5 BugsMCR: Software for MCR Temperature Reconstruction from Beetle Assemblages

This chapter describes the BugsMCR climate reconstruction component of the BugsCEP software. Some developmental aspects are described, such as the improvements in BugsMCR over previous software, but the primary focus is on the implementation of the methodology itself, its advantages and disadvantages, and possible improvements. Instructions on the use of BugsMCR are given in section 3.4.4, and some practical applications can be found in Chapter 6. Whilst the MCR, and prediction by MCR, program modules are fully functional in the current release of BugsCEP, some of the more advanced techniques described below are not publicly available and will be released in conjunction with later publications. They are presented here to prepare the ground and to enable the discussion of future developmental strategies.

Fossil beetle assemblages have been used for the reconstruction of Quaternary palaeoclimates since the late 1950s, when Russell Coope first used them to reconstruct late Quaternary environments at Chelford in Cheshire (Coope, 1959) and Upton Warren in Worcestershire (Coope *et al.,* 1961). The Mutual Climatic Range method (MCR) (Atkinson *et al.,* 1986) was developed to provide quantitative climate reconstructions, using the overlap of modern species thermal envelopes to predict/retrodict the temperature regime in which all species in a fossil assemblage would have been able to survive. During the late 1980s and early 1990s, two software suites were developed for the generation of thermal envelopes and calculation of MCR, commonly referred to as MCRBirm and MCRUEA after their respective development institutions (Birmingham University and the University of East Anglia). The reconstruction components of these software, called RECON and RECON2 respectively, run in the MS-DOS environment, and there has for some time been the need for a more user-friendly format using MS Windows, which is now provided in BugsMCR.

Much has been written on the MCR method and its applications (see references throughout this chapter), although detailed descriptions of its development and mechanics are rare, and almost entirely restricted to unpublished PhD theses (see section 5.1.1).

5.1 Background and Software Development

Although detailed descriptions of the earlier MCR software are hard to find (e.g. Perry, 1986), the MCR method itself is described in a number of articles (e.g. Atkinson *et al.,* 1986; 1987; Lowe & Walker 1997). BugsMCR was initially developed, by the author of this thesis, to improve upon the original MS-DOS software, as a standalone program for use in research and teaching, and has been subsequently incorporated into the latest version of BugsCEP, with a number of improvements. This allows for a more integrated approach to fossil beetle studies, combining climate change with ecology and biogeography. Sites can easily be analysed using the full suit of BugsCEP tools without the need for transferring data between programs.

5.1.1 The mutual climatic range (MCR) method in brief

The mutual climatic range is the term used to define the set of temperature values[i] in which a group of beetles, or indeed any organism, can all survive. The method overlays the known thermal tolerances, or thermal envelopes, of the taxa in a sample and simply reads off the extremes of the area of greatest overlap (Figure 5.1). The greatest overlap is typically expressed as a percentage of the number of MCR species, that is to say the species with thermal envelopes, in the sample. By repeating this process for samples in a stratigraphic sequence it is possible to gain a picture of climate change over

[i] Additional climate variables have been used in the application of the MCR method to other proxies, e.g. Sinka & Atkinson (1999).

time, should there be sufficient dating evidence to support it. Examples are provided in Chapter 6 of this thesis.

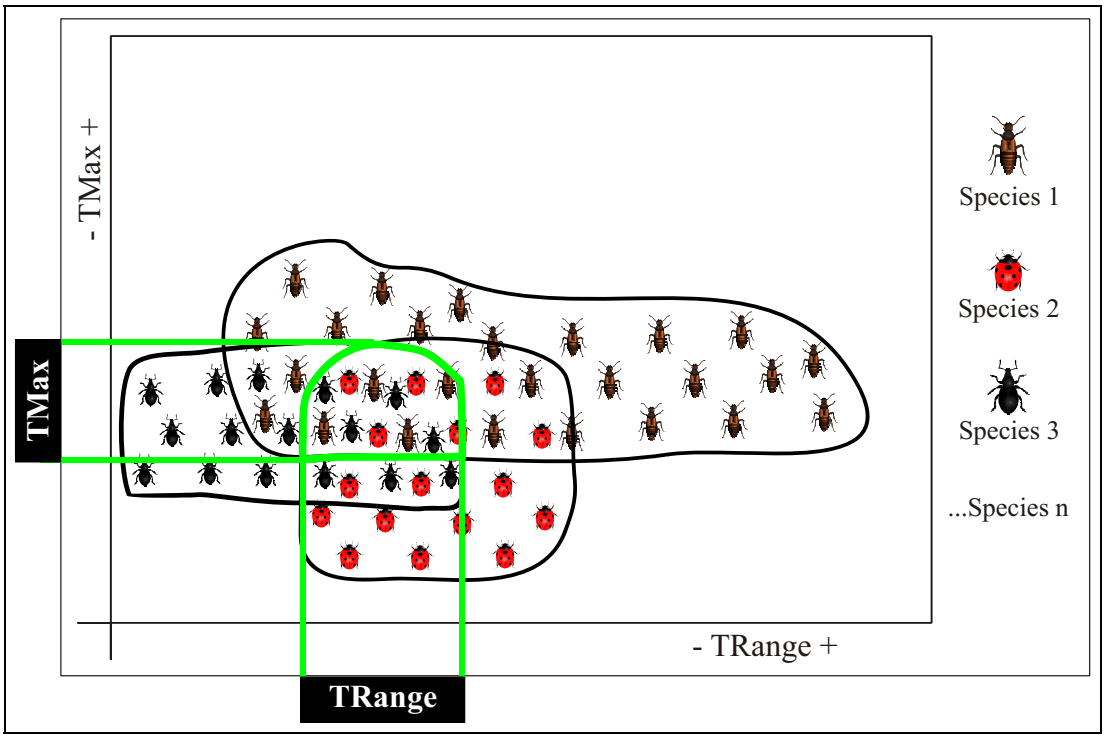


Figure 5.1. An illustration of the derivation of temperature values (TValues) using the MCR method, showing the mutual climatic range (MCR) for three species in climate space.

The method may be classed as an 'indicator-species approach using two or more climatic variables' according to Birks (1981), and could be said to have its roots in the works of Iversen (1944), and derivatives, looking at the climatic indicator value of a limited number of plant species[ii]. Much of the theoretical, mathematical and computational groundwork for MCR was undertaken in the 1970s and 1980s as components in palaeoentomological PhD theses at Birmingham, UK (Morgan, 1970; Joachim, 1978; Moseley, 1982; Perry, 1986). Ordination was used to show that many beetle distributions are primarily controlled by summer temperatures, and the difference between the summer and winter temperature – summarized in the MCR dataset as TMax: mean temperature of the warmest month, and TRange: difference between TMax and the mean temperature of the coldest month (TMin)[iii]. TRange is essentially an index of continentality, in that more continental climates show a greater difference between the extremes of summer and winter. The envelopes are stored as TMax versus TRange, and TMin can be calculated by deducting TRange from TMax for any point in TMax/TRange climate space. The reference dataset uses a 1°C cell matrix, making these calculations relatively simple, and leading to reconstructions with a resolution of 1°C in all three thermal dimensions.

MCR relies on the tendency of mobile populations to migrate in the face of climate or environmental change, rather than genetically adapt to the changes and remain in the same location. Remaining in the same location is not an option when the environment changes dramatically over a short period of time, and insects, especially those with wings, are able to react rapidly to abrupt changes (Coope, 1978). Thus extinctions throughout the Quaternary have been few, and the anthropogenic habitat

[ii] It must be noted that Birks, for a number of reasons that are discussed below, appears to ascribe little value to the MCR method as a quantitative reconstruction technique.

[iii] Note that occasionally authors (e.g. Huppert & Solow, 2004) have mistakenly cited the use of July and January temperatures instead of the warmest and coldest months. The difference is especially important when considering past shifts in continentality or seasonality, where the warmest and coldest months may change.

fragmentation and destruction of recent centuries may prove to have been more damaging than any other event in prehistory (Thomas *et al.,* 2004)[iv]. Insects are also among the first organisms to colonise newly exposed land, such as in front of a retreating glacier, or the shores of a drying lake or sinking sea level (see Ashworth, 2001, for a detailed analysis of responses to climate change). A number of omnivorous, aquatic and predatory beetles are particularly mobile and make up a large part of the MCR dataset. It is this rapid colonization ability that first gave proxy evidence for the rapid amelioration at the end of the last Ice Age (Devensian) (Osborne, 1972), and has subsequently revealed a number of other rapid climate change events that floral data, hampered by slower colonization rates, could not resolve. This has lead to a significant steepening of the established climate curves, and an intense debate between beetle and chironomid people on the one hand and pollen people on the other, which was only really resolved by the emergence of the Greenland Ice Core data (Alley *et al.*, 1993) showing a similar, if not *more* dramatic set of changes.

5.1.2 The BugsMCR implementation

The usage of BugsMCR has already been described in section 3.4.4, and readers should refer to that section for instructions. The definitions of the variable which specify the reconstructed temperature ranges are repeated here in Table 5.1 for convenience. Although BugsMCR uses the same reference dataset as the Birmingham RECON software, that is where the similarities end. RECON is a piece of compiled FORTRAN software functioning in an MS-DOS environment, and rather than attempting to reverse engineer the source code, it was decided to implement the MCR method from the bottom up using MS Access and VBA. In this respect, although BugsMCR is a natural progression from RECON, it owes nothing to it programmatically. BugsMCR was developed as part of the groundwork for this thesis, and the time for development has been somewhat limited due to other priorities. As a result, some of the useful functions provided in RECON (and its associated programs) have not been replicated in BugsMCR. In particular, it does not provide the facility to view the individual species envelopes, or manually build up overlaps by selecting species. This was a useful investigative and teaching facility included in the MCRUEA software 'NOD'. Another RECON feature not yet implemented in BugsMCR is that of calculating the warm/cold components of assemblages which do not display a significant overlap. This feature, although it has some theoretical problems, is a useful investigative tool and is considered in more detail below (5.2.5).

Table 5.1. Explanation of MCR results terms, repeated from Chapter 3. See chapters 3 and 6 for worked examples and outputs. The reconstructed temperature range limits are collectively referred to as TValues.

Column	Explanation
Sample	Sample name from database
TMaxLo	Lower limit of reconstructed mean temperature of warmest month
TMaxHi	Upper limit of reconstructed mean temperature of warmest month
TMinLo	Lower limit of the reconstructed mean temperature of the coldest month
TMinHi	Upper limit of the reconstructed mean temperature of the coldest month
TRangeLo	Lower limit of the reconstructed mean temperature ranges (TMax – TMin)
TRangeHi	Upper limit of the reconstructed mean temperature ranges (TMax – TMin)
NSPEC	Number of taxa used in reconstruction
Overlap	Percentage of sample taxa in the area of maximum overlap, used to calculate the temperature values

BugsMCR utilizes the site/countsheet database in BugsCEP, and any site in the database can be processed towards climate reconstruction. This is not to say that all sites are suitable for MCR, and archaeological deposits, in particular with elements thermally cushioned by man-made heat islands,

[iv] Wikipedia also includes an excellent overview of the ongoing Holocene extinction event: http://en.wikipedia.org/wiki/Holocene_extinction_event

should be treated with extreme caution (see 5.2.2). Abundance data should be entered or imported into BugsCEP as described in section 3.4.2, before they can be accessed through the BugsMCR program component.

The use of MS Access theoretically allows several otherwise complicated calculations and data manipulations to be performed easily and quickly through the use of database queries (cf. stored procedures in SQL-Server), but the data intensive nature of MCR calculations proved incompatible with this technique due to stability and file bloating problems[v]. A set of routines was subsequently developed to perform all calculations using arrays in VBA, from which results could be exported to MS Excel for graphing and subsequent user access. In comparison to the previous MS-DOS programs, the facilities for developing a Graphical User Interface (GUI) within MS Access allowed for a more user friendly and intuitive system to be developed (see section 3.4.4 for screenshots). In addition, the use of MS Excel as the output format allowed for easy graphing and compatibility with other statistical packages, although some of the text file outputs of the older versions were more portable. MS Excel, however, is infinitely more flexible in terms of what can be put into the output files, and the current version includes graphing of reconstructed temperatures by sample, the export of raw results, thermal envelopes and species lists, as well as more advanced statistics in versions currently under development (see section 5.1.2.4). MS Excel is also easily integrated with MS Access and VBA, being fully object orientated, and is ubiquitous in academic circles. This enables users to perform subsequent statistical and graphical analyses easily, including the calibration/correction of temperature values if so desired (although see section 5.2.3 on the problems with calibration).

5.1.2.1 Species thermal envelopes

The thermal envelope data have been imported and converted from the existing MCRBirm software, and consist of binary grids of 1°C presence/absence data, which were stored in a file called 'beetle.dat'. Figure 5.2 shows the thermal envelope for *Carabus problematicus* Hbst. as stored in MCRBirm (beetle.dat) and BugsCEP respectively. The import process was not without its problems, and due to taxonomic revisions or variations in spellings, 93 of the original taxa had to be manually matched with BugsCEP taxa. The full list of MCR taxa, with their BugsCEP and MCRBirm names can be seen by clicking the Show All MCR Species link in the BugsMCR interface. This list also includes the numbers used in input files in the original RECON component of the MCRBirm software (Figure 5.3). The latter are provided for backward compatibility and, along with details of the name conversions, to allow for cross-checking of any unexpected problems in the BugsMCR reconstructions.

Although not of the resolution commonly claimed in other climate reconstruction methods, the 1°C grid has proven a reliable system for estimating past temperatures and has been tested against modern, external data sets (Coope *et al.,* 1998). There are currently 436 taxa in the BugsMCR calibration set, although there are plans to increase and refine this, eventually including other climatically sensitive insect groups such as the caddis flies (Trichoptera) (Greenwood *et al.,* 2003). BugsMCR is programmed modularly, the calculation routines and functions are held in modules independent of the interface forms, and can be called from any part of the program. They can thus be easily upgraded should new routines be needed.

[v] This is a problem peculiar to MS Access, and the original routines have been preserved for later use in an SQL-Server type version.

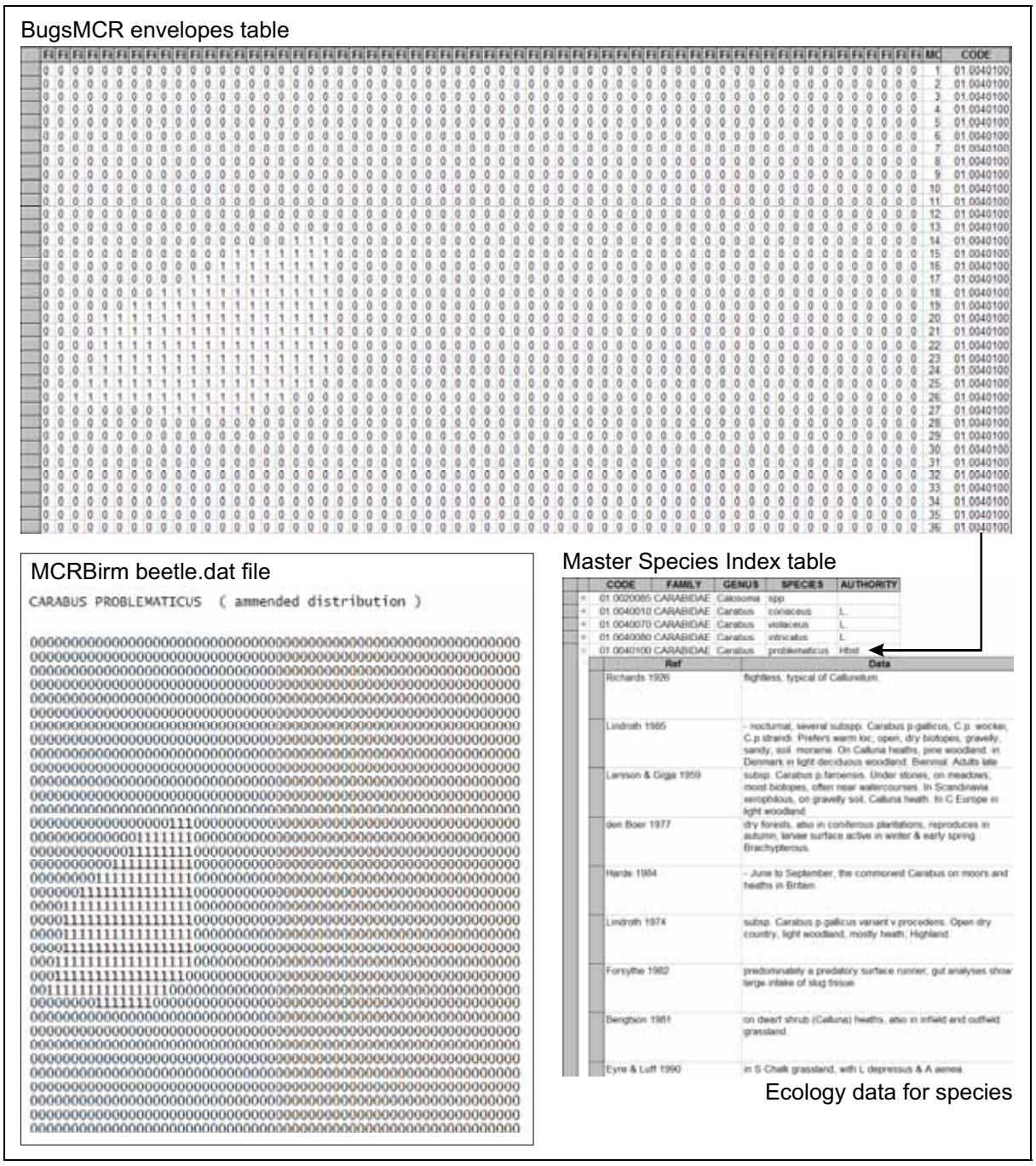


Figure 5.2. Thermal envelope for *Carabus problematicus* Hbst. as stored in BugsCEP, showing how taxonomic code links the envelope data to ecology data through the master species index. The original envelope, as stored in the beetle.dat data file for the MCRBirm RECON software is shown in the inset to the bottom left.

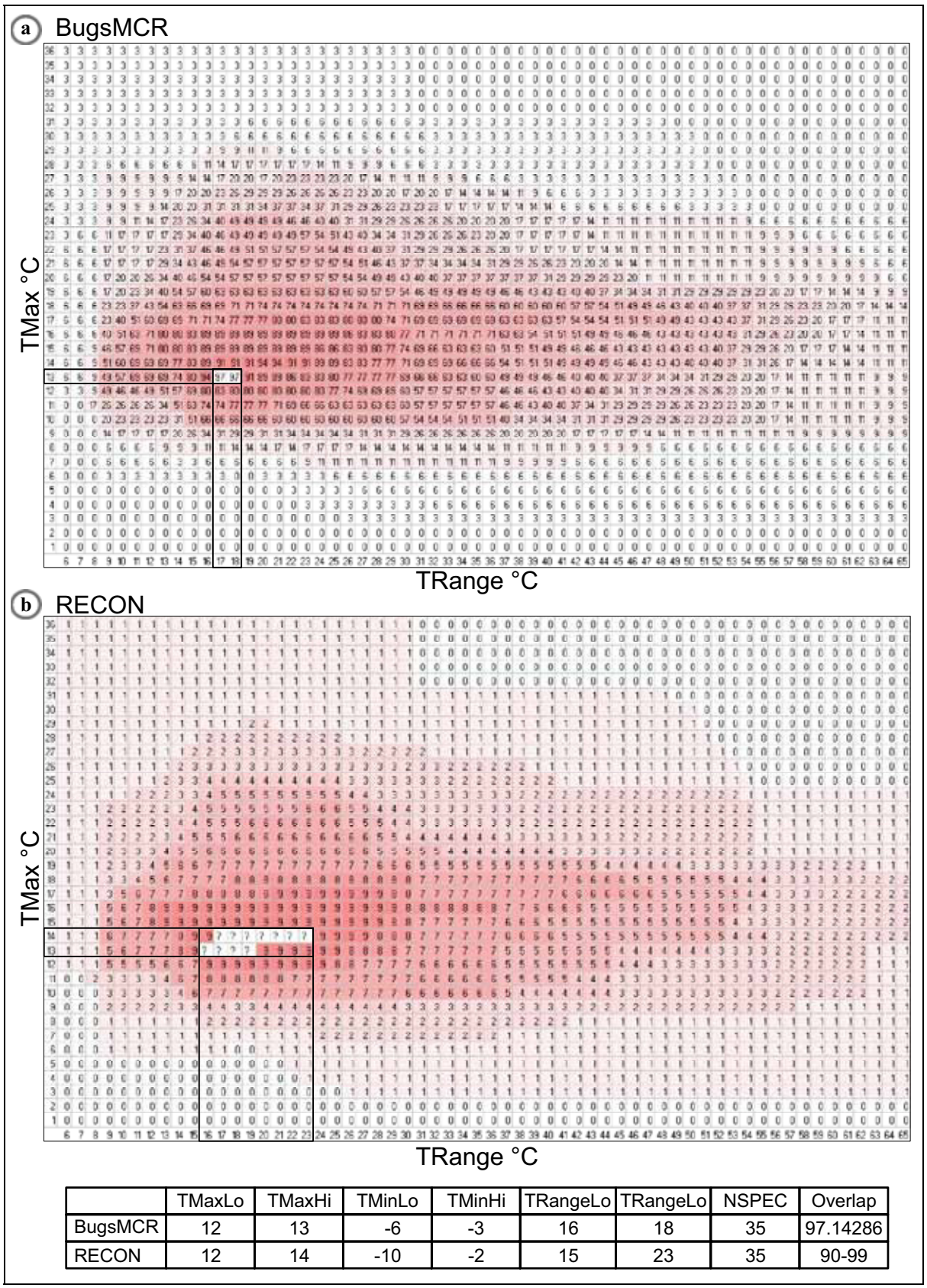
CODE	FAMILY	GENUS	SPECIES	AUTHORITY	RECON Nr	RECON Name
01.0010020	CARABIDAE	Cicindela	sylvatica	L.	273	Cicindela sylvatica L.
01.0010070	CARABIDAE	Cicindela	campestris	L.	274	Cicindela campestris
01.0020010	CARABIDAE	Calosoma	inquisitor	(L.)	271	CALOSOMA INQUISITOR
01.0020050	CARABIDAE	Calosoma	reticulatum	(F.)	270	Calosoma reticulatum
01.0040100	CARABIDAE	Carabus	problematicus	Hbst.	283	CARABUS PROBLEMATICUS (ammended distribution)
01.0040120	CARABIDAE	Carabus	granulatus	L.	286	CARABUS GRANULATUS L.
01.0040140	CARABIDAE	Carabus	clatratus	L.	288	Carabus clathratus L.
01.0040172	CARABIDAE	Carabus	convexus	F.	287	CARABUS CONVEXUS F. (=TOMOCARABUS)
01.0040180	CARABIDAE	Carabus	nitens	L.	284	CARABUS NITENS L.
01.0040341	CARABIDAE	Carabus	maeander	Fisch.	285	Carabus maeander
01.0050010	CARABIDAE	Cychrus	caraboides	(L.)	253	Cychrus caraboides

Figure 5.3. Screenshot: Comparison of BugsCEP taxa with names of taxa as stored in the original MCRBirm software. The 'RECON Nr' field shows the numbers used as input strings in the original RECON(struction) component of the MCRBirm software..

5.1.2.2 Calculations and overlaps

Whilst the earlier software did not calculate temperature values for assemblages where the area of maximum overlap contained < 90 % of the taxa in the sample, it provided the option of sub-setting these faunas on the basis of their warm or cold tolerance (see 5.2.5). BugsMCR currently does not provide warm/cold component estimations, but it does provide the facility to calculate temperatures for any degree of maximum overlap, thus allowing the user to decide on the acceptable minimum percentage. The percentage overlap is given in the 'Overlap' column in the results file (see Figure 5.4). It could be postulated that the lower the percentage overlap, the greater the probability that the sample represents a period of time in which there was a degree of climate change greater than the tolerance levels of the individual species found. This is a function of the resolution of the sample, and the rate of climatic change, and not easy to resolve without entering into circular reasoning (see 5.2.5). The broad application of an arbitrary 90 % minimum overlap often prevents reconstruction from large assemblages or samples, where the fauna in its entirety represents the most probable extremes of the temperature that occurred during the terminal depositional lifespan of the sample. Note that the MCR values *do not* represent the average temperature for the period, due to the fact that MCR works on thermal limits rather than means. It is possible that, since MCR calculates the extreme limits of possible temperatures, i.e. the widest ranges, from the processed fauna, the presentation of any reconstructed values are valid as long as the percentage overlap is given. Exceptions may apply in situations where there is evidence, such as differential preservation of fragments or sedimentological indications, of secondary deposition, where the assemblage may represent more than one geographically or chronologically disparate fauna.

For each cell in the 1°C climate space map for a sample, RECON calculated envelope overlaps to the nearest 10 %, as shown in the overlap matrix in Figure 5.4b. BugsMCR theoretically calculates overlaps with up to 28 decimals precision, and can thus more accurately define the area of maximum overlap, when compared to the 90 % or 100 % limits used in RECON. This is sometimes reflected in small differences in the reconstructed temperatures produced by each program – BugsMCR producing a narrower set of ranges than RECON (Figure 5.4). Whether or not this is to be called an increase in accuracy will depend on the user's acknowledgement of the usefulness of 90 % of the assemblage as an acceptable proportion of the assemblage for reconstruction, or whether a narrower range defined by more taxa is preferable. It may be so that the reliability of a reconstruction is more dependent on the actual species used than the number of them, and more work is clearly needed in assessing the relative reliability of assemblages. A possible method, using jackknifing variants, is suggested below (5.2.6 and 5.2.6.1).



	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeLo	NSPEC	Overlap
BugsMCR	12	13	-6	-3	16	18	35	97.14286
RECON	12	14	-10	-2	15	23	35	90-99

Figure 5.4. Comparison of exported climate space maps for Saint Bees (Coope & Joachim, 1980) sample s50 as processed by (a) BugsMCR and (b) RECON. Note the difference in reconstructed temperatures caused by the definition of maximum overlap cells. Both maps have been shaded, had scales added and the area of maximum overlap highlighted. The BugsMCR output has been rounded to the nearest percent for clarity, and the RECON values are in precent/10 as output by the program. The scales indicate the upper boundary of climate cells in degrees Celsius.

5.1.2.3 Graphs

The original Birmingham MCR software suite included a program called 'Graphs' which was able to plot a series of thermal ranges (TMax and TMin) against sample dates. Although BugsCEP does graph the results, there was unfortunately not time to duplicate the facility to scale the x-axis by sample date, and samples are simply plotted in order of entry. The graphing motor in MS Excel is not designed for graphs too far removed from its standard types, and improved scaling would require some trickery in terms of 'drawing' with data. A prototype has been created, and this feature will be added at a later date. For the moment users requiring a scaled time axis must import the data into another graphing package, or use graphics software to scale the graphs. In addition, BugsMCR does not attempt to unify the temperature scales of the individual TMax and TMin graphs produced, and this must also be undertaken manually.

5.1.2.4 Advanced MCR

A button in the 'Tools' section of the BugsMCR interface give access to the experimental 'Advanced MCR' interface (Figure 5.5). This is not fully tested, and the meaning of the statistics that it produces is not yet fully understood[vi]. The two main features of the advanced interface are the ability to see sample summary data and select samples before running calculations, and the ability to jackknife MCR calculations and produce a number of related statistics. The potential uses for jackknifed MCR calculations are discussed in sections 5.2.6 and 6.7. Multiple removal, or 'delete-d' jackknifing can also be performed, and the options are briefly discussed in section 5.2.6.1. The intention is to add more features to this interface with time.

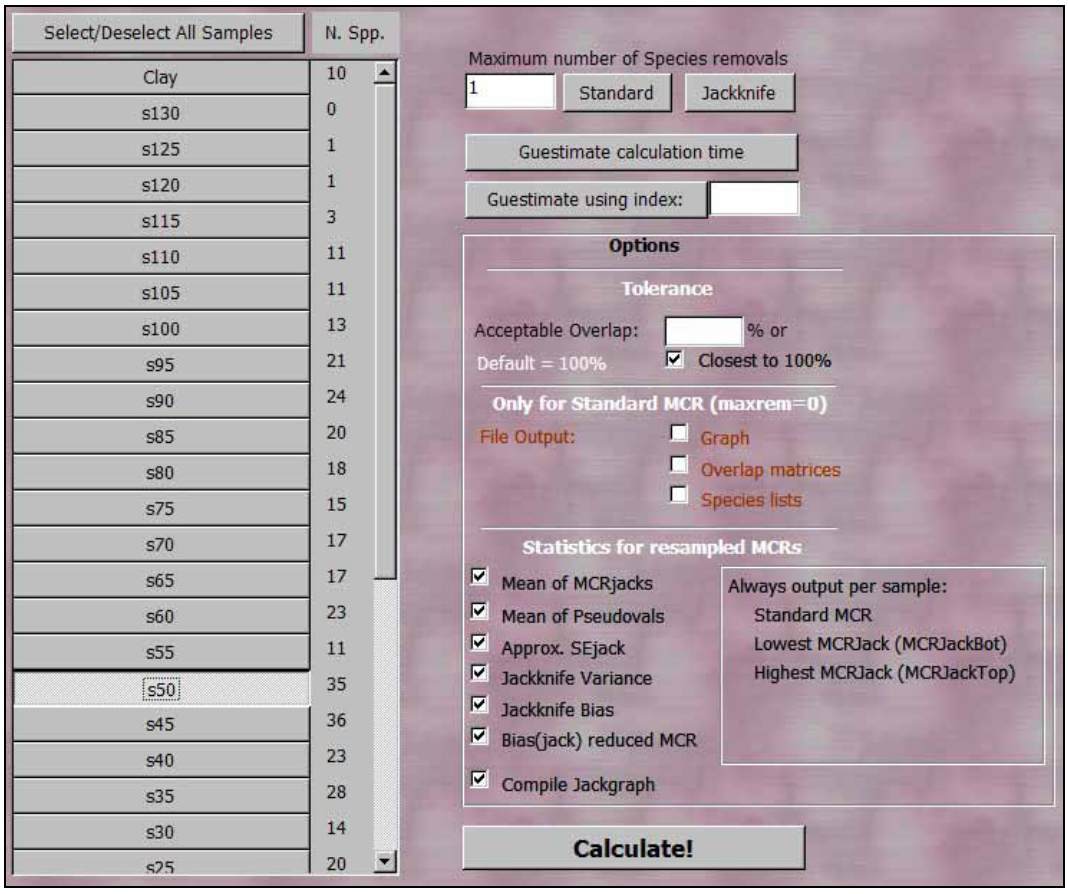


Figure 5.5. Screenshot: Advanced MCR interface, showing the sample selection panel on the left and numerous options on the right.

[vi] The interface is password protected at the time of publication, and will be made available on its completion.

5.1.3 Predicting potential changes in geographical range

The 'Predictions' module of BugsMCR is a simple query engine for retrieving lists of taxa that comply with specific thermal limits or values. It is similar in purpose to the 'Pest' program described by Perry (1986), although this was not available for comparison. At the time of writing, the predictions module uses only the extreme limits of the thermal variables, i.e. TMaxHigh, TMaxLow etc, rather than the actual envelopes. This is by design, and allows the system to be slightly optimistic in the species lists it retrieves, although with the loss of some accuracy. It also partly compensates for the poor quality of a number of the species thermal envelopes in the MCR dataset. An alternative, using the actual thermal envelopes, will be implemented at a later date, as this could potentially be a more powerful method.

As Perry (1986) suggests, the MCR method can be inverted, and the thermal tolerance of species used to predict their potential geographical distribution under ideal conditions[vii]. Perry (1986) used the Pest program to test the viability of beetle distribution by ice rafting, and investigated the percentage of carabid populations found on North Atlantic islands in proportion to the potential richness under different climate scenarios. He showed a clear distance decay model in line with Scandinavian and northern British origins for the faunas of Shetland, Faeroe, Iceland and Greenland. Vickers (2006) has used the BugsMCR predictions module to discuss tabula-rasa/refugia theory in the North Atlantic, and there is considerable potential for experimentation in many research areas from historical biogeography to the prediction of predator or pest species distributions with global warming (see also Vickers & Buckland, *in prep.*).

The predictions pop-up window, accessible by clicking the [Predictions] button on the BugsMCR interface, gives the user access to the thermal limits of all the MCR species, and Figure 5.6 shows those for the stenothermic carabid *Diacheila arctica* (Gyll.). The current distribution of *D. arctica* is restricted to the far north of Scandinavia, North West Russian, and possibly into Siberia, although there is little collection data currently available from Siberia. The beetle is characterised by an extremely narrow tolerance for summer temperatures (TMax), and is known fossil from a number of Late Glacial and Younger Dryas sites in the British Isles, often being cited in evidence for the cold, continental climate of that time (e.g. Ashworth, 2001).

By copying the thermal range data for *D. arctica* into the 'Ranges' panel, they become available as search criteria, and the user can simply click the [Find Species that are...] button to see which other species can survive within these limits. As it happens, none can survive within the exact limits of *D. arctica*, which gives us scope for expanding the ranges, or simulating changes in temperature. Any range value may be either adjusted, or omitted, but if specific TMax and TMin values are to be used, then both must be included. TRange, although a useful indication of continentally, and the second most important variable for defining the thermal limits of the beetles in the MCR dataset, is more difficult to visualize than summer and winter temperatures. If the TRange values for *D. arctica* are deleted, and the button clicked again, it opens up the possibility for more, or less, continental species to be found, as can be seen in Table 5.2.

[vii] A similar, although more complex approach has also been applied for assessing the impact of climate change on plants (Dockerty & Lovett, 2003).

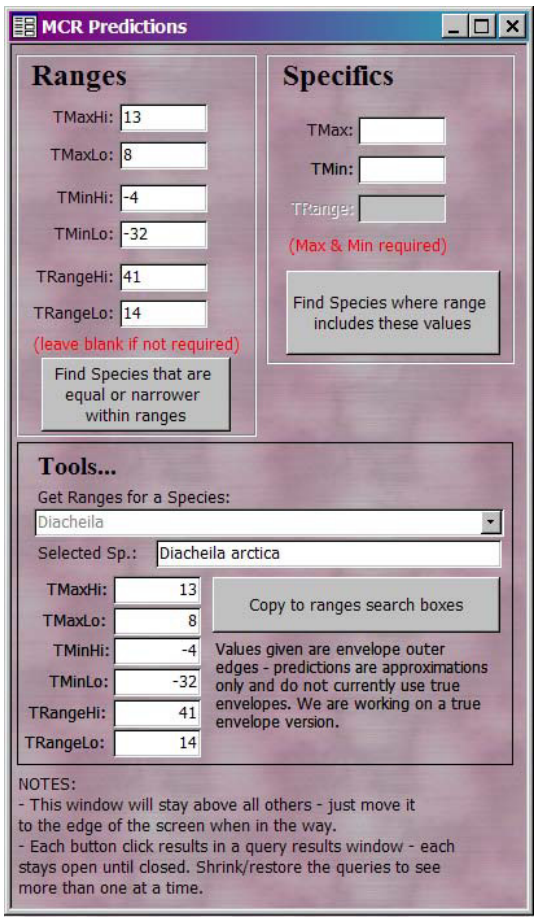


Figure 5.6. Screenshot: The BugsMCR Predictions interface with the thermal envelope limits for *Diacheila arctica* (Gyll.) selected and copied to the 'Ranges' panel.

Pterostichus kokeilii Miller (Table 5.2) is slightly more cold stenothermic than *D. arctica*, but does not appear to be able to survive as cold winters. The ranges of these two species do not overlap in geographical space, *P. kokeilii* being restricted to central and eastern European Alpine areas (Koch, 1989; Mani, 1968), but this result shows that they could theoretically exist in the same climate. This is, of course, highly simplified reasoning, and there are a large number of factors that need to be considered when investigating the potential ranges of species during different climatic conditions. Species competition is also a factor to consider when experimenting with ranges. Many of the MCR species are low density predators, and the arrival of a new species due to climate change could upset the predator-prey relationships that exist in an area. In this case, however, *P. kokeilii* is classed as a *Meadowland* species in BugsCEP, whereas *D. arctica* is classed as a *Heathland & moorland* species, and it is perhaps unlikely that they would compete for similar habitats or food sources.

Table 5.2. Species list return from Predictions module when searching for species with TMin and TMax spans equal to or narrower than *Diacheila arctica* (Gyll.).

CODE	Taxon	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi
01.0111010	*Diacheila arctica*	8	13	-32	-4	14	41
01.0510410	*Pterostichus kokeilii*	8	11	-28	-4	13	36

Simulating temperature changes through the adjustment of range extremes is a difficult business, and it is perhaps easier to deal with single temperature values such as mean values for TMax and TMin. The 1961-1990 average temperature for the far northern tip of Sweden is around 10°C for July, and -14°C for January (SMHI, 2005; Naimakka weather station, 68.7° N, 21.5° E). If these values are

entered into the 'Specifics' TMax and TMin boxes, and the [Find Species where range includes these values] button pressed, a list of 192 species is retrieved. This surprisingly large list is retrieved due to the fact that all species whose ranges overlap the entered values are found, including the cold stenotherms discussed above, and more eurythermal species such as *Calathus melanocephalus* (L.), which can survive summer temperature from 8°C to 36°C. A simple 2°C global warming scenario can be simulated by raising the TMax and TMin values to 12°C and –12°C respectively, and then running the query again. This retrieves a list of 246 species, more than half the MCR dataset, which could theoretically survive at the new temperatures. It would appear that a uniform two degree rise in the mean summer and winter temperatures would allow more MCR species to survive in northern Sweden. The means, however, give a very limited picture of the climate, as the monthly mean temperatures will have varied from year to year around these values.

For the sake of experiment, this variation can be simulated by setting hypothetical limits to the range of temperatures expected. Focussing on the summer temperature, which is more accurately recorded in the species envelopes, one can produce an alternative list of species that could inhabit the far northern tip of Sweden. Clearing all range boxes and entering 14°C and 7°C for TMaxHi and TMaxLo returns a list of 12 species (Table 5.3). Subsequently raising TMaxHi and TMaxLo by two degrees, to 16°C and 9°C, actually reduces the number of species to 9 (Table 5.4), illustrating the important point that this function retrieves *only* those species that have ranges narrower or equal to the values entered. Rather than just telling us which species could potentially colonise the area with a rise in temperature, this experiment has told us which species are at risk of local extinction (although it must be remembered that not all of those listed will actually live at the location – the MCR software has no geographical awareness). In addition, the experiment retrieves a list of several, slightly more warm tolerant, stenothermic species which could theoretically move in. These would, according to their thermal envelopes, not have been able to survive the lower extremes of the 7-14°C TMax summers. The advantage of this method over the use of means, is that the maximum survival limits of species are taken into consideration, and thus the retrieved list are considerably shorter.

Additional query functions, and the refinement of the prediction module to include envelope, rather than range, based querying would allow these lines of enquiry to be explored in more detail, and build up a fuller picture of potential distribution changes. At the moment, prediction envelopes can only be seen by importing the query results (e.g. Table 5.3) into a BugsCEP site and running MCR on the list.

Table 5.3. List of species, and their thermal tolerance extremes, which have TMax ranges equal to or narrower than 7-14°C. Species that would not be able to cope with an increase in summer temperature ranges of 2°C are in **bold**.

CODE	Taxon	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi
01.0111010	**Diacheila arctica**	**8**	**13**	**-32**	**-4**	**14**	**41**
01.0111020	**Diacheila polita**	**7**	**12**	**-38**	**-5**	**15**	**49**
01.0120007	Elaphrus lapponicus	9	13	-36	3	10	47
01.0290045	**Bembidion lapponicum**	**8**	**14**	**-37**	**-5**	**19**	**49**
01.0290141	**Bembidion hyperboraeorum**	**8**	**13**	**-39**	**-7**	**20**	**47**
01.0510410	**Pterostichus kokeilii**	**8**	**11**	**-28**	**-4**	**13**	**36**
01.0510578	**Pterostichus middendorffi**	**7**	**11**	**-39**	**-8**	**19**	**46**
01.0510580	**Pterostichus vermiculosus**	**7**	**11**	**-40**	**-17**	**28**	**47**
01.0620071	Agonum chalconatum	10	14	-25	-6	20	35
01.0620285	Agonum consimile	9	14	-27	-2	14	36
23.0260081	**Olophrum boreale**	**8**	**14**	**-21**	**0**	**14**	**29**
23.0300043	Acidota quadrata	9	13	-30	-2	15	39

Table 5.4. List of species, and their thermal tolerance extremes, which have TMax ranges equal to or narrower than 9-16°C. Stenothermic species that would not have been able to survive a 2°C lower TMax value are in **bold**.

CODE	Taxon	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi
01.0120007	Elaphrus lapponicus	9	13	-36	3	10	47
01.0290240	**Bembidion virens**	**9**	**16**	**-27**	**5**	**8**	**36**
01.0290541	**Bembidion petrosum**	**10**	**16**	**-37**	**1**	**13**	**49**
01.0620071	Agonum chalconatum	10	14	-25	-6	20	35
01.0620285	Agonum consimile	9	14	-27	-2	14	36
23.0240010	**Deliphrum tectum**	**9**	**16**	**-21**	**5**	**10**	**30**
23.0260121	**Olophrum rotundicolle**	**9**	**15**	**-21**	**2**	**13**	**30**
23.0300043	Acidota quadrata	9	13	-30	-2	15	39
23.0350060	**Anthophagus bicornis**	**9**	**15**	**-16**	**1**	**14**	**25**

Although the majority of species in the MCR list have been chosen for their lack of ties to specific vegetation types, it is quite probable that a number of them still have other specific habitat needs. The ecology of many species is poorly understood, especially at their geographical or climatic limits, and it has previously been argued that regional variation in the microhabitat preference of carabids reduces the usefulness of MCR as a climate reconstruction method (Andersen, 1993; 1996). Coope & Lemdahl (1996) argue that the microclimate (as described by Andersen, 1993) exists as a subcomponent of the macroclimate used when constructing the species thermal envelopes, which are built from the entire geographical range of the species, and these variations are thus catered for in the method. Even so, care must be taken to look at the geographical possibility for species migrations, past or future, when predicting ranges from climate data. The problems of habitats and geographical ranges are discussed further in section 6.7.

In the examples given above, the influence of the dataset scope on retrieved species lists is potentially large. The fact that the MCR dataset has a large Scandinavian component makes this less of a problem in this case, but should the same experiments be carried out for Central or Eastern Europe, the results would probably be unreliable in that a large number of important species would be missing. There is, as is mentioned at several places in this chapter, a great need for the enhancement and expansion of the MCR dataset. In addition, the combination of the prediction module with a GIS system would greatly increase the potential for investigating the past, present and future biogeography of beetles, perhaps by including their present geographical distributions in the prediction algorithms. The addition of phytophagous species, for example, could make the system interesting for forestry and agriculture in the prediction of changing pest patterns due to global warming. It is possible that additional variables would have to be added to complement TMax and TMin, as these may not be the limiting factors for all species (Parmesan *et al.*, 2005).

5.2 MCR – Problems and Possibilities

5.2.1 Requirements for quantitative reconstructions

Birks (2003) lists nine major requirements for quantitative reconstructions, two of which the MCR method could be considered as failing to meet. Firstly, the method does not "...model the non-linear relationships between modern taxa and their environment and take account of the numerical properties of the biological data.". There are a number of reasons for this, the primary one being that MCR is a presence/absence method by definition, and numbers of individuals are, mathematically, uninteresting. A single find of a species has as much weight in the final reconstruction as any number of individuals, and this allows MCR to reconstruct temperatures from very poor faunas. There is, of course, a risk that the identifications are incorrect, or that the sample does not represent the environment that is to be reconstructed due to redeposition or contamination, for example. These are, however, taphonomic concerns, and the domain of the individual doing the identification and processing the samples, and

these are factors that cannot easily be quantified in the reconstruction methodology without resorting to guesswork. This is true for any quantitative reconstruction method, irrespective of proxy data source. Palaeoentomology has the advantage, however, that the taxonomic resolution of identifications is most often far greater than that possible for a number of other proxies.

A number of authors have attempted to either build population density functions around the original collection data, or apply general population response models to the thermal envelopes in an effort to access the information potentially contained in abundance data (e.g. Huppert & Solow, 2004). The former method is ambitious, and requires not only a considerable improvement in the amount of beetle collection data, but also the application of a number of assumptions upon that data in order to smooth it into a probability density function for the species. The quality of the underlying distribution data are variable, and spatial abundance data are rare, the majority of beetle distribution data being point finds. In addition, pitfall trap data are often biased, being the results of habitat specific surveys, and often must be statistically treated before they can be used to estimate reliably the population densities of species (Krebs, 1999; Southwood & Henderson, 2000; Brown & Lomolino, 1998). It is possible to combine species data collected by multiple methods (e.g. Graham & Hijmans, 2006), but whether abundance data simulated from this would be any more realistic than general models is difficult to assess.

Theoretically, the population density of any species will vary within its climatic range, tending to decay towards the edges of survivability. A unimodal model is often chosen to approximate this, with a central peak spread over the theoretical optimum levels of each variable. Although the models work well with a number of statistical treatments, and allow for the estimation of errors, there is limited empirical evidence supporting their use to describe abundance or population density as a response to temperature. They should therefore be treated with as much care as presence/absence models, or data based simulations, especially for broad applications over wide geographical areas. Unimodality is a reasonable assumption, but applications often ignore the potential for skewed distributions or thresholds (such as freezing) in response to variables. There has been a large amount of recent work assessing the various attempts to model the limits of species ranges in terms of environmental variables (cf. Parmesan *et al.,* 2005). A comparison of a number of models, along with an alternative to MCR for New Zealand, is presented by Marra *et al.* (2004).

At the other end of the reconstruction process is the fossil beetle assemblage which should represent the palaeoclimate in question. Due to the problems of taphonomic loss and sample representativeness, it difficult to know as to whether the abundance patterns in the sample accurately represent the species populations that were alive at the time of deposition. As a result of this, it is equally difficult to know whether the abundance data are relevant to the particular model being applied. Again, this is an issue that permeates all proxy data sources in all forms of reconstruction, and must be considered during the application of models and the interpretation of their results. One should, of course remember that "all models are wrong, some are useful" (Box, 1987: p424), and that the above concepts may still provide useful approximations to reality that allow us to model the past more accurately. More work is certainly necessary in this area, and cooperation between ecologists, (palaeo-)entomologists and biogeographers is essential.

The second of Birks' (2003) criteria not met by the MCR method in its coleopteran form is that of the reliable estimation of sample specific errors. Quaternary science is accustomed to the presentation of mean and standard deviation values for temperature reconstructions, and Atkinson *et al.* (1987) attempted to provide this from the MCR method by constructing a linear regression based correction equation. This method has problems (see section 5.2.3), and there is currently no other method used for providing a measure of the reliability of an MCR reconstruction. The use of resampling statistics may provide at least part of a solution, allowing the internal reliability of each set of species to be tested, as discussed below (5.2.6).

5.2.2 MCR and urban deposits

When reconstructing palaeotemperatures it is very important to be aware of what the assemblage in the samples represents. Climate reconstructions have sometimes been undertaken from archaeological urban deposits (e.g. Hellqvist & Lemdahl, 1996), and although there is evidence that some species in these deposits may reflect background environments (Kenward, 1985), the interpretation may be problematic. The effect of urban areas is not only to warm the ambient temperature, and often reduce the variability of annual temperatures, in a dome like 'urban heat island' (Camilloni & Barros, 1997), but also create artificially warm environments which allow species to survive in regions outside of their natural geographical range. They often provide a variety of indoor and ground level microhabitats which can support a wider fauna than the surrounding natural environment. These microhabitats often have raised temperatures, due to human activities such as heating, covering and waste disposal, which allow species that would not naturally be able to survive in the area to maintain populations. This is particularly evident from northern Europe, where work on Norse and medieval farm sites has provided considerable evidence for the artificially warmed interior of structures supporting species with more southerly origins (Buckland *et al.*, 1996). If the beetles that occupy these environments are also used to reconstruct temperatures using MCR, then they could lead to warmer reconstructions than the ambient temperature outside of the settlement. By using MCR on an urban fauna it is the temperature of these additional microhabitats that are most likely being reconstructed, and not the regional temperature, or even the urban heat island, as some would assume. The variable nature of such microhabitat creation, added to the possibilities for a context to capture individuals from them, makes it extremely difficult to interpret such an MCR signal. To try to deconstruct the fauna then into local and background components, from which different reconstructions can be made, is a dangerous game which can easily lead to a reliance on circular reasoning.

Although more work is necessary on urban deposits, it should be undertaken cautiously with respect to temperature reconstruction, which should only be undertaken along with a thorough investigation into the habitats represented by the species used for the thermal reconstruction, in addition to the environments represented by the rest of the fauna. There are many potentially interesting research angles related to archaeological deposits and biogeography, including dispersal issues and the persistence of species upon the abandonment of sites.

5.2.3 Problems with MCR correction/calibration

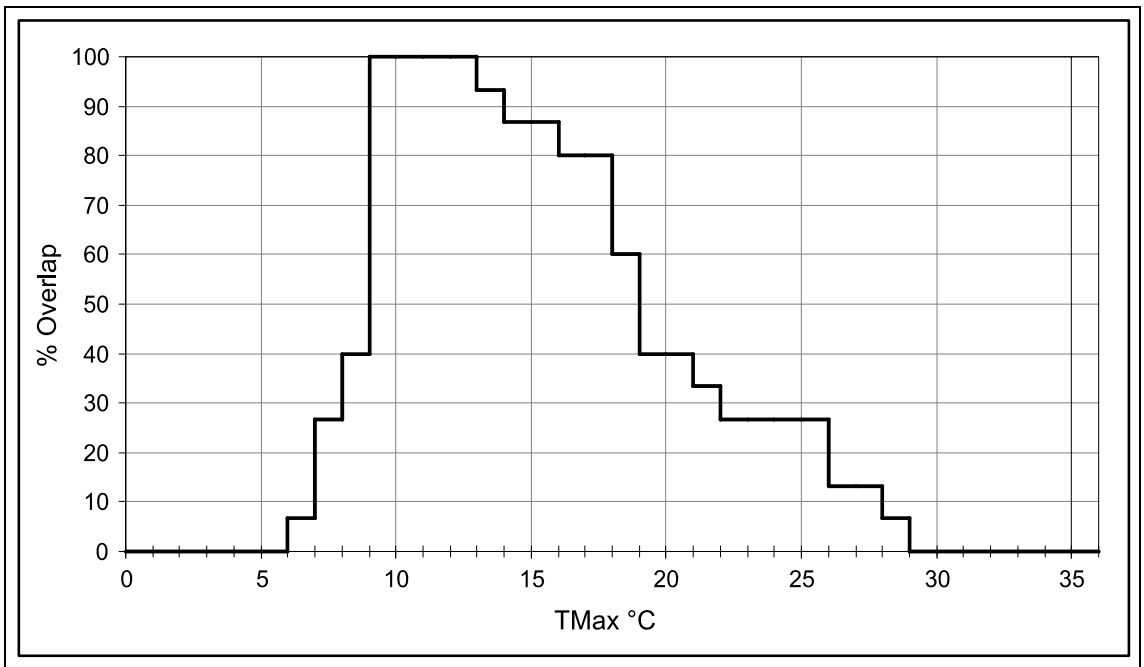
The MCR method's ability to reconstruct palaeotemperatures has been successfully validated by the reconstruction of independent modern faunas (Atkinson *et al.*, 1987). The validation method has also been suggested for correcting MCR temperatures to compensate for the systematic bias exhibited by MCR values when tested on an independent modern dataset. The calibration technique uses linear regression of median values to derive formulae for correcting TMax for its tendency to reconstruct the summers warm climates as too cold, and TMin for its tendency to underestimate the severity of cold climates. It is also often cited as the most probable value of the MCR, with the corrected values providing "...unbiased estimates of the most probable palaeoclimate within the MCR..." (Atkinson *et al.*, 1987: p588; but see also Walkling & Coope, 1996 and Coope *et al.*, 1998, where the equation is refined). Unfortunately this is not true. Due to the binary nature of the species thermal envelopes (Figure 5.2), each and every grid square is equally probable to represent a climate in which the species can survive. A consequence of this is that the area of maximum overlap for any group of species also represents a uniform probability surface (Figure 5.7) – there is nothing in the method that allows for one grid cell of this area to be more probable than any other, including the median value. In addition, the median, defined as the middle value between the extremes of an envelope, may not necessarily be the most appropriate measure of centre for either a species envelope or an MCR, due to the non-symmetrical nature of the matrices, and the variable nature of their source data.

A further problem with the calibration method is the assertion of precision (c. ±2°C for TMax and c. ±5°C for TMin), which, although correctly derived for the regression equation, it is doubtful as to whether these values can be reliably transferred to other reconstructions. Standard deviation is the

RMS (root mean square) deviation of values from an arithmetic mean, in this case derived from the linear regression comparing reconstructed medians with independent modern data. The errors, then, are for the calibration attempt, and not the actual reconstructed medians themselves. In addition, the quality of the species envelope data is variable, and hence assemblages will vary in their internal reliability. The quantification of the internal reliability of assemblages is discussed below (5.2.6), but such errors are difficult to assess, and an evaluation of individual envelope reliability (as suggested in Perry, 1986) should be used to better quantify errors.

An alternative to calibrating the median would be to calibrate the range limits (TMaxLo, TMaxHi, etc.), in the same way as described above. Unlike the median, range limits are significant values, representing the outer bounds of the uniform area of greatest overlap. Testing of these values against an independent modern dataset, and the derivation of standard errors through regression could help identify the accuracy of the range boundaries. This does not, however, address the problem of quantifying the reliability of the reference data, which is a problem common to any quantitative reconstruction method, and rarely evaluated. It also represents a loss of information in that the species envelopes are not rectangular, and thus the range limits only have a limited ability to describe them.

The question still remains as to whether there is actually any real reason for trying to estimate the most probable value within the range. Palaeoecological samples, especially those taken for beetles, almost always encompass a variable time depth, from a moment in time in some archaeological deposits (the 'Pompeii effect' (Schiffer, 1987)), to several hundred, if not several thousand years. The climate within any extended time span will most likely have varied, and in many cases an indication of the range of temperatures represented by the assemblage will be more useful than an mean value. Calculation of the mean value represents a significant simplification of the available information when compared to the range limits. The demands for mean and standard deviation, not least amongst the Quaternary community, and the desire to present more and more 'accurate' reconstructions in all measurements may be largely to blame for the aversion to specifying thermal limits.



Sample	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi	NSPEC	Overlap
s75	9	13	-27	-3	16	36	15	100

Figure 5.7. Cross section of a sample climate space map, along the TRange = 21°C line, showing % of species in each TMax 1°C climate cell. Note the square nature of the curve, and the plateau like nature of the 100 % area, indicating the equal probability of any cell in this area.

5.2.4 Ubiquity analysis

Bray *et al.* (2006) suggest the use of ubiquity analysis to refine the MCR estimates, although they do not present an actual method for obtaining temperature values. Bray *et al.* map the point occurrence data of the original MCR reference dataset into frequency of occurrence in gridded European climate cells. This grid is then used to derive a 'ubiquity score' by standardizing the occurrence of each species in a particular climate cell against the frequency of occurrence of the climate cell in Europe. The 'ubiquity score' is essentially a measure of the probability of occurrence of a particular species in a particular climate cell. Unfortunately, the method compounds the problems inherent in the irregularity of insect collection data, and produces a frequency of thermal occurrence map which is entirely tied to the accuracy of the base data. In other words the system does not show "…how much of a particular sector of climate space … a species actually occupies" (Bray *et al.,* 2006), but the relative frequency of collection of a species in a particular climate sector. Whilst the method undoubtedly has research potential, utilizing redundant information in the original dataset, it does not seem to provide any refinements to the accuracy of reconstructions as yet. In common with the original MCR method, it is also severely restricted to the range of climate space cells available in the original dataset, and its ability to extrapolate beyond appears limited without addition to the MCR base data. Criticisms aside, ubiquity analysis appears to present one potential method for constructing a data based probability density function for approximating the thermal envelopes of species in more dimensions. The problems in the reliability and scope of the base, thermal envelope, dataset remain, and must be resolved before any method, no matter how it manipulates the data, can be expected to refine the accuracy of reconstructions.

5.2.5 Calculation of relative warm/cold components

The RECON software used the overlap of species envelopes with two somewhat arbitrarily selected grid cells to identify warm and cold faunal components (Table 5.5) in assemblages that provided too little overlap for MCR calculation (Perry, 1986). This could be used to help provide information on thermal anomalies with shorter durations than the resolution of the samples, separate out the extreme components of a gradient, or identify other reasons for the non-overlap situation. These cells had "...no intrinsic merit" (Perry, 1986), and gave a somewhat abstract division of assemblages, and, although useful, limited the investigative power of the function.

Table 5.5. Warm/Cold reference cells used in RECON.
Reproduced from Perry (1986:131).

	TMax	TRange
Warm reference	17 - 18°C	19 - 20°C
Cold reference	8 - 9°C	30 - 31°C

These reference values are most certainly not adequate for dividing all assemblages, and a system has been devised, through the work behind this thesis, to use the centre of gravities (COG)[viii] of the individual species envelopes to define the warm/cold reference cells on a sample by sample basis. BugsMCR calculates a sample specific COG using all the species in a sample, and then compares the relative warm/cold position of each species envelope COG to this. As there are a number of options for calculating a COG, this allows for some flexibility and experimentation in the resolution of warm/cold faunal components. It also provides the possibility for a more context specific breakdown of non-overlap assemblages, which may help resolve the reasons behind the diversity of the fauna. Most importantly, it allows for the separation of relative measures of warm/cold, e.g. a relatively cold and relatively warm component within a generally warm phase. This could possibly be especially useful in helping to resolve short duration events, such as the 8 200 cal. yr BP event.

[viii] Note that this should not be confused with the envelope means or medians, which are specific measures of central tendency, and can be used as methods in the calculation of a COG.

Care must be taken, however, as was equally the case when using RECON, not to give these experimental reconstructions the same worth as those calculated from full assemblages. The COG of the unsymmetrical binary species envelopes is in itself somewhat arbitrary, and although it has useful scientific value, there is no statistical foundation behind it at present. This module is currently incomplete, but will be made available in the near future as an experimental tool.

5.2.6 The use of jackknifing to investigate or enhance the reliability of results

The lack of standard error calculation in the MCR method has lead to some criticism of its use, and MCR is sometimes overlooked as a viable quantitative method as a result of this (e.g. Birks, 2003). Apart from the successful testing of the method against independent modern data (Atkinson *et al.*, 1987), from which the regression based correction technique described above (section 5.2.3) is derived, the MCR method, as applied to beetles, has no internal verification capacity. Although Witte *et al.* (1998) use bootstrapping and Monte Carlo simulations to test the reliability of thermal gradients derived through MCR, no attempt has been made to test the reliability of the MCR reconstructions themselves using resampling.

The resampling method of jackknifing, or leave-one-out analysis, has been used in a variety of fields to provide a measure of internal reliability of data sets (e.g. Manly, 1997). Improvements in computer performance have been instrumental in the increasing use of resampling methods, which are by their nature computationally intensive. The system described below has been developed, and tested, but is not in a state sufficiently advanced or understood to be comprehensively utilized. There are still many questions that need to be answered on the validity and interpretation of the results, and these will be presented in a forthcoming publication. The intention is to construct software that is able to provide an indication of the reliability of reconstructed sample temperature range limits (TMaxHi, TMaxLo, etc.). A worked example is provided in Chapter 6, and a more detailed examination of a single sample from the Saint Bees' site (Coope & Joachim, 1980) is given below.

Resampling techniques are a set of conveniently simple methods for simulating larger datasets using only the data available, and in many cases providing confidence intervals for the results obtained. A number of resampling methods are available, but few are useful on presence/absence data. Jackknifing works, as do most resampling methods, by duplicating the current dataset with a minor variation, and then running the original calculations on the new dataset. In the case of jackknifing, the variation is caused by the removal of one data item, or in our case taxon, and replacing it before removing the next. The process is simple, as follows:

1. Calculate MCR on the full dataset
2. Remove first taxon, and calculate MCR on the reduced dataset (MCR_{J1})
3. Replace the first taxon, remove the second, and calculate MCR on the new reduced dataset (MCR_{J2})
4. Repeat the process for all taxa, so that a set of MCR_{Ji} results is created
5. Calculate statistics and limits from the results

The computer implementation is equally simple, in the form of a couple of nested loops and counters to provide the taxon removal sequence, and simply calling the existing MCR calculation module on each inner loop. The manipulation of the output data, which is geometrically proportional to the number of taxa in each sample, however, is not so simple. After initial tests using tables and queries, a VBA solution was arrived at, due to the former leading to enormous expansion and instability in the database. The routine performs calculations entirely in arrays in memory, and dumps results into a prepared MS Excel file. Statistics are similarly calculated from the results array, stored in a new array, and then dumped to MS Excel. A number of worksheets are used to organize the output so that it is more manageable, and the user can select which of these to include (see Figure 5.5). Results are also output in a form which may easily be graphed using MS Excel's built in 'Stock Market Open-High-Low-Close' chart (Table 5.6), although some additional manipulation may be necessary to produce ideal graphics (Figure 5.8).

The results of each jackknifed calculation are exported, to allow users to examine the implications of each and every species removal. In the example provided below (Table 5.7), it can be seen that only the removal of two species (in *italics*) lead to a change in the MCR reconstruction. The example represents a stable reconstruction, where only about 5.7 % of the species removals cause a change in the reconstructed temperatures. The two species concerned, *Helophorus sibiricus* (Mots.) and *Boreaphilus henningianus* Sahl., both have arctic distributions that extend into Siberia (Hansen, 1987; Mani, 1968), but they affect the MCR in slightly different ways. The hydrophilid *H. sibiricus* has a poorly defined thermal envelope, but appears to prefer a more continental climate, and its removal expands the TRange lower limit, suggesting a very slightly less continental climate. Its removal also decreases the upper value of TMin by 1°C, suggesting slightly colder winters, although this is probably a consequence of the approximate nature of the TRange extension of the envelope. *B. henningianus* is a relatively cold stenothermic wetland species, the removal of which leads to a slightly warmer TMax, colder TMin and more continental TRange, the last two being a consequence of each other. Closer examination of the MCR output shows that removal of this species highlights a bimodality in the overlap matrix, symptomatic of mixed faunas, which would require further investigation if this experiment was to be followed up. *Calathus erratus* (Sahl.) (in bold in Table 5.7) could be responsible for this, being the only species who's removal leads to 100 % overlap of the remaining species envelopes. It is a relatively warm and eurythermal species when compared to the rest of the fauna.

Where one sample is being examined, the extended limits produced by the jackknifing routine can be plotted on a single graph for convenience (Figure 5.8), or overlain onto the standard TMax and TMin graph where a sequence of samples are examined (see example in Chapter 6). The percentage of species the removal of which causes a change in the reconstructed temperatures, output as *PctSppTDiff* in the results files (Table 5.8), may in itself be a useful indication of the internal reliability of samples. Jackknifing gives the opportunity to produce a number of other statistics from the resampled results, some of which may be used to assess the stability of TValues with species removals.

Table 5.6. Jackknife statistics for sample s50, Saint Bees (Coope & Joachim, 1980), calculated from the results shown in Table 5.7. See Table 5.8 for more details.

Sample	Stat	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi
s50	MCRStd	12	13	-6	-3	16	18
s50	MCRJackBot	12	13	-8	-3	15	18
s50	MCRJackTop	12	14	-6	-2	16	21
s50	VJack	0	0.94	3.77	0.94	0.94	8.49
s50	BJack	0	0.97	-1.94	0.97	-0.97	2.91
s50	MCRJackMean	12	13.03	-6.06	-2.97	15.97	18.09
s50	PseudoMean	12	12.03	-4.06	-3.97	16.97	15.09
s50	SEJack	0	0.97	1.94	0.97	0.97	2.91
s50	BRedJack	12	12.03	-4.06	-3.97	16.97	15.09

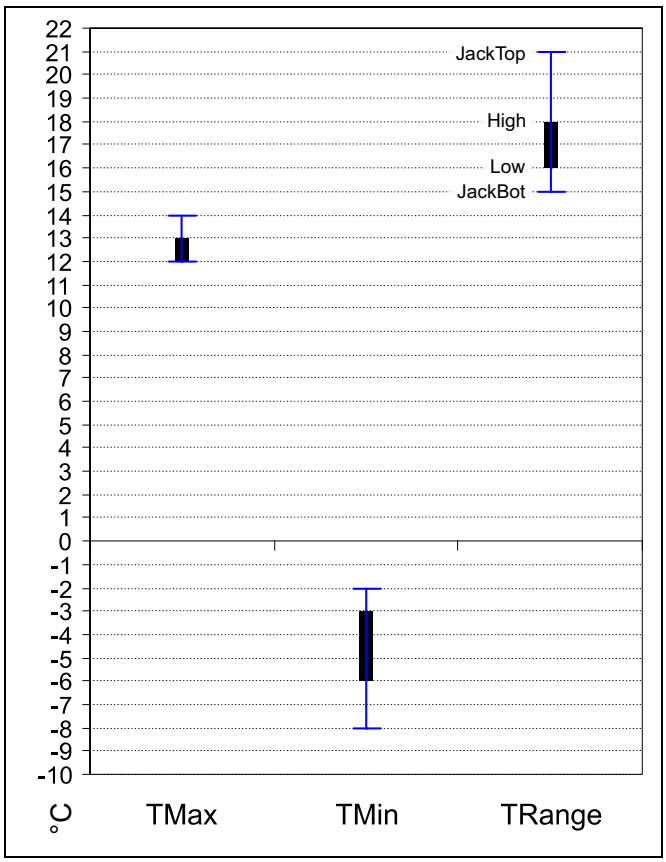


Figure 5.8. Chart showing jackknife limits for all temperature variables for Saint Bees sample s50. The thick bars show the standard MCR results, and the extensions the jackknife extremes. The source data is presented in Table 5.6.

Table 5.7. Jackknife process output for sample s50, Saint Bees site, slightly modified as follows: Species whose removal causes a change in the TValues are in *italics*; species whose removal leads to a 100 % overlap area are in **bold**.

Sample	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi	NSPEC	Overlap	NSpecRemoved	RemovedCODE1	Species
s50	12	13	-6	-3	16	18	35	97.14286	0		
s50	12	13	-6	-3	16	18	34	97.05882	1	1.00401	Carabus problematicus
s50	12	13	-6	-3	16	18	34	97.05882	1	1.021001	Epaphius secalis
s50	12	13	-6	-3	16	18	34	97.05882	1	1.029092	Bembidion doris
s50	12	13	-6	-3	16	18	34	97.05882	1	1.032001	Patrobus septentrionis
s50	12	13	-6	-3	16	18	34	97.05882	1	1.032002	Patrobus assimilis
s50	12	13	-6	-3	16	18	34	97.05882	1	1.051019	Pterostichus nigrita
s50	12	13	-6	-3	16	18	34	97.05882	1	1.051022	Pterostichus minor
s50	**12**	**13**	**-6**	**-3**	**16**	**18**	**34**	**100**	**1**	**1.056002**	**Calathus erratus**
s50	12	13	-6	-3	16	18	34	97.05882	1	1.056006	Calathus melanocephalus
s50	12	13	-6	-3	16	18	34	97.05882	1	1.062028	Agonum fuliginosum
s50	12	13	-6	-3	16	18	34	97.05882	1	1.0620285	Agonum consimile
s50	12	13	-6	-3	16	18	34	97.05882	1	4.007002	Hygrotus inaequalis
s50	12	13	-6	-3	16	18	34	97.05882	1	4.007003	Hygrotus quinquelineatus
s50	12	13	-6	-3	16	18	34	97.05882	1	4.0080015	Hydroporus notabilis
s50	12	13	-6	-3	16	18	34	97.05882	1	4.008005	Hydroporus tristis
s50	12	13	-6	-3	16	18	34	97.05882	1	4.008012	Hydroporus erythrocephalus
s50	12	13	-6	-3	16	18	34	97.05882	1	4.023022	Agabus congener
s50	12	13	-6	-3	16	18	34	97.05882	1	4.0230261	Agabus arcticus
s50	12	13	-6	-3	16	18	34	97.05882	1	4.024005	Ilybius subaeneus
s50	12	13	-6	-3	16	18	34	97.05882	1	4.027001	Colymbetes fuscus
s50	12	13	-6	-3	16	18	34	97.05882	1	5.002003	Gyrinus marinus
s50	*12*	*13*	*-6*	*-2*	*15*	*18*	*34*	*97.05882*	*1*	*7.0050065*	*Helophorus sibiricus*
s50	12	13	-6	-3	16	18	34	97.05882	1	9.003019	Cercyon tristis
s50	12	13	-6	-3	16	18	34	97.05882	1	9.008001	Hydrobius fuscipes
s50	12	13	-6	-3	16	18	34	97.05882	1	9.015001	Chaetarthria seminulum
s50	12	13	-6	-3	16	18	34	97.05882	1	23.0120013	Pycnoglypta lurida
s50	12	13	-6	-3	16	18	34	97.05882	1	23.024001	Deliphrum tectum
s50	12	13	-6	-3	16	18	34	97.05882	1	23.026004	Olophrum fuscum
s50	12	13	-6	-3	16	18	34	97.05882	1	23.026006	Olophrum assimile
s50	12	13	-6	-3	16	18	34	97.05882	1	23.0260081	Olophrum boreale
s50	12	13	-6	-3	16	18	34	97.05882	1	23.028001	Eucnecosum brachypterum
s50	12	13	-6	-3	16	18	34	97.05882	1	23.030001	Acidota crenata
s50	12	13	-6	-3	16	18	34	97.05882	1	23.033003	Geodromicus nigrita
s50	*12*	*14*	*-8*	*-3*	*16*	*21*	*34*	*97.05882*	*1*	*23.038001*	*Boreaphilus henningianus*
s50	12	13	-6	-3	16	18	34	97.05882	1	23.117017	Tachinus corticinus

Table 5.8. Statistics calculated by the BugsMCR jackknife routine.

Abbreviation	Description
MCRStd	Standard MCR calculation results (TMaxHi, TMaxLo etc.)
MCRJackTop and MCRJackBot	The extreme values created by the jackknifed calculations
MeanOverJ	The mean maximum percentage overlap produced by the jackknifed faunas
PctSppTDiff	The percentage of species whose removal caused a change in any of the temperature variables
Jackknife statistics	For each variable, the following are calculated from the jackknife results: VJack – jackknife variance BJack – jackknife bias MCRJackMean- mean temperature of the jackknife values PseudoMean – used only in calculations SEJack – jackknife standard error BRedJack – Bias reduced jackknife TValue

Preliminary testing on a small number of sites suggests that jackknife standard error (SEJack) is often loosely proportional to 1/NSpec, and that PctSppTDiff is generally proportional to 1/log(NSpec), although this may be strongly influenced by the choice of test sites. More work is needed before the accuracy, usefulness or even validity of the other statistics can be discussed, although the system appears to work at least as an informal investigative tools.

5.2.6.1 Multiple removal jackknifing as a reliability index

As an experiment, the jackknifing routine was enhanced so that an increasing number of species could be removed on consecutive passes, a method sometimes known as delete-d, or multiple delete-d jackknifing. In other words, after running a jackknifed MCR with each and every taxon removed individually, the routine was run again with each and every combination of two taxa removed, then three, and so on, until the number of taxa in the sample was reached. This could then be used to plot changes in reconstructed temperature values against numbers of taxa removed, and thus provide an indication of the reconstruction stability inherent in a fauna.

This is an extremely computer intensive routine, but is proving to provide some interesting results. Preliminarily, it can be seen that faunas display threshold numbers beyond which reconstruction quality declines, although it is too early to say if there are any patterns related to the type of faunas involved. The reconstruction of some samples, most likely those that cover climatic gradients, the pattern appears to be more complex, and the data management involved in interpreting these is proving restrictive. New summary measures and automated data manipulation routines will be programmed, and this work will be published separately in the near future.

5.2.6.2 Potential problems with jackknifing and MCR

Whilst the jackknife processes outlined above undoubtedly produce useful results for investigating the implications of the species used in a reconstruction, there is a possibility that some of the statistics are invalid under certain situations. In particular, jackknifed MCRs that produce no thermal values will upset jackknife means, unless they are excluded from the calculations. Jackknife estimators may also not be valid where resampling gives the same values as standard calculations (MCR) (M. Ekström, *pers. comm.*), although this must be investigated more thoroughly. There is, however, evidence that delete-d jackknifing can provide more consistent standard errors than the standard jackknife (Chi & Russell [online], 1999), although as to whether this is true for MCR data is yet to be thoroughly investigated.

In addition, jackknifed values rarely lead to a reduction in the apparent extent of the area of maximum overlap, as defined by the temperature values. This is methodologically logical where simple sample

overlaps are concerned, but the effects of more complex, multimodal overlap scenarios on the statistics require further examination at the individual sample level.

5.3 Conclusions and Future Directions

An advantage of the MCR method is that it calculates on the presence/absence of species, which allows for reconstructions based on very low abundances. In fact, abundance has no effect on reconstructions, although this in itself could be considered as detrimental to the method's ability to provide error estimations for reconstructions. The current state of knowledge on the effects of climate on the relative abundance of all species is, however, too poor for this aspect of the MCR method to be developed further without a considerable amount of work on the primary dataset. There have been recent attempts to extract a probability based abundance surrogate, in the form of the probability of occurrence (presence) of taxa in European gridded climate cells, under the name of ubiquity analysis (Bray *et al.*, 2006). Although this method reveals interesting information on the climate preference of the taxa *as represented in the MCR dataset*, it has a number of problems which currently prevent it from improving on the existing MCR method. The probabilities derived are limited to the scope of the dataset, a problem common to any method that derives secondary calibration data from the primary calibration set[ix]. The use of resampling methods can provide a measure of reliability by supplementing an independent control dataset with (at least n-1) resampled calculations, and may thus be able derive resampled standard errors.

What is essential at this point is an expansion of the calibration set to include more species, especially continental ones, and a refinement of the envelopes for the existing species. With present day computing power, there is little need for the 1°C cell resolution, and more complex envelopes can be stored and manipulated relatively simply due to improvements in database management and programming tools (although one could question whether a greater resolution would actually lead to a *real* increase in reconstruction accuracy). The collation of this data would, as always, probably be the most time consuming part of the development. The original thermal envelopes used in the construction of the MCR dataset were compiled through examination of a variety of published distribution maps, museum records and collection reports spanning c. 150 years of collection data (Perry, 1986). The reliability of this data is variable, and there is a need to reassess and supplement them with more modern data. In addition, it is now possible, through the increase in commonly available computer power, to match collection dates against high resolution climate data and improve on the accuracy of the envelopes.

The expansion of the dataset to include phytophagous species would expand the usefulness of the method into other aspects of entomology, although because distribution may be limited by host plant their inclusion might cause theoretical problems in the reconstruction of Quaternary climates. The option to exclude these species from reconstructions would ensure backward compatibility with previous reconstructions.

There are a number of alternative systems for climate reconstruction from fossil insects evolving around the world (e.g. Huppert & Solow, 2004; Marra *et al.*, 2004; Bray *et al.*, 2006; Porch, 2006). Each method appears to have its own set of advantages and disadvantages, and it is unlikely that any single method will be universally applicable for all regions and timescales. The comparison of methods is essential, including a rigorous understanding of the quality of the primary data for each, in assessing the most appropriate methods.

[ix] Much in the same way that ordination of fossil assemblages can only reveal grouping within the assemblage itself, and cannot provide an indication of the presence of these groupings in relation to habitats not represented by the fauna.

6 Case Studies – testing BugsCEP with real data

This chapter presents the application of BugsCEP to specific research problems. It compares the results and usefulness of the software with published modern and fossil work, and presents the analysis of this author's own investigations (Hemavan and Lockarp). Although BugsCEP is primarily aimed at palaeoecology, the testing of its features on modern data sets is essential in order to understand and validate the results produced by the BugStats system. The tools may also be of use to ecologists, especially when investigating faunal changes over time. The sites which are the topic of the primary discussions are shown in Figure 6.1, and readers should refer to the BugsCEP software for the location of any other sites mentioned.

The BugStats diagrams presented here have been tidied up, but the representation of the data is the same as the files exported by BugsCEP, and all results, unless otherwise specified, are reproducible through the program. There will be little discussion of confidence intervals or error margins associated with either the environmental reconstructions or the correlation coefficients calculated below. It is doubtful whether this would be meaningful for the reconstructions, given the semi-quantitative nature of the BugStats system (see Chapter 4). Confidence intervals for the correlation coefficients have been omitted for the sake of brevity, and due to the fact that these are only used as general indicators to support the patterns of sample similarities observed in the EcoFig diagrams.

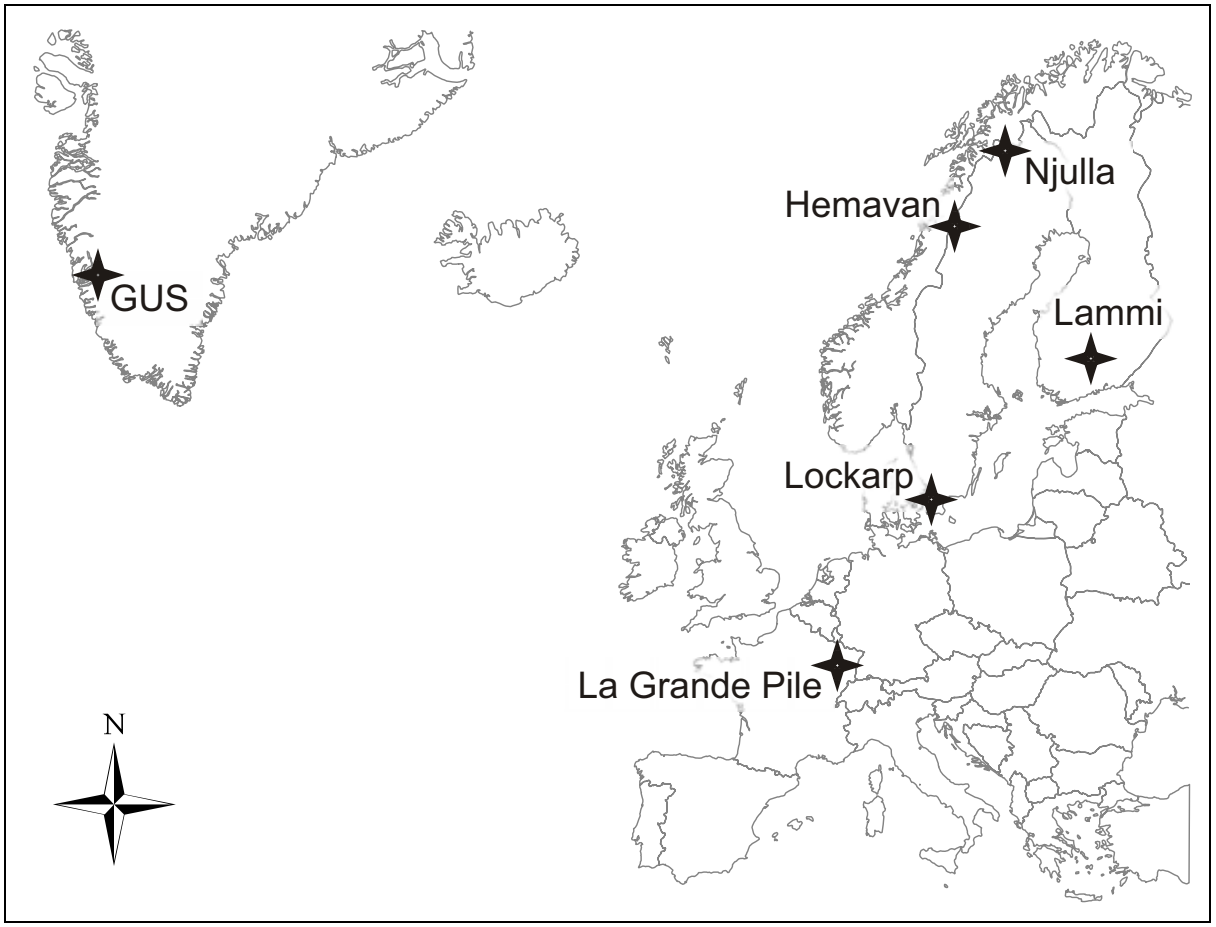


Figure 6.1. Map of case study sites discussed in this chapter. See BugsCEP for the location of other sites mentioned.