


# Chironomids can be reliable proxies for Holocene temperatures. A comment on Velle et al. (2010)

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## Abstract

Velle et al. (*The Holocene* 20 (2010) 989–1002) discussed discrepancies between Scandinavian Holocene chironomid-inferred temperature estimates, which they attribute to the response of chironomids to environmental variables other than temperature and to taxonomic shortcomings. They suggest ways in which the reliability of chironomid-based paleotemperature reconstructions could be improved by taking into account ecological complexity. While we agree with many of their recommendations, based on the results of other work, we think their paper is unnecessarily pessimistic regarding the ability of existing chironomid-based temperature inference models to provide reliable estimates of past temperature. We offer a critique of the main points discussed by Velle et al. (2010) and provide evidence that chironomid-based temperature inference models can reliably reconstruct mean July air temperature in the Lateglacial and Holocene over millennial and centennial timescales.

## Keywords

chironomids, Holocene, lake depth, lake trophic state, pH, temperature inference

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## Introduction

The paper of Velle et al. (2010) has re-opened the 20 year old debate (Hann et al., 1992; Walker and Mathewes, 1989; Warwick, 1989) concerning whether chironomid assemblages are reliable quantitative indicators of past summer temperatures. Velle et al. (2010) acknowledge that chironomid-based temperature records can provide reliable reconstructions of climatic variability during the Lateglacial period. They focus their discussion on temperature reconstruction during the climatologically more stable Holocene and discuss a subset of Holocene temperature reconstructions from Scandinavia, pointing out differences between these reconstructions and arguing that parameters other than temperature may be responsible for these differences. They suggest that similar issues may detract from the reliability of chironomid-based Holocene temperature reconstructions in other regions.

We agree that, like all climate reconstruction methods based on proxies, chironomid-based temperature reconstructions can be influenced by confounding factors (Brooks, 2006; Heiri and Lotter, 2003, 2005). This has long been recognized and Velle et al. (2010) provide a useful review of some of the problems. However, we wish to clarify that there is no doubt that chironomids *can* provide reliable estimates of past temperatures, including robust estimates of the associated prediction error which incorporate the response to other variables. This is demonstrated by the many chironomid records that have provided accurate temperature reconstructions for the Lateglacial and Holocene, as evaluated by comparison with independent climate proxies (e.g. Brooks and Birks, 2000; Clegg et al., 2010; Heiri et al., 2007; Levesque et al., 1993), and that have reflected the small-scale fluctuations apparent in meteorological records over the last 100+ years (Langdon et al., 2011; Larocque and Hall, 2003;

Larocque et al., 2009). Chironomids offer several advantages over other quantitative temperature proxies (Brooks, 2003) and the requirement for multiproxy and multisite studies to separate signal from noise is equally true for other climate proxies, including lacustrine proxies and proxies from other archives such as tree rings, peats, speleothems and ice cores.

Like any proxy method, chironomid-based temperature reconstructions should not be applied uncritically. Analogue statistics are routinely calculated to detect non-analogue situations (e.g. Axford et al. 2011; Heiri et al., 2007; Larocque-Tobler et al., 2010a), although WA-PLS methods work well in non-analogue situations (Birks et al., 2010). Telford and Birks (2011) have provided a method to test the statistical significance of a temperature reconstruction against random data, but the results of this test must be considered alongside other palaeoecological and environmental evidence because failure of the test does not necessarily mean a reconstruction is unusable, rather that it should be treated more cautiously. The challenge for palaeoecologists is to identify further

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strategies that can detect non-temperature artefacts in chironomid-based temperature records and to constrain *a priori* the types of environments in which chironomids perform well in tracking past temperature changes. Velle et al. (2010) provide a valuable set of recommendations for successful chironomid analysis which we largely endorse. However, the paper also makes several assertions that are not generally supported by the breadth of chironomid studies conducted over the past two decades. Here we seek to advance the discussion by providing another perspective on the utility of chironomids for reconstructing palaeotemperatures and evaluating some of the possible complications discussed by Velle et al. (2010).

## Temperature as a driver of chironomid distribution and abundance

Calibration data sets based on samples of modern chironomids across long temperature gradients show a strong relationship between chironomid assemblage composition and summer air temperature (e.g. Brooks and Birks, 2001; Larocque et al., 2001; Lotter et al., 1997; Olander et al., 1999). For this reason chironomid-based temperature inference models can be developed with excellent performance statistics. However, Velle et al. (2010) imply that the main reason for the high performance of these models is because the temperature gradient is maximised in the calibration data set and the gradients of other environmental variables are minimised, rather than temperature being a particularly significant variable in driving the composition of chironomid assemblages. The reader may gain the impression that chironomids could be used to infer any variable provided the gradient length of the parameter is as long as possible and the influence of other variables is reduced. However, this overlooks the fact that the performance statistics of chironomid-based temperature inference models far exceed the performance statistics of other chironomid-based models designed to infer other variables such as total phosphorus (Brooks et al., 2001; Langdon et al., 2006), total nitrogen (Brodersen and Anderson, 2002), dissolved oxygen (Quinlan and Smol, 2001), dissolved organic carbon (DOC) (Larocque et al., 2006), chlorophyll *a* (Brodersen and Lindegaard, 1999) and lake depth (Korhola et al., 2000). These observations emphasise the over-riding influence of summer temperature on the distribution and abundance of chironomid species at the local to regional scale.

## The influence of other environmental variables on chironomid distribution and abundance

Velle et al. (2010) discuss several environmental variables that can influence chironomid assemblages and potentially affect chironomid-based temperature estimates. We commend them on this discussion and agree that a better understanding of the influence of non-climatic parameters on chironomid-based temperature reconstruction is essential for further improvement of the method. However, we believe some of their discussion of how factors, such as trophic state and pH, influence chironomid-based temperature estimates overlooks important points, so we provide a contrasting perspective on some specific issues below.

### Lake trophic state

Velle et al. (2010) focus much of their discussion on the potential confounding effects of lake trophic change. They provide conceptual

models that demonstrate different ways that lake trophic state and nutrient conditions may co-vary with temperature. We agree that there are situations in which it may be difficult to distinguish between responses to trophic change versus temperature, because taxa characteristic of warm waters are also often characteristic of eutrophic waters, and taxa characteristic of cold waters are also often characteristic of oligotrophic waters. Velle et al. (2010) suggest that this may be problematic for palaeoclimate reconstructions because relationships between climate and trophic variables could change over time, especially in the earliest Holocene when nutrients may have been suddenly released following deglaciation. However, Velle et al. (2010) do not provide compelling evidence that this situation is common as only two (SPA and RAT) of the ten lakes they analyse include early-Holocene chironomid assemblages that may be indicative of enhanced lake productivity during that time. More generally, there are many chironomid-inferred temperature (C-IT) records from the early Holocene that capture climatic oscillations at 11.3, 10.3, 9.3 and 8.2 ka BP (e.g. Axford et al., 2009; Brooks, 2003; Brooks and Birks, 2000; Caseldine et al., 2006; Lang et al., 2010a), in agreement with reconstructions from Greenland ice cores and other climate proxy-data. These examples demonstrate that trophic influences do not obscure the response of chironomids to climate changes at those sites during the early Holocene.

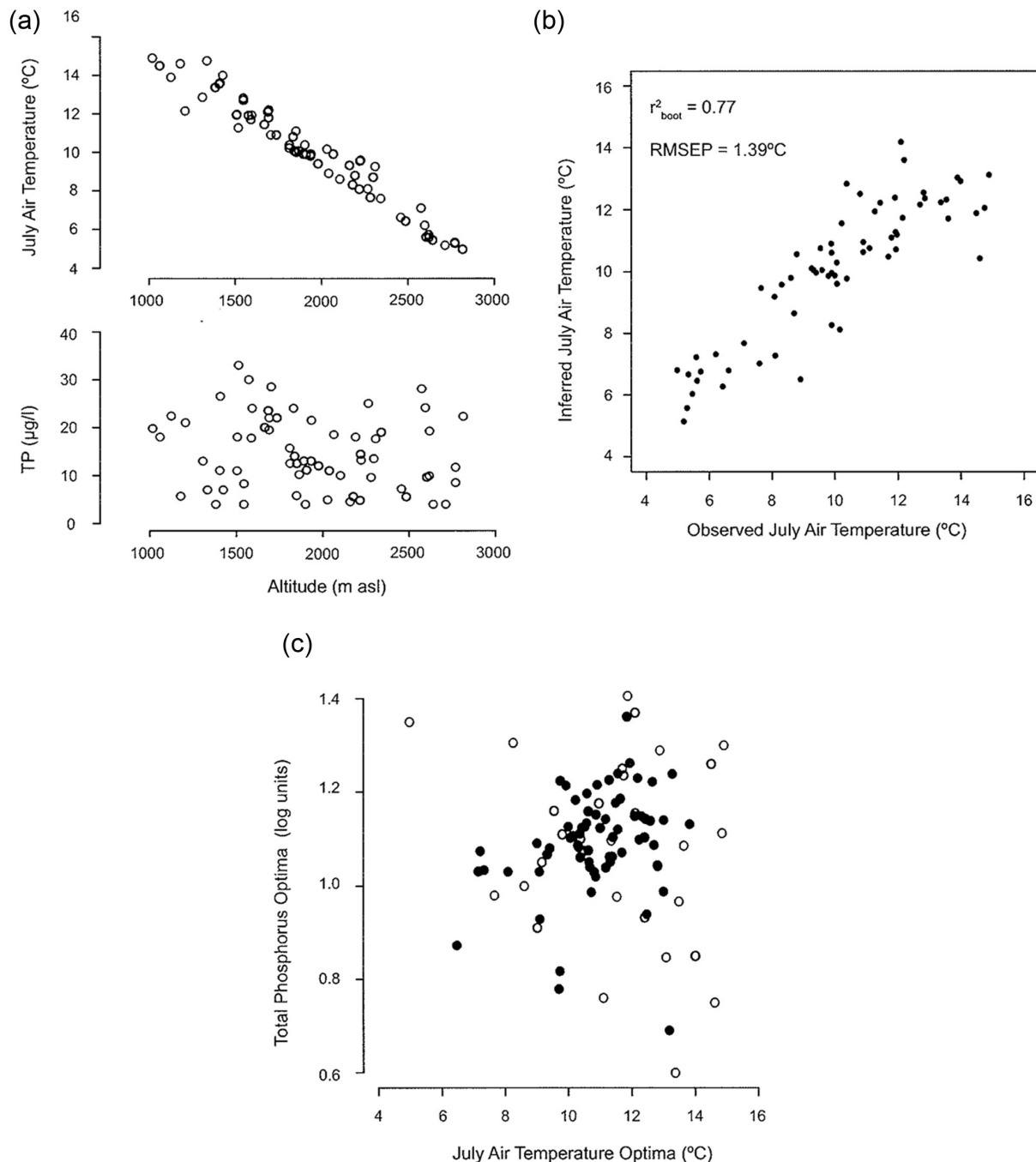
One circumstance in which lake trophic state may indeed decouple from climate, and obscure the chironomid-temperature relationship, is when local human activities strongly affect the nutrient-loading of lakes and lead to trophic shifts unrelated to climate. Gathorne-Hardy et al. (2007) showed that the trophic influence of early Viking settlements in the Faroe Islands was distinguishable in the chironomid record. Conversely, Gathorne-Hardy et al. (2009) showed that during human settlement and tree clearance on Iceland chironomid assemblages were relatively complacent but did respond to climate cooling during the 'Little Ice Age'. Similarly, Heiri and Lotter (2003, 2005) describe a chironomid record that was strongly affected by early human activity and the resulting lake anoxia during the Bronze Age. These studies demonstrate that human impacts can be discerned and distinguished from climate responses in chironomid records.

We would also emphasise that the correlation between lake trophic state and temperature is not as universal as suggested by Velle et al. (2010) and therefore cannot be invoked to explain all of the chironomid-temperature correlations strongly expressed in many data sets. The authors cite a data set (Brodersen and Anderson, 2002) from near Kangerlussuaq, western Greenland, which comes from a set of lakes exhibiting a wide range of catchment characteristics, in some cases strongly influenced by evaporative enrichment of nutrients, and representing a limited and unevenly distributed range of temperatures. This sampling strategy maximizes the statistical impact of lake catchment characteristics and minimizes the effect of temperature. At least partly because the warmer lakes are more affected by evaporative enrichment, nutrient concentrations in the sampled lakes were strongly correlated with temperature (Anderson et al., 2001; Brodersen and Anderson, 2002). Consequently, the calculated optima of individual chironomid taxa with respect to nutrient concentrations and temperature are necessarily correlated as well. Notwithstanding the above, an indication of the underlying strength of the temperature gradient is that it still accounted for about 20% of the variability in the chironomid assemblages reported.

Velle et al. (2010) suggest that a data set in which lake nutrient concentrations are not correlated with temperature is needed to demonstrate the chironomid-temperature relationship. Such a data set is easily constructed from available chironomid-temperature calibration data sets. For example, if the chironomid-temperature calibration data set from the European Alps (Heiri and Lotter, 2005, 2010) is truncated to include only lakes with total phosphorus concentrations below 50 µg/l and July air temperatures cooler

than 15°C (Figure 1a), then the relationship between lake total phosphorus and July temperature is effectively eliminated ( $r = 0.15$ ,  $p = 0.23$ ; Figure 1c). Nevertheless, a chironomid-based inference model for reconstructing temperature can be developed from this restricted data set ( $n = 65$ ) with an almost identical prediction error as in the original 100 lake inference model (Figure 1b) (bootstrapped error statistics of  $r^2 = 0.77$  and  $\text{RMSEP} = 1.39^\circ\text{C}$ , compared with  $r^2 = 0.89$  and  $\text{RMSEP} = 1.41^\circ\text{C}$  in the full model). The reduced  $r^2$  is related to the shorter temperature range included in the truncated model than in the full model. If the temperature optima of the chironomids are compared with the optima

calculated for total phosphorus concentrations it becomes apparent that the relationship between the two is not nearly as strong as has been suggested (Figure 1c). No correlation is apparent if the optima of all taxa are examined ( $r = 0.04$ ) and only a very weak relationship exists if only abundant taxa are examined ( $r = 0.26$ ). This correlation occurs because cold lakes are typically nutrient-poor and therefore only a few cold-adapted chironomids can be identified in the data set that have a preference for high nutrient concentrations. However, in warmer climates there are clearly chironomids that have a wide range of preferences with respect to trophic state.



**Figure 1.** (a) Distribution of lakes in the modern Swiss calibration set showing relationship between altitude and temperature (above) and total phosphorus (TP) (below). The calibration set has been truncated to include only lakes with total phosphorus concentrations below 50 µg/l and July air temperatures cooler than 15°C. (b) Comparison of chironomid-inferred temperature and observed temperature in the truncated modern Swiss calibration set. The performance statistics of the chironomid-based temperature inference model from the truncated data set (65 lakes) are only slightly inferior to the full data set of 100 lakes. (c) Comparison of TP optima and temperature optima of the most abundant taxa (solid circles) ( $r = 0.26$ ) and all taxa (open circles) in the truncated moderns Swiss calibration set ( $r = 0.04$ ).

These calculations clearly show that lake trophic state is not the driving force behind the relationship between chironomids and temperature in the European alpine region. Furthermore, since most of the chironomid taxa in the Alpine chironomid-based temperature inference model also occur in other European calibration data sets and regions, our results contradict the assertion by Velle et al. (2010) that a close correlation between temperature and nutrient optima is the rule for chironomid taxa.

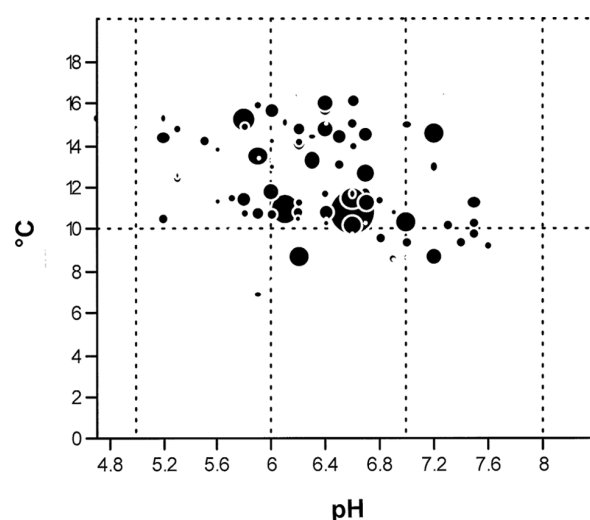
### pH

At pristine sites on acid bedrock a more common reason for unreliable chironomid-inferred temperature estimates than trophic change may be the influence of pH change. In at least two of the examples chosen by Velle et al. (2010), Giltjärnen (GIL) and Bjørnfjelltjønn (BJØ), the strong response of chironomids to pH change during the mid Holocene may have reduced the reliability of the chironomid-inferred temperature estimates. Other Holocene sites that appear to have been influenced by pH change include Holebudalen (Velle et al., 2005) and Lochnagar (Dalton et al., 2005). These pH changes appear to be driven by forest or bog development in the lake catchment and so this problem could be avoided by studying lakes which remain above (or below) the treeline throughout the Holocene or which are buffered against pH change (e.g. carbonate lakes). The influence of pH on chironomid assemblages is clearly identifiable by characteristic changes in the chironomid assemblage. Acid-tolerant chironomid assemblages often include both warm and cool stenothermic taxa, although they tend to be dominated by taxa that favour the oligotrophic conditions typical of acidified lakes. As a result, many acidophilic taxa have low temperature optima and chironomid assemblages in acidified lakes may be expected to underestimate summer air temperature. This is contrary to Velle et al. (2010) who state that these assemblages will produce unrealistically high temperature estimates. This conclusion is based on an analysis by Velle et al. (2010) of the response of the warm stenothermic *Microtendipes pedellus*-type, which is apparently acid-tolerant in cool temperatures. However, this assertion is not supported by published data (e.g. Brodin, 1986; Dalton et al., 2005; Schnell and Willassen, 1996), which suggest that this taxon is acid intolerant, or by Woodcock et al. (2005) (referred to by Velle et al., 2010) who do not discuss any species of *Microtendipes*. Furthermore, our analysis of the distribution of *Microtendipes pedellus*-type in the modern Norwegian calibration set does not show any evidence for a positive relationship between *Microtendipes pedellus*-type and pH at low temperatures (Figure 2).

Nevertheless, even in acidifying lakes, a response to temperature change may be discernable. For example, at Holebudalen, western Norway (Brooks, 2003), although the C-IT appears to underestimate summer temperature when compared to pollen-inferred estimates, the C-IT trends reflect falling summer insolation and the well-known temperature declines at around 4.6 ka and 2.7 ka BP are clearly indicated (Velle et al., 2005). Similarly, at Lochnagar, Scotland, the C-IT indicates cool phases in the mid Holocene which correlate well with independent records from elsewhere in northern Britain (Langdon et al., 2004).

### Effects of lake depth

Lake shallowing, which naturally occurred in many lakes during the Holocene, may result in overestimates of summer temperature as shallowing lakes become dominated by littoral and semi-terrestrial taxa, which tend to have high temperature optima. Conversely, lake deepening may result in increasing abundance of profundal taxa, which tend to have cold temperature optima. Such changes are usually identifiable because of characteristic assemblage changes or can be detected by the combination of multiple



**Figure 2.** Mean July air temperature and pH of lakes in the modern Norwegian calibration set in which *Microtendipes pedellus*-type occurs. The size of the circle is proportional to the abundance of *M. pedellus*-type in each lake.

proxies. For example, at Tsuolbmajavri (TSU) a shallowing of the lake in the late Holocene is thought to have contributed to the gradual rise in C-IT (Korhola et al., 2002). This problem was recognized in the original study, and otherwise the inferred trends from this site agree well with climate reconstructions from other independent proxies.

The C-IT from Toskaljavri, Finland (TOS) are lower than expected when considering terrestrial vegetation development at the site, and this may be because the lake is relatively deep (21.5 m) and dominated by profundal taxa with low temperature optima. Nevertheless, the chironomid-inferred Holocene temperature trend derived from this site (Seppä et al., 2002) agrees closely with Holocene trends in the oxygen isotopes from Greenland.

### Taxonomic resolution

Velle et al. (2010) suggest that taxonomic inconsistency, especially where this involves high taxonomic resolution, may lead to problems in quantitative and qualitative palaeoenvironmental interpretations. Unfortunately, they do not provide evidence to support this statement. We would argue that low taxonomic resolution is more likely to cause unreliable temperature estimates than high taxonomic resolution, given that low resolution reduces the specificity of environmental information that may be gleaned from an assemblage. As taxonomic resolution is increased, the performance of chironomid-based inference models improves (Brooks, 2006; Larocque, 2008), as does the reliability of palaeotemperature reconstructions (Heiri and Lotter, 2010). Jones (2008) also emphasises that to detect small-scale processes taxonomic resolution at species level is necessary. Given the evidence that increased taxonomic resolution can improve the reliability of chironomid-based temperature estimates, and the problems that have resulted from low resolution in the past, we encourage the pursuit and use of the highest taxonomic resolution possible.

### Remarks on the Scandinavian data sets

Velle et al. (2010) state that correlation between chironomid-inferred temperatures from different sites in the same climatic region should be expected if temperature has an over-riding influence and suggest this is not apparent in the Scandinavian



sites they review. However, we caution against assuming that modern correlation of year-to-year temperature variability within an area as large as Scandinavia should indicate that decadal-scale to centennial-scale temperature variability during the Holocene would have to correlate as well. In mountainous areas, such as Norway and Sweden, and at spatial scales of hundreds to thousands of kilometres, changes in climatic forcing factors during the Holocene may well have led to differential regional climatic responses. Thus, it is not surprising that some of the records presented by Velle et al. (2010) show somewhat different reconstructed temperature patterns. However, it is notable that records from sites in close vicinity of each other do largely show consistent results, certainly within the prediction errors (about 1.0°C) of the applied temperature inference models and considering the chronological uncertainties (reaching 500 years in some cases). In Iceland two closely located sites showed almost identical early-Holocene chironomid-inferred temperature histories (Caseldine et al., 2006).

## Conclusions

We agree with many of the recommendations made by Velle et al. (2010). Calibration data sets and sites for downcore records should be carefully selected, chironomid-based temperature reconstruction should be undertaken within a multiproxy framework, chironomid data should be interpreted using autoecological data, and fossil assemblages should be carefully evaluated for modern analogues and tested against random data (Telford and Birks, 2011). Most of these recommendations are already followed by many researchers employing chironomid-based temperature reconstructions. Several studies have incorporated multiple chironomid-based temperature records to generate robust regional palaeotemperature reconstructions (e.g. Axford et al. 2007; Caseldine et al. 2006; Lang et al., 2010b; Larocque and Hall, 2004). In many studies chironomid-based temperature reconstructions are similar to independent temperature reconstructions based on other proxies, such as glacial extent (e.g. Langdon et al., 2011; Larocque-Tobler et al., 2010b), oxygen isotopes (e.g. Bedford et al., 2004; Heiri and Millet, 2005), borehole palaeothermometry (Young et al., 2011), tree rings (Clegg et al., 2010) and treeline fluctuations (Heiri et al., 2004), and are supported by results from vegetation modelling (Heiri et al., 2006) and climate models (Renssen et al., 2009).

Evidence from studies over the past 20 years in Europe and North America overwhelmingly points to summer temperature as one of the dominant drivers governing the distribution and abundance of lacustrine chironomid species in those regions. Chironomids have been used at many sites to generate Lateglacial and Holocene summer air temperature estimates that are in close agreement to independent proxy-based reconstructions and instrumental data. Unlike some temperature proxies, chironomids can be analyzed at geographically diverse and widespread sites, at high temporal resolution, and used to reconstruct both decadal-scale trends in recent centuries and millennial-scale temperature trends over long timescales. Palaeoecologists would be ill-advised to dismiss this useful method, but rather should continue to refine their understanding of this proxy and use methods, such as careful site selection and model development, multisite consensus approaches, multiproxy comparisons and analogue tests, to alleviate or detect possible complications.

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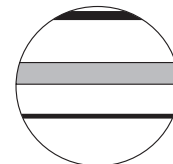
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# Inconsistent results should not be overlooked: A reply to Brooks et al. (2012)

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## Abstract

Empirical data in the form of many chironomid-based temperature reconstructions give an excellent opportunity to assess the chironomid approach to temperature reconstruction by testing its reproducibility. Brooks et al. (*The Holocene* 22(12) 2012 (this issue)) offer a critique of points discussed in Velle et al. (*The Holocene* 20 (2010) 989–1002), but fail to explain the poor reproducibility found when Holocene chironomid-based temperature reconstructions are compared. We discuss the issues raised by Brooks et al. (2012) and cite studies that demonstrate the complexity involved. We are grateful to Brooks et al. (2012) for contributing to the discussion. However, they overly rely uncritically on transfer functions and the resulting reconstructions as representatives of true patterns in nature. A major source of bias involved when chironomids are used as a palaeoenvironmental proxy is the response to confounding gradients. Many of the challenges discussed in the Forum Article, in the comment, and in the reply are also valid for other research fields within palaeoecology. The challenges should still be properly addressed in chironomid research.

## Keywords

chironomids, confounding gradients, palaeoenvironmental proxies, reconstruction validation, temperature, training-set

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## Validation of results

### *Inconsistent temperature reconstructions*

As Brooks et al. (2012) note, Velle et al. (2010a) have re-opened a 20 year old debate on biological indicators. Twenty years ago there was an active discussion about whether chironomid assemblages are reliable indicators of past temperatures. There is, however, one important difference between the situation today and 20 years ago. Now, there are empirical data in the form of many chironomid-based temperature reconstructions. So far, more than 20 Holocene chironomid-based temperature reconstructions have been published from Norway, Sweden, and Finland (Antonsson et al., 2006; Bigler et al., 2002, 2003; Heider, 2004; Heinrichs et al., 2005; Korhola et al., 2002; Larocque and Bigler, 2004; Lüder, 2007; Luoto et al., 2010; Paus et al., 2011; Seppä et al., 2002; Velle et al., 2005a, 2005b, 2010b, 2011). Many more have been published worldwide. The Velle et al. (2010a) Forum Article was written to shed light on a striking problem that empirical data and reconstructions have revealed: when Holocene temperature reconstructions from different sampling localities are compared there are many instances of strongly mismatching curves (Figure 1). We feel that many investigators have overlooked this problem and we hope that our Forum Article and ensuing discussion and research would contribute towards resolving the problem. Similarities with other proxies or multiple sites are needed to confirm results, but the results are too uncertain to assess whether discordances are real or are caused by confounding factors.

Velle et al. (2010a) show ten reconstructions and argue that these are so different that it seems unlikely they can solely be attributed to local site differences in microclimate. Brooks et al. (2012) caution against assuming that decadal-scale to centennial-scale temperature variability in Scandinavia should correlate. However, studies of the instrumental record of the last 100–250 years (Casty et al., 2007; Dobrovolny et al., 2010; Jones and Moberg, 2003; Luterbacher et al., 2004; Meier et al., 2007;

Moberg et al., 2005; Nordli et al., 2003) and of reconstructions from documentary proxy evidence during the last 500 years (Brazdil et al., 2010; Casty et al., 2005; Dobrovolny et al., 2010; Meier et al., 2007) suggest that temperatures do correlate, not only in Scandinavia, but also across Europe. Brooks et al. (2012) are rightly concerned that chronological uncertainties can obscure a comparison between sites. In a study on six Holocene chironomid-stratigraphies, Velle et al. (2005a) tested the numerical relationship among unsmoothed and smoothed inferred temperature curves. Since only two of 15 comparisons were statistically significantly positively correlated, uncertainties associated with chronologies were tested. The correlation analysis indicated no correlation, whereas by disregarding the dating model, there was series of matching temperatures events, but only when the original age–depth models were displaced by more than 1000 years (Velle et al., 2005a: figure 11). In this context, it is of little meaning to search for discordances that are, or are not, within the prediction errors of the temperature inferences, as Brooks et al. (2012) do. At many sites, the chironomid-inferred temperatures are too erratic to be climatically useful. For most sites, it is of little

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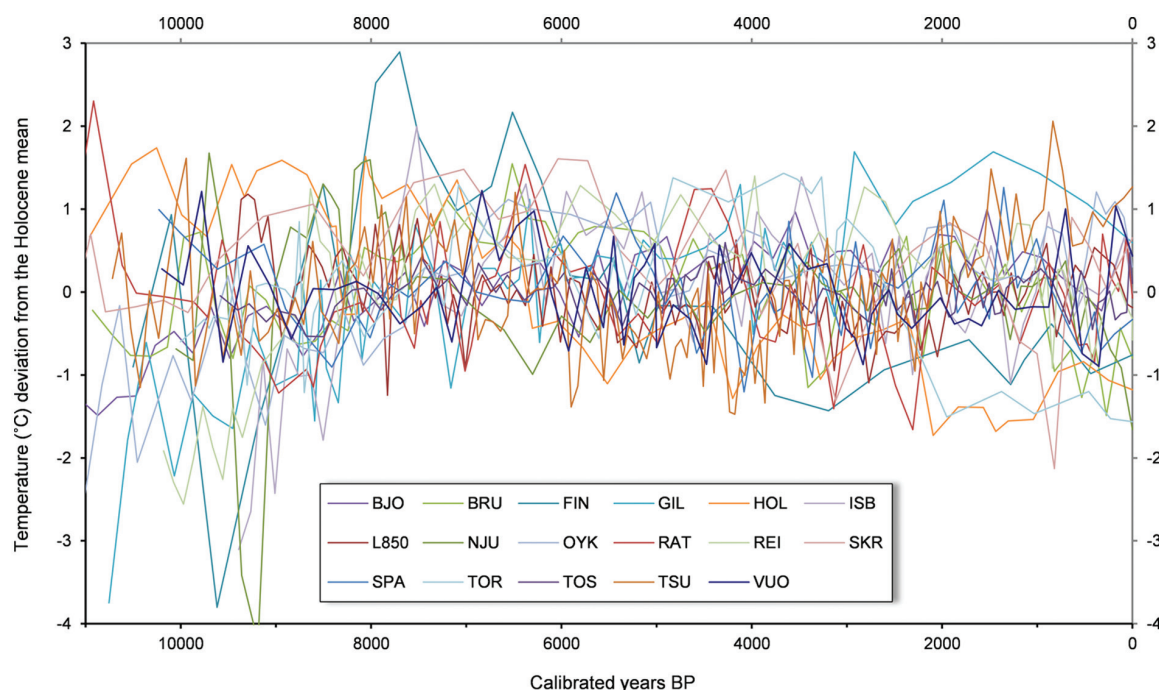
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**Figure 1.** Chironomid-inferred mean July air temperatures adjusted for glacioisostatic rebound. BJO: Bjørnfeldtjønn (Brooks, 2006); BRU: Brurskardet (Velle et al., 2010b); FIN: Finse Stasjonsdam (Velle et al., 2005a); GIL: Giltjärnen (Antonsson et al., 2006); HOL: Holebudalen (Velle et al., 2005a); ISB: Isbentjønn (Lüder, 2007); L850: Lake 850 (Larocque and Bigler, 2004); NJU: Njulla (Bigler et al., 2003); OYK: Vestre Økjamyrjønn (Velle et al., 2005a); RAT: Råtåsøen (Velle et al., 2005b); REI: Reiardalsvatnet (Lüder, 2007); SKR: Stora Kroksjön (Heider, 2004); SPA: Spåime (Hammarlund et al., 2004); TOR: Lilla Torkelsjön (Heider, 2004); TOS: Toskaljavri (Seppä et al., 2002); TSU: Tsuolbmajavri (Korhola et al., 2002); VUO: Vuoskkujävi (Bigler et al., 2002).

value to interpret temperature fluctuations that are inside the prediction errors estimated by statistical cross-validation, as many chironomid workers continue to do.

Strong differences prevail when more sites than those presented in Velle et al. (2010a) are included in the comparison (i.e. three sites from western Norway (Velle et al., 2005a), two from southern Norway (Lüder, 2007), and two from southern Sweden (Heider, 2004); Figure 1). Chironomids have produced encouraging results (Larocque et al., 2009), but there is no doubt that chironomids have also produced discouraging results Norway (Velle et al., 2005a). In all instances, quantitative proxies will only produce reliable estimates of past environmental conditions with robust errors if the assumptions of the reconstruction method are met (Birks et al., 2010). While Brooks et al. (2012) make some valuable comments, they fail to acknowledge the underlying concern of Velle et al. (2010a): Why are the chironomid-inferred Holocene temperatures from Fennoscandia so different? We have initiated a re-analysis of most chironomid data sets from Norway, Sweden, Finland, Iceland, and UK. This is a joint project, including some of the Comment authors and others, which hopefully will help to identify at what sites and at what periods the chironomid approach is reliable (e.g. Figure 2).

#### Validation with instrumental records

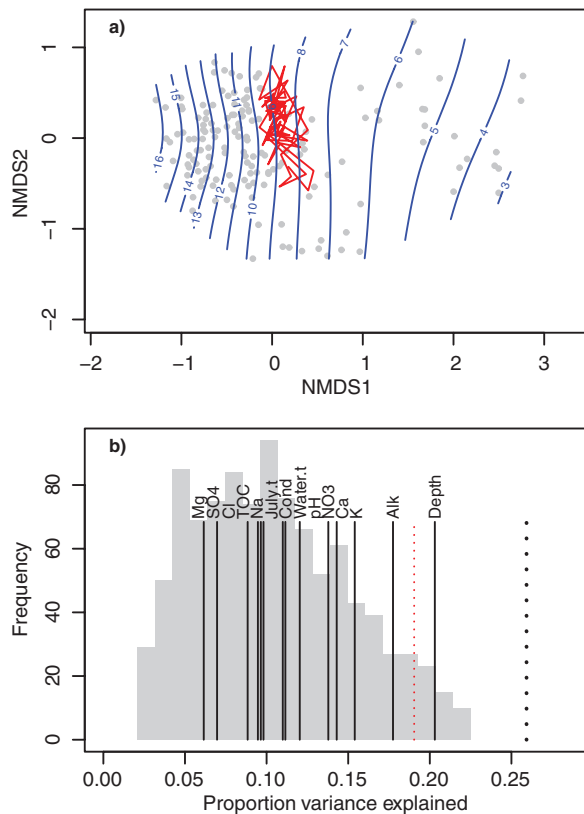
As Brooks et al. (2012) point out, chironomids have been assessed as a palaeoclimatic proxy by comparing the reconstructed temperatures with instrumental records for the last 100–150 years. This validation has given promising results, but studies that failed to find a correlation between chironomids and the instrumental temperature record should not be overlooked (e.g. Axford et al., 2009; Cameron et al., 2002; Lotter et al., 2002). In addition, it is important to consider potential confounding factors when down-core chironomids and the instrumental temperature record are

compared: (1) Any comparison and numerical correlation should be corrected for temporal auto-correlation, as there is a lack of statistical independence in the fossil record and in the instrumental record (Tian et al., 2011). The auto-correlation violates the assumptions of many statistical tests and can cause overoptimistic estimates of the correlation coefficient. A correction for auto-correlation is usually not performed in chironomid-temperature validation, but as Tian et al. (2011) show, such a correction can easily be achieved using a block bootstrap similar to *h*-block cross-validation (Burman et al., 1994). (2) A correlation during the instrumental record for the last 100–150 years does not imply that the chironomid record will provide reliable temperatures for the entire Holocene. This was very evident in Lake 850 in Sweden. Here, there was a good match between the instrumental record and inferred temperatures for the last 100 years (Larocque and Hall, 2003). However, based on inconsistencies in a Holocene multiproxy study, Larocque and Bigler (2004) concluded that temperature was not the most important factor to explain the distribution and abundance of chironomids prior to 2500 cal. yr BP.

#### Validation with independent proxies

Brooks et al. (2012) cite studies where results obtained from chironomids correspond well with the results obtained from other proxies or with independent records, such as the Greenland ice-cores. We agree that a comparison with independent records is a principal assessment of results. However, we note the following: (1) it is unclear to us why Brooks et al. (2012) assume that temperatures throughout Scandinavia should not necessarily correlate, while Scandinavian chironomid temperature reconstructions should correlate with ice-core records from Greenland. (2) We caution against the risk of circularity of argument. In their conclusions, Brooks et al. (2012) write that chironomid-based temperature reconstructions are supported by results from vegetation





**Figure 2.** (a) Non-metric multidimensional scaling (NMDS) of fossil chironomids from Råtåsøyen (red line) added passively into the NMDS space of samples in the modern Norwegian calibration data set (grey dots). The contours (blue) represent temperature change (°C) of samples in the Norwegian calibration data set (Brooks and Birks, 2001, unpublished data, 2001–2010). The fossil samples change along some unknown secondary gradient, NMDS2. (b) Proportion of variance in the Råtåsøyen fossil data explained by environmental variables in the modern calibration data set. The only statistically significant environmental variable is lake depth, suggesting that the secondary gradient found from the NMDS is lake depth. The dashed line to the far right shows the proportion explained by the first axis of a PCA, while the red dashed line shows the threshold from which the environmental variables explain more of the variance than 95% of 999 random reconstructions. For details on the method, see Telford and Birks (2011).

modelling. A correlation between inferred temperatures and vegetation modelling is not surprising given that the vegetation model they cite (Heiri et al., 2006) was driven by chironomid-inferred temperatures. Our interpretation is that Brooks et al. (2012) find the chironomid-inferred temperatures supported since the chironomid temperature-driven vegetation model produced vegetation dynamics that mimic an independent pollen record. (3) A general visual similarity with independent climate proxies should also be quantified and assessed for statistical significance (e.g. Dobrovolsky et al., 2010; figure 6). According to Bennett (2002), testable hypotheses are needed or it becomes difficult or impossible to disentangle what is based on data and what is based on opinions. (4) There are many multiproxy studies that have pointed out inconsistencies between temperatures obtained from chironomids and other proxies, or studies that have suggested temperature was not the main driver for the full or parts of the down-core chironomid distribution (Bigler et al., 2002; Dalton et al., 2005; Heinrichs et al., 2005; Heiri and Lotter, 2003; Heiri et al., 2003; Korhola et al., 2002; Larocque and Bigler, 2004; Lüder, 2007; Nyman et al., 2008; Velle et al., 2010b).

## Gradient length and response to confounding variables

### Gradient length in training-sets

We do not think that chironomids are a useful proxy for any environmental variable provided the gradient is long enough, as Brooks et al. (2012) give the impression that we do. However, based on training-set statistics, any environmental variable will appear to be reconstructable if the gradient is long enough and other gradients are short. This is demonstrated by the many environmental variables that chironomids appear to respond to in training-sets (Table 1).

Brooks et al. (2012) state that the performance statistics of chironomid-based temperature inference models exceeds by far the performance statistics of other chironomid-based models. We agree that the numerical performance of chironomid-based temperature-inference models is good (Table 1), but miss data from Brooks et al. (2012) that confirm their statement. To our knowledge it has not been tested whether temperature-inference models out-perform the numerical performance of training-sets based on other environmental variables. The coefficient of determination ( $r^2$ ) measures the strength of the relationship between observed and predicted values and will increase with gradient length, while RMSEP and bias statistics are not dependent on the range of the observed environmental gradient (Birks, 1998). Different units of measurement (e.g. chlorophyll *a* (µg/l), water depth (m) or temperature (°C)) are not comparable unless standardised. Hence, a comparison among training-sets based on dissimilar environmental variables is valid if the gradient lengths are similar and the environmental data are standardised to a comparable unitless scale.

### Relationship to temperature

Most chironomid-temperature training-sets show significant responses to temperature and to secondary variables, such as organic carbon, alkalinity, conductivity, solar radiation, magnesium, precipitation, altitude, lake depth, and lake productivity (e.g. Barley et al., 2006; Larocque et al., 2001, 2006; Lotter et al., 1997, 1998; Olander et al., 1999; Rees et al., 2008; Velle et al., 2005a). In surprisingly many training-sets designed for long temperature gradients, the response to environmental variables other than temperature overrides the response to temperature. Such variables include pH (Porinchu et al., 2009; Rees et al., 2008), loss-on-ignition (LOI) (Larocque et al., 2001; Olander et al., 1999), lake depth (Porinchu et al., 2009), total carbon (Langdon et al., 2008), or total nitrogen (Porinchu et al., 2009). Chironomids in data sets that are not designed for training-set purposes will respond most significantly to one of several environmental variables, such as tropho-dynamic status, DOC, sediment organic content, chlorophyll *a*, bottom oxygen content, lake size, location of the lake, water chemistry, or altitude (Bigler et al., 2006; Brodersen and Lindegaard, 1999; Catalan et al., 2009; Fjellheim et al., 2009; Kernan et al., 2009; Nyman et al., 2005; Real and Prat, 1992). Many of these environmental variables co-vary with temperature or with one or more of the other variables listed above.

There is a lack of understanding on the relationship between chironomids and temperature, and it seems that indirect effects of temperature can play an important role (Eggermont and Heiri, 2011). When this is the case, it is wise to interpret down-core reconstructions cautiously. All training-sets will produce results when applied down-core (Birks et al., 2010). Can chironomids provide reliable estimates for temperature change or for change along any of the other environmental variables from training-sets (Table 1) backwards in time? In principle yes, but only if the environmental variable of interest is the dominating gradient at the

**Table 1.** Examples of chironomid training-sets developed to infer diverse environmental variables.

Environmental variable	Region	$\lambda_1/\lambda_2$	Model	$r^2_{\text{jack}}$	Reference
July temperature	Sweden		WA <sub>inv</sub>	0.44	Rosén et al. (2001)
July temperature	Norway and Switzerland	1.17	WA-PLS 2	0.87	Heiri et al. (2011)
Water T	Sierra Nevada, USA	0.87	WA <sub>classical</sub>	0.73	Porinchu et al. (2002)
Water depth	Finland	0.68	PLS 2	0.70	Korhola et al. (2000)
Total phosphorus	UK	1.21	WA <sub>inv</sub>	0.60	Brooks et al. (2001)
Salinity	Tibetan plateau	0.73	WA-PLS 2	0.80	Zhang et al. (2007)
Late summer anoxia	Ontario, Canada	0.40	WA <sub>inv tol</sub>	0.56	Quinlan and Smol (2001)
Late winter anoxia	Southern Finland	0.77	WA-PLS 1	0.72	Luoto and Salonen (2010)
Stream flow/turbulence	Finland, intra-lake	0.95	WA <sub>classical</sub>	0.77	Luoto (2010)
Chlorophyll <i>a</i>	Denmark	1.38	WA <sub>inv</sub>	0.67	Brodersen and Lindegaard (1999)
Continentality	Russia and Norway	0.48	WA-PLS 2	0.73	Self et al. (2011)
Distance to littoral vegetation	Finland, intra-lake	0.77	WA <sub>classical</sub>	0.71	Luoto (2010)
pH	Tasmania	0.90	WA-PLS 1	0.74	Rees and Cwynar (2010)

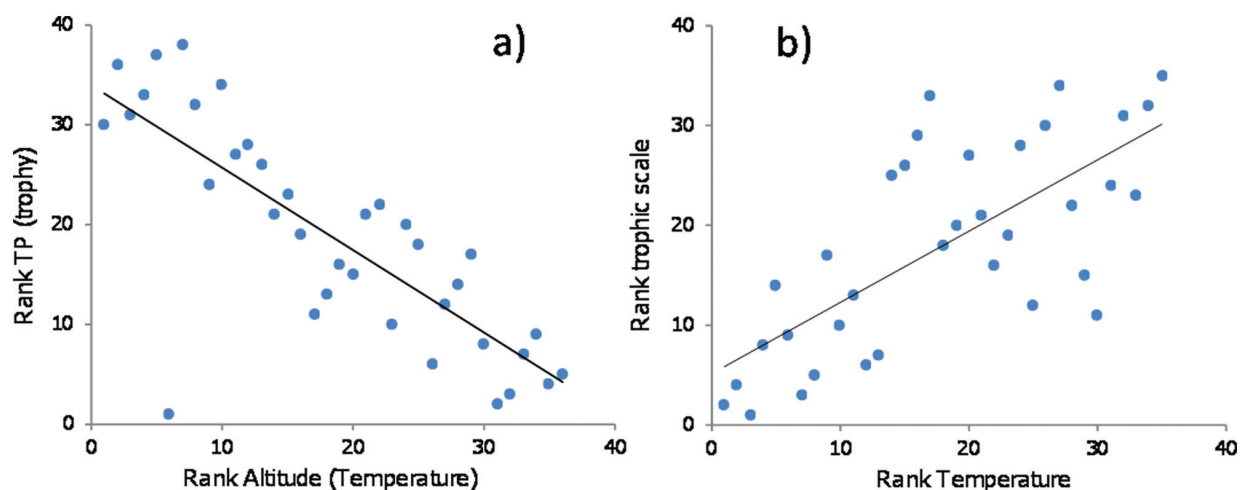
For reference on model performance, the average  $r^2_{\text{jack}}$  for 23 published chironomid–air temperature training-sets is 0.75. WA: weighted averaging; PLS: partial least squares; WA-PLS: weighted averaging partial least squares; inv: inverse deshrinking; classical: classical deshrinking; tol: tolerance downweighting. The number after WA-PLS refers to the number of WA-PLS components considered.

time of interest (Birks et al., 2010). Many chironomid researchers have been concerned about issues of confounding gradients. Brooks (2006) stressed that soil development and the resulting changes in pH, nutrients, dissolved oxygen (DO), and dissolved organic carbon (DOC) can have a greater influence than temperature on the composition of some midge assemblages. Larocque et al. (2006) suggested that it was hard to dissociate the combined effects of temperature, DOC, LOI, and depth when performing down-core temperature reconstructions. According to Langdon et al. (2008) it is a major challenge to separate the effects of temperature, LOI, and lake depth on subfossil chironomid sequences.

#### Correlation between temperature optima and trophic optima

Brooks et al. (2012) agree that taxa characteristic of warm waters are also often characteristic of eutrophic waters, and taxa characteristic of cold waters are also often characteristic of oligotrophic waters. However, based on optima in a truncated data set they argue the correlation between trophic optima and temperature is not as universal as we suggested. First, we point out

that a relationship between trophic optima and temperature optima should not be expected for all taxa in a data set since the optima for rare taxa are inevitably poorly defined. Only common taxa are relevant and performing a more robust correlation with outliers removed would drastically improve the correlation (see Brooks et al., 2012: figure 1). Second and most important, concerning the relationship between temperature and trophic status (nutrients, chlorophyll, Secchi-depth, DOC), it is not a matter of our opinion, or of transfer-function performance and statistical prediction errors, but a question of well-described ecological and limnological phenomena in nature (Brodersen and Anderson, 2002; Brodersen and Lindegaard, 1999; Brooks et al., 2001; Brundin, 1949, 1956; Lenz, 1925; Lotter et al., 1997; Sæther, 1979; Thienemann, 1928, 1954; Walker et al., 1991; Wiederholm and Erikson, 1979). Several examples of significant positive correlations between temperature and trophic variables are reviewed by Eggermont and Heiri (2011). These relationships are responsible for the evolutionary outcome that warm-water taxa, with a higher metabolic activity, are also adapted to productive lakes (and streams, see Velle et al., 2010a: figure 6) rich in available food for growth. This should not be



**Figure 3.** (a) Rank correlation between chironomid altitudinal optima in the Swiss Alps (Lotter et al., 1997: figure 6) and trophic optima (Lotter et al., 1998: figure 6). The correlation between temperature and total phosphorus (TP) in the Swiss Alps is  $r = 0.57$ ,  $p < 0.01$  in the non-truncated data set. (b) Rank correlation between chironomid temperature optima for northwest North America (Barley et al., 2006) and trophic rank (Sæther, 1979). Average rank numbers for trophyl were used where adjustment to subfossil genus/type was necessary.

surprising and can be shown for many data sets (Figure 3a). Comparison of independent data will, in many cases, give the same rather convincing result (Figure 3b). However, even if we could succeed in selecting lakes to produce the ideal training-set with no correlations among the variables, as Brooks et al. (2012) attempt, nature will still expose the same relationship based on all the thousands of lakes that were not sampled for the optimised data set. Modern data sets aimed and designed for high precision and accuracy for single variables may perform well for that purpose, but will not necessarily reflect the true complexity in nature in space and time because they are optimised for a single variable at one point in time. If this ecological knowledge is acknowledged, it can be used positively to understand palaeoecological records and contradictions in inferred environmental variables.

### *Trophic optima in a Greenland data set*

Velle et al. (2010a) cite a study from West Greenland where Brodersen and Anderson (2002) demonstrate there is a strong correlation between temperature optima and trophic optima. Brooks et al. (2012) argue that the West Greenland data set maximises the statistical impact of lake catchment characteristics (nutrients) and minimises the impact of temperature. If Brooks et al. (2012) see this as a problem, we point out that such a sampling strategy with single environmental gradients maximised is common in chironomid temperature training-sets and other proxy-based training-sets (e.g. Brooks and Birks, 2001). Brodersen and Anderson (2002) realised that the nutrient gradient in the Greenland data was long and that temperature significantly explained 20% of the variation in the chironomid data. However, instead of publishing a seemingly good temperature transfer function, they attempted to interpret ecologically the multivariate complexity in their data set. Theoretically, Brodersen and Anderson (2002) could have maximised the temperature gradient simply by including an artificial climate gradient uphill. This would have been a classic example of a data set that would have obscured the strong local influence of catchment characteristics, and have ignored the true limnological processes that probably also occurred in the lakes (down-core) over the Holocene in that region.

### *Trophic influence down-core*

Brooks et al. (2012) provide examples of sites where trophic influence is thought not to obscure the response of chironomids to climate change during the early Holocene, and argue that trophic influence is therefore not a problem. We agree that sites with small confounding gradients are ideal candidates for quantitative palaeoecology (see Velle et al., 2010a: figure 5). However, it is important to be cautious with samples from the early Holocene and from sites formed in recent deglaciations given (1) the relationship between chironomid temperature optima and trophic optima (Figure 3) (Brodersen and Anderson, 2002; Velle et al., 2010a), and (2) that leaching and lake-catchment nutrient-ontogeny is a natural process following deglaciation (Boyle, 2007; Engstrom and Fritz, 2006; Engstrom et al., 2000; Norton et al., 2011; Reuss et al., 2010; Saros et al., 2010). A response of chironomids to the input of phosphorous in mineral colloids from glaciers was described more than 50 years ago (Brundin, 1956, 1958). Of the ten sites presented by Velle et al. (2010a), multiproxy studies indicate that four of the chironomid-based temperature inferences, and not two as stated by Brooks et al. (2012), could be obscured by an early-Holocene increase in productivity (SPA: Hammarlund et al., 2004; L850: Larocque and Bigler, 2004; RAT: Velle et al., 2005b; BRU: Velle et al., 2010b). Furthermore, an increase in rainfall may result in enhanced in-wash of nutrients into water bodies (Chang et al., 2001; Kundzewicz et al.,

2007). If this happened in the past, the chironomid-inferred temperatures could accordingly be overestimated. A response to nutrient-input was illustrated in a study on experimental fertilization in Alaska. During the six study years, the dominating chironomid genus in the fertilised side of the lake changed from *Heterotrissocladius* to *Phaenopsectra* (Hershey, 1992). There were no corresponding changes in the test side of the lake. *Phaenopsectra* has higher temperature optima than *Heterotrissocladius* (Eggermont and Heiri, 2011), and any temperature inference at this site would accordingly be overestimated.

### *Down-core influence of human impact, pH, and depth*

Brooks et al. (2012) recognise that human impact can influence the temperature reconstructions, but that the influence from humans can be discerned and distinguished from climate responses in chironomid records. We agree that potential human impact can be detected at sites where background information exists on the timing and extent of human influence and from multiproxy studies, such as those cited in Brooks et al. (2012). For many sites, however, information on human impact or impact along other confounding gradients is missing. At such sites, the confounding impact would potentially be interpreted as a temperature signal. Because of biases in the inferred temperatures associated with human impact in the Alpine region, Heiri and Lotter (2005) recommended a multiproxy approach to palaeoenvironmental reconstruction. According to Heiri and Lotter (2005), it is clearly essential to keep a close control on changes in local human activity during the late Holocene, even at high elevations and in remote mountain lakes.

When it comes to the influence of lake depth and pH, Brooks et al. (2012) agree that there is a possible problem of confounding gradients that can cause unreliable chironomid-inferred temperature estimates.

## **Training-sets as representatives of true pattern in nature**

The complexity and multidimensionality in chironomid responses to environmental variables in modern data sets and in down-core sequences, as demonstrated above and in Velle et al. (2010a), suggest that transfer functions should not be interpreted as representatives of true ecological patterns in nature. Training-sets can help build ecological hypothesis, but should be seen as empirical models that mimic a small fraction of the biological response mechanisms. It is important to separate responses in static and optimised training-sets in space, from responses along gradual changes within single lakes in time. As an example, Axford et al. (2009) found that some taxa appeared to exhibit different temperature preferences in a core from Iceland and in the Iceland calibration data set. We concur with Huntley (2012), who cautions against using biological proxies to reconstruct variables in isolation since most organisms respond concurrently to several variables. A strong implication is that chironomids can be used as a proxy for combinations of variables that often occur together, such as tropho-dynamic status sensu Catalan et al. (2009). Tropho-dynamic status is a combination of variables, including productivity (DOC, total phosphorus), thermal conditions, and littoral habitat features.

## **Concluding remarks**

All scientific results should be subject to rigorous testing. This is not straightforward when we use proxies to infer some unknown environmental variable of the past (Birks et al., 2010). In this context, we do not see how Brooks et al. (2012) have provided



evidence that Holocene chironomid-based temperature reconstructions are reliable, as they state. Similarities with other proxies or multiple sites are needed to confirm results and the similarities should be tested for statistical significance. We do not believe these challenges involved are unique to chironomids as a palaeoenvironmental proxy (e.g. Huntley, 2012). This was highlighted in the title of the Velle et al. Forum Article as ‘lessons for palaeoecology’. As Brooks et al. (2012) noted ‘... the requirement for multiproxy and multisite studies to separate signal from noise is equally true for other climate proxies, including lacustrine proxies and proxies from other archives such as tree rings, peats, speleothems and ice cores’. These are general challenges that we hope experts in their respective fields of palaeoenvironmental sciences will take seriously. Recognising that other sciences have challenges is no excuse not to take these challenges seriously in chironomid research. We do not wish palaeoecologists to dismiss their biological proxies, but rather to use more resources to understand the underlying ecological processes and to refine their palaeoecological methods. Then, the resulting palaeoenvironmental inferences will hopefully be more robust.

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