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We the undersigned declare that this manuscript is original, has not been published before and is not currently being considered for publication elsewhere.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We understand that the Corresponding Author is the sole contact for the Editorial process. He/she is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs.

Signed by all authors as follows:

A handwritten signature in blue ink, appearing to read 'Scott A. Elias', written over a light blue rectangular background.

Professor Scott A. Elias

A handwritten signature in blue ink, appearing to read 'Ian P. Matthews', written over a light blue rectangular background.

Dr. Ian P. Matthews

31 May 2013

Dr. Norm Catto, Editor-in-chief,

Quaternary International

Dear Norm,

Ian Matthews and I are pleased to submit our manuscript, entitled '**Late glacial temperature reconstructions for the British Isles: a comparison of reconstructions based on aquatic and terrestrial beetle assemblages**,' for inclusion in the issue of *Quaternary International* dedicated to the life and career of Russell Coope. This manuscript represents our own, original work, and has not been submitted for publication elsewhere. We feel it makes a significant contribution to a topic of some controversy in paleoenvironmental research: the noted discrepancy between mean summer temperature estimates based on beetle assemblages vs those made from chironomid assemblages. This was a topic close to Russell's heart.

Best regards,

A handwritten signature in blue ink, appearing to read 'Scott Elias', is positioned above the printed name.

Scott Elias

**A comparison of reconstructions based on aquatic and terrestrial beetle
assemblages: Late glacial-Early Holocene temperature reconstructions for the
British Isles**

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Abstract:

This paper presents the results of a study of MCR estimates of mean July temperature (TMAX) during the late glacial interval from four British sites, comparing estimates based on terrestrial and aquatic species. We have generated precise age models for three of these datasets, and have found that in most cases the terrestrial-based estimates agree with the aquatic-based estimates. The temperatures across the late glacial are consistent and warm in the early interstadial, however, differences exist in the later interstadial where Llanilid seems to be slightly warmer than either St Bees or Gransmoor. The small-scale discrepancies between aquatic and terrestrial beetle MCR temperature estimates that were found from these sites appear to occur during the transition into the late glacial interstadial, during the transition into the Younger Dryas cooling, and during the Younger Dryas interval. We tentatively attribute these discrepancies to the presence of meltwater from snowbanks surrounding the study sites during the stated intervals, and suggest that MCR studies of late glacial beetle assemblages from northwest Europe should adopt the protocol of generating separate aquatic and terrestrial estimates, for comparative purposes.

1. Introduction

The Mutual Climatic Range method of paleoclimatic reconstruction was developed for use with insect fossil assemblages by Atkinson et al. (1987). Since then, fossil beetle assemblages from more than 90 British sites have undergone MCR paleotemperature reconstructions (Elias, 2010). The results of these analyses have generally demonstrated that Late Pleistocene temperatures in Britain often oscillated rapidly and on large scales. The pace and amplitude of these changes often contradicted the reconstructions of past climate based on other terrestrial proxies, such as pollen, but the results of beetle MCR studies, notably during the late glacial

interval, were amply supported by the oxygen isotope records from Greenland ice cores since the 1990s (Lowe et al., 1995).

The late glacial interval has received intensive study in Britain and elsewhere, because it comprises a series of rapid, large scale climatic oscillations in a relatively brief time span at the end of the last glaciation. The late Russell Coope devoted a great deal of effort to working out the timing and intensity of these climatic changes in Britain, and he developed a regional model of climate change to compare with other regions of northwest Europe (Coope and Lemdahl, 1995) that has prompted much discussion in amongst paleoclimate researchers in the past 20 years.

In the past few years, paleotemperature reconstructions based on fossil chironomid (midge) assemblages have become widely popular in many parts of the world, including Britain (Brooks and Birks, 2000; Barley et al., 2006; Heiri et al., 2007). There have only been a few attempts to directly compare late glacial temperature reconstructions based on chironomids and beetles. For instance, Brooks and Birks (2000) reconstructed late glacial mean July air temperatures from Whitrig Bog in southeast Scotland. They noted that while the broad-scale trends of their chironomid-inferred reconstruction were similar to beetle-inferred best-estimate TMAX (mean temperature of the warmest month) reconstructions for Britain, the latter are about 2-4°C higher than the correlative chironomid estimates from Whitrig, for the early part of the interstadial. When the two data sets are plotted on the same temperature and time scales, it becomes readily apparent that the chironomid TMAX reconstruction is substantially cooler than the British beetle TMAX reconstruction throughout the late glacial interval (Fig. 1). This result raises several research questions that will be addressed in this paper:

- 1) Do aquatic insect assemblages from the British late glacial interval consistently reflect colder temperatures than terrestrial insects?
- 2) If so, does this trend cease in the early Holocene?

One logical explanation for the disparity between the thermal 'signal' from aquatic and terrestrial insects during the late glacial might be that lakes and ponds which were in relatively close proximity to sources of glacial meltwater, or derived there water primarily from seasonal snowmelt might have supported relatively cold-adapted aquatic faunas during the late glacial, even though regional air temperatures were considerably warmer. If this were the case, then we would expect to see any disparity between aquatic- and terrestrially-derived insect palaeotemperature reconstructions come to an end when regional ice cover disappeared in the early Holocene. Alternatively, if glacial meltwater lakes were sufficiently large, they may well have chilled the air for distances up to several tens of kilometres on the surrounding landscape. This phenomenon was noted by one of us (SE) in a study of late glacial beetle assemblages from the Great Lakes region of eastern North America (Elias et al., 1996). Sites that were in proximity to large lakes being fed by glacial meltwater yielded both aquatic and terrestrial beetle assemblages reflecting mean summer temperatures (TMAX) that were 3-5°C colder than other sites in the region which were distant from these lakes. Indeed the Norwegian chironomid temperature calibration data of 111 lakes notes 2 outliers where the calibration model predicted temperatures to be much higher than were actually observed. In these modern samples it was possible to exclude these 2 sites which had water primarily derived from glacial sources (Brooks and Birks, 2001). These factors are less well defined for palaeolake systems and it is possible that temperatures in large proglacial lakes were influenced by meltwater fluxes, and shallow small lakes influenced by seasonal snow melt. In

these cases the relationship between summer air temperature and water temperatures may be questionable as suggested for Loch Ashik during the late Younger Dryas period (Brooks et al., 2012).

2. Regional Setting

The four study sites were all in close proximity to margins of Devensian ice at the end of the last glaciation (Figure 2). All of the deposits sampled from these sites for insect and other fossil assemblages represent in-filled kettle holes that formed as blocks of stagnant ice melted *in situ*, near the retreating margins of the Devensian ice sheet.

Kettle holes are ephemeral features on recently deglaciated landscapes, generally filling in with sediments over intervals from a few centuries to a few thousand years.

The sites were chosen for this study because they met three criteria: (1) They yielded abundant, well-preserved insect fossil assemblages, (2) the assemblages span the late glacial interval, and (3) the water feeding the kettle hole ponds would have been predominantly melt-water, at least for the first few decades to centuries after their creation, and it is likely they were strongly influenced by seasonal snow melt during the Younger Dryas.

2.1 St. Bees, Cumbria

The kettle hole exposed at a coastal bluff near St. Bees yielded a 4.5-m sequence of organic-rich sediments, studied by Coope and Joachim (1980). The basal radiocarbon date of $12,560 \pm 170$ yr BP on woody macrofossils indicates that the pond formed about 14,900 years ago. The authors rejected a basal radiocarbon date of $13,290 \pm 310$ from the same sampling horizon, as it was based on bulk sediments that may have been contaminated by weathered limestone at the site. The youngest age on woody macrofossils comes from a sample just below a clay layer that capped the kettle hole deposit. This sample yielded an age of $11,150 + 96$ yr BP, indicating that the pond

filled in about 13,000 years ago. These dates plus those listed in Walker (2001) were remodelled here (see below). However, subsequent calibration of radiocarbon ages from a sample 55 cm below this clay layer yielded an age of $12,414 \pm 175$ cal yr BP, so the macrofossils from just below the clay layer must be at least several centuries younger than this.

2.2 Gransmoor, East Yorkshire

This kettle hole is part of kettle and kame topography that formed adjacent to the Late Devensian ice sheet. The 2.35 m-deep sequence of organic-rich sediments was deposited over several metres of glaciofluvial deposits (Walker et al., 1993) in a working sand and gravel pit. Peat from a depth of 195 cm in the profile yielded a humic carbon date of $12,845 \pm 45$ yr BP. The organic sequence was originally thought to span about 4000 years. Our calibrated radiocarbon age model indicates that the upper 235 cm of the sequence accumulated from about 14,600 to 11,850 yr BP. There are eleven samples below the 235-cm horizon from a separate monolith (B) that remain undated. The youngest of these samples is greater than 14,600 cal yr BP.

2.3 Glanllynau, North Wales

The late glacial deposits at Glanllynau are much like those from Gransmoor, representing the infillings of a kettle hole in a kettle and kame topographic setting, near the modern coast on the south side of the Llyn Peninsula. The exposure occurred below a shallow cliff backing the foreshore (Coope and Brophy, 1972). The basal date for the organic deposits was $14,470 \pm 300$ yr BP. The organic sequence is thought to span about 3000 years, though there are not sufficient radiocarbon ages available from the sequence to allow an age calibration model to be created.

2.4 Llanilid, South Wales

The late glacial deposits at Llanilid were exposed in an open cast coal pit, and represent about 1.8 m of organic deposits that formed in a kettle hole (Walker et al., 2003). These sediments overlie several metres of till, glaciofluvial and glaciolacustrine deposits. The coal mining operation destroyed the exposure shortly after sampling. A basal radiocarbon date on the humic fraction was $13,200 \pm 75$ yr BP. Our age calibration model indicates that the organic deposits from the site range in age from about 14,300 to 10,500 cal yr BP.

3. Materials and Methods

As discussed above, direct comparison between chironomid and beetle temperature reconstructions has thus far only been possible from one site in Britain. However, several British late glacial fossil sites contained sufficiently large numbers of both aquatic and terrestrial beetles to allow independent palaeotemperature reconstructions to be made on both sets of insects, following the Mutual Climatic Range (MCR) method described by Atkinson et al. (1987). In this study, we estimated only the average temperature of the warmest month of the year (TMAX), as there would seem to be little difference between meltwater-fed lake temperatures and other lake temperatures during winter, when air temperatures dropped at or below freezing. Thus we used the MCR method to determine the range of temperatures within which the actual mean monthly temperature for the warmest month is most likely to have fallen, based on the overlaps of the climate envelopes of the species in each assemblage. Four British late glacial sites contained sufficient numbers of both aquatic and terrestrial beetle faunas to allow these comparisons to be made for most of the late glacial interval (Tables 1 and 2). A total of 234 species in 17 families of beetles were used in the MCR reconstructions.

Using the MCR facility in the BUGS CEP database (Buckland and Buckland, 2006), we performed separate MCR reconstructions for the aquatic and terrestrial species of predators and scavengers in each of the fossil beetle assemblages from the four sites. The mutual climatic ranges, expressed as vertical bars, were then plotted (Figures 4-6) using different colour schemes: black for aquatic taxa and red for terrestrial taxa. In order to assess the temporal consistency of any observed changes between these sequences, new age models were defined for Llanilid and Gransmoor, while an age model was constructed for the late glacial interstadial interval from St Bees for the first time. Although Bayesian age models have previously been generated for Llanilid and Gransmoor, these were based on relatively simplistic modelling and the IntCal98 calibration data (Blockley et al., 2004). Here we made use of a more sophisticated model construct and outlier detection. All age models were constructed in OxCal v4.2 (Bronk Ramsay, 2009a) utilising the IntCal09 calibration curve (Reimer et al., 2009). Depositional models based on a Poisson depositional principle were constructed according to Bronk Ramsay (2008) and outlier detection was specified using the 'General' model of Bronk Ramsay (2009b). However, due to the large number of outliers for each of the three sequences, OxCal could not resolve a final model and some degree of pre-modelling data filtering was deemed necessary. The data filtering used all available stratigraphic information and followed the criteria established by Blockley et al., (2004). It should be noted that, due to the differences in the calibration curve and the differing model construct from that available to Blockley et al., (2004), dates previously accepted using these criteria are now rejected and *vice versa*. This approach has generated robust age models with total chronological uncertainties of ca. 200 years throughout much of the late glacial interstadial period with larger uncertainties in the early Interstadial and early Holocene.

All of the beetles labelled as terrestrial in Table 2 live their entire lives (i.e., as larvae, pupae and adults) on land. So all life stages must cope with terrestrial temperatures, albeit most beetles in temperate and cold climates overwinter in some environment that is protected from winter air temperatures. This is done in all life stages. Some beetles overwinter in the egg stage, with the eggs laid under leaf litter, in the soil, beneath the bark of trees, etc. Some beetles overwinter as larvae or pupae in similar sheltered environments. A few species, notably arctic beetles, may overwinter as adults. These likewise seek shelter beneath snowpack, in the soil, beneath rocks, in clumps of vegetation, etc. (Danks, 1981). In contrast to this, the beetle species listed as aquatic in Table 2 spend their entire lives in the water. The only exception to this is that some aquatic beetles lay their eggs on the emergent parts of aquatic plants. However, nearly all aquatic beetles spend the winter in the water, as eggs, larvae, pupae or adults. This ensures that they are not exposed to winter air temperatures.

3. Results

The fossil beetle records from the four British sites extend back in time to about 15,000 cal yr. All of the records extend through much of the late glacial interval. Many of the earliest late glacial assemblages contained insufficient numbers of stenothermic aquatic species to yield narrowly constrained TMAX estimates based on aquatic taxa alone. Site-specific results are as follows:

3.1 St Bees (Figure 3)

This site yielded 27 faunal assemblages, and of these, all but two yielded terrestrial fauna MCR TMAX estimates that overlap with the aquatic beetle TMAX estimates. In 24 of the assemblages the terrestrial component of the fauna yielded more tightly constrained TMAX estimates than the aquatic component.

3.2 Gransmoor (Figure 4)

The Gransmoor faunal sequence included 32 assemblages for which both terrestrial and aquatic MCR estimates of TMAX could be made. Seven of these assemblages yielded terrestrial TMAX estimates that failed to overlap with the aquatic TMAX estimates. In the older part of the sequence (samples >15,000 cal yr BP), a series of three assemblages (B10-B12) yielded aquatic TMAX estimates that ranged from about 4.5 to 14.5°C, while the terrestrial TMAX estimates ranged from 15.5-18.5°C. However, in the subsequent sample (B8) the situation was reversed, so that the terrestrial TMAX estimate was 12-13°C, while the aquatic estimate was 13-14°C. Higher up in the sequence, the samples from 125 and 140 cm depths (ca. 12,400-12,375 cal yr BP) both yielded terrestrial TMAX estimates of 9-11.5 °C and the aquatic TMAX estimates were 12-14.5°C. The same pattern of estimates was repeated for the sample from 95 cm (ca. 11,950 ± 95 cal yr BP). For all the remaining assemblages examined in this study, there is no separation between the terrestrial and aquatic MCR estimates at Gransmoor. In 11 out of the 32 assemblages, the terrestrial MCR estimates are more tightly constrained than the aquatic estimates, but in ten instances the situation is reversed.

3.3 Glanllynau (Figure 5)

Ten of the eleven fossil beetle assemblages from this site yielded terrestrial fauna MCR TMAX estimates that overlap with the aquatic beetle TMAX estimates. In all cases, the terrestrial-based estimates are more narrowly constrained than the aquatic-based estimates. In only one case did the two sets of MCR estimates fail to overlap: for sample from the -25 cm horizon. In that case, the terrestrial TMAX estimate was 14-16°C, while the aquatic TMAX estimate was 7-14°C. The age of this sample remains unknown, but it was certainly >15,500 cal yr BP.

3.4 Llanilid (Figure 6)

The Llanilid site had 18 faunal assemblages for which both aquatic and terrestrial MCR estimates of TMAX could be obtained. Of these, all but one assemblage had aquatic and terrestrial estimates that overlapped. The one exception was sample N ($12,975 \pm 63$ cal yr BP), for which the aquatic TMAX estimate was 12-13°C and the terrestrial estimates was 13-14°C. In five cases, the terrestrial estimate was more tightly constrained than the aquatic, and in one case the aquatic estimate was the more tightly constrained.

4. Discussion

In general, the MCR TMAX estimates based on terrestrial species are more tightly constrained than those based on aquatic species. In spite of the sites being kettle-hole ponds, the water beetles that inhabited the ponds generally had more cosmopolitan modern distributions than the terrestrial beetles that lived along the edges of the kettle holes. Nevertheless, there were very few instances of disagreement between the two sets of estimates. All told, 11 out of 88, or 12.5% of the faunal assemblages showed some level of disagreement between aquatic- and terrestrial-based estimates of TMAX. Of these 11 sets of discrepancies, six pairs of aquatic- and terrestrial-based estimates differed by only 1°C, one differed by 2°C, and four pairs had contiguous estimates, i.e., the upper limit of one estimate matched the lower limit of the other. These results tend to confirm the concept that aquatic insects should be considered reliable proxies for regional air temperature regimes, in spite of the fact that they are not regularly exposed to air temperatures. The idea behind this supposition is that lakes and ponds are developed and maintained only within certain climates, so their insect faunas indirectly reflect those climates (Elias, 2010). Williams (1988) compared paleoclimate reconstructions from fossil caddisfly (aquatic larvae) and

terrestrial beetle assemblages the Great Lakes region of North America, and concluded that the two groups respond nearly identically to climate change. Statistical analyses of data on the distribution and abundance of chironomid taxa across long climatic gradients in both North America and Europe repeatedly demonstrated that summer air and water temperatures were highly correlated with midge distributions, and summer climate is now recognized as potentially the single most important variable regulating midge distributions (Walker, 2007).

The issue of the comparability between coleopteran and chironomids in the reconstruction of past air temperatures leads us back to the two research questions posed in the introduction: Do aquatic insect assemblages from the British late glacial interval consistently reflect colder temperatures than terrestrial insects? If so, does this trend cease in the early Holocene? Based on the comparative MCR estimates presented here, the answer to the first question appears to be 'No.' In fact, there are no consistent differences between the aquatic and terrestrial MCR estimates. At Llanilid, the single assemblage that yielded different temperatures estimates had a warmer TMAX estimate from the terrestrial fauna than from the aquatic fauna. At St Bees, one assemblage yielded a warmer aquatic TMAX estimate, and one marginally warmer terrestrial estimate. The Glanllynau faunas yielded one assemblage in which the terrestrial estimate was marginally warmer than the aquatic estimate. The Gransmoor faunal assemblages included three of the early (undated) assemblages that yielded warmer terrestrial estimates, and one assemblage that yielded a marginally warmer aquatic estimate. Three assemblages from the Younger Dryas interval yielded warmer terrestrial estimates than aquatic.

On the other hand, there are some noticeable trends in the discrepancies between aquatic and terrestrial beetle MCR estimates from these four sites, even if they are not

strong differences. As shown in Table 3, the slight disagreements between the two sets of data all occur during transitions into the late glacial interstadial (i.e., from about 16,200 to 15,600 cal yr BP), or during the transition into the Younger Dryas, and the during the Younger Dryas interval, itself (13,000-11,900 yr BP). Each of these discrepancies show up at multiple sites, during the earlier transitional period at both Gransmoor and Glanllynau, and during the Younger Dryas at Llanilid, St Bees and Gransmoor. We hypothesize that the timing of these discrepancies is linked with meltwater entering these ponds – especially the input of meltwater from local snowbanks around the edges of the ponds.

Can this interpretation of events help unravel the discrepancy between the colder chironomid-based late glacial temperature reconstructions from Whitrig Bog and the warmer beetle-based reconstructions from the British Isles? The answer remains unknown, but may ultimately be found in the local environmental conditions at the site, the statistical measures used for the reconstruction of air temperatures, or differences in seasonality leading a relative shift in the statistically important variables for insect survival. Brooks et al. (2012) noted that their chironomid assemblages from the Younger Dryas interval have a poor fit-to-temperature, which suggests that ‘air temperature may not have been the main influence on chironomid distribution and abundance at that time.’ They also pointed out that ‘increased winter precipitation may also have resulted in the expansion of long-lasting snow beds in the catchment of Loch Ashik resulting in cold melt-water entering the lake.’ These conclusions agree with our interpretation of the reason for the discrepancies between aquatic and terrestrial beetle MCR reconstructions during the Younger Dryas at Llanilid and St Bees.

As has been noted in previous studies (Atkinson et al., 1987; Elias et al., 1996), MCR reconstructions of TMAX tend to overestimate temperatures in the temperature range from 5-12°C, based on comparisons between predicted and observed modern temperatures for a series of localities across Eurasia and North America. This is one of the reasons that linear regression models were developed: to compensate for these overestimations of very low summer temperatures. For northwest Europe, the regression equation is:

$$\text{TMAX (calibrated)} = (\text{mean predicted TMAX} - 3.88) \times 1.26$$

Therefore, a 'raw' TMAX estimate of 10°C would yield a calibrated estimate of 7.7°C, and a 'raw' estimate of 15°C would yield a calibrated estimate of 14°C. The use of linear regressions to calibrate MCR estimates has more recently been abandoned (Blockley et al., 2006), because it has been demonstrated that some beetle distributions in climate space are not normally distributed. However, the original comparisons between predicted and observed modern temperatures estimated from beetle assemblages do show this systematic difference, i.e., overestimation of cold temperatures, so this may be one of the reasons why beetle-estimated TMAX values for the colder intervals between 16,000 and 11,000 cal yr BP are warmer than the chironomid-based estimates.

What is clearly needed are more studies where both beetle and midge fossil assemblages are studied in tandem. Although such directly comparable studies have yet to be published, there is nevertheless generally good agreement between regional chironomid and beetle temperature reconstructions.

Watson et al. (2010) analysed a late glacial fossil chironomid sequence from Lough Nadourcan in Ireland, and found that the pattern of chironomid-inferred temperature change is similar to the beetle-derived temperature reconstructions for

northern Europe by Coope et al. (1998), as well as the chironomid-inferred temperature curves from Hawes Water, northwestern England (Bedford et al., 2004), and Whitrig Bog, southern Scotland (Brooks and Birks, 2000). However, they noted that the Whitrig Bog temperature reconstructions were based on an earlier 109-lake training set (Brooks and Birks, 2000b). This may be one reason why the Whitrig Bog interpretation of late glacial temperatures was colder than most others. However, the peaks of interstadial warmth noted in the British late glacial beetle assemblages appear to be muted in the Lough Nadourcan midge record. The latter shows TMAX values remaining at or below modern levels throughout the interval of 15,000-11,000 cal yr BP, whereas the former show TMAX values possibly greater than modern from 15,000-13,900 at Llanilid, Gransmoor and St Bees, and warmer than modern again from about 13,500-13,100 cal yr BP at Llanilid (Figure 7). These results are broadly in line with $\delta^{18}\text{O}$ results from the NGRIP ice core in Greenland, in which $\delta^{18}\text{O}$ values are between -40 and -35 from 14,700 to 14,000 cal yr BP, and again from 13,900-13,300 cal yr BP.

We recommend that in future, beetle MCR reconstructions for the late glacial interval in Britain and elsewhere in northwest Europe are done so that reconstructions are based both on aquatic species and on terrestrial species, facilitating comparisons.

Conclusions

Our study has made the following findings:

1. We have demonstrated consistency between terrestrial and aquatic records
2. We have generated precise age models for three Lateglacial beetle datasets
3. Except in two intervals (see points 7 and 8), these lakes appear to be unresponsive to meltwater or seasonal snowmelt and this may relate to their size which is neither too large nor too small.

4. If the same exercise is carried out at Croftamie where a lake is known to be fed by glacial meltwater, still no significant differences are observed and this most probably relates to the shallow water depth at these sites.
5. The temperatures across the late glacial are consistent and warm in the early interstadial (figure 7) however, differences exist in the later interstadial where Llanilid seems to be slightly warmer than either St Bees or Gransmoor.
6. All sites record a brief increase in temperature around 13.2-13 ka, before temperatures declined into the Younger Dryas.
7. The small-scale discrepancies between aquatic and terrestrial beetle MCR temperature estimates from these sites appear to occur during the transition into the late glacial interstadial, during the transition into the Younger Dryas cooling, or during the Younger Dryas interval.
8. We tentatively attribute these discrepancies to the presence of meltwater from snowbanks surrounding the study sites during the stated intervals.

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Table 1. Sample information for the study sites

Site	Age range of samples (cal yr BP X 1000)	Number of samples in MCR	Sediment volume per sample	Number of species used in MCR	References
St. Bees, Cumbria	14.8-11.2	27	5 liters	51	Coope & Joachim, 1979
Gransmoor, Yorkshire	Ca. 15.5-11.7	32	2 liters	137	Walker et al., 1993
Glanllynau, Gwynedd	Ca. 16.5-13.5	11	5 liters	117	Coope & Brophy, 1972
Llanilid, Glamorgan	14.7-11.3	16	2 liters	64	Walker et al., 2003

Table 2. Taxonomic list of beetle species from the four study sites, showing their ecology (order of families and genera follows Duff, 2012)

Species	Ecology	St Bees	Gransmoor	Glanllynau	Llanilid
COLEOPTERA					
Gyrinidae (Whirligig beetles)					
<i>Gyrinus marinus</i> Gyll.	A/P	X	X	X	
<i>Gyrinus minutus</i> F.	A/P		X	X	
<i>Gyrinus opacus</i> Sahl.	A/P	X	X	X	
<i>Gyrinus natator</i> (L.)	A/P			X	
Noteridae (Burrowing water beetles)					
<i>Noterus crassicornis</i> (Müll.)	A/P		X		
Haliplidae (Crawling water beetles)					
<i>Haliplus fulvus</i> (F.)	A/O		X		
Dytiscidae (Predaceous diving beetles)					
<i>Agabus arcticus</i> (Payk.)	A/P		X		X
<i>Agabus bipustulatus</i> (L.)	A/P	X	X	X	X
<i>Agabus congener</i> (Thun.)	A/P		X	X	
<i>Agabus labiatus</i> (Brahm)	A/P			X	
<i>Agabus serricornis</i> (Payk.)	A/P		X		
<i>Agabus sturmi</i> (Gyll.)	A/P		X	X	
<i>Ilybius aenescens</i> Thoms.	A/P		X		
<i>Ilybius ater</i> (Deg.)	A/P	X	X		
<i>Ilybius fenestratus</i> (F.)	A/P	X			
<i>Ilybius subaeneus</i> Er.	A/P		X		
<i>Platambus maculatus</i> (L.)	A/P		X		
<i>Colymbetes dolabratus</i> (Payk.)	A/P		X		X
<i>Colymbetes fuscus</i> L.	A/P			X	
<i>Colymbetes paykulli</i> Er.	A/P		X		
<i>Colymbetes striatus</i> (L.)	A/P				X
<i>Rhantus exsoletus</i> (Forst.)	A/P		X		
<i>Rhantus (Nartus) grapii</i> (Gyll.)	A/P		X		
<i>Rhantus notatus</i> (F.)	A/P		X		
<i>Dytiscus circumflexus</i> F.	A/P		X		
<i>Dytiscus lapponicus</i> Gyll.	A/P		X		X
<i>Graptodytes granularis</i> (L.)	A/P			X	
<i>Hydroporus palustris</i> (L.)	A/P				X
<i>Coelambus impressopunctatus</i> (Schall.)	A/P		X		
<i>Coelambus novemlineatus</i> (Steph.)	A/P		X		
<i>Hygrotus decoratus</i> (Gyll.)	A/P		X		
<i>Hygrotus inaequalis</i> (F.)	A/P		X		
<i>Hygrotus quinquelineatus</i> (Zett.)	A/P		X		
<i>Suphrodytes dorsalis</i> (F.)	A/P		X		
<i>Stictotarsus griseostriatus</i> (Deg.)	A/P		X		
<i>Nebrioporus assimilis</i> (Payk.)	A/P		X		X
<i>Nebrioporus depressus</i> (F.)	A/P				X
<i>Nebrioporus elegans</i> (Panz.)	A/P		X		
<i>Oreodytes alpinus</i> (Payk.)	A/P		X		
<i>Boreonectes multilineatus</i> (DeG)	A/P		X	X	X
<i>Hygrotus inaequalis</i> (F.)	A/P		X	X	X
<i>Hyphydrus ovatus</i> (L.)	A/P		X		
Carabidae (Ground beetles)					
<i>Cicindela campestris</i> L.	T/P			X	
<i>Carabus clatratus</i> L.	T/P	X			
<i>Carabus convexus</i> F.	T/P	X			
<i>Carabus glabratus</i> Payk.	T/P	X			
<i>Carabus nitens</i> L.	T/P	X			

Species	Ecology	St Bees	Gransmoor	Glanllynau	Llanilid
<i>Carabus problematicus</i> Hbst.	T/P	X		X	
<i>Leistus terminatus</i> (Hellwig)	T/P	X			
<i>Nebria livida</i> (L.)	T/P		X		
<i>Nebria nivalis</i> (Payk.)	T/P		X		
<i>Nebria rufescens</i> (Ström.)	T/P		X		
<i>Pelophila borealis</i> (Payk.)	T/P		X	X	
<i>Notiophilus aquaticus</i> (L.)	T/P	X	X	X	
<i>Notiophilus palustris</i> (Duft.)	T/P	X	X		
<i>Blethisa multipunctata</i> (L.)	T/P	X			
<i>Diacheila arctica</i> (Gyll.)	T/P		X		
<i>Diacheila polita</i> (Fald.)	T/P		X		
<i>Elaphrus cupreus</i> Duft.	T/P		X	X	
<i>Elaphrus lapponicus</i> Gyll.	T/P		X		
<i>Elaphrus riparius</i> (L.)	T/P		X	X	
<i>Loricera pilicornis</i> (F.)	T/P		X	X	
<i>Clivina fossor</i> (L.)	T/P	X			
<i>Dyschirius globosus</i> (Hbst.)	T/P		X	X	
<i>Dyschirius salinus</i> Schaum	T/P		X		
<i>Dyschirius septentrionum</i> Munst.	T/P		X		
<i>Trechus obtusus</i> Er.	T/P			X	X
<i>Trechus rivularis</i> (Gyll.)	T/P		X		
<i>Trechus secalis</i> (Payk.)	T/P		X	X	X
<i>Trechoblemus micros</i> (Hbst.)	T/P			X	
<i>Bembidion aeneum</i> Germ.	T/P			X	X
<i>Bembidion bipunctatum</i> (L.)	T/P		X	X	
<i>Bembidion clarkii</i> (Dawson)	T/P			X	
<i>Bembidion difficile</i> (Mots.)	T/P				X
<i>Bembidion doris</i> (Panz.)	T/P			X	X
<i>Bembidion fellmanni</i> (Mann.)	T/P		X	X	
<i>Bembidion femoratum</i> Sturm	T/P			X	
<i>Bembidion fumigatum</i> (Duft.)	T/P			X	
<i>Bembidion gilvipes</i> Sturm	T/P		X		
<i>Bembidion grisvardi</i> Dew.	T/P		X		
<i>Bembidion guttula</i> (F.)	T/P			X	X
<i>Bembidion hastii</i> Sahl.	T/P			X	
<i>Bembidion humerale</i> Sturm	T/P		X		
<i>Bembidion lunatum</i> (Duft.)	T/P			X	X
<i>Bembidion minimum</i> (F.)	T/P	X		X	
<i>Bembidion obliquum</i> Sturm	T/P		X	X	
<i>Bembidion varium</i> (Ol.)	T/P		X	X	
<i>Bembidion obscurellum</i> Mots.	T/P		X		
<i>Bembidion octomaculatum</i> (Goeze)	T/P			X	X
<i>Bembidion properans</i> (Steph.)	T/P			X	
<i>Bembidion punctulatum</i> Drap.	T/P			X	
<i>Bembidion quadrimaculatum</i> (L.)	T/P			X	
<i>Bembidion quadripustulatum</i> Serv.	T/P			X	
<i>Bembidion semipunctatum</i> (Don.)	T/P			X	
<i>Bembidion schueppelii</i> Dej.	T/P			X	
<i>Bembidion transparens</i> (Gebler)	T/P		X		
<i>Patrobus septentrionis</i> Dej.	T/P	X	X	X	X
<i>Patrobus assimilis</i> Chaud.	T/P	X	X	X	
<i>Poecilus lepidus</i> (Lesk.)	T/P			X	
<i>Poecilus versicolor</i> (Sturm)	T/P			X	
<i>Pterostichus adstrictus</i> Esch.	T/P			X	
<i>Pterostichus anthracinus</i> (Ill.)	T/P	X			
<i>Pterostichus diligens</i> (Sturm)	T/P	X	X	X	X
<i>Pterostichus gracilis</i> (Dej.)	T/P	X		X	
<i>Pterostichus macer</i> (Marsham)	T/P	X	X	X	
<i>Pterostichus minor</i> (Gyll.)	T/P	X		X	X
<i>Pterostichus niger</i> (Schall.)	T/P			X	
<i>Pterostichus nigrita</i> (Payk.)	T/P	X		X	
<i>Pterostichus strenuus</i> (Panz.)	T/P			X	
<i>Pterostichus vernalis</i> (Panz.)	T/P	X		X	

Species	Ecology	St Bees	Gransmoor	Glanllynau	Llanilid
<i>Calathus erratus</i> (Sahl.)	T/P	X		X	
<i>Calathus fuscipes</i> (Goeze)	T/P	X		X	
<i>Calathus melanocephalus</i> (L.)	T/P	X	X	X	X
<i>Olisthopus rotundatus</i> (Payk.)	T/P				X
<i>Agonum consimile</i> (Gyll.)	T/P				X
<i>Agonum fuliginosum</i> (Panz.)	T/P	X	X	X	X
<i>Agonum gracile</i> Sturm	T/P		X		X
<i>Agonum sexpunctatum</i> (L.)	T/P	X	X		
<i>Agonum thoreyi</i> Dej.	T/P	X			
<i>Agonum viduum</i> (Panz.)	T/P	X			
<i>Amara aulica</i> (Panz.)	T/P	X		X	
<i>Amara bifrons</i> (Gyll.)	T/P			X	
<i>Amara convexiuscula</i> (Marsham)	T/P		X		
<i>Amara equestris</i> (Duft.)	T/P			X	
<i>Amara infima</i> (Duft.)	T/P	X			
<i>Amara lunicollis</i> Schiödte	T/P	X			
<i>Amara quenseli</i> (Schön.)	T/P		X	X	X
<i>Amara plebeja</i> (Gyll.)	T/P			X	
<i>Curtonotus alpinus</i> (Payk.)	T/O	X	X	X	X
<i>Oodes helopioides</i> (F.)	T/P	X			
<i>Badister bullatus</i> (Schrank)	T/P		X		
<i>Cymindis angularis</i> Gyll.	T/P		X	X	
<i>Cymindis humeralis</i> (Geoff.)	T/P			X	
<i>Cymindis macularis</i> Fisch.	T/P			X	
<i>Microlestes minutulus</i> (Goeze)	T/P			X	
<i>Syntomus truncatellus</i> (L.)	T/P			X	
Helophoridae (Helophorid beetles)					
<i>Helophorus aequalis</i> Thoms.	A/S		X		
<i>Helophorus aquaticus</i> (L.) auct.	A/S		X	X	
<i>Helophorus brevipalpis</i> Bedel	A/S		X	X	
<i>Helophorus flavipes</i> F.	A/S		X	X	
<i>Helophorus glacialis</i> Villa	A/S		X		X
<i>Helophorus grandis</i> Ill.	A/S		X		
<i>Helophorus nanus</i> Sturm	A/S		X	X	
<i>Helophorus obscurellus</i> Popp.	A/S		X	X	
<i>Helophorus sibiricus</i> (Mots.)	A/S		X	X	X
<i>Helophorus splendidus</i> Sahl	A/S			X	
Georissidae (Georissid beetles)					
<i>Georissus crenulatus</i> (Rossi)	A/S		X	X	
Hydrochidae (Hydrochid beetles)					
<i>Hydrochus brevis</i> Hbst.	A/S		X		X
Hydrophilidae (Water scavenger beetles)					
<i>Berosus luridus</i> (L.)	A/S				X
<i>Berosus signaticollis</i> (Charp.)	A/S			X	
<i>Chaetarthria seminulum</i> (Hbst.)	A/S		X	X	X
Species	Ecology	St Bees	Gransmoor	Glanllynau	Llanilid
<i>Enochrus quadripunctatus</i> Hbst.	A/S			X	X
<i>Hydrobius fuscipes</i> (L.)	A/S	X	X		X
<i>Hydrophilus piceus</i> (L.)	A/S				X
<i>Cercyon convexiusculus</i> Steph.	A/S		X		X
<i>Cercyon marinus</i> Thoms.	A/S		X		
<i>Cercyon tristis</i> (Ill.)	A/S		X		X
<i>Megasternum obscurum</i> (Marsham)	A/S		X		X
Hydraenidae (Minute moss beetles)					
<i>Hydraena riparia</i> Kug.	A/O			X	
<i>Limnebius nitidus</i> (Marsham)	A/O			X	
<i>Limnebius truncatellus</i> (Thun.)	A/O				X

Species	Ecology	St Bees	Gransmoor	Glanllynau	Llanilid
<i>Ochthebius bicolon</i> Germ	A/O		X		
<i>Ochthebius marinus</i> (Payk.)	A/O		X	X	
<i>Ochthebius minimus</i> (F.)	A/O		X	X	X
<i>Ochthebius pedicularis</i> Kuw	A/O		X		
<i>Ochthebius viridis</i> Peyr.	A/O		X		
Silphidae (Carrion beetles)					
<i>Thanatophilus dispar</i> (Hbst.)	T/C		X		
<i>Silpha atrata</i> (L.)	T/C	X		X	X
<i>Necrophorus vestigator</i> Hersch.	T/C			X	X
Staphylinidae (Rove beetles)					
<i>Acidota crenata</i> (F.)	T/P	X	X		X
<i>Acidota cruentata</i> Mann.	T/P		X		X
<i>Acidota quadrata</i> (Zett.)	T/P		X		X
<i>Anthophagus caraboides</i> (L.)	T/P		X		
<i>Arpedium brachypterum</i> (Grav.)	T/P		X	X	X
<i>Deliphrum tectum</i> (Payk.)	T/P		X	X	
<i>Geodromicus nigrita</i> (Müll.)	T/P	X	X		X
<i>Lesteva longolytrata</i> (Goeze)	T/P	X	X	X	X
<i>Olophrum assimile</i> (Payk.)	T/P		X	X	X
<i>Olophrum boreale</i> (Payk.)	T/P		X		X
<i>Olophrum consimile</i> (Gyll.)	T/P		X		
<i>Olophrum fuscum</i> (Grav.)	T/P	X		X	X
<i>Olophrum rotundicolle</i> (Sahl.)	T/P		X		
<i>Euedectus giraudi</i> Redt.	T/P		X		
<i>Pycnoglypta lurida</i> (Gyll.)	T/P		X	X	
<i>Boreaphilus henningianus</i> Sahl.	T/P		X	X	X
<i>Holoboreaphilus nordenskiöldi</i> (Mäkl.)	T/P		X		
<i>Eusphalerum minutum</i> (F.)	T/P		X		X
<i>Omalius excavatum</i> Steph.	T/P		X		
<i>Pselaphus heisei</i> Hbst.	T/P		X		X
<i>Tychus niger</i> (Payk.)	T/P			X	
<i>Mycetoporus angularis</i> Muls. & Rey	T/P		X		
<i>Tachinus corticinus</i> Grav	T/P		X	X	
<i>Tachinus elongatus</i> Gyll.	T/P		X	X	
<i>Tachinus marginellus</i> (F.)	T/P		X		
<i>Tachinus rufipes</i> (L.)	T/P		X	X	
<i>Tachyporus chrysomelinus</i> (L.)	T/P		X		
<i>Gymnusa brevicollis</i> (Payk.)	T/P		X	X	
<i>Dinarda dentata</i> (Grav.)	T/P		X		
<i>Anotylus insecatus</i> (Grav.)	T/P		X		
<i>Anotylus nitidulus</i> (Grav.)	T/P			X	
<i>Anotylus rugosus</i> (F.)	T/P				X
<i>Platystethus comutus</i> (Grav.)	T/P		X		X
<i>Platystethus nodifrons</i> Mann.	T/P			X	X
<i>Stenus juno</i> (Payk.)	T/P	X		X	X
<i>Euaesthetus bipunctatus</i> (Ljungh)	T/P			X	
<i>Euaesthetus laeviusculus</i> Mann.	T/P			X	
<i>Ochthephilum fracticorne</i> (Payk.)	T/P		X		
<i>Philonthus decorus</i> (Grav.)	T/P		X		
<i>Othius angustus</i> Steph.	T/P			X	
<i>Staphylinus erythropterus</i> L.	T/P		X		
<i>Ocypus fortunatarum</i> (Woll.)	T/P			X	
<i>Ocypus fuscatus</i> (Grav.)	T/P			X	
<i>Creophilus maxillosus</i> (L.)	T/P	X			
<i>Tasgius ater</i> Grav.	T/P	X			
	T/P				
Scarabaeidae (dung beetles)					
<i>Aegialia sabuleti</i> (Panz.)	T/S		X		X
<i>Aphodius ater</i> (Deg.)	T/D				
<i>Aphodius depressus</i> (Kug.)	T/D	X			
<i>Aphodius erraticus</i> (L.)	T/D			X	

Species	Ecology	St Bees	Gransmoor	Glanllynau	Llanilid
<i>Aphodius fimetarius</i> (L.)	T/D		X		
<i>Aphodius luridus</i> (F.)	T/D	X			
<i>Aphodius plagiatus</i> (L.)	T/D	X			
<i>Aphodius prodromus</i> (Brahm)	T/D		X		
Elmidae (Riffle beetles)					
<i>Elmis aenea</i> (P. Müller)	A/S				X
<i>Esolus parallelepipedus</i> (P. Müller)	A/S			X	X
<i>Limnius volckmari</i> (Panz.)	A/S		X	X	X
<i>Normandia nitens</i> (P. Müller)	A/S			X	
<i>Oulimnius tuberculatus</i> (P. Müller)	A/S			X	X
Heteroceridae (Variegated mud-loving beetles)					
<i>Heterocerus intermedius</i> Kies.	A/O		X		
Coccinellidae (Ladybird beetles)					
<i>Nephus redtenbacheri</i> (Muls.)	T/P		X		
<i>Anisosticta novemdecimpunctata</i> L.	T/P		X		
<i>Hippodamia arctica</i> Schneid.	T/P		X		
<i>Hippodamia tredecimpunctata</i> (L.)	T/P			X	
<i>Coccinella hieroglyphica</i> L.	T/P	X			
<i>Coccinella septempunctata</i> L.	T/P	X	X		
<i>Coccinella undecimpunctata</i> L.	T/P		X		

Ecological codes: A – aquatic; C – carrion feeder; D – dung feeder; O – omnivorous; P – predator; S – scavenger; T – terrestrial.

Table 3. Calibrated radiocarbon ages of intervals for which the aquatic and terrestrial MCR estimates disagree

Sample age	Site
Ca 16,200	Gransmoor
Ca 16,000	Gransmoor
Ca 16,000	Glanllynau
Ca 15,800	Gransmoor
Ca 15,600	Gransmoor
13,000	Llanilid
12,400	Gransmoor
12,400	St Bees
12,350	Gransmoor
12,200	Gransmoor
11,900	St Bees

Figure captions:

Figure 1. Composite MCR reconstruction of mean July temperatures for the British isles (black) compared with the chironomid reconstruction of mean July temperatures for the Whitrig Bog site, Scotland. Data from Coope et al., 1998 (beetle MCR) and Brooks and Birks, 2000 (chironomid reconstruction). The black line represents single estimates for each MCR range, calibrated using a linear regression model that fits predicted to observed TMAX values for modern beetle assemblages (see Atkinson et al., 1987).

Figure 2. Map of the British Isles, showing the location of sites discussed in the text. LGM ice limits (dashed line) based on data in Chiverrell and Thomas, 2010. Loch Lommond Stadial ice limits in Scotland based on data in Ehlers et al., 1992.

Figure 3. Mutual climatic range estimates of TMAX from the St Bees site, based on aquatic beetle species (black bars) and terrestrial beetle species (red bars). The age scale represents calibrates years before present.

Figure 4. Mutual climatic range estimates of TMAX from the Gransmoor site, based on aquatic beetle species (black bars) and terrestrial beetle species (red bars). The age scale represents calibrates years before present.

Figure 5. Mutual climatic range estimates of TMAX from the Glannynau site, based on aquatic beetle species (black bars) and terrestrial beetle species (red bars). The age scale represents calibrates years before present.

Figure 6. Mutual climatic range estimates of TMAX from the Llanilid site, based on aquatic beetle species (black bars) and terrestrial beetle species (red bars). The age scale represents calibrates years before present.

Figure 7. Combined TMAX reconstructions (all species) for the Llanilid, Gransmoor and St Bees beetle assemblages, compared with the $\delta^{18}\text{O}$ record from the NGRIP ice core (NGRIP members, 2007). The full range of estimated TMAX values for each

assemblage is shown as the area within the shaded colours; a heavy, coloured line is shown for the mid-point of each TMAX bar. This line does not represent a most likely scenario; it is there merely to facilitate the observation of trends in the data.

Figure 1.jpg
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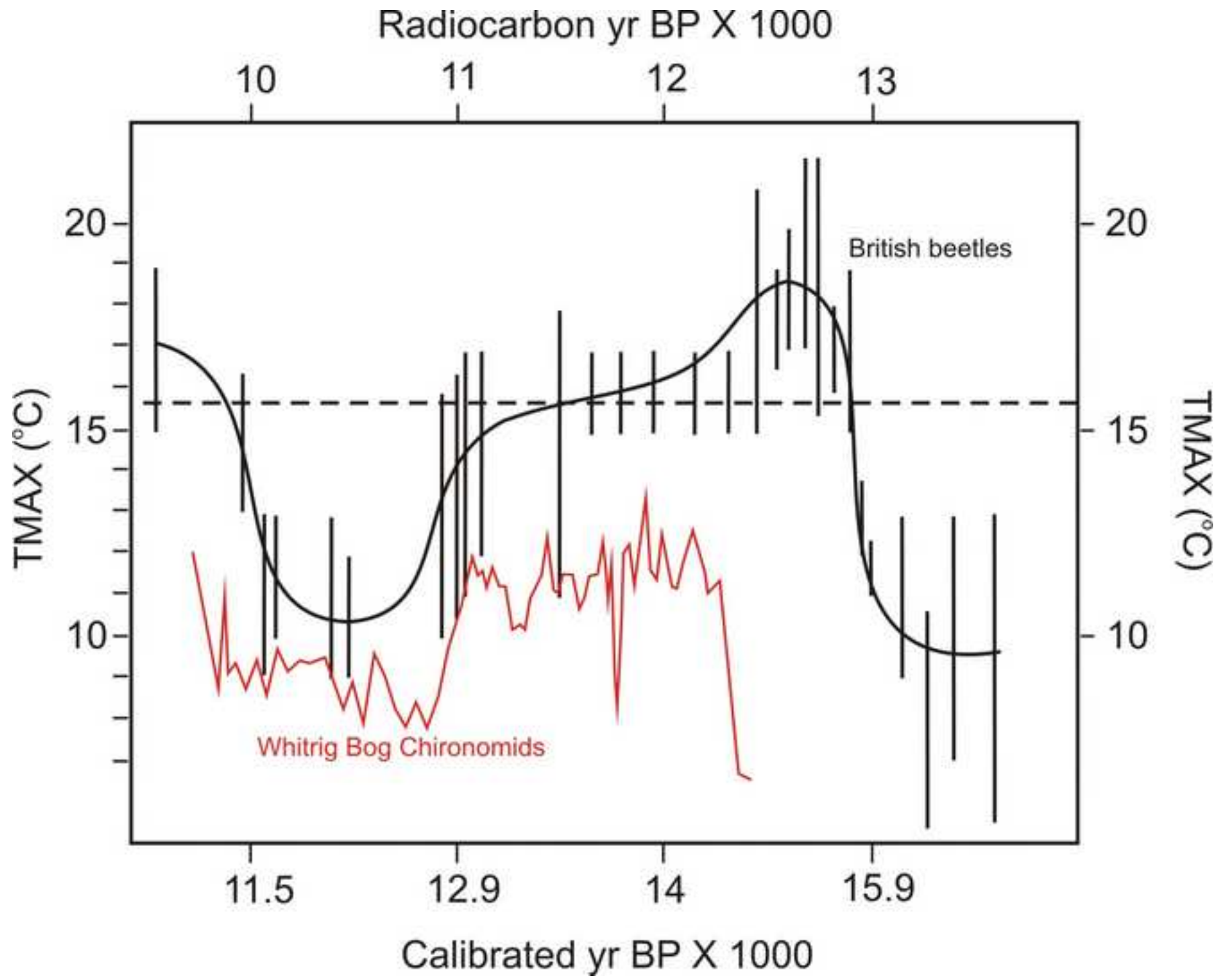


Figure 2.jpg
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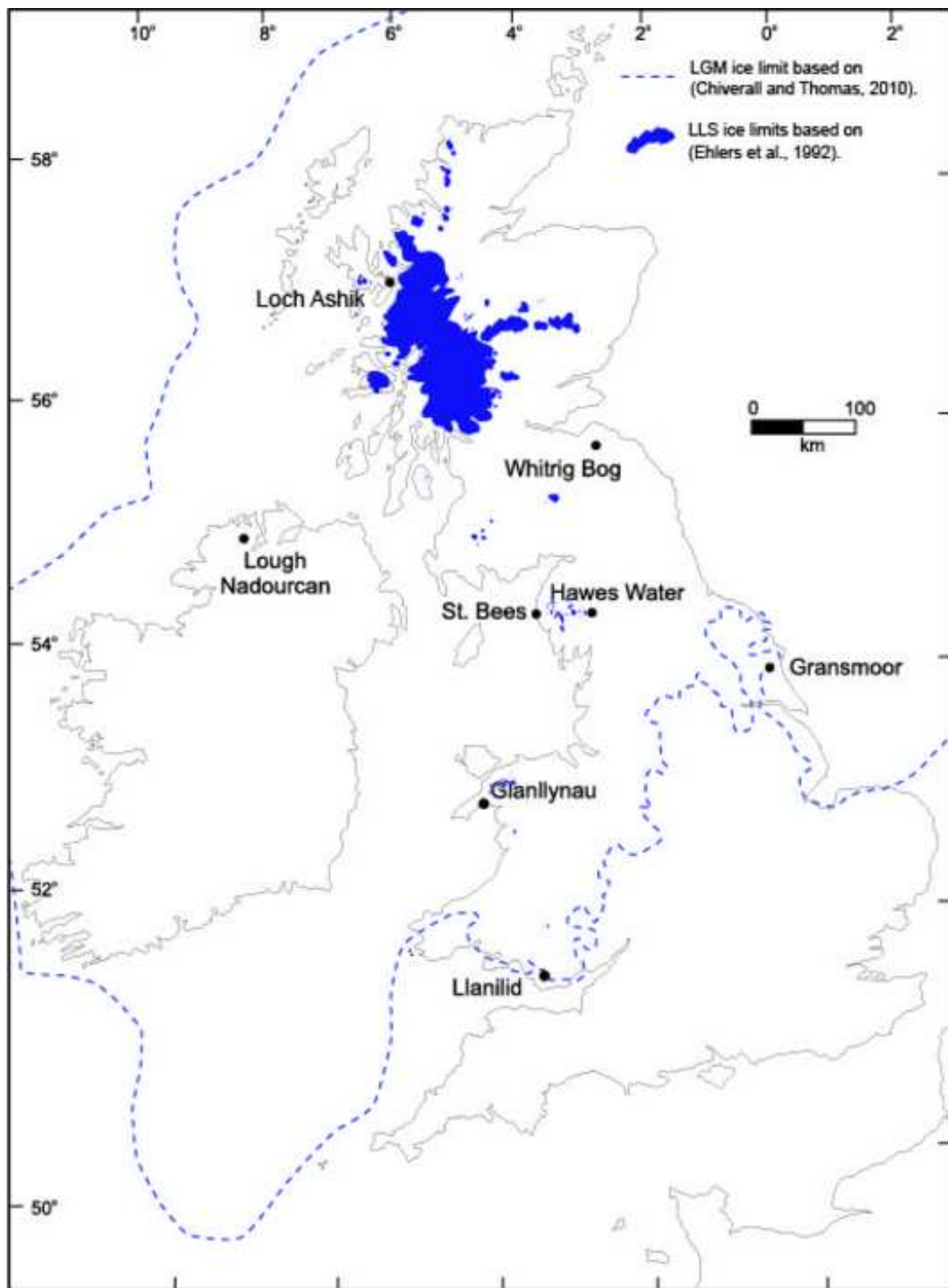


Figure 3.jpg
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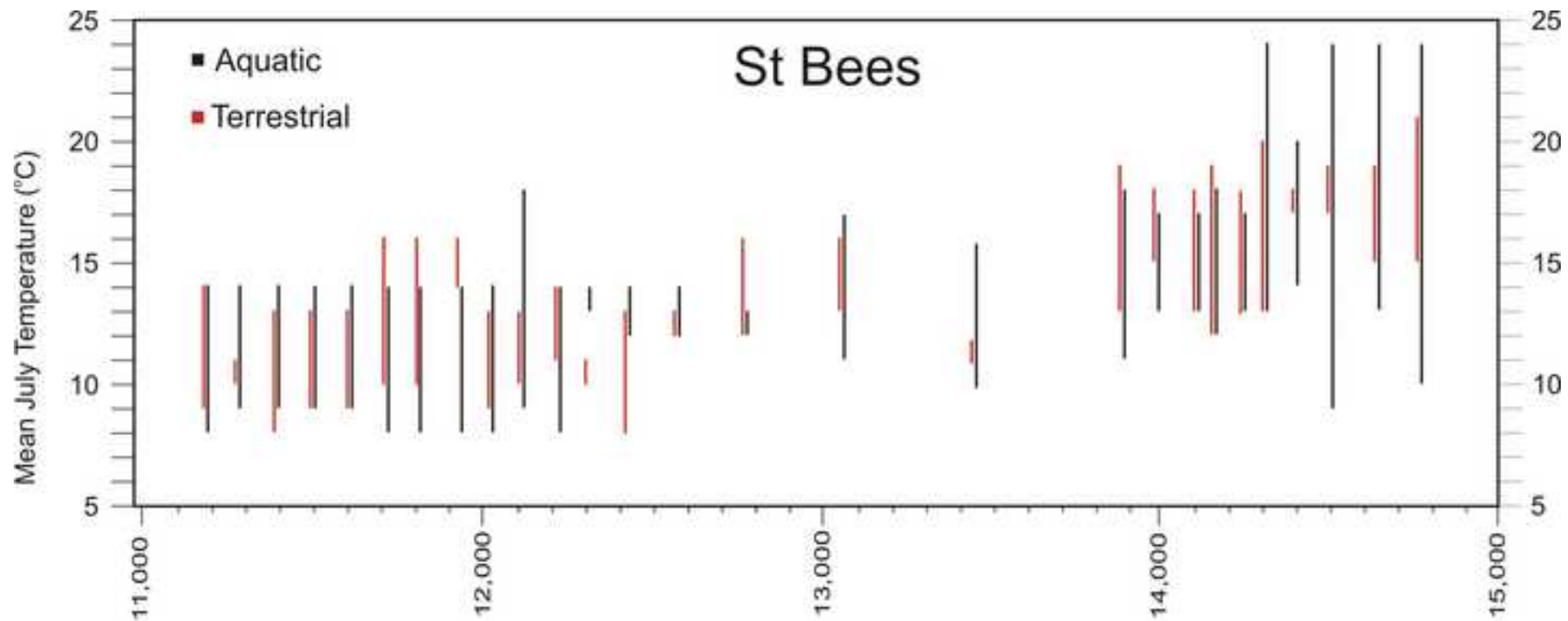


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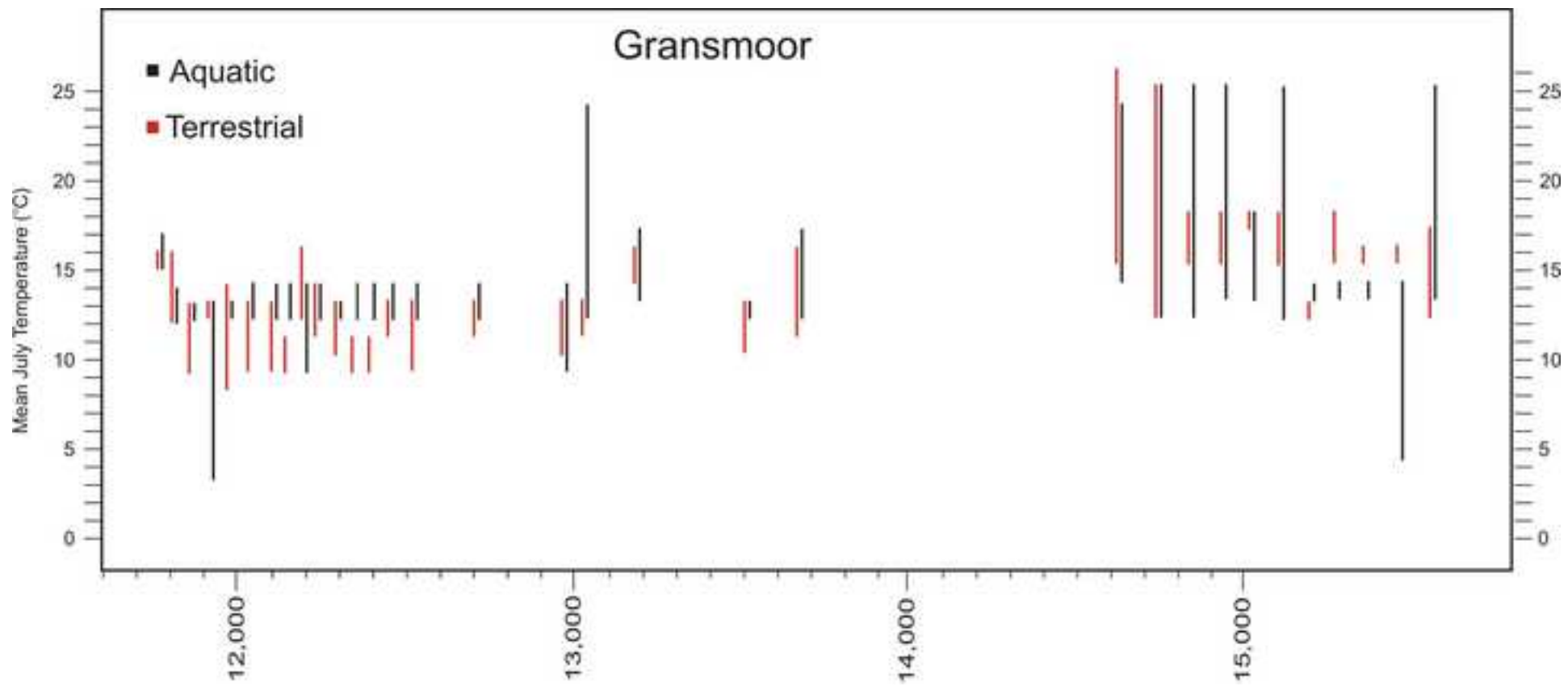


Figure 5.jpg
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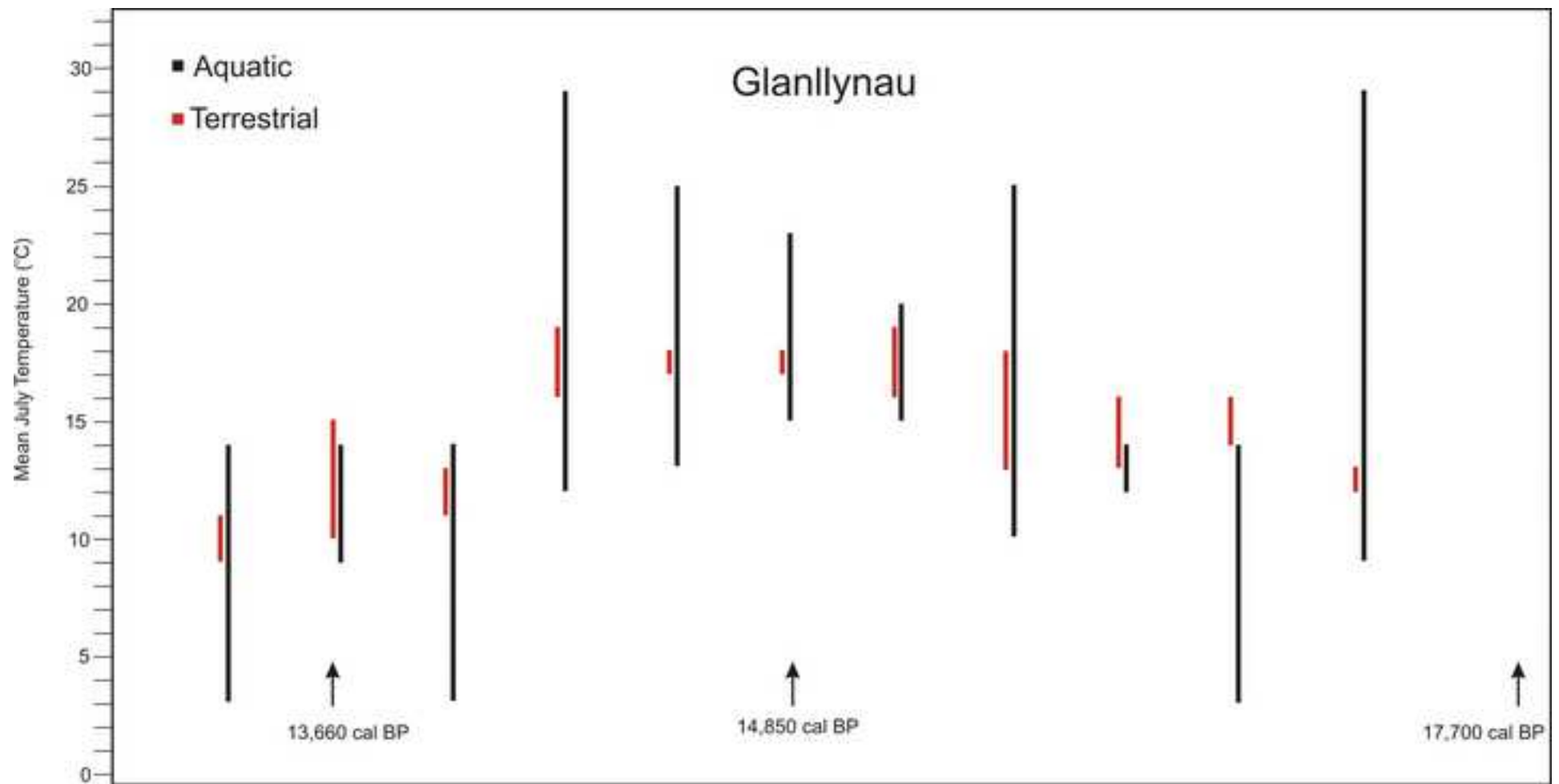


Figure 6.jpg
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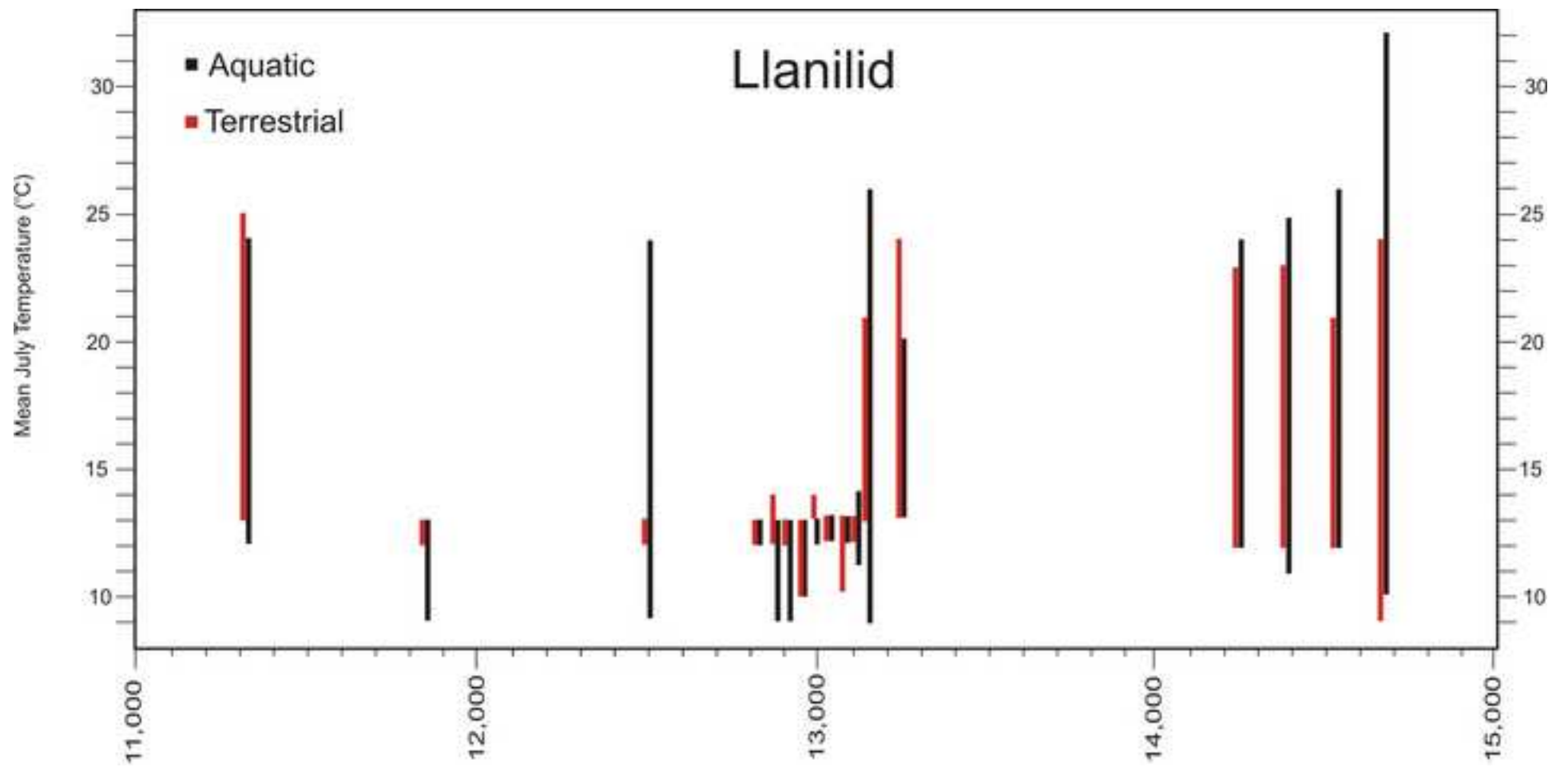
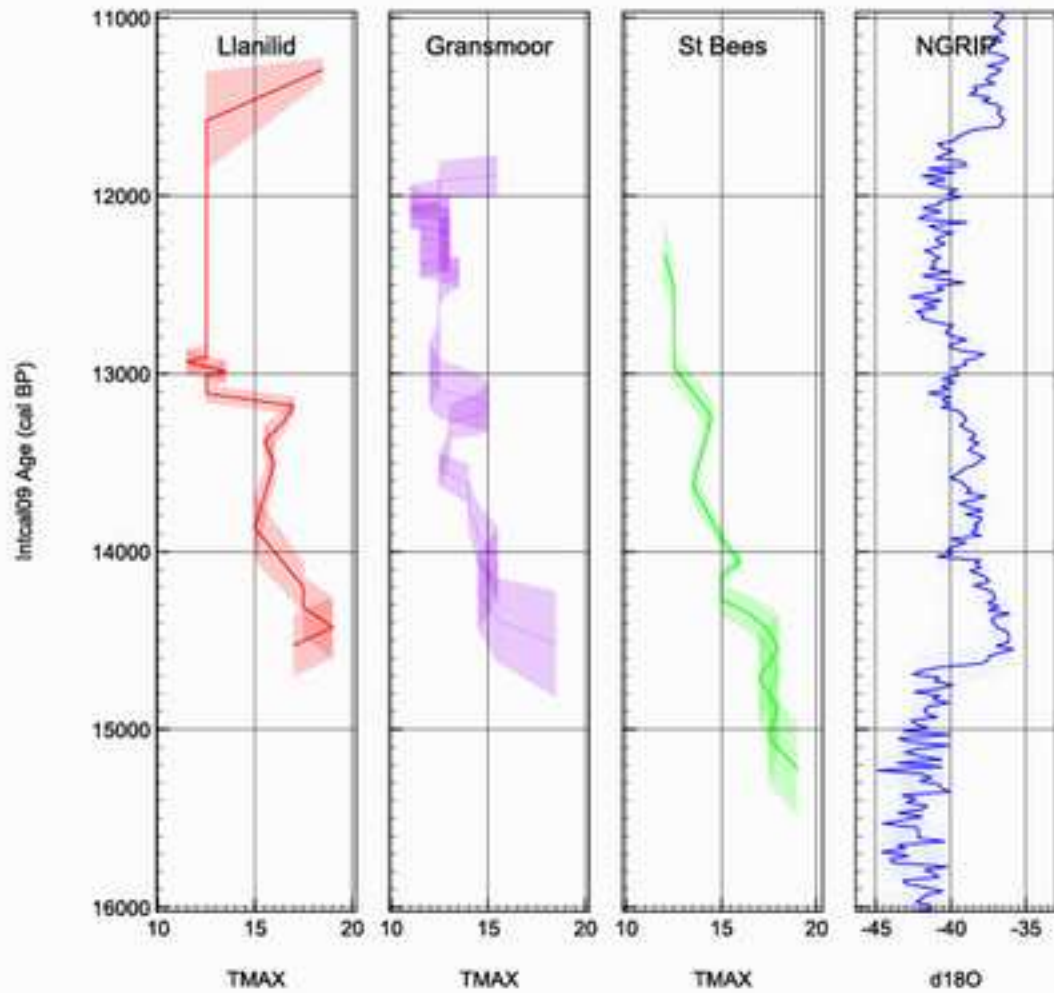


Figure 7.jpg

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Review for QUATINT-D-13-00349

The article “Late glacial temperature reconstructions for the British Isles: a comparison of reconstructions based on aquatic and terrestrial beetle assemblages” written by Scott Elias and Ian Matthews has mostly methodological goal. It compares results of the temperature reconstruction using aquatic and terrestrial insects. The reconstruction of the Late glacial temperature itself seems to be secondary here (by my imagination). Besides that, the article describes also Early Holocene. I guess, the authors should correlate the article title to something like this - “a comparison of reconstructions based on aquatic and terrestrial beetle assemblages and Late glacial – Early Holocene temperature reconstructions for the British Isles”.

Response: Done

This article has been written for the Russell Coope Honourary Volume. This volume provides rare opportunity to gather insect papers and it will be attractive collection not only for usual readers of QI, but also for entomologists. Following this thought, I would like to recommend some improving. The article should include:

- 1 method of fossil insect sampling and volume of the tested sediment,
- 2 list of studied insects

Response: Done as follows: we created a new table showing age ranges, sample volumes, and number of species used in MCR estimates, and a second table showing which species were used in the MCR from the four sites.

- 3 insect species and families names in the text,

Response: We have not added species information to the manuscript text, as the full information on which species of predators and scavengers were identified from each of the sites is now available in the second table, discussed above.

- 4 maybe pictures of the most remarkable species.

Response: We have not added such photos, as the manuscript already contains six figures.

Presence of the insect list will make the article much more interesting and open for discussion. Now a reader has no information which species were selected for MCR. What mean “predators and scavengers? How strong is the definition? The interpretation could be different, one considers Helophorus is scavenger, another can say the beetle is polyphagous with phytophagous adult, but anyway, the genus is always used for MCR. We need more detailed criteria for selection.

Response: In the second table discussed above, we have included ecological codes for each species, indicating whether they are aquatic or terrestrial, predators, scavengers, omnivores, dung feeders, or carrion feeders.

In geological point of view, it will be interesting to see the scheme and photo of the studied sections and their geological description. It can help to understand the discussion about post-glacial water bodies, shallow or deep water, flooding, etc.

Response: We have not added these for two reasons. First, all of this information is available to interested readers in the original publications we cite. Second, the point of this paper is to discuss the differences (if any) between aquatic and terrestrial species in late glacial MCR estimations, not to go over the site stratigraphy and deposition history again.

I think the paper needs minor revisions to be acceptable for publication, but the publication will be better with medium revision.

Reviewer #2: This a valuable study comparing results of beetle MCR and chironomid transfer function palaeotemperature methods, and exploring the effects of carrying out separate MCR analyses for aquatic and terrestrial beetles. We need more multiproxy comparisons like this! The results and their implications are well-presented and argued, and I have only a few (relatively minor) critical comments for the author's consideration, which are detailed below.

1. For those of us not familiar with beetles (or chironomids) could you perhaps clarify precisely what is meant by aquatic and terrestrial? Do they complete their entire life cycle in aquatic and terrestrial environments respectively, or do, e.g. some terrestrial beetles have an aquatic larval stage? The answer to this question could have implications for some of the discussion.

Response: We have added a paragraph discussing the nature of these adaptations in beetle ecology.

2. Material and methods: It is stated that: "In this study, only the average temperature of the warmest month of the year (TMAX) was considered...". This could be interpreted in two ways: (a) you use the MCR method to determine the range of temperatures within which the actual mean/average monthly temperature for the warmest month must have fallen, or (b) you use the MCR method to determine that range and then use an average value derived from the reconstructed range.

It would be helpful to clarify this; I have the impression (from looking at Fig. 7) that it is (b), and if so, please explain how average temperatures are obtained from the MCR method. As presented by Atkinson et al. (1987), the cited reference, this method provides a range; the actual temperature could have been anywhere within that range. How do you get from Figs 4-6, which show ranges, to Fig. 7, which apparently shows curves based on plots of single values, with shading to represent the ranges (at least I assume that is what it shows; this is not explained in the caption)? I know there are rationales for deriving an "average" value from such ranges but this aspect of the method is controversial and needs some explanation / discussion here. This is one of the difficulties of comparing chironomid transfer function results with those from the beetle MCR method: the former gives you a single value with +/- bars and the latter gives you a range without (in the strict application of the method) a single mean /median / average value.

Response: We have clarified this in the text. The MCR estimates shown as vertical bars in figures 3-6 represent the range of TMAX (mean July temperature) values suitable to all the predaceous and scavenging species in a given fossil assemblage. In Fig. 7, we have changed the caption as follows, 'The full range of estimated TMAX values for each assemblage is shown as the area within the shaded colours; a heavy, coloured line is shown for the mid-point of each TMAX bar. This line does not represent a most likely scenario; it is there merely to facilitate the observation of trends in the data.'

3. The discussion touches on the issue of the size of training sets (in relation to calibration for the chironomid method). This is an issue that could usefully be explored and discussed further in relation to beetles as well. The number of lakes in a chironomid training set is relatively unimportant; more significant is the range of temperatures that they cover. What is the extent, in climate space as well as geographical space, of the training set used with the beetle MCR method? Do the training sets capture the full climatic ranges of the beetles and chironomid taxa in question? I suspect that in some cases they do not (and I have seen chironomid papers that determined palaeotemperatures that lay outside the range covered by the training set used) and that this might contribute to some of the discrepancies observed.

Response: The beetle MCR method does not use training sets in the standard meaning of the phrase. Training sets are needed when palaeontologists are unable to identify their fossil

specimens to the species level. They therefore rely on training sets: associations of taxa found living together in certain environmental settings, to help them interpret their faunal or floral assemblages by finding patterns of similarity with those modern assemblages. In contrast to this, all of the specimens used in beetle MCR reconstructions are identified to the species level. MCR paleoclimate estimation is based on the overlap of the individual species climate envelopes, based on the climatic parameters associated with the known modern distributions of those species. The chironomid training sets are based on established modern data sets which have been discussed and reviewed at length in the wider literature; we already reference many of the key papers in the manuscript. The most recent of these is Heiri et al. (2011) who combined the Swiss and Norwegian training sets in order to include lakes with different geomorphic and geological controls, alongside generating a longer environmental gradient of Mean July air temperatures. While we agree with the reviewer that the number of lakes is not an indicator *per se* of robustness, it is directly linked to the environmental gradient and the ability to assess a taxon's response to change along the gradient of interest. We are not aware of chironomid articles which reconstruct temperatures outside of the calibration data but agree with the reviewer that this is an interesting area for discussion. However, we do not think this can be meaningfully addressed in this manuscript without a rather long explanation and this would detract from the focus of the rest of the text. Rather, we think this needs to be followed up by subsequent articles.

4. What does the curve shown in Fig. 1 represent? I would have assumed that it somehow links mean or median values in the MCR ranges shown, but the curve misses one of the range bars entirely. And what does the horizontal dashed line represent? Maybe some explanation could be included in the figure caption.

Response: As discussed in the text, and now added to the figure caption, the black line represents single estimates for each MCR range, calibrated using a linear regression model that fits predicted to observed TMAX values for modern beetle assemblages (see Atkinson et al., 1987).

Dave Horne 17th June 2013