since many taxa have long life cycles, and their dispersal, although fast compared to many other biological proxies (Wu et al. 2015), can take up to 7 yr (Pinder 1986). The correlation between reconstructed and observed temperatures was higher than in a previous study where the latitudinal Finnish model was used (Luoto & Ojala 2017), clearly suggesting that the new model has better prediction accuracy and reliability compared to the original model.

Since the model had solid performance statistics and it was able to reconstruct similar temperatures with the observational record in southern Finland, we also applied it to a long core taken from the Żabieniec paleolake in Poland. Importantly, the chironomid-inferred values showed significant correlation with the primary ordination axis scores, verifying that chironomids respond to temperature in the Żabieniec record. A previous study at the Polish site demonstrated that chironomid-based temperature models from outside the geographical area reconstructed partly differing temperatures (Płóciennik et al. 2011). The present results show that the developed East European model reconstructed temperatures that mostly resemble those reconstructed using the Russian model (Self et al. 2011; our Fig. 7), whereas distinct differences were apparent when compared with the Swiss (Heiri & Lotter 2005) and Norwegian models (Brooks & Birks 2001; our Fig. 7). These differences include very low temperatures in the initial part of the record and the absence of the late Holocene cooling trend (Wanner et al. 2015). The early phase of the record may be connected with the warm Kamion phase previously described from Poland (Manikowska 1995); however, this remains uncertain due to a lack of detailed chronological control in the bottom part of the Żabieniec sediment sequence. Although the present interpretations are based solely on mean July air temperature and there is no data on winter conditions or vegetational season length, it may still be speculated that the climate conditions during the early phase of the record were glacial, but because of high continentality, summers were warm as in Siberia (Klimanov 1997). This interpretation would be logical also considering that the East European and Russian models produce similar warm temperatures for this phase differing from those derived using the Swiss and Norwegian models (Fig. 6).

It is possible that the Late Glacial temperatures could have been colder in Żabieniec than the lowest temperatures represented by the calibration sites. However, the reconstructed temperatures are not close the limits of the model (11°C), but remain at >14°C (Fig. 7). If the actual temperatures would have been colder and the chironomid taxa would have consisted solely of taxa with the coldest temperature preferences, the WA-PLS model would have the potential to extrapolate beyond the cold gradient end (Velle et al. 2011). This was not the case in the present data, where Late Glacial sequences consisted of taxa with intermediate temperature optima, such as *Procladius* and *Tanytarsus pallidicornis*-type (Fig. 7). These taxa are also known to have wider trophic tolerances (Brodersen & Quinlan 2006), which could reflect elevated nutrient condition during the early part of the sediment profile. In contrast, the Norwegian, Russian and Swiss calibration models all reconstruct consistently colder Late Glacial temperatures than the East European model. This is probably related to the compared calibration models having generally colder lakes among the training set sites, and hence, the new model would benefit from inclusion of even colder sites than it currently has. Despite the extrapolation capabilities of the WA-PLS method, it is clear that the East European model can be reliable only within its temperature gradient (11–20°C), with decreasing reliability towards the gradient ends. Consequently, the coldest and warmest episodes in long sediment records, such as the Żabieniec record, should be considered cautiously when observing the reconstructed values, although at the same time the trends may be realistic. It is also noteworthy that the Late Glacial chironomid assemblages had poor modern analogues in the calibration set, which decreases the reliability of the new reconstruction during this early phase of the record.

Similar to the other chironomid-based reconstructions, the new reconstruction did not depict a significant temperature drop during the cold Younger Dryas period. There are also no distinct changes in the taxonomic composition at this time (Płóciennik et al. 2011; our Fig. 7) that could indicate other driving factors that would potentially reduce the temperature signal. This period was unusually cold in Scandinavia (Brooks & Birks 2001, Wohlfarth et al. 2018), but in several studies from Poland (Pawłowski et al. 2015, 2016a,b, Zawiska et al. 2015) and Central Europe (Larocque-Tobler et al. 2010), the summer temperature drop during the Younger Dryas was relatively muted compared to the British Isles, the Baltic region and the northern parts of the continent (Heiri et al. 2014). Therefore, the present results are consistent with previous studies from Poland showing intra-European differences. Compared to the other chironomid-based reconstructions from Żabieniec, the East European model reconstructs similar 16–17°C temperatures, with the exception of the Norwegian model, which indicates slightly lower temperatures (Fig. 7).

Compared to hemispheric temperatures reflected by the GISP2 ice core record (Cuffey & Clow 1997, Alley 2000), the current reconstruction does not suggest a similar increase in early Holocene temperatures (Fig. 7). The rapid early Holocene temperature increase has been described from several lake sediment records from northern Europe (Brooks & Birks 2001, Engels et al. 2014, Luoto et al. 2014, Shala et al. 2017, Helmens et al. 2018) and the European Alps (Samartin et al. 2012). The increase in *Lauterborniella* between 10 000 and 8000 cal yr BP can be related to nutrient conditions, since in addition to high temperature optimum, it is known to thrive in more nutrient-enriched lakes (Brooks et al. 2007). However, the warming associated with the increase in *Lauterborniella* is consistent with the increased temperatures in the GISP2 record following the cold early Holocene. The late Holocene cooling trend is not apparent in the GISP2 record, although it is clearly seen from the present results and several other records from Poland (Pawłowski et al. 2015, 2016b, Zawiska et al. 2015), suggesting regional deviation from hemispheric temperatures. Nonetheless, it should be noted that the temperature decrease reconstructed from Żabieniec between 2000 and 1000 cal yr BP is not reliable owing to a dominance of semiterrestrial chironomid taxa and low count sums (Płóciennik et al. 2011). Compared to the reconstructions performed using the other chironomid-based models and the GISP2 record, the temperatures reconstructed using the East European model showed a distinct warming during the past 1000 yr, with a short-lived drop in temperatures during the Little Ice Age. In general, the reconstruction of the Holocene temperatures in the Żabieniec paleolake closely resembles those from elsewhere in Europe (Davis et al. 2003, Luoto et al. 2010, Engels et al. 2014) combined with distinct local features (Pawłowski et al. 2015, 2016b, Zawiska et al. 2015), hence signifying the reliability of the reconstruction.

5. CONCLUSIONS

Merging the Finnish and Polish chironomid-based training sets resulted in a valid calibration model for mean July air temperature with an extended temperature gradient and improved applicability. The temperature indicators were similar to what has been found in previous studies; however, the numerical optima are more accurately adjusted for the study area. The statistical tests showed that chironomids were responding most strongly to temperature, hence enabling construction of the enhanced model. Compared to previous chironomid-temperature models in general, the new East European model has solid performance statistics.

The model validation in a Finnish annually laminated lake sediment record, covering the observational temperature period beginning from the 1830s, showed that the model better predicts paleotemperatures compared to the original Finnish model. Since the inferred temperatures correlated strongly with the instrumental record, the model can be considered solid with respect to its predictive abilities and applicability in downcore profiles from Eastern Europe. The reconstructed temperatures using the East European model in the long core from the Polish paleolake Żabieniec, covering the past ~20 000 yr, were more similar to temperatures reconstructed using the Russian chironomid-based model than the ones reconstructed using the Swiss and Norwegian models. The reconstructed temperature trends were comparable to previous studies from Poland, but significantly different from hemispheric paleotemperature estimates, signifying the importance of local reconstructions in understanding past climate oscillations.

Although the model is designed for Finnish and Polish sites as a preset, it can be useful in other areas of Eastern Europe as well. In the future, the East European model can be further developed, especially by including additional calibration sites from the Baltic countries, which would promote stability of the model. In all, the present results demonstrate the usability and sensitivity of fossil chironomids as quantitative paleoclimate indicators.

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