Quaternary Research 81 (2014) 50–62

Contents lists available at ScienceDirect

Quaternary Research

journal homepage: www.elsevier.com/locate/yqres

New evidence of warm early-Holocene summers in subarctic Finland based on an enhanced regional chironomid-based temperature calibration model

Tomi P. Luoto [a,]*, Marjut Kaukolehto [b], Jan Weckström [c], Atte Korhola [c], Minna Väliranta [c]

[a] *Division of Geology, Department of Geosciences and Geography, University of Helsinki, P.O. Box 64, 00014, Finland*
[b] *Division of Atmospheric Sciences, Department of Physics, University of Helsinki, P.O. Box 48, 00014, Finland*
[c] *Environmental Change Research Unit (ECRU), Department of Environmental Sciences, University of Helsinki, P.O. Box 65, 00014, Finland*

ARTICLE INFO

Article history:
Received 6 February 2013
Available online 30 October 2013

Keywords:
Chironomidae
Climate change
Lapland
Paleoclimatology
Paleolimnology
Plant macrofossils
Transfer function

ABSTRACT

Paleoclimate reconstructions based on biological proxies present methodological challenges, especially during non-analog conditions, such as the early Holocene. Here, two chironomid-based training sets from Finland were amalgamated to create a more accurate transfer function of summer air temperature. The aim was to reconstruct Holocene paleoclimate in northernmost Lapland, in an area that has been either too warm or too cold for reliable reconstructions using the original calibration models. The results showed that the combined calibration model had improved performance statistics. The temperature trends inferred from the downcore chironomid record using the original and combined models were very similar. However, there were major changes in their absolute values with the combined model showing greatly improved accuracy. The chironomid-based temperature reconstruction showed significant correlation with the previous pollen-based reconstructions from northwestern Finnish Lapland. However, differences were observed in the temperature trends of the early Holocene, when the chironomid-inferred temperatures rapidly increased, but the pollen-based reconstructions lagged behind suggesting that a cool climate continued for much longer. However, similar to the chironomid record, new plant macrofossil evidence from northwestern Finland also showed warmer-than-present early Holocene temperatures. Therefore, we conclude that the early Holocene was probably warm in northern Lapland.

Introduction

Climate change projections for the future suggest increased temperatures outside the magnitude of observational records (Carter et al., 2004). Therefore, knowledge of past climates is needed to increase our understanding of climate variability and its influences on the natural environment. Due to the short time span of observational records (Vesajoki and Holopainen, 1998), paleoclimatological proxies from geological and related archives are invaluable. Paleolimnological data from lake sediments provide a major data source for understanding causes and dynamics of climate changes (Smol, 2008) and one of the major proxies used for paleoclimatic inferences are (sub)fossil remains of chironomids (Insecta: Diptera: Chironomidae) (Brooks, 2006; Walker and Cwynar, 2006; Eggermont and Heiri, 2012). Typical species composition can be assigned for different climate conditions using training sets collected from multiple lakes along a temperature gradient. These training sets of modern species–environment relations can be used to construct calibration models (calibration-in-space) to quantitatively reconstruct past climate dynamics from downcore sediment profiles (Brooks and Birks, 2001). In general, regional calibration models perform most reliably on downcore sediment records, except for late glacial chironomid records which often contain taxa that are no longer regionally abundant (Larocque-Tobler, 2010), whereas application of chironomid-based inference models based on taxon optima from different biogeographical or climatic regions has a larger potential for error (Heiri et al., 2011).

The rapid response of insect communities to climate change (Elias, 1991) and the sensitivity of chironomids, in particular, to prevailing temperature conditions have made fossil chironomids one of the most utilized biological proxies in paleoclimatology. Recent methodological advancement, including improvements in fossil taxonomy (Brooks et al., 2007), has increased the reliability of chironomid-based temperature reconstructions (Heiri and Lotter, 2010), while in the meantime, more accurate paleoclimate reconstructions are required for putting the present climate change into a long-term perspective (Wanner et al., 2008). Although there is some debate on the relative roles of direct versus indirect effects of temperature in shaping the chironomid–climate correlation and apparent inconsistencies in chironomid-inferred temperatures (Brodersen et al., 2004, 2008; Velle et al., 2010, 2012), chironomids are accepted as one of the most useful paleoindicators of temperature (Brooks, 2006; Walker and Cwynar, 2006; Brooks et al., 2012; Eggermont and Heiri, 2012). To establish reliable chironomid-based temperature reconstructions, calibration data sets and downcore sites must be carefully selected, ecological characteristics comprehensively

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* Corresponding author.
E-mail address: tomi.luoto@helsinki.fi (T.P. Luoto).

http://dx.doi.org/10.1016/j.yqres.2013.09.010

considered, fossil assemblages evaluated for modern analogs, and reconstructions tested for their significance and validated against other proxy records (Velle et al., 2010; Brooks et al., 2012).

In this study, through taxonomic harmonization, two existing chironomid-based training sets from Finland (Nyman et al., 2005; Luoto, 2009a) are amalgamated to provide more reliable and accurate regional paleoclimate reconstructions. The longer temperature gradient of the combined training set is hypothesized to strengthen the relationship between chironomid species assemblages and temperature, and the increased number of sites and taxa is expected to enhance the precision of estimated taxon optima that would lead to more accurate paleoclimate reconstructions. The developed model is applied to an AMS ^{14}C dated Holocene sediment profile from Lake Várddoaijávri, located in northernmost Finnish Lapland, in an area where the modern summer temperatures are either in the upper or lower end of the temperature gradients covered by the existing regional chironomid-based inference models, which potentially makes the original models unreliable for this site. A special focus of this paper is on the regional temperature development during the early Holocene, when pollen-based reconstructions have indicated low temperatures until ~8000–7000 cal yr BP (Seppä and Birks, 2001, 2002), but contradictory evidence exists from the area that the climate was warm already during the early Holocene (Korhola et al., 2002a; Väliranta et al., 2005; Sarmaja-Korjonen et al., 2006; Szeroczyńska et al., 2007). For comparison with the chironomid-based reconstruction, we also use plant macrofossil records from three sites to reconstruct the early Holocene temperature development in northern Lapland.

Regional setting

The original chironomid-based training set from northwestern Finnish Lapland (67°82′–69°27′N, 20°67′–24°87′E) consists of 62 lakes of which 17 are located in barren tundra, 26 in mountain birch woodland and 19 in pine and birch forest zone (Table 1; Fig. 1). The bedrock consists of acidic Precambrian plutonic and metamorphic rocks and in the northernmost study area of Palaeozoic schists and gneisses. The mean July air temperature (T_{Jul}) varies from 7.9 to 13.8°C along an altitudinal gradient from 197.5 to 1024.4 m asl. The sampling depth of the lakes varies from 0.9 to 25 m. The chironomid-based training set from northwestern Lapland was originally collected by Olander et al. (1999) and Korhola et al. (2002a), and the chironomid identifications were updated by Nyman et al. (2005). The chironomid-based temperature calibration model used as a part of the new combined dataset in this study was first introduced and used by Seppä et al. (2002). More details about the study area and sites are given in Weckström and Korhola (2001) and Korhola et al. (2002b).

Table 1
Comparison of the chironomid-based temperature calibration sets from Finland.

	Nyman et al. (2005)	Luoto (2009a)	New combined
Number of sites	62	77	139
Barren tundra sites	17	1	18
Mountain birch woodland sites	26	11	37
Pine and birch forest sites	19	11	30
Spruce, pine, and birch forest sites	0	54	54
Mean air T_{Jul} gradient (°C)	5.9 (7.9–13.8)	5.8 (11.3–17.1)	9.2 (7.9–17.1)
Best model type	WA-PLS, comp. 2	WA-PLS, comp. 1	WA-PLS, comp. 2
Number of taxa in model	71	84	117
R^2_{jack}	0.75	0.78	0.88
RMSEP (°C)	0.754	0.721	0.839
Mean bias (°C)	0.009	0.018	0.005
Maximum bias (°C)	1.095	0.794	1.088

The original training set along the latitudinal gradient in Finland (60°13′–69°53′N, 22°00′–30°13′E) by Luoto (2009a) consists of 77 lakes (with 5 outliers removed). One of the lakes is located in barren tundra, 11 in mountain birch woodland, 11 in pine and birch forest zone and 54 in mixed boreal forests with spruce, pine, and birch (Fig. 1; Table 1). The training set is situated in the central part of the Precambrian Fennoscandian Shield. In general, rocks of the shield are younger towards southwest Finland occupying the main part of the transitional zone between dominantly Archaean and Palaeoproterozoic rocks, mostly granites. The mean air T_{Jul} varies within the training set between 11.3 and 17.1°C and elevation between 11.6 and 404.0 m asl. The gradient in sampling depth is from 0.5 to 9.0 m. The study area and sites are described in more detail by Luoto (2009a) and Kultti et al. (2011).

The downcore study site, Lake Várddoaijávri (69°53′N, 26°31′E), is situated in northeastern Finnish Lapland, close to the Norwegian border and outside the region of the training set from northwestern Finnish Lapland and at the northern part of the latitudinal training set (Fig. 1). The ~26 ha lake with maximum depth of ~5 m lies at 409.4 m asl. The lake is located in barren tundra with a rocky surface with patchy thin soil cover. The catchment area is ~150 ha with two small seasonal streams flowing into the lake from the south and southeast. The area belongs to a granulite belt. The vegetation in the catchment of Lake Várddoaijávri consists of low shrubs, lichen and mosses. The climate in the area of the lake is subarctic with an air temperature of −2.6°C and mean air T_{Jul} of 11.3°C. The pH of the lake was 6.3 on April 2005. The ultraoligotrophic lake is currently occupied by a small-bodied Arctic char (*Salvelinus alpinus* L.) population, while other fish species are absent (Lehtonen, 1998). For more details on the site, see Luoto and Sarmaja-Korjonen (2011).

Material and methods

Sampling and sediments

The chironomid-based training sets from northwestern Finnish Lapland (Nyman et al., 2005) and from the latitudinal gradient in Finland (Luoto, 2009a) are based on fossil assemblages in the uppermost 0–1 cm of lake sediments. The sampling depths vary in both of the training sets (from sublittoral to profundal samples) and it should be noted that they do not necessarily equate to the maximum lake depths. A 296-cm downcore sediment sequence from Lake Várddoaijávri was cored from ice cover at a water depth of 393 cm in April 2005 using a Russian peat corer. The whole sediment profile consisted of gyttja. The age–depth model is based on eight AMS radiocarbon dates (with two outliers excluded) and on retreat of the Weichselian ice sheet from the area between ~11,500 and 11,000 cal yr BP (Johansson and Kujansuu, 2005). Details on the training sets (Olander et al., 1999; Korhola et al., 2002a; Nyman et al., 2005; Luoto, 2009a; Kultti et al., 2011) and the core (Luoto and Sarmaja-Korjonen, 2011) can be found in the previous publications.

Fossil analyses and numerical methods

Fossil chironomid analyses were performed applying standard methods (see Olander et al., 1999; Nyman et al., 2005; Luoto, 2009a; Luoto and Sarmaja-Korjonen, 2011) at 1-cm slices in the training sets and at 3–5 cm intervals from 1-cm slices in the downcore sequence. The identification was mainly based on the identification guides by Wiederholm (1983) and Brooks et al. (2007). Descriptions by Heiri et al. (2004) and Rieradevall and Brooks (2001) were used to identify the Tanytarsini and Tanypodinae, respectively. The nomenclature for the chironomid morphotypes in the new combined training set follows that of Brooks et al. (2007). Taxonomic harmonization of the two training sets was achieved through close collaboration between the chironomid analysts.

The previous chironomid-based training sets from Finland were combined to achieve a new enhanced temperature training set with a longer temperature gradient (7.9–17.1°C). Detrended correspondence analysis was used to assess the gradient lengths in the chironomid assemblage data for determining whether to use linear or unimodal methods in further numerical analyses. Subsequently, unimodal canonical correspondence analysis (CCA) was used for ordinations and to test the strength of temperature in determining chironomid distribution in the dataset. The DCA and CCAs were run with square-root transformed species data and downweighting of rare species in the program CANOCO, version 5 (ter Braak and Šmilauer, 2012). The CCAs were run both with mean air T_{Jul} as the sole constraining variable and with water depth, a mutual variable in the training sets and an important environmental determinant for chironomid distribution in Finland (Olander et al., 1999; Nyman and Korhola, 2005; Luoto, 2010, 2012), as a co-variable. This was done to reveal whether temperature retains its unique explanatory power or whether it gains from the covariance with depth. Although loss-on-ignition (LOI) was also found to be an important regulator for chironomid spatial distribution in the altitudinal training set (Nyman et al., 2005), this variable was not measured from the latitudinal training set due to lack of available sediment material (Luoto, 2009a). Mean air T_{Jul} optima for chironomid taxa in the Finnish training sets were calculated using weighted averaging.

The new calibration model was developed from untransformed relative species abundances using weighted averaging-partial least squares (WA-PLS) regression and calibration techniques (ter Braak and Juggins, 1993) and also other model types, including WA, PLS, and the modern analog technique (MAT), were tested. The number of regression calibration components to be used was assessed using leave-one-out cross-validation in the program C2 (Juggins, 2007). Components were accepted if they were classified as useful (5% reduction in prediction error) and statistically significant ($p \leq 0.05$). The cross-validated model performance and error statistics were assessed according to the coefficient of determination (R^2) between predicted and observed values, root mean squared error of prediction (RMSEP), and the mean and maximum biases.

Mean air T_{Jul}s were reconstructed based on the chironomid stratigraphy of the Lake Várddoaijávri record published by Luoto and Sarmaja-Korjonen (2011), who used the chironomid assemblages to reveal Holocene effective-moisture fluctuations. In the current study, mean air T_{Jul} reconstructions were performed using the original Finnish chironomid-based temperature transfer functions and the new combined model. Comparison of the models' performance statistics and other training set characteristics are shown in Table 1. Sample-specific standard errors of prediction (eSEPs) for the downcore reconstruction using the combined model were calculated using random re-sampling (bootstrapped cross-validation with 999 iterations). Lake Várddoaijávri was omitted from the training set in the core analysis to prevent a bias in the reconstruction.

To identify significant relationships between chironomid taxa and the reconstructed environmental variable in the expanded calibration set, taxon response models were constructed using generalized linear models (GLM). The GLMs were set to a quadratic degree and Poisson distribution. The GLMs were run with CanoDraw, a component of the CANOCO program. In addition, the reliability of reconstruction was assessed by calculating the percentage of fossil taxa represented in the training set (cut-off value 90% for good representativeness) and by examining the distance of modern analogs between fossil and training set samples using the modern analog technique (MAT) (Birks, 1998). A good analog was considered to have a chord distance less than the upper 90/95% confidence interval of the mean minimum dissimilarity coefficient of the training set. The applicability of the training data for the core samples was also assessed using the CCA by plotting the core

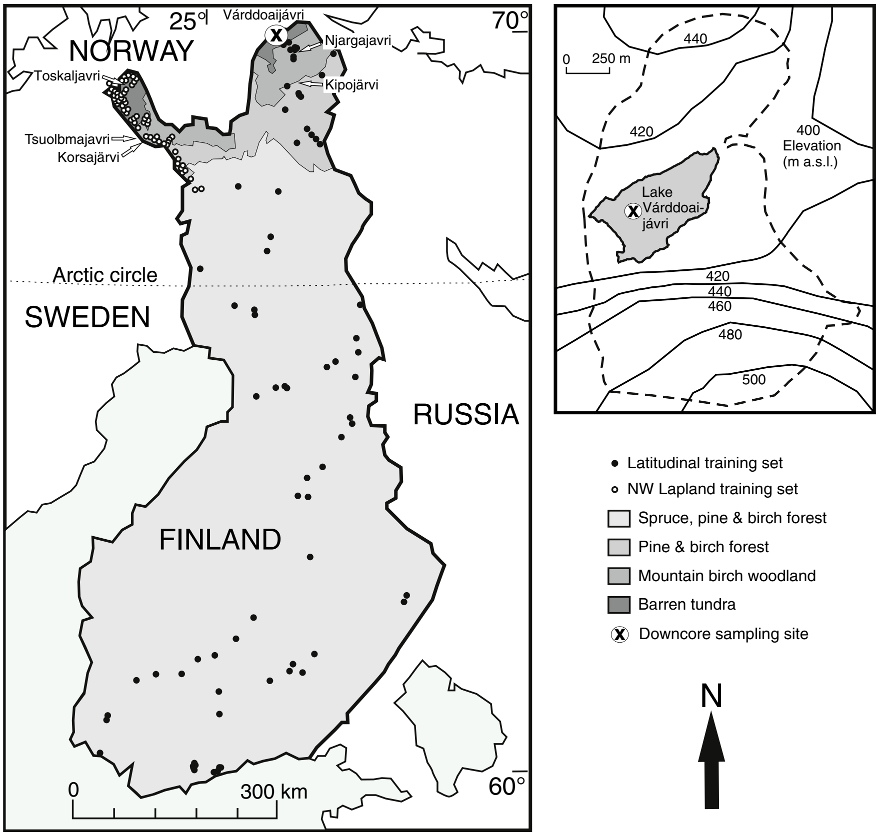


Figure 1. Location of the training set lakes in Finland and the downcore study site Lake Várddoaijávri (marked with a cross) in northern Finnish Lapland. In addition, study sites of previous paleotemperature reconstructions are shown.

samples passively on the training samples (Bigler et al., 2003). The core data was further tested by examining the correlation (Pearson product–moment correlation coefficient) between DCA axis 1 scores (beta diversity = rate of faunal turnover) and the reconstructed temperatures in particular chironomid faunal zones, which were determined by using the optimal partitioning method and a broken-stick model (see Luoto and Sarmaja-Korjonen, 2011). The statistical significance of the chironomid-based temperature reconstructions was tested using the random TF method (Telford and Birks, 2011). This method was used to determine whether the present reconstructions explained larger proportion of the variance in fossil data than 95% of 999 reconstructions of random environmental data. Statistical significance test calculations were performed using the R statistical software (R development Core Team, 2009) package palaeoSig.

Early Holocene temperature reconstructions based on plant macrofossils from Lake Njargajavri (69°46′N, 27°20′E; 355 m asl), Lake Korsajärvi (68°49′N, 22°05′E; 530 m asl), and Lake Kipojärvi (69°11′N, 27°17′E; 160 m asl) were used for comparison of summer temperature trends. The macrofossil record from Lake Njargajavri is described in Väliranta et al. (2005) and the record from Lake Kipojärvi in Väliranta et al. (2011a, 2011b), whereas the macroscopic indicator species from Lake Korsajärvi are described in this study. The macrofossil-based paleotemperature reconstructions were made based on presence of indicative plant taxa. We used species distribution maps of Lampinen and Lahti (2013) to define the current distribution of indicator species in Finland, and compared these distributions to calculated mean T_{Jul}s (1961–2000) based on daily measurements by the Finnish Meteorological Institute (Venäläinen et al., 2005). This comparison yields a minimum mean T_{Jul}, but temperatures may have been higher. It should be notated that macrofossil records are not continuous in a similar way as for instance pollen records. However, this approach has been successfully applied in previous studies, where the macrofossil-based temperature reconstructions concurred well with for instance chironomid-based temperature reconstructions (Väliranta et al., 2009; Engels et al., 2010).

Results

The new training set consisted of 139 lakes covering the latitudinal and elevation gradients in Finland (Fig. 1) with catchments representing all vegetation types. The DCA of fossil chironomids indicated gradient lengths of 3.5 SD for axis 1 and 2.2 SD for axis 2 that suggests use of unimodal methods. Consequently, CCA was used to determine chironomid relationships with temperature. The CCA results showed that the chironomid–temperature relations were statistically significant in all the training sets (Table 2). Importantly for the present study, there was no improvement in this relationship when water depth was used as a co-variable that could hamper the development of the combined calibration model due to influence of conditional effects. In the CCA ordination (Fig. 2), the first axis explained 12.6% and the second 2.9% of the total variance. A trend from warm- to cold-indicating taxa was apparent from the results with a tendency of the coldest taxa, such as *Micropsectra radialis*-type and *Heterotrissocladius maeaeri*-type, being associated also with the deepest sites. Furthermore, the CCA plot for samples indicated that the chironomid assemblages between the original training sets were dissimilar, with only minor overlap. When comparing the temperature optima of mutual common taxa that also occur in the sediment profile from Lake Várddoaijávri between the original training sets and in the combined training set, the results are consistent (Fig. 3). However, there is a clear trend in which the optima are lowest in the altitudinal training set and highest in the latitudinal training set with the estimated optima of the combined training set in between.

Table 2
Canonical correspondence analysis (CCA) results from the original and combined chironomid-based training sets of temperature. The relationships between chironomid assemblages and mean air T_{Jul} is tested for its marginal effects and conditional effects with water depth as a co-variable.

Training set	Variable	λ_1:λ_2	Species–environment correlation	% variance explained	*p*
Combined	T_{Jul}	1.178	0.915	11.6	0.001
	T_{Jul} with depth	1.047	0.915	8.2	0.001
NW Lapland	T_{Jul}	1.045	0.810	13.4	0.001
	T_{Jul} with depth	0.809	0.843	8.3	0.001
Latitudinal	T_{Jul}	1.400	0.927	10.7	0.001
	T_{Jul} with depth	1.424	0.930	11.0	0.001

Similar to the original training sets, the new combined calibration model was developed using WA-PLS method. The 2-component model had an R^2_{jack} of 0.88 and an RMSEP of 0.84°C with mean and maximum biases of 0.005 and 1.088°C, respectively (Fig. 4, Table 1). Addition of the second calibration regression component decreased the RMSEP by 22.2% with randomization *t*-test significance of 0.001, whereas the use of third component showed no significant improvement on the prediction error. Despite the strong correlation between observed and inferred temperatures, a statistically significant trend ($p < 0.01$, $R^2 = 0.17$) was found from the model residuals. This bias was concentrated on the coldest lakes, which showed consistently higher inferred temperatures than were observed (Fig. 4). The other model types did not achieve the performance level of WA-PLS (Table 3).

Of the most abundant chironomid taxa in the Lake Várddoaijávri core, only *Psectrocladius sordidellus*-type and *Microtendipes pedellus*-type had no significant relationship with temperature in the combined calibration set based on the GLMs (Fig. 5). *M. pedellus*-type was abundant in the early (maximum abundance of 11% in all chironomids) and mid-Holocene (14%) sediment sequences, but *P. sordidellus*-type (38%) was abundant throughout the core. The most common taxa having significant relationship with temperature included *Corynocera ambigua* (most abundant during the mid-Holocene, 33%), *Psectrocladius septentrionalis*-type (early Holocene, 22%), *Sergentia coracina*-type (late Holocene, 15%), and *H. maeaeri*-type (late Holocene, 16%). Most of the taxa had lower temperature optima than the calibration set average temperature of 13.3°C. Overall, the diversity of chironomids was relatively high for a subarctic Finnish lake (Nyman et al., 2005) throughout the core, with at least 13 taxa present in every sample. The abundance of taxa without significant relationship with temperature was highest in the sample at 58 cm (39.3%), whereas the number of these taxa (*N*) was highest in the sample at 83 cm (4 of the total 24 taxa) (Fig. 6). Samples at 228

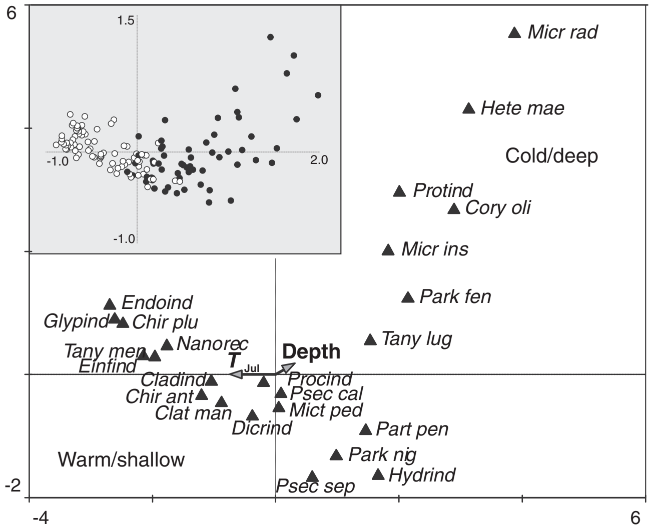


Figure 2. Canonical correspondence analysis (CCA) results from the combined training set of fossil chironomids for taxa and environmental variables (large figure) and for samples (small figure). Only the most common indicator taxa are shown and the taxa coding system follows Schnell et al. (1999). Variance explained by the first CCA axis is 12.6% and by the second axis 2.9%.

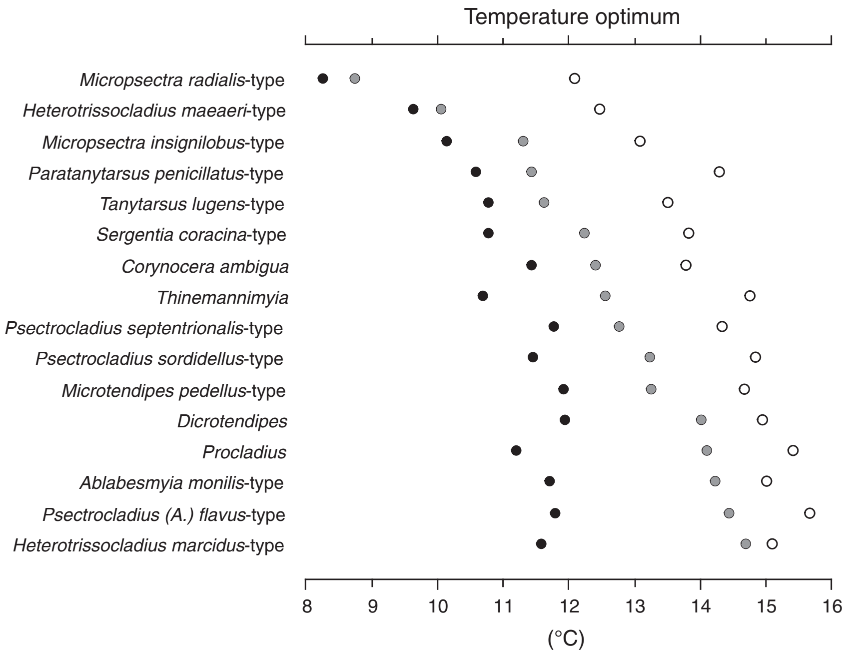


Figure 3. Mean air T_{Jul} optima of 16 mutual chironomid taxa in the Finnish training sets that also occur in the sediment core record from Lake Várddoaijávri, northeastern Lapland. The black circles represent taxon optima from the latitudinal training set, white circles from the longitudinal training set and gray circles from the combined training set.

and 295 cm depth had fewer than 90% fossil taxa present in the calibration set and samples at 38, 83, and 88 cm depth had no close analog in the modern data (5% chord distance in MAT) (Fig. 6). According to the CCA, the passively added fossil core samples were clustered between the training set samples from the two original calibration sets (Fig. 7).

The chironomid-inferred mean air T_{Jul}s using the three different models showed strong correlation in their trends; the linear correlation (r) between the reconstructions using the original models was 0.49 ($p < 0.01$), between the reconstruction using the altitudinal model and combined model 0.77 ($p < 0.01$), and using the latitudinal model and combined model 0.76 ($p < 0.01$). Regardless of the similar trends, the magnitude was different among the reconstructions. The lowest values were reconstructed using the altitudinal model and highest using the latitudinal model, with the values inferred using the combined model in between (Fig. 5). The combined model inferred the present day value (uppermost sediment sample) most accurately with overestimation of only 0.36°C, which is clearly within the model's RMSEP of 0.84°C and within the sample-specific eSEP of 0.86°C. The underestimation using the altitudinal model was 0.67°C and the overestimation using the latitudinal model was as high as 2.36°C, which clearly exceeds the model's RMSEP of 0.72°C. According to the reconstruction significance test (random TF), the reconstructions using the altitudinal ($p = 0.01$) and latitudinal ($p = 0.01$) models were statistically valid, but the reconstruction using the combined model ($p = 0.14$) failed this test. The reconstruction using the combined model showed statistically significant correlation ($r = 0.51$, $p < 0.001$) with the primary chironomid ordination axis (DCA axis 1) scores in the sediment profile. In chironomid zone 1 (Fig. 5), there was no significant correlation ($r = 0.12$, $p = 0.611$), but in zones 2 ($r = 0.65$, $p < 0.001$) and 3 ($r = 0.77$, $p < 0.001$) there were

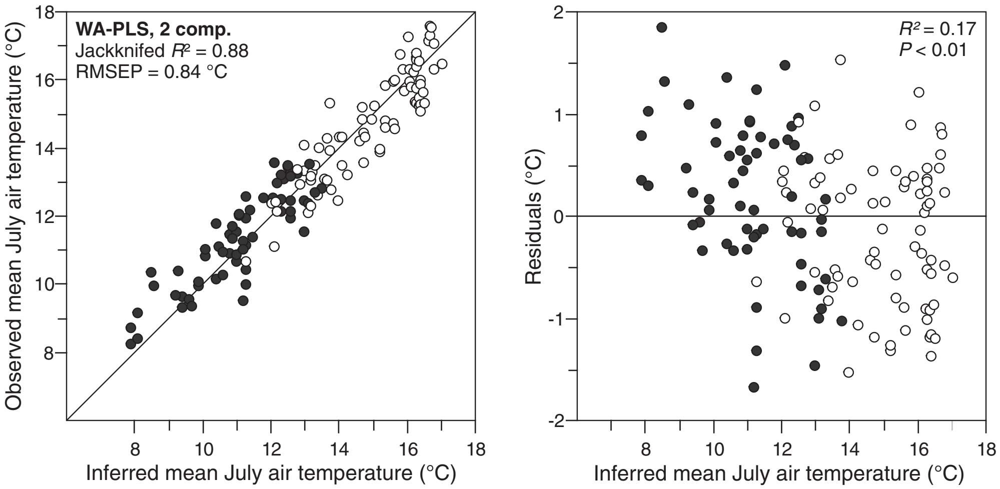


Figure 4. Relationship between measured and inferred temperatures in the new combined chironomid-based calibration model and the residuals along the temperature gradient.

Table 3
Comparison of the tested calibration models based on weighted averaging (WA), partial least squares (PLS), WA-PLS, and modern analog technique (MAT) in the combined Finnish training set. The best performance level (bold type) was achieved using a two-component WA-PLS model.

Model type	R^2_{jack}	RMSEP	Mean bias
$\text{WA}_{\text{inverse deshrinking}}$	0.80	1.082	0.006
$\text{PLS}_{\text{component2}}$	0.83	1.002	0.014
$\mathbf{WA\text{-}PLS}_{\textbf{component 2}}$	**0.88**	**0.839**	**0.005**
MAT	0.85	1.008	0.344

strong and significant correlation between the DCA axis 1 scores and inferred temperatures.

In the plant macrofossil record from Lake Korsajärvi, a number of species that have indicative temperature value were detected, despite that the macrofossil sample volumes were very small; only few cubic centimeters. The following species were used to reconstruct the mean minimum July temperatures for Korsajärvi, with the modern minimum mean July temperature limit (°C) indicated in brackets: narrow-leaved *Potamogeton* spp., including for instance *P. filiformis* (13°C); *Callitriche cophocarpa* (14°C); and *C. hermaphroditica* (12°C). Only these taxa are presented in Fig. 8. These taxa were accompanied by, for instance, tree-type *Betula* and various herbs, such as *Comarum palustre*, *Ranunculus* sect. *sceleratus*, and aquatic organisms such as *Bryozoa*.

Discussion

Training sets

As the altitudinal training set from northwestern Lapland suffered from the absence of warm lakes located at the boreal forest zone, and the latitudinal model from the scarcity of cold barren tundra sites, the combined model had an even distribution of lakes along the climate gradient in Finland. The more uniform distribution of training set lakes along the temperature and vegetation type gradients should improve the estimation of taxa temperature optima that inevitably lead to more accurate reconstructions. The taxa associated with cold or warm lakes in the combined Finnish training set (Figs. 2, 3) are very similar to those found elsewhere in Europe (Heiri et al., 2011; Eggermont and Heiri, 2012) with *M. radialis*-type, *H. maeaeri*-type, *Protanypus*, *Corynocera oliveri*-type, *M. insignilobus*-type, *Parakiefferiella nigra*-type, *Hydrobaenus*, and *Tanytarsus lugens*-type being typical of cold lakes and *Glyptotendipes*, *Endochironomus*, *Chironomus plumosus*-type, *T. mendax*-type, and *Einfeldia* of warm lakes. However, the temperature optima in the southern lakes can partly be misleading due to limnological effects of human activities (Luoto, 2011), whereas the lakes from northwestern Lapland suffer from the covariance between air temperature and water depth (Korhola et al., 2000a). Disregarding that the general trends in the temperature optima were consistent between the training sets, the tendency of the altitudinal training set having lower optima and the latitudinal training

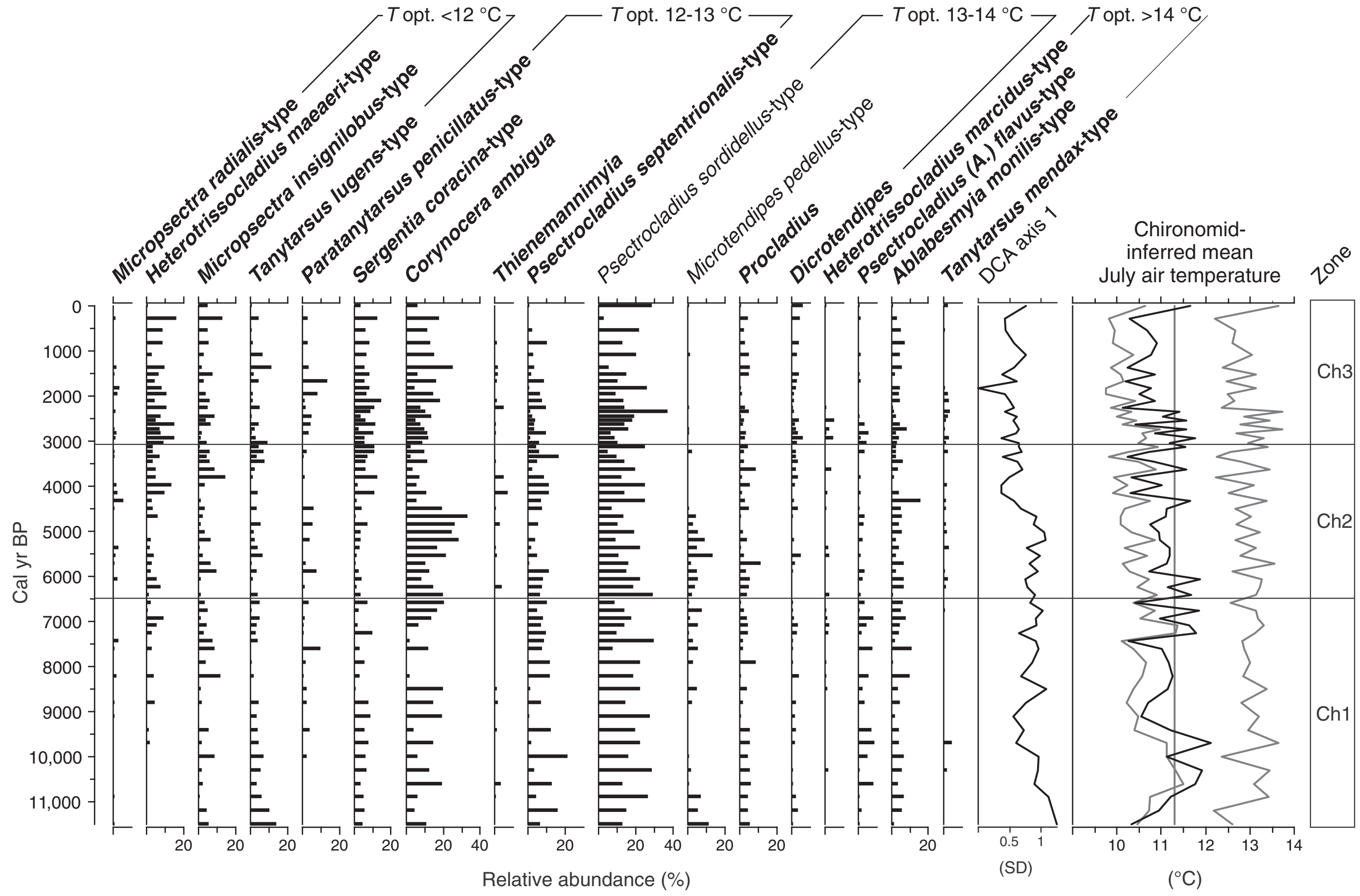


Figure 5. Most common chironomid taxa in Lake Várddoaijávri as relative abundances, detrended correspondence analysis (DCA) axis 1 scores, and the chironomid-inferred mean air T_{Jul} using the models from northwestern Finnish Lapland (gray line with lower values) and along the latitudinal gradient in Finland (gray line with higher values) and also using the new combined model (black line). The taxa are arranged according to their WA temperature optima in the combined Finnish training set and taxa having significant linear relationships (generalized linear models) with temperature in the calibration data are marked in bold type. The faunal zones are determined using the optimal partitioning method.
The chironomid stratigraphy was previously published by Luoto and Sarmaja-Korjonen (2011).

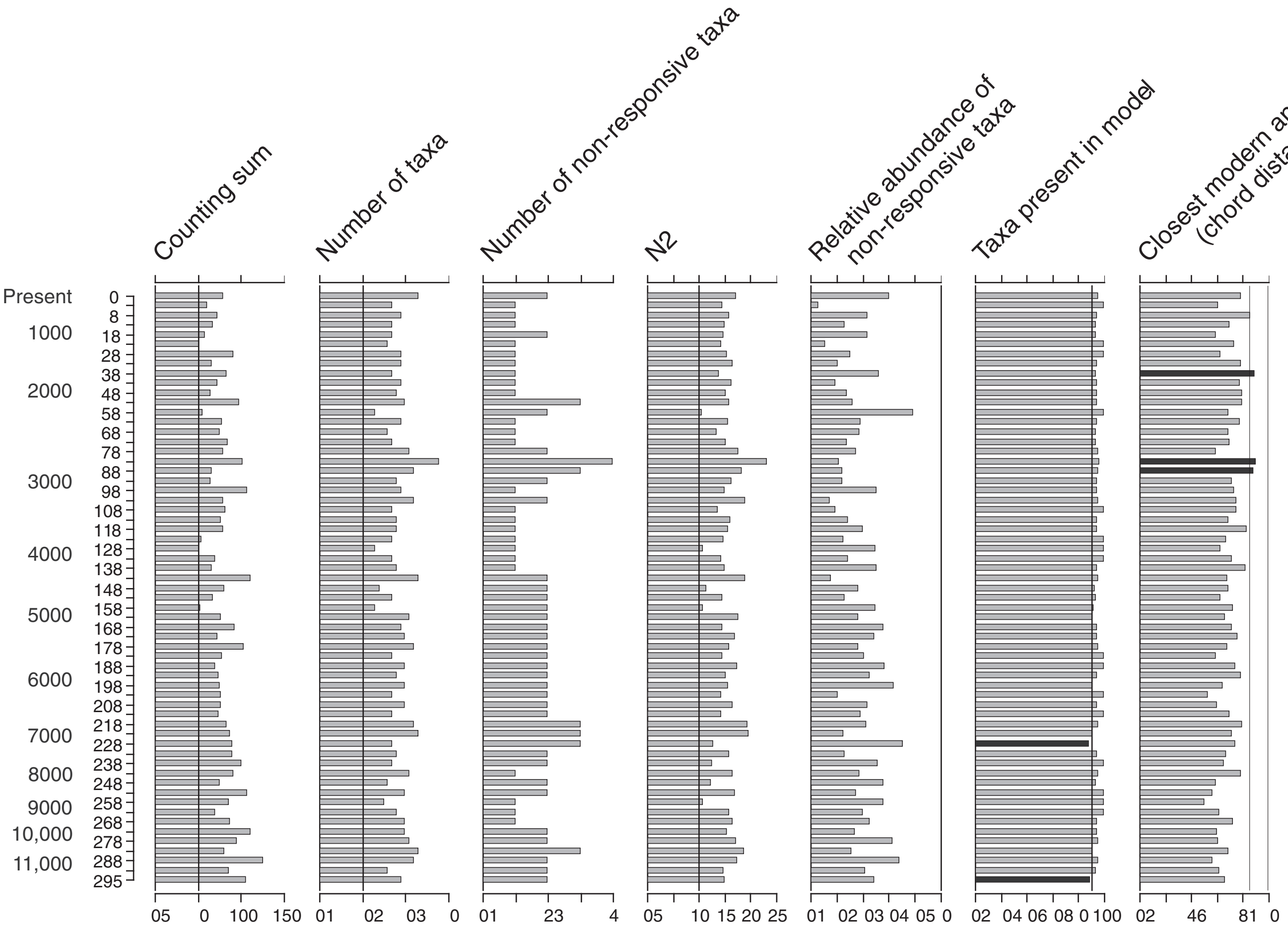


Figure 6. Chironomid counting sum, number of taxa and taxa without significant relationship with temperature, the effective number of occurrences (N2), relative abundance of taxa non-responsive to temperature and not present in the calibration model, and the closest modern analogs in the training set for Lake Várddoaijávri. Samples with taxa coverage of <90% in the training set and samples with poor modern analogs (<5% chord distance) are marked with black.

set having higher optima is not surprising considering the temperature gradients of the respective data sets. This suggests that instead of the original training sets with underestimated or overestimated taxon optima, the combined training set provides the most accurate estimations of ecological preferences, and subsequently the most accurate paleotemperature estimates in downcore reconstructions.

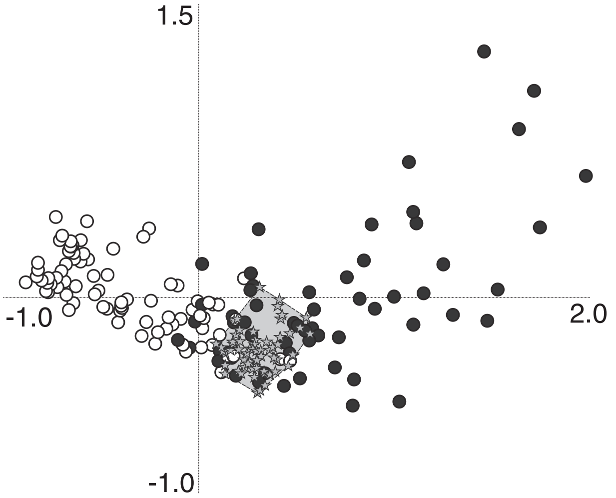


Figure 7. Canonical correspondence analysis (CCA) ordination of the training set chironomid assemblages and passively added core assemblages from Lake Várddoaijávri. The white circles represent the samples from the latitudinal training set, black circles from the altitudinal training set, and the stars highlighted with a gray area represent the core samples. The horizontal CCA axis 1 approximates the temperature gradient.

The CCA results indicated that the relationship between chironomid assemblages and temperature gained from the covariance of depth in the latitudinal dataset, but the altitudinal and combined models did not (Table 2). The CCA plot of the combined dataset also indicates that the coldest taxa favor deep lakes (Fig. 2). This potentially hampers chironomid-based temperature inferences during events of increased lake level, when the inferred temperatures may become unrealistically low. In fact, a test on the influence of depth on temperature inferences using the latitudinal model along an intra-lake water depth gradient from a lake in eastern Finland have shown that realistic temperatures can be reconstructed from shallow and intermediate depths but the risk of underestimated temperatures increase markedly in samples taken from the deepest sites (Luoto, 2010). It is also potentially possible that under a decreasing lake level, the associated decrease in cold-water (profundal) chironomids could lead to overestimated chironomid-inferred temperatures.

Compared to the original models, the combined model showed a greatly improved R^2_{jack} (Fig. 4; Table 1), which relates to a stronger species–environment relationship. However, the RMSEP increased by ~0.1°C, which is most likely due to the longer temperature gradient. Regardless that the RMSEP increased, the mean bias of the combined model reduced indicating that the observed and inferred temperatures were more in balance than in the original models, most likely due to the more even distribution of lakes along the temperature gradient. The combined model otherwise showed a good correlation between inferred and observed temperatures, with the exception of the coldest lakes, which had overestimated inferred values. Non-linear distortions at the ends of gradients are an intrinsic problem in unimodal-based methods that use WA (ter Braak and Juggins, 1993). In this case, the samples were more unevenly distributed in the cold end of the temperature gradient (Fig. 5), which may explain the significant distortion. Therefore, it should be noted that when reconstructed temperatures are less than ~9°C, the true values may have been even slightly colder.

Chironomid-based temperature reconstruction from Lake Várddoaijávri

Lake Várddoaijávri is located in barren tundra at the end of the temperature gradients of the original datasets. The majority of the core taxa had temperature optima less than ~13°C in the combined calibration dataset and taxa with temperature optima >14°C were scarce (Fig. 5). This is realistic, because the modern mean air T_{Jul} at the lake is 11.3°C. As most of the core taxa were cold indicators, the inferred values using the combined model were closer to those inferred with the model from northwestern Lapland than with the latitudinal model (Fig. 5). Although the reconstructed values using the combined model were closer to those derived using the altitudinal model, all the reconstructions correlated strongly and significantly and the same general trends were apparent in all the temperature curves. Due to these close similarities in their trends, it is peculiar that the reconstruction using the combined model failed the reconstruction significance test introduced by Telford and Birks (2011), whereas the reconstructions using the original models appear to be statistically valid. The random TF method is sensitive to the trajectory of the core samples through calibration space and also to sample size and amount of processable data. Therefore, the test does not provide here a reliable estimation of reconstruction reliability due to the relatively short trajectory of fossil data compared to the increased size of the calibration space (Fig. 7). As stated by Brooks et al. (2012), the results of this test must be considered alongside other paleoecological and environmental evidence because failure of the test does not necessarily mean a reconstruction is unusable, rather that it should be treated more cautiously. One possibility for the failure of the test is poor analog situations. However, the fossil samples of the current study were closely clustered between the temperature gradients of the original models in the CCA without distinct outlier samples (Fig. 7) and the MAT identified only three samples with poor modern analogs (Fig. 6). Furthermore, although the combined model had increased number of potential analogs following the merging of the original training sets and yet failed the significance test while the original models passed the test, poor analog conditions cannot be the causal factor in this case. Instead, the magnitude of variability in the measured temperatures in the original training sets (5.8/5.9°C) was much lower compared to the variability in the combined training set (9.2°C) when examined in relation to the reconstructed variability in the core data (2.0°C) that could explain the failure of the significance test. Therefore, it is likely that the random TF method is sensitive to the size of training data, as the variability in the reconstructed variable tends to diminish relative to the increase in training set samples.

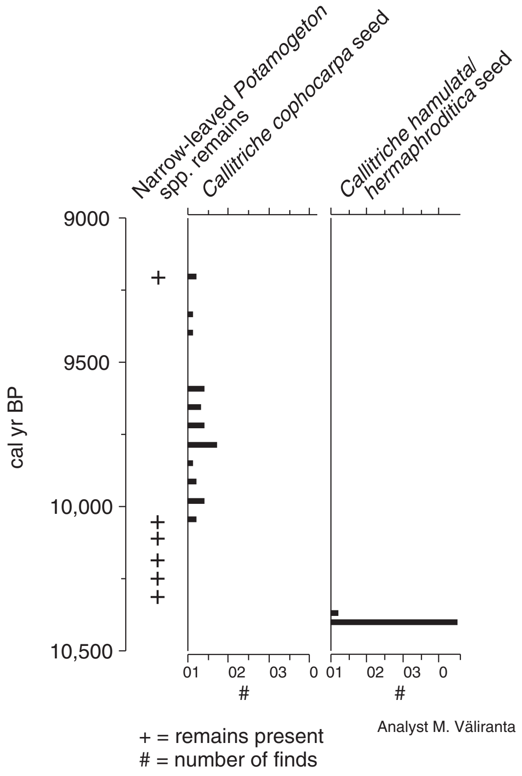
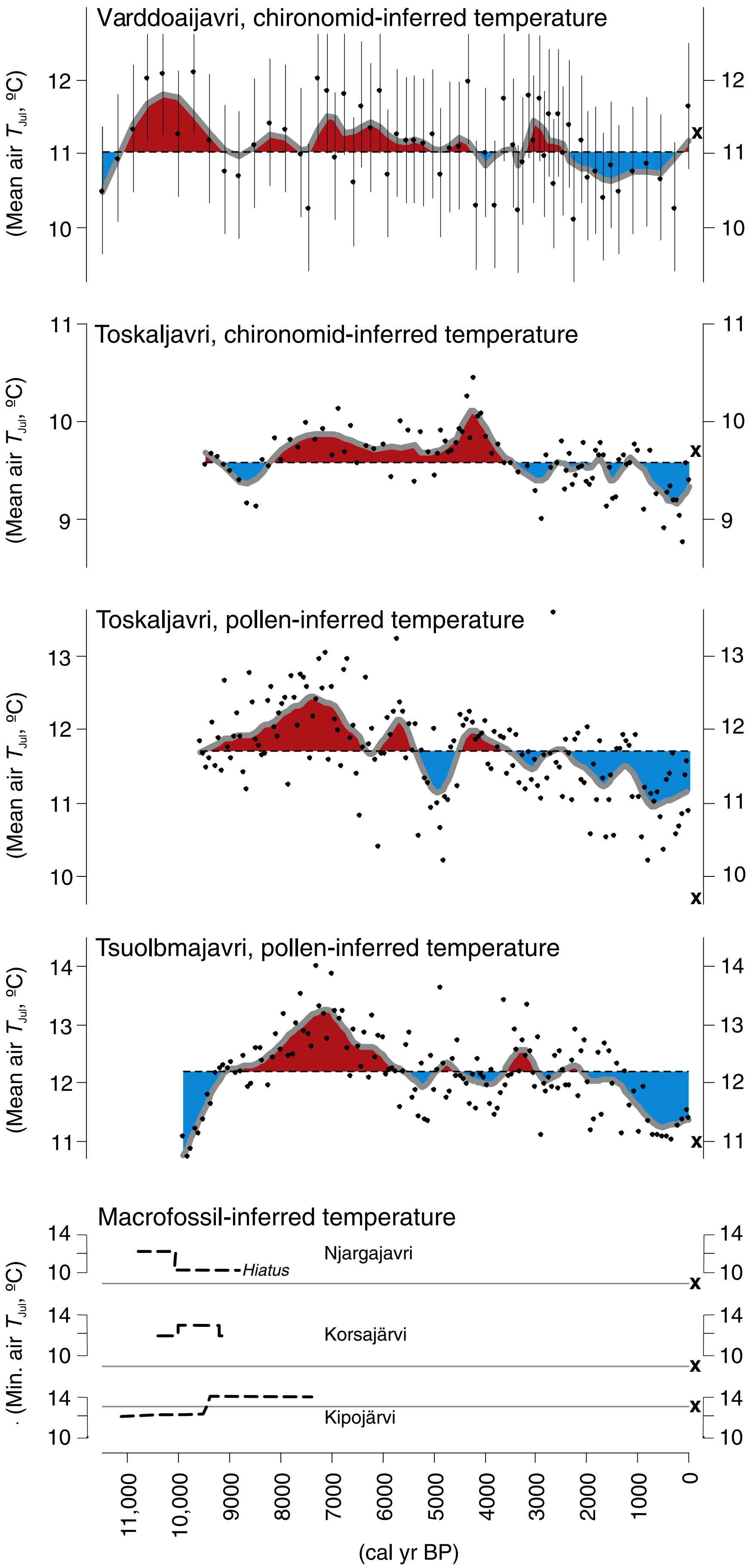


Figure 8. Macroscopic plant indicator species from Lake Korsajärvi, northwestern Lapland.

The most abundant taxa in the downcore data, including *P. sordidellus*-type, *C. ambigua*, *S. coracina*-type, and *P. septentrionalis*-type, are common taxa in both training sets (Nyman et al., 2005; Luoto, 2009a) and of these, only *P. sordidellus*-type did not have a significant relationship with temperature in the calibration data. Another non-responsive taxon with regard to temperature was *M. pedellus*-type. In Finland, *P. sordidellus* has been found to be associated with littoral vegetation (Tolonen et al., 2001) and hence, a possible factor behind the abundance of *P. sordidellus*-type in the sediment profile may have been the occurrence of macrophytes, which is determined in Finnish Lapland mainly by climate variables and lake depth (Sarmaja-Korjonen et al., 2006; Väliranta, 2006; Siitonen et al., 2011; Väliranta et al., 2011a, 2011b). In fact, Luoto and Sarmaja-Korjonen (2011) showed that the abundance of *P. sordidellus*-type in Lake Várddoaijávri may have been controlled by effective precipitation, as the distribution of *P. sordidellus*-type has significant correlation with sampling depth in Finnish lakes. Hence, the taxon may not be directly related to temperature, but it does appear to be indirectly related to climatic factors through occurrence of macrophyte and changes in effective precipitation.

The lowermost sample failed to reach 90% representativeness of taxa in the training set, although the sample did have a good modern analog (Fig. 6). However, there were three poor modern analog samples with cut-off value of 5% chord distance, of which two occurred around 3000 cal yr BP and one around 2000 cal yr BP (Fig. 6). With the cut-off for a good assemblage of 10% chord distance, these samples had good matches in the training set. Furthermore, the passively added core samples in the CCA were clustered within the training set samples (Fig. 7), being located at the warm end of the temperature gradient of the altitudinal training set and the cold end of the latitudinal training set. These results suggest that the temperature variability in Lake Várddoaijávri can be most reliably estimated by using the combined model. In a previous chironomid-based lake depth reconstruction from Lake Várddoaijávri, only about half of the taxa showed significant relationship with water depth and less than half with temperature in the calibration data of 68 lakes in Finland (Luoto and Sarmaja-Korjonen, 2011). In this study, this situation has changed as >90% of the core taxa had significant temperature relation in the combined calibration data, enabling a more reliable temperature reconstruction. The previous water-depth reconstruction and the current temperature reconstruction can be considered independent in the sense that water depth has no correlation with temperature in the calibration set (Luoto, 2009b), but according to the tests on reliability it seems that the current temperature reconstruction is more reliable.


Varddoaijavri, chironomid-inferred temperature
Toskaljavri, chironomid-inferred temperature
Toskaljavri, pollen-inferred temperature
Tsuolbmajavri, pollen-inferred temperature
Macrofossil-inferred temperature
Njargajavri
Hiatus
Korsajärvi
Kipojärvi
(Mean air T_{Jul}, ºC)
(Min. air T_{Jul}, ºC)
x
11,000
10,000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
(cal yr BP)

Attempts to reconstruct non-causal surrogate environmental variables and from the effects of secondary variables causes problems for paleolimnological reconstruction (Juggins, 2013). Lake nutrient conditions are correlated with air temperature in Finnish lakes (Luoto, 2011), hence providing a major error source for chironomid-based temperature reconstructions if changes in nutrient condition occur due to other factors (e.g., following morphometric nutrient enrichment). However, Eggermont and Heiri (2012) showed that there exists an independent influence of temperature from that of the nutrient–temperature relationship on chironomids. These influences can be recognized using indicator taxa, such as in the present study by using the GLMs (Fig. 5). Similarly, the simultaneous influence of lake depth changes on chironomid-inferred temperatures can be assessed using indicator taxa (Luoto et al., 2010). In addition to the problem of possible influence of non-causal variables on paleoenvironmental reconstructions, models may have reduced predictive power outside their current spatial setting (Juggins, 2013). This argument is well supported by the present results indicating that, although having consistent trends, the taxon optima between the original training sets have marked divergence (Fig. 3). We solved this confounding factor by merging the training sets to be geographically and climatically suitable for the Lake Várddoaijávri core.

Although it could have been expected that events of high lake-level increase the number of cold-indicating chironomids due to the covariance found between depth and temperature in the dataset, there was no particular evidence on lower chironomid-inferred temperatures during periods of suggested elevated lake level in Lake Várddoaijávri. Increasing number of deep water chironomids and higher reconstructed lake levels occurred in Lake Várddoaijávri between ~11,000 and 9000, ~7000 and 6000, ~5000 and 4000, and at ~3000 cal yr BP (Luoto and Sarmaja-Korjonen, 2011), but instead of lower chironomid-inferred temperatures during these phases, no pattern between lake depth and temperature was found when compared with the pollen-based temperatures. Most importantly, the suggested elevated lake level during the early Holocene did not seem to influence the chironomid-based temperature reconstruction, because the inferred temperatures were increased at that time. Therefore, it seems that the community response may diminish the influence of secondary variables and the effect of lake level change on chironomid-based temperature reconstructions could be relatively insignificant. However, this interpretation is based solely on the results of this study and more research is needed to reveal the influence of lake-depth dynamics on chironomid-based temperature reconstructions.

There was a strong correlation between the chironomid-inferred temperatures using the combined model and chironomid DCA axis 1 scores in the entire sediment sequence (Fig. 5) suggesting that the assemblages were indeed responding to the inferred variable. However, unlike chironomid zones 2 and 3, no significant correlation was found in the initial zone 1, between 11,500 and 6500 cal yr BP. This may indicate that also other environmental variables besides temperature influenced the chironomid community composition during the early Holocene, though the samples had good modern analogs according to the MAT and CCA (Figs. 6, 7).

Temperature dynamics in northern Lapland—warm or cold early Holocene?

Previous paleolimnological temperature records from Lake Toskaljavri (69°12′N, 21°28′E; 704 m asl) (Seppä and Birks, 2002; Seppä et al., 2002) and Lake Tsuolbmajavri (68°41′N, 22°05′E; 526 m asl) (Seppä and Birks, 2001) in northwestern Lapland suggest similar general trends compared to the present reconstruction of Holocene summer temperatures (Fig. 9). A significant correlation was found between the present mean air T_{Jul} reconstruction from Lake Várddoaijávri and the chironomid-based reconstruction from Lake Toskaljavri (Pearson $r = 0.32$, $p = 0.018$), and furthermore, significant correlations were found between the present reconstruction and the previous pollen-based reconstructions from Lake Toskaljavri ($r = 0.43$, $p = 0.001$) and Lake Tsuolbmajavri ($r = 0.41$, $p = 0.002$). Although significant correlations between the series were found for the whole Holocene sequence, a major difference between the chironomid-based reconstruction from Lake Várddoaijávri and pollen-based temperature inference from Lake Tsuolbmajavri occurred during the early Holocene (Fig. 9).

The retreat of the Fennoscandian Ice Sheet after the Younger Dryas stadial (12,800–11,500 cal yr BP) lagged behind in northwestern Finnish Lapland (Johansson and Kujansuu, 2005). This explains the absence of equally old sediment material in Lake Tsuolbmajavri and Lake Toskaljavri than that retrieved from Lake Várddoaijávri, which is situated farther east. The very cold (<11°C) chironomid-inferred temperatures in Lake Várddoaijávri had already increased rapidly during the earliest Holocene, and present-day temperatures were reached at ~11,000 cal yr BP (Fig. 9). Based on the chironomid record from Lake Várddoaijávri, the warmest temperatures of the Holocene (>12°C) occurred between ~11,000 and 10,000 cal yr BP.

In contrast, the pollen-based reconstructions from Lake Tsuolbmajavri still showed very cold temperatures (<11°C) at ~10,000 cal yr BP, with temperatures reaching the Holocene maximum between ~8000 and 7000 cal yr BP. In addition, a diatom-based temperature reconstruction from Lake Tsuolbmajavri showed a slow temperature increase with maximum temperatures reached as late as ~6000 cal yr BP (Korhola et al., 2000b). Consistent with pollen-inferences from Lake Tsuolbmajavri and Lake Toskaljavri, pollen-based temperatures from the Norwegian side of Lapland indicated that the maximum temperatures were reached at ~7000 cal yr BP (Bjune et al., 2004).

However, a chironomid-based reconstruction from Jansvatnet in Hammerfest, northernmost Norway, suggests rapidly increasing temperatures already at 11,000 cal yr BP and the warmest Holocene temperatures at 10,000 cal yr BP (Birks et al., 2012). The pollen-inferred temperatures from Jansvatnet indicate a much later timing of the Holocene thermal maximum (HTM) (Birks et al., 2012), thus suggesting a lag in the pollen record compared to the chironomid evidence. However, these results cannot be compared with the results from the Finnish lakes (Fig. 9), which represent sites from different locations. Consistently with the chironomid record from Lake Várddoaijávri, recent pollen-based and plant macrofossil-based reconstructions from elsewhere in Finnish Lapland have shown that the temperatures reached present-day or even higher values already at the very beginning of the Holocene (Väliranta et al., 2005, 2011a, 2011b; Salonen et al., 2013, Fig. 9).

A chironomid-based temperature reconstruction from a closely located lake (Sarmaja-Korjonen et al., 2006) indicated elevated temperatures (~1°C warmer than present) for the earliest Holocene; however, this record suffered from a hiatus between ~9000 and 5000 cal yr BP making it more difficult to use for closer comparison. Nevertheless, the consistency on the chironomid-based indication of warm early Holocene is further evidenced by the chironomid record and reconstruction from Lake Tsuolbmajavri (Korhola et al., 2002a). A

Figure 9. Mean air T_{Jul} reconstructions from Finnish Lapland: chironomid-based reconstruction from Lake Várddoaijávri (69°53′N, 26°31′E; 409 m asl) in northeastern Lapland, chironomid (Seppä et al., 2002) and pollen-based (Seppä and Birks, 2002) reconstructions from Lake Toskaljavri (69°12′N, 21°28′E; 704 m asl) and pollen-based reconstruction from Lake Tsuolbmajavri (68°41′N, 22°05′E; 526 m asl) (Seppä and Birks, 2001) in northwestern Lapland. A locally weighted scatterplot smooth with a span of 0.1 is applied to each of the mean air T_{Jul} reconstructions and fitted against the mean inferred temperatures in each of the cores (dashed horizontal lines). To estimate macrofossil-based paleotemperatures from Lake Njargajavri (69°46′N, 27°20′E; 355 m asl), Lake Korsajärvi (68°49′N, 22°05′E; 530 m asl), and Lake Kipojärvi (69°11′N, 27°17′E; 160 m asl), plant species distribution maps of Lampinen and Lahti (2013) were used to define the current area of distribution of several indicator species in Finland, and these distributions were compared to calculated mean air T_{Jul} data (1961–2000) based on daily measurements by the Finnish Meteorological Institute (Venäläinen et al., 2005). The modern measured mean air T_{Jul}s for each site are marked with a cross.

similar pattern of more rapidly increasing chironomid-inferred temperatures compared to pollen records has also been evident in sediment profiles from southern Finland (Heikkilä and Seppä, 2003; Luoto et al., 2010) and the lag of pollen-based reconstructions is also suggested by Cladocera-inferred length of ice-covered period from southern Finland (Nevalainen et al., 2012). In addition to the Finnish evidence, isotopic records (Shemesh et al., 2001) and megafossils of mountain birch (Kullman, 2004) from Swedish Lapland support the scenario of warm early Holocene.

It is possible that the pollen-based temperature reconstructions of early Holocene are underestimated due to the slow response of terrestrial vegetation development to climate change in newly glacial retrieved areas compared to insects, such as chironomids (Elias, 1991; Massaferro and Brooks, 2002). The slow catchment vegetation development can be attributable to factors such as long duration of soil development and slow-paced floral immigration of certain species (Väliranta et al., 2011a, 2011b). It may also be that compared to chironomid reconstruction, the pollen-based reconstructions are more influenced by the potential poor analog situations and the increased continentality during the early Holocene (Salonen et al., 2013). It is also possible that the chironomids responded to some other environmental factor than temperature during the earliest Holocene that would have increased the inferred temperatures. This is suggested by the lack of correlation between chironomid-inferred temperatures and chironomid DCA axis 1 scores (main direction of community variance) between 11,500 and 6500 cal yr BP. In fact, Nyman et al. (2008) showed from a treeline lake in northwestern Fennoscandia that the early Holocene (~10,500–8300 cal yr BP) chironomid communities were responding to changes in water quality, namely pH, which was inferred from diatom assemblages. Based on diatom records, it is common that the early Holocene lake ontogeny in Finnish sites is characterized by elevated trophic status and higher pH (Seppä and Weckström, 1999; Luoto et al., 2012) and it has also been shown that chironomids with elevated trophic optima tend to inhabit warm lakes (Luoto, 2011; Eggermont and Heiri, 2012). Therefore, it can be that minerogenic material washed into Lake Várddoaijávri from the undeveloped soil after the retreat of continental ice sheet and increased the nutrient content enabling the success of chironomids, which favor higher trophic status. In the early Holocene chironomid stratigraphy from Lake Várddoaijávri, the only taxon with such preference was *M. pedellus*-type (Fig. 5), which has an oligo-mesotrophic optimum in Finnish lakes (Luoto and Raunio, 2011) and no linear relationship with temperature in the training set, causing its temperature optimum to be rather warm compared to the other core data. However, the relatively low abundance of *M. pedellus*-type during the early Holocene (~5–10%) together with a decreasing trend along with the temperature increase suggests that this cannot solely explain the elevated temperatures. Instead, the early Holocene chironomid samples had very close modern analog assemblages in the core data and the number of temperature indicator taxa was high (Figs. 5, 6), which suggests that the chironomid-inferred temperatures were indeed reliable and the more probable cause for the divergence compared to the pollen-based results was the lag time in vegetation immigration and colonization.

The lag in vegetation development is likely also due to the later deglaciation of the sites where the pollen-based reconstructions were derived from; thus, the differences may reflect variability in local climate conditions between the northeastern and northwestern Lapland. This theory would be supported by the pollen-based results of Solovieva et al. (2005) showing warmer climate conditions for the early Holocene from the adjacent Kola Peninsula compared to the reconstructions from Lake Tsuolbmajavri and Lake Toskaljavri. It should be noted that all the pollen records were only ~9000–10,000 years long, therefore missing the earliest Holocene and making the comparison of temperatures during this period impossible at these sites. Nevertheless, it is also worth mentioning that the activity of the sun was most intense during the early Holocene (Solanki et al., 2004). Due to the spatial differences in deglaciation that are reflected in the paleoenvironmental records of northern Europe, we cannot say whether the pollen records lag behind the chironomid evidence. These records do suggest earlier HTM in the northeastern part of Lapland coinciding with maximum summer insolation, while the western part with delayed deglaciation continued to be cold for much longer despite the intensive solar activity. It is noteworthy though that the macrofossil-based reconstruction from Lake Korsajärvi, located very close to Lake Tsuolbmajavri (Fig. 1), suggests very warm early Holocene also for the northwestern part of Lapland with climate conditions warmer than present already at ~10,500 cal yr BP (Fig. 9).

Following the early Holocene maximum temperatures, the chironomid-inferred mean air T_{Jul}s in Lake Várddoaijávri decreased until ~9000 cal yr BP (Fig. 9); and from then onwards, the chironomid and pollen records suggest similar temperature development. Coinciding with the HTM (Kaufman et al., 2004; Renssen et al., 2012), the climate first warmed until ~7000 cal yr BP and then turned into late Holocene cooling after ~5000 cal yr BP, a period well characterized from northern Europe (Tiljander et al., 2003; Salonen et al., 2011). This cooling was interrupted in all the reconstructions by a short-lived warm period at ~4000/3000 cal yr BP that is evident also from other records from Finnish Lapland (Korhola et al., 2002a; Salonen et al., 2013). Another distinct common feature between the reconstructions was the most recent climate warming (Fig. 9). The inferred temperatures of the most recent sediment samples have remained lower than during the warm periods of HTM and the ~4000/3000 cal yr BP event, though the present-day temperature at Lake Toskaljavri was greatly overestimated by the pollen-based reconstruction. The slight underestimation in the chironomid-inferred temperature for the surface sample in Lake Várddoaijávri might have been caused by the possible recent introduction of Arctic char causing changes in the macrobenthic communities unrelated to climate.

Conclusions

The combination of the two original chironomid-based temperature training sets enabled the construction of a calibration model with a longer temperature gradient and a more uniform distribution of lakes along the climatic gradient in Finland. The relationship between chironomid assemblages and temperature became stronger with the expanded dataset and the number of taxa markedly increased. As the species–environment relations became more significant, the calibration model improved with respect to its correlation between observed and predicted mean air T_{Jul}.

As a consequence of the increased environmental gradient and number of taxa, almost all of the core taxa from Lake Várddoaijávri had statistically significant relationships to temperature, which allowed for a more reliable paleotemperature reconstruction. Compared with reconstructions made using the original models, the combined model inferred similar temperature trends for the Holocene but with different magnitudes. Based on the value reconstructed for the surface sample representing the present, the combined model showed improved accuracy with regard to the observed modern value.

Significant correlations were found between the chironomid-inferred temperatures from Lake Várddoaijávri and chironomid- and pollen-based reconstructions from northwestern Lapland over the Holocene. However, a considerable difference was also apparent, as the chironomid record from Lake Várddoaijávri indicated rapidly increased temperatures already during the earliest Holocene (~11,000–10,000 cal yr BP) whereas the pollen-based reconstructions showed a much slower temperature increase that ended as late as ~8000–7000 cal yr BP. The discrepancy was possibly caused by spatial differences in deglaciation patterns between northwestern and northeastern Lapland, although the macrofossil evidence from Lake Korsajärvi also suggested a warm early Holocene for the northwestern part. The temperature development for the rest of the Holocene was more uniform between the aquatic and terrestrial proxies, with characteristically increased temperatures during the HTM, late Holocene cooling interrupted by a short-lived warm episode at ~4000/3000 cal yr BP, and the recent climate warming.

The results of this study show that longer temperature gradients can improve estimation of taxon optima in training sets and increase model performance and reliability. One of the benefits of the new combined calibration set is that, although it has a longer temperature gradient, it still has the advantage of representing regionally estimated temperature optima for the taxa. Another important implication demonstrated in this study is that chironomids, as well as other insects, may respond considerably faster to climatic change compared to vegetation, which may have a long lag time especially in newly exposed terrains.

Acknowledgments

This study was supported by the ILMAVEIVI project (Academy of Finland, grant no. 250343) for T.P. Luoto and the CLICHE project (Academy of Finland, grant no. 1140900) for J. Weckström, A. Korhola, and M. Väliranta. We thank Heikki Seppä for fruitful discussions and making the pollen-based reconstructions available. We are also grateful for the two journal reviewers for their detailed and constructive comments that greatly improved the value of this paper.

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