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Mammal associations in the Pleistocene of Britain: Implications of Ecological Niche Modelling and a Method for Reconstrucing Palaeoclimate

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The climatic envelope of a species is a multivariate space whose axes are climatic variables and whose boundaries are the upper and lower values of those variables that occur within the species' geographic range. If climate limits the geographic ranges of species, then the climate envelope can be used to predict which ones will occur together in a palaeofauna or to reconstruct palaeoclimate based on the species found in a fossil site. We evaluated these possibilities using ten living mammal species, four that are now found in cold climates (*Alopex lagopus*, *Lemmus lemmus*, *Ovibos moschatus* and *Rangifer tarandus*), three that are now found in warm climates (*Crocuta crocuta*, *Panthera leo*, and *Hippopotamus amphibius*), and three that are broadly spread through temperate climates (*Arvicola terrestris*, *Cervus elaphus*, and *Sus scrofa*). The WorldClim dataset of 19 climatic variables was used to characterize climate distributions for the 10 species. Out of the 45 possible pairings of the 10 species, 22 pairs have geographic ranges that do not overlap, but only 12 pairs have climatic envelopes that do not overlap. We looked at 22 palaeofaunas from the British Quaternary palaeofauna: 44% of them had species whose climatic envelopes do not overlap today (these are climatically 'non-analogue' or 'disharmonious' faunas), whereas 82% of the faunas had species whose geographic ranges do not overlap (these are geographically non-analogue faunas). The 'index of disharmony' (I_R) was $I_R = 0.38$ when geographic non-overlap was used as a criterion (higher than in similar aged North American faunas) but only $I_R = 0.12$ when climatic non-overlap was used. A maximum-likelihood function was used to estimate the most probable climate for the 22 palaeofaunas based on the modern climatic distribution of the 10 species. The reconstructions were generally compatible with other quantitative estimates of palaeoclimate at the same sites.

Keywords: Britain, climate envelope, *Crocuta crocuta*, mammals, palaeoclimate reconstruction, *Panthera leo*, Quaternary.

1. Introduction

The climatic envelope of a species is a multivariate space: its axes are climatic variables; its boundaries are the upper and lower values of those variables that occur across the species' geographic range; and its purpose is to describe the climatic limits experienced by the species. Many studies equate the climate envelope with a species' niche, but it is only when the factors that limit the existence of the species are, in fact, climatic that the climate envelope is a good proxy for the fundamental niche in the Grinnellian sense, in other words that the envelope describes the full range of climate conditions that permit a species to live (Hutchinson, 1957; Soberón and Peterson, 2005; Soberón, 2007).

Climate envelopes and Grinnellian fundamental niches are implicit in the notion of "non-analogue" Pleistocene faunas. Non-analogue faunas are ones which contain combinations of species that today do not have overlap in their geographic ranges (Hibbard, 1960; Lundelius *et al.*, 1983; Graham and Mead, 1987; Lundelius, 1989; Webb and Barnosky, 1989; Graham *et al.*, 1996; Alroy, 1999; Stewart *et al.*, 2003; Bell *et al.* 2005; Graham, 2005; Stewart, 2008). Non-analogue species are conflicting indicators of palaeoenvironment because they imply that two environments, as they are recognized today,

A. *Alopex lagopus* (Arctic Fox)

F. *Lemmus lemmus* (Norway Lemming)

B. *Arvicola terrestris* (Water Vole)

G. *Ovibos moschatus* (Musk Ox)

C. *Cervus elaphus* (Red Deer)

H. *Panthera leo* (Lion)

D. *Crocuta crocuta* (Spotted Hyaena)

I. *Rangifer tarandus* (Reindeer)

E. *Hippopotamus amphibius* (Hippo)

J. *Sus scrofa* (Wild Boar)

Figure 1. Approximate modern geographic ranges of the species included in this study (red).

overlapped in the past such that species could coexist that cannot live together today. This environmental interpretation of non-analogue faunas assumes that species had the same climate envelopes as they do today, that their geographic range is and was determined by their climate envelopes, and that the non-analogue palaeoclimate had a different combination of climate values than exists today (Jackson and Overpeck, 2000). If these assumptions are correct, then it follows that (1) species found in association in the past will have overlapping climate envelopes today, even if their geographic ranges do not presently overlap; and that (2) the palaeoclimate of a site should be predictable from the combined climate envelopes of the species that lived there, regardless of whether the palaeofauna is non-analogue or not. These principles implicitly form the basis on which palaeoenvironments are reconstructed from the species found in the fossil record, principals that we explore in this paper.

Fossil faunas and floras have been used to infer palaeoclimate in many ways, both qualitative and quantitative. While plants, insects and reptiles are the most established taxa for reconstructing past environments (*e.g.*, Stuart, 1979; Atkinson *et al.,* 1987; Wilf *et al.*, 1998; Grandjouan, 2000; Jackson and Overpeck, 2000; Head *et al.*, 2009), mammal remains have a long-established and expanding role in palaeoclimatic inference (*e.g.*, Hokr, 1951; Legendre, 1986; Janis *et al.*, 2000; Fortelius *et al.*, 2002; Stewart *et al.*, 2003). Most but not all of the approaches for reconstructing past climates from mammal fossils depend upon a species' geographic range being correlated with one or more climate parameters such as temperature (mean annual, maximum, minimum), precipitation (total annual, driest month, wettest month) or seasonality. Classic approaches to climate inference from mammal faunas range from qualitative assessments of warm or cold environments based indicator species such as reindeer, lemming, musk-ox or hippo (*e.g.*, Koenigswald, 2003) to the more complicated matching of a fossil fauna to the modern geographic location of its most similar living fauna (*e.g.*, Semken and Falk, 1987).

In this study, we evaluated the climate and the faunal associations of selected British Quaternary sites on the basis of ten key species that are still living today (**Figure 1**). We studied four species that now live in cold climates (*Alopex lagopus*, *Lemmus lemmus*, *Ovibos moschatus* and *Rangifer tarandus*), three that now live in warm climates (*Crocuta crocuta*, *Panthera leo*, and *Hippopotamus amphibius*), and three that are broadly spread through temperate climates (*Arvicola terrestris*, *Cervus elaphus*, and *Sus scrofa*). Based on our ten key species: (1) we determined which combinations of species are geographically and climatically non-analogue today; (2) we determined what geographic areas in the world today have climates compatible with each species' modern climate envelope (this determination is usually known as "ecological niche modelling", but we refer to it here as "bioclimatic niche modelling" to emphasize that we are only looking at climatic variables); (3) we identified British Quaternary sites that had three or more of the ten species present and determined which of those had geographically and climatically non-analogue faunas; (4) we estimated climatic parameters for those sites based on the modern climatic envelopes of the key species found there; and (5) we evaluated the implications of the Quaternary associations for the assumptions of ecological niche modelling, especially whether species coexisted that do not have overlapping climate envelopes today.

2. Materials and Methods

2.1 Extant mammals

Ten extant mammal species were analysed: *Alopex lagopus*, the arctic fox; *Arvicola terrestris*, the water vole; *Cervus elaphus*, the red deer (also known as wapiti or elk in North America); *Crocuta crocuta*, the spotted hyena; *Hippopotamus amphibius*, the hippo; *Lemmus lemmus*, the Norway lemming; *Ovibos moschatus*, the musk-ox; *Panthera leo*, the lion; *Rangifer tarandus*, the reindeer (or Caribou in North America); and *Sus scrofa*, the wild boar. These species were chosen because they are found in British Quaternary fossil sites and today they represent polar, temperate and tropical biomes.

The geographic ranges of the species were derived from World Wildlife Fund's species distributions (WWF WildFinder, http://www.worldwildlife.org/science/). The ranges are based on occurrences lists for the ecoregion divisions of Olson et al. (2001). Ecoregions are contiguous regions across which environmental conditions are similar, as are the fauna and flora. The ranges from this data set are estimated by identifying the ecoregions where the species is present and then making the assumption that the species distribution is ecoregion-wide. The ranges used here are thus overestimated, covering a larger geographic region than is actually inhabited by the species; this is unproblematic for this study because the range of climatic conditions associated with the species is not affected by these extensions (since the additional areas belong to the same ecoregions, which have by definition the same climate) and because the ranges estimated here are only minorly different from ranges reported in the literature. For further details see Olson et al. (2001). Even though some species, such as the lion, had a wider geographic range in the recent past, we purposefully chose to use current geographic ranges rather than Holocene ones because climate is continually changing and we wanted our geographic ranges and climate data to match.

We converted the WildFinder data to a gridded format with a resolution of 0.5º latitude and longitude for grid cells (ca. 55 km at the equator, 720 x 360 cells) and recorded all the species present within each cell. When more than one ecoregion was included in the area of a cell, we chose the ecoregion with the highest proportion of area within the cell. After the conversion we exported all the grid cells associated with each of our species. The resulting geographic ranges are shown in **Figure 1**.

2.2 Climate data

We used the WorldClim global climate data set as the basis for our climate envelopes. The data consist of temperature and precipitation layers for the period 1950-2000 (see Hijmans et al., 2005 for information on the original sources of the data and their processing of those data). GIS layers for these data were obtained the DIVA climate format from http://www.diva-gis.org/climate.htm (2.5 minute resolution).

For climate analysis, we used the nineteen bioclimatic (BIOCLIM) variables that are contained in the WorldClim data set. These variables, which are widely used for bioclimatic niche modelling, were originally defined by Nix (1986) and modified by ANUCLIM project (http://fennerschool.anu.edu.au/) as likely to be important for limiting species ranges. The variables are: (1) mean annual temperature; (2) mean diurnal temperature range, which is the mean daily temperature range for each month; (3) isothermality, or the proportion of the mean diurnal range to the annual temperature range (Var 2 / Var 7); (4) temperature seasonality (100 * standard deviation of temperature); (5) maximum temperature of the warmest month; (6) minimum temperature of the coldest month; (7) annual temperature range (Var 5 minus Var 6); (8) mean temperature of the wettest quarter; (9) mean temperature of the driest quarter; (10) mean temperature of the warmest quarter; (11) mean temperature of the coldest quarter; (12) total annual precipitation; (13) precipitation of the wettest month; (14) precipitation of the driest month (15) precipitation seasonality, coefficient of variation of precipitation; (16) precipitation of the wettest quarter; (17) precipitation of the driest quarter; (18) precipitation of the warmest quarter; and (19) precipitation of the coldest quarter. Temperatures are in degrees Celsius and precipitation is in millimetres. Quarters are defined as the contiguous twelve-week block that maximises or minimises the variable in question. Elevation was not used as a climate variable because its primary effect is on precipitation and temperature, which are already included here.

2.3 Climate envelopes and bioclimatic niche models

Values for the 19 bioclimatic variables were extracted for each species at each grid point of their modern geographic ranges. These data were used to determine the median and range of climate conditions for each species, to construct multidimensional climate envelopes, to generate "ecological" or bioclimatic niche models, and to generate probability distributions for the climate associated with each species. Our climate envelopes were thus the volume occupied by a species in the 19-dimensional space defined by the bioclimatic variables. DIVA-GIS was used to extract data from the climate layers and to generate the ecological niche models (http://www.diva-gis.org/). All other calculations were performed in Mathematica 6.0.

We used rectilinear climate envelopes, which are orthogonal polyhedrons whose edges are linear, the length of each edge defined by the minimum and maximum values of the species on each variable (see discussion of alternative kinds of envelopes and justification for using the rectilinear envelope in section 4.2.1). We calculated envelopes for each species in two ways: first with the full range of the species on each bioclimatic variable and again after dropping the outermost 0.1% of each species' points.

The volume of climatic envelopes was calculated as the product of the lengths of each side in the 19-dimensional climatic space. Bioclimatic variables were each first standardized to have a mean of 0.0 and a variance of 1.0 (all species were pooled for the standardization). Because volumes increase geometrically with the number of dimensions, they are reported as the *n*th root of their full volume for convenience:

$$V_S = \sqrt[n]{\prod_{i=1}^{n} range_i} \ , \qquad (1)$$

where V_S is the scaled volume, n is the number of bioclimatic variables (19 in this case), and $range_i$ is the range of the species on bioclimatic variable i. As mentioned, volumes were calculated for the full set of points and with 0.1% of the outliers on each bioclimatic variable dropped.

Volumes of overlap in the climatic envelopes of two species were calculated the same way, with $range_i$ being the overlapping range on bioclimatic variable i.

Bioclimatic niche models were constructed using the BIOCLIM method (Busby, 1991) with the algorithm implemented in DIVA-GIS Version 5.2 (http://www.diva-gis.org/).

2.4 *Fossil occurrences*

British Quaternary fossil faunas that contain at least three of the ten species from the same stratigraphic horizon were identified from the Ancient Human Occupation of Britain (AHOB) database (http://AHOBProject.org/). The sites in the database are not exhaustive and there are other British faunas with three or more of our species than the ones we considered here.

2.5 *Indices of Disharmony*

Alroy's (1999) index of disharmony (I_D) was calculated for each fossil fauna based on the ten species. The index reports the proportion of non-analogue or disharmonious species pairs ("conjunctions") in a fauna as

$$I_D = C_D \,/\, (C_H + C_D) \quad , \qquad (2)$$

where C_D is the number of non-analogue pairs in the fauna and C_H is the number of analogue pairs. As Alroy (1999) pointed out, this index can be misleading because the complete mixing of species from two environments does not necessarily yield a value that even approaches 1.0: if two equal sized faunas were mixed, for example, then $I_D = 0.5$ because the species in each fauna are "harmonious" with one another. Furthermore, small sample sizes can inflate the index because a fauna of two species that happened to be non-analogous then I_D=1.0. The index can be rescaled to correct this by adjusting the denominator by the expected number of randomly harmonious pairs given the size of a fauna:

$$I_R = C_D \,/\, (C_H + C_D - C_E) \quad , \qquad (3)$$

where I_R is the rescaled disharmony index and C_E is

$$C_E = ([C_D + C_H] \,/\, M) \times (C_H \,/\, M), \qquad (4)$$

where M is the number of pairs for an N-sized fauna: $M = (N^2\text{-}N) \,/\, 2$. The normal and rescaled indices were each calculated twice for each fauna, once for geographic disharmony and once for climatic disharmony.

2.6 *Maximum-likelihood estimation of palaeoclimate parameters*

The most likely value for each of the 19 bioclimatic variables was reconstructed for each fossil site based on the combination of the ten species found there. Climate variables are highly correlated with one another (*e.g.*, mean annual temperature is necessarily correlated with the maximum and minimum temperatures), which means that estimation of any one parameter needs to be made while taking into accounts its covariances with the other variables. To do this, we first rotated the entire climate data set to the principal components (PCs) of its covariance matrix after mean centring the variables, thus creating a new set of PC climate variables that are uncorrelated with one another but which still preserve the variance and distribution of the original climate data. The eigenvectors (U) and eigenvalues (W) of the principal component axes were found using singular value decomposition; only those vectors whose eigenvalues were significantly different from zero were retained. Principal components scores were found for the climate data associated with each species by projecting them onto the principal components as

$$Y = U.T \quad , \qquad (5)$$

where Y is the matrix of PC scores, U is the matrix of eigenvectors and T is the matrix of mean-centred climate data.

A frequency distribution was calculated for each PC variable for each species based on the climate sampled from that species' modern geographic distribution. Frequency counts were made using 1000 equal-sized bins for each variable. The resulting frequency curve can be thought of as the probability of the species occurring at any given point along the PC axis, which is to say with any given combination of the correlated climate parameters that are associated with that PC:

$$P\,(species \mid cl) \quad , \qquad (6)$$

where P is the probability and cl is the bioclimatic variables associated with the PC. Because the PC axes are uncorrelated (orthogonal), their associated probabilities can be multiplied to find the most probable point in the bioclimatic space represented by the PC axes. The most likely climate at a given fossil site can be estimated by combining the probabilities off all the species that occur there using maximum likelihood (Edwards, 1992):

$$L\,(\mathrm{cl} \mid \mathrm{fauna}) = \prod_{\mathrm{i}=1}^{\mathrm{n}} P(species_i \mid cl) \quad , \qquad (7)$$

where L (cl | $fauna$) is the likelihood of the bioclimatic value given the fauna and n is the number of species in that fauna. The log-likelihood support function is thus:

$$l(cl \mid fauna) = \sum_{i=1}^{n} \log[P(species \mid cl)] + c\,, \qquad (8)$$

where l (cl | $fauna$) is the log-likelihood of the climate value given the fauna and c is a constant of proportionality equal to the maximum of the sum of the logged probabilities of the species given the climate (the constant standardizes the curve so that its maximum is zero). The most likely point for the fauna in the multidimensional climatic space can thus be obtained by maximizing Equation 8 across all the PC axes. The ML estimates on these axes are scores in the principal components space, which can be converted back into the original bioclimatic variables as

$$\hat{T} = U^T.CL + \overline{X} \quad , \qquad (9)$$

where $\hat{T}$ is the vector of 19 estimated bioclimatic parameters, U^T is the transpose of the eigenvectors, CL are the scores in the multidimensional climate space, and $\overline{X}$ is the vector of bioclimatic means that were subtracted before the eigenvectors were calculated.

3. Results

3.1 Climate ranges of extant species

Temperature and seasonality distinguish the species more than precipitation did. The histograms in **Figure 2** show the distribution of climate parameters for the points we sampled from each species' modern geographic range. The peak of each histogram shows the mode for that species, and the spread of the histogram represents the variety of climate conditions across that species' geographic range. The numbers in **Table 1** report the median condition and the total range of each species for all of the variables.

Temperature and seasonality are the variables that most strongly distinguish the three African species from two of the arctic species, arctic fox and musk-ox, but less clearly from the lemming (**Figure 2**). Interestingly, the cold extremes appear to matter more than the warm ones: maximum temperature of the warmest month, annual temperature range, and mean temperature of the warmest quarter do not separate the species as distinctly as the other temperature variables. This pattern may be similar to plants, where the length of the growing season and the winter minimum temperatures affect plant distributions more than summer high temperatures (Walther et al., 2002). Red deer and wild boar have temperature and seasonality distributions that are intermediate between the arctic and African species, overlapping extensively with both. Interestingly, the water vole's mean annual temperatures and seasonalities are more like those of arctic species than temperate ones, thanks to the water vole's Siberian range. Even though the water vole's moist microhabitats are different from the harsher ones associated with musk-ox and reindeer, the climates of all three are surprisingly similar when viewed at this coarse resolution.

Precipitation patterns do not readily distinguish any of the species (**Figure 2**). Most species have low modal values with a long tails toward the high end of all of the precipitation variables. Small parts of the ranges of the three African species have heavy rains, which produce long tails on some precipitation variables, especially total annual precipitation. The

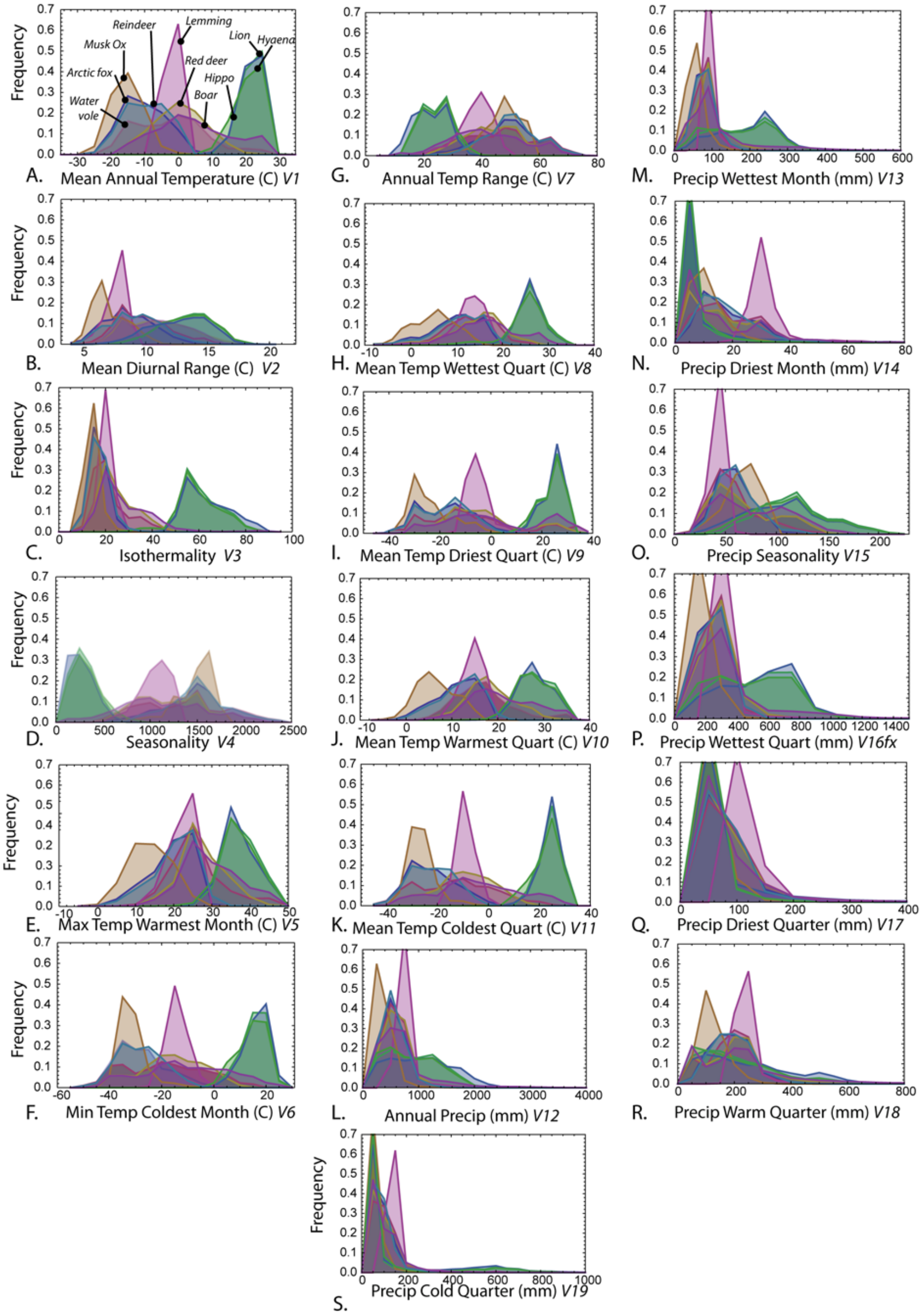


Figure 2. Histograms of the associations between the species and 19 bioclimatic variables based on their modern geographic ranges. Histograms describe the distribution of each bioclimatic variable for each species. Species are labelled A and the same colour scheme is used in B-S. The median and range of each species for all 19 bioclimatic variables is reported in Table 1.

Table 1. The median and (range) of nineteen bioclimatic variables for each of ten extant species for points sampled at 0.5º degree intervals across their global modern geographic range.

Bioclimatic Variable	*Alopex lagopus*	*Arvicola terrestris*	*Cervus elaphus*	*Crocuta crocuta*	*Hippopotamus amphibius*
Annual Mean Temp (C)	-8.1 (-23.3 - 8.9)	0.3 (-23.3 - 27.9)	2.7 (-16.6 - 27.5)	25.0 (11.0 - 30.8)	24.8 (7.4 - 30.4)
Mean Diurnal Range (C)	8.9 (4.0 - 16.1)	10.0 (4.0 - 17.3)	11.2 (4.0 - 21.3)	13.9 (6.0 - 20.5)	13.4(5.8 - 20.5)
Isothermality (100 * V2 / V7)	19.0 (11.1 - 36.1)	22.3 (13.4 - 54.6)	25.3 (13.4 - 61.7)	62.1 (39.5 - 92.2)	63.9 (42.9 - 92.2)
Temp Seasonality (100 * SD)	1439 (358 - 2366)	1319 (329 - 2366)	1167 (271 - 2343)	217 (19 - 616)	184 (19 - 678)
Max Temp of Warmest Month (C)	18.0 (-6.3 - 26.7)	22.8 (5.5 - 46.4)	24.1 (5.5 - 46.4)	34.6 (19.8 - 43.7)	33.5 (17.9 - 43.7)
Min Temp of Coldest Month (C)	-31.9 (-55.9 - -0.3)	-21.4 (-55.9 - 17.3)	-18.2 (-50.0 15.6)	14.1 (-2.1 - 22.5)	14.6 (-4.8 - 22.7)
Temp Annual Range (C) (V5 - V6)	47.8 (13.5 - 72.4)	45.8 (13.0 - 72.4)	43.3 (13.9 - 72.4)	22.1 (10.2 - 35.3)	20.5 (9.5 - 35.0)
Mean Temp of Wettest Quarter (C)	9.5 (-27.6 - 18.6)	12.5 (-8.5 - 30.1)	14.5 (-11.5 - 31.7)	25.3 (11.7 - 34.7)	25.0 (8.9 - 34.0)
Mean Temp of Driest Quarter (C)	-19.4 (-45.5 - 12.3)	-12.7 (-45.5 - 36.1)	-9.1 (-38.2 - 36.1)	23.6 (9.1 - 34.7)	23.9 (2.4 - 30.6)
Mean Temp of Warmest Quarter (C)	10.5 (-10.9 - 18.6)	15.2 (0.3 - 36.1)	16.6 (0.3 - 36.1)	26.9 (12.6 - 35.3)	26.2 (11.9 - 35.3)
Mean Temp of Coldest Quarter (C)	-25.8 (-50.0 - 2.1)	-15.3 (-50.0 - 22.0)	-11.5 (-43.8 - 20.4)	22.6 (9.1 - 28.6)	22.9 (2.3 - 28.6)
Annual Precip (mm)	389 (59 - 2939)	433 (18 - 2689)	462 (14 - 3356)	761 (13 - 3236)	899 (0 - 4139)
Precip of Wettest Month (mm)	62 (11 - 435)	66 (3 - 338)	73 (3 - 747)	181 (5 - 1033)	198 (0 - 1060)
Precip of Driest Month (mm)	13 (0 - 137)	14 (0 - 124)	12 (0 - 124)	0 (0 - 72)	1 (0 - 164)
Precip Seasonality (CV)	49.2 (10.2 - 122.2)	45.8 (7.9 - 169.9)	52.7 (7.9 - 160.0)	108.5 (25.0 - 245.7)	100.1 (0 - 346.4)
Precip of Wettest Quarter (mm)	167 (32 - 1084)	179 (9 - 965)	197 (7 - 2029)	464 (8 -2412)	510 (0 - 2514)
Precip of Driest Quarter (mm)	45 (4 -493)	49 (0 - 418)	44 (0 - 418)	2 (0 - 276)	5 (0 -582)
Precip of Warmest Quarter (mm)	161 (26 - 667)	165 (0 - 663)	181 (0 - 1782)	159 (0 - 1031)	194 (0 - 1031)
Precip of Coldest Quarter (mm)	55 (4 - 825)	67 (1 - 778)	59 (0 - 1393)	6 (0 - 2412)	14 (0 - 2514)

Bioclimatic Variable	*Lemmus lemmus*	*Ovibos moschatus*	*Panthera leo*	*Rangifer tarandus*	*Sus scrofa*
Annual Mean Temp (C)	0.8 (-5.8 - 6.7)	-12.8 (-23.3-3.5)	24.3 (6.1 - 30.8)	-6.9 (-23.3 - 11.4)	6.1 (-16.6 - 29.1)
Mean Diurnal Range (C)	8.2 (4.3 - 9.6)	7.1 (4.2 - 12.7)	13.8 (5.9 - 20.5)	9.6 (4.1 - 16.5)	11.2 (4.6 - 18.2)
Isothermality (100 * V2 / V7)	22.1 (18.0 - 31.3)	16.5 (11.1 - 30.2)	60.9 (27.3 - 92.2)	19.6 (11.1 - 42.1)	26.8 (13.4 - 92.0)
Temp Seasonality (100 * SD)	1007 (421 - 1280)	1468 (495 - 1717)	237 (19 - 832)	1435 (450 - 2366)	1019 (22 - 2343)
Max Temp of Warmest Month (C)	20.4 (9.3 - 23.9)	10.9(-6.3 - 22.7)	34.0 (16.0 - 43.7)	19.0 (-6.3 - 31.6)	25.8 (5.5 - 46.4)
Min Temp of Coldest Month (C)	-16.7 (-27.1 - -1.0)	-35.0 (-44.7 - -5.0)	13.4 (-5.6 - 22.5)	-30.9 (-55.9 - -2.9)	-14.1 (-50 - 23.6)
Temp Annual Range (C) (V5 - V6)	36.7 (15.6 - 46.4)	45.7 (18.3 - 56.3)	22.8 (9.8 - 40.2)	48.4 (17.4 - 72.4)	39.2 (7.2 - 72.4)
Mean Temp of Wettest Quarter (C)	12.2 (-8.4 - 17.7)	4.3 (-27.6 - 14.9)	24.8 (3.5 - 34.7)	10.2 (-27.6 - 22.8)	15.5 (-10.9 - 36.9)
Mean Temp of Driest Quarter (C)	-7.8 (-19.7 - 8.1)	-27.9 (-40.1 - 1.8)	23.3 (1.1 - 34.7)	-18.7 (-45.5 - 20.8)	-3.8 (-38.2 - 36.1)
Mean Temp of Warmest Quarter (C)	13.6 (3.9 - 17.7)	4.8 (-10.9 - 14.9)	26.1 (10.0 - 35.3)	11.3 (-10.9 - 22.8)	18.6 (0.3 - 36.9)
Mean Temp of Coldest Quarter (C)	-11.5 (-21.0 - 1.2)	-29.5 (-40.9 - -1.9)	21.9 (1.1 - 28.6)	-24.7 (-50.0 - 1.8)	-7.6 (-43.8 - 27.0)
Annual Precip (mm)	598 (394 - 2642)	215 (59 - 1688)	689 (13 - 3236)	393 (59 - 2230)	486 (14 - 9121)
Precip of Wettest Month (mm)	78 (55 - 327)	39 (11 - 172)	164 (3 - 1033)	64 (11 - 264)	77 (3 - 2417)
Precip of Driest Month (mm)	27 (14 - 119)	7 (0 - 111)	0 (0 - 79)	13 (0 - 129)	9 (0 - 224)
Precip Seasonality (CV)	32.9 (16.5 - 53.5)	61.6 (10.7 - 91.0)	103.0 (11.6 - 245.7)	50.9 (10.1 - 132.4)	64.2 (7.9 - 175.8)
Precip of Wettest Quarter (mm)	213 (151 - 936)	101 (32 - 452)	414 (8 -2412)	171 (32 - 653)	205 (7 - 6145)
Precip of Driest Quarter (mm)	91 (49 - 416)	23 (4 - 384)	4 (0 - 317)	45 (1 - 423)	34 (0 - 723)
Precip of Warmest Quarter (mm)	208 (142 - 559)	89 (26 - 425)	149 (0 - 1031)	164 (26 - 633)	181 (0 - 4785)
Precip of Coldest Quarter (mm)	108 (57 - 754)	25 (4 - 452)	9 (0 - 2412)	53 (1 - 609)	53 (0 - 3196)

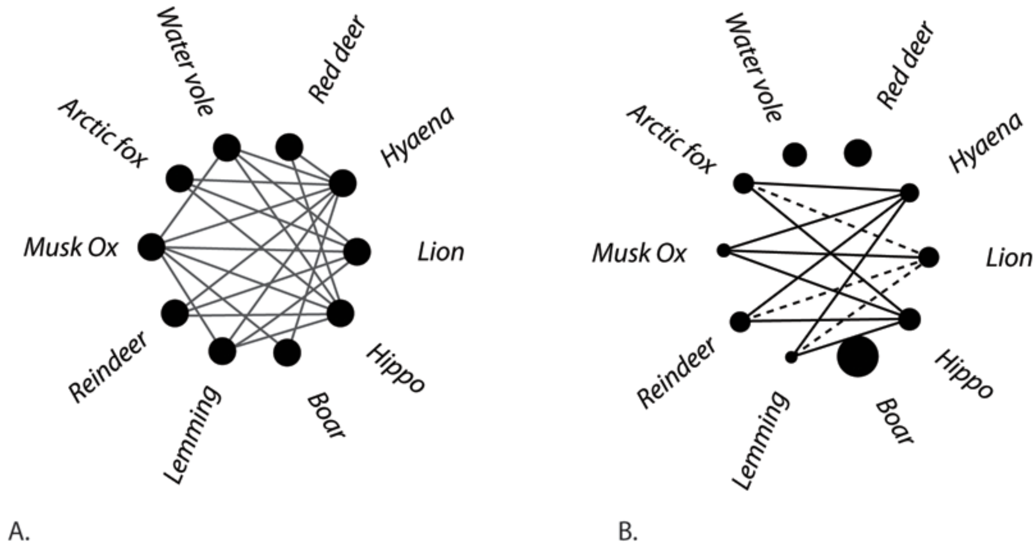


Figure 3. Non-analogue species pairs. **A.** Geographic non-analogous pairs of species. The grey lines connect species whose modern geographic ranges **do not** overlap. Geographic disjunctions are based on the ranges in Figure 1 and do not take into account historic ranges. **B.** Climatically non-analogous pairs of species. Lines connect species whose climate envelopes **do not** overlap (broken lines connect species that do not overlap when the outermost 0.1% of climatic outlying points are omitted). These species would **not** be expected to occur together in the fossil record if climate truly limits their modern distribution and if their climate tolerances have not changed over time. Species are arranged from cold-climate on the left to warm climate on the right. The diameter of the circles in part B indicates the relative volume of each species' climate envelope (volumes and overlap of climatic envelopes are reported in Table 2).

seasonality of precipitation in some parts of Africa means that modal precipitation in the wettest months is higher for the species there than elsewhere. Interestingly, the Norway lemming is the most distinctive species in terms of precipitation. The lemming's Scandinavian habitats have comparatively high precipitation year round: compared to the other Arctic species, the lemming's climate is mild, wet, and homogenous.

3.2 Geographically and climatically non-analogue species pairs

Nearly half of the species pairs have disjunct geographic ranges (22 out of 45 pairs, or 49%) (**Figure 3A**). Notably, none of the African species overlap geographically with any of the other seven species, except for co-occurrence of the lion with red deer and wild boar in northern Africa, and the North American musk-ox never occurs with the exclusively old world water vole or wild boar. When any of these disjunct pairs appear together in a palaeofauna, the result is a geographically non-analogue fauna.

In contrast, less than a third of the species pairs have bioclimatic envelopes that are disjunct if the full climate envelop is used (12 out of 45 pairs, or 27%), and only a fifth of them are climatically disjunct when the outlying 0.1% of the climate points are excluded from the envelopes (9 out of 45 pairs, or 20%) (**Figure 3B**, **Table 2**). Notice that those species envelopes that are smallest (**Table 2**) are the ones least likely to overlap with another envelope.

3.3 Bioclimatic niche models

Bioclimatic niche models for the ten extant species show which regions now have climate conditions that are compatible with the conditions experienced by these species in their modern geographic ranges (**Figure 4**). These models are essentially the climate envelopes mapped geographically using today's climate. Yellow, orange or red colours indicate areas that are highly

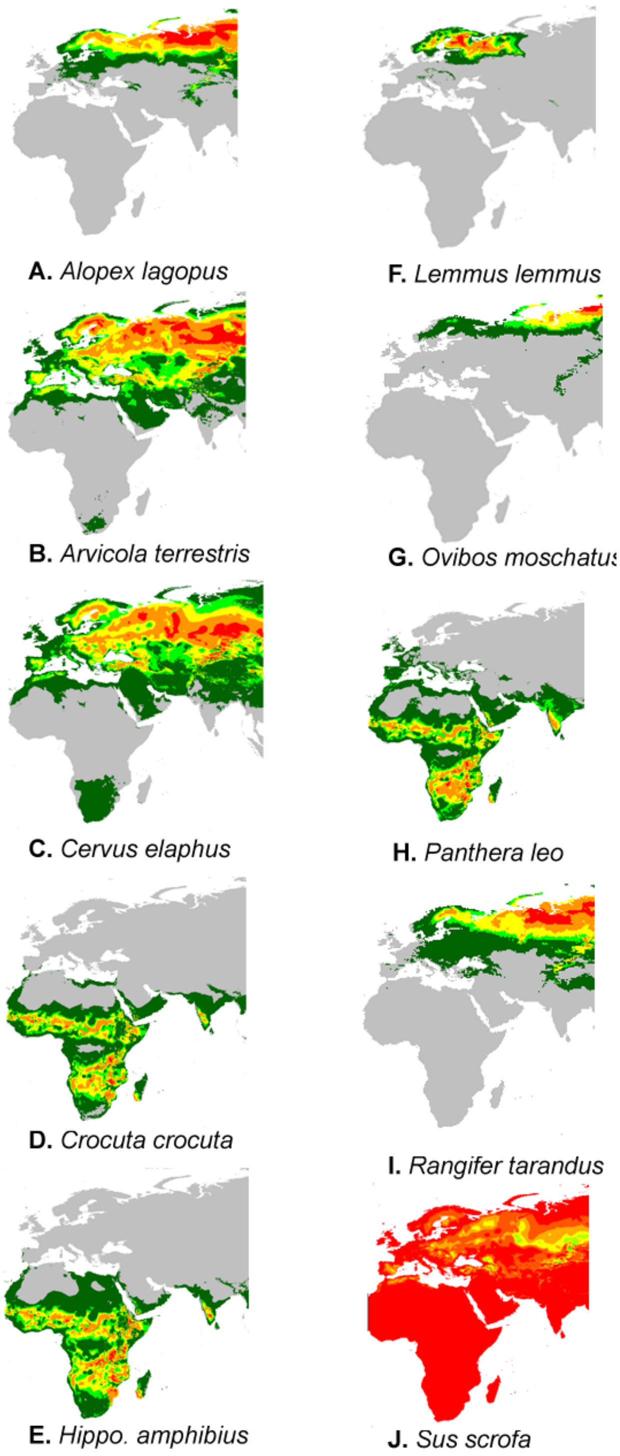
Table 2. The total volume (diagonal) and volume of overlap (off-diagonal) of bioclimatic envelopes of ten extant species. The volume of each envelope was calculated after standardizing the nineteen bioclimatic variables (mean=0.0, standard deviation=1.0). Volumes are reported as the nineteenth root of the actual volume (i.e., $\mathrm{vol}_{\mathrm{reported}}^{19} = \mathrm{vol}_{\mathrm{actual}}$).

Full envelopes

Arctic Fox	**Water Vole**	**Red Deer**	**Hyaena**	**Hippo**	**Lemming**	**Musk Ox**	**Lion**	**Reindeer**	**Wild Boar**	
4.2	3.7	3.7	0.0	0.0	2.5	2.9	1.6	3.7	3.8	**Arctic Fox**
	4.6	4.5	2.4	2.8	2.8	2.7	2.9	3.7	4.5	**Water Vole**
		5.5	2.9	3.3	2.9	2.6	3.5	3.6	5.4	**Red Deer**
			3.6	3.6	0.0	0.0	3.6	0.0	3.6	**Hyaena**
				4.3	0.0	0.0	3.9	0.0	4.2	**Hippo**
					2.3	1.7	1.0	2.4	3.0	**Lemming**
						2.8	0.0	2.9	2.7	**Musk Ox**
							4.1	1.6	4.1	**Lion**
								3.9	3.6	**Reindeer**
									8.0	**Wild Boar**

Envelopes excluding 0.1% outliers

Arctic Fox	**Water Vole**	**Red Deer**	**Hyaena**	**Hippo**	**Lemming**	**Musk Ox**	**Lion**	**Reindeer**	**Wild Boar**	
3.4	3.2	3.1	0.0	0.0	2.1	2.4	0.0	3.0	3.1	**Arctic Fox**
	4.0	3.9	1.8	2.1	2.4	2.3	2.4	3.0	3.9	**Water Vole**
		4.5	2.1	2.4	2.5	2.2	2.6	2.9	4.4	**Red Deer**
			3.0	3.0	0.0	0.0	3.0	0.0	2.9	**Hyaena**
				3.5	0.0	0.0	3.1	0.0	3.4	**Hippo**
					2.1	1.4	0.0	1.9	2.7	**Lemming**
						2.3	0.0	2.3	2.2	**Musk Ox**
							3.4	0.0	3.3	**Lion**
								3.1	2.9	**Reindeer**
									6.0	**Wild Boar**



A. *Alopex lagopus*

B. *Arvicola terrestris*

C. *Cervus elaphus*

D. *Crocuta crocuta*

E. *Hippo. amphibius*

F. *Lemmus lemmus*

G. *Ovibos moschatu*

H. *Panthera leo*

I. *Rangifer tarandus*

J. *Sus scrofa*

Figure 4. Bioclimatic niche models for the species included in this study. Coloured regions indicate areas that have the same climatic conditions that exist in the species' current geographic range. Coloured areas have a climate that falls within the full climate envelope of the species (grey areas fall outside). Dark green indicates the outermost 5 percentile of points, areas that fall on the outer margin of the climate envelope (low suitability), light green indicates the next 5 percentile (medium suitability), yellow the next 10 percentile (high suitability), orange the next 20 percentile (very high suitability), and red the remaining innermost points (excellent suitability).

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suitable for a species based on the combination of climate variables in that area and green colours indicate areas that are at best marginally suitable; these colour schemes are equivalent to quartiles of the histograms in **Figure 2**.

3.3.1 Arctic Fox (Alopex lagopus)

The climate envelope of *Alopex lagopus* extends south beyond its actual geographic range in the modern world, into non-maritime continental Europe as far as the southern Alps and into the Altai Mountains of central Asia (**Figure 4A**). Isolated pockets of suitable habitat are found in montane areas such as Scotland, the Massif Central of France, the Pyrenees, the Balkans, and the Caucuses. This species is not found in Britain today, but its climate tolerances are compatible with it living in the higher elevations of the island.

3.3.2. Water Vole (Arvicola terrestris)

Suitable habitat for *Arvicola terrestris* extends beyond its current geographic range in northern Africa, a pocket of southern Africa, and the mountains of central Asia, western China, and northern Pakistan and India (**Figure 4B**). The water vole is found in Britain today, but the climate there is on the outer margins of its climate envelope.

3.3.3. Red Deer (Cervus elaphus)

Cervus elaphus has the second largest climate envelope of the ten extant species (**Table 2**), which is reflected by suitable habitat found all across Eurasia, except for southern India, southeast Asia, harsh deserts in Pakistan, Iran and the Arabian Peninsula, and the mid-latitudes of Africa (**Figure**

4C). It lives in Britain today and has continuously since the Pleistocene.

3.3.4. Spotted Hyena (Crocuta crocuta)

Suitable habitat for *Crocuta crocuta* extends beyond its current geographic range into northern Africa, the Arabian Peninsula, southern India and beyond (**Figure 4D**). Small isolated patches exist along the coasts of southern Spain, but no suitable habitat is found anywhere near Britain today.

3.3.5. Hippo (Hippopotamus amphibius)

In addition to its existing geographic range, *Hippopotamus amphibius* can find suitable habitat on the eastern and western margins of the Sahara, coastal areas of the Arabian Peninsula, and through southern India and beyond (**Figure 4E**). Like the hyena, isolated pockets of southern coastal Spain might also be suitable for hippos, but not Britain or anywhere else in Europe.

3.3.6. Norway Lemming (Lemmus lemmus)

The lemming is today confined to Scandinavia and the northern reaches of European Russia; suitable habitat for *Lemmus lemmus* is nearly as restricted, extending only slightly beyond its current geographic range with the exception of habitats in the most alpine areas of the Alps (**Figure 4F**). No habitat suitable for the lemming exists in Britain today.

3.3.7. Musk-Ox (Ovibos moschatus)

Today *Ovibos moschatus* is restricted to the arctic areas of North America, but suitable habitat also exists in similar environments of Scandinavia, northern Siberia, and mountainous areas of central Asia (**Figure 4G**). A couple of tiny points in alpine Europe would be suitable for the musk-ox, but nowhere in or near Britain.

3.3.8. Lion (Panthera leo)

Because of the Mediterranean climates of the northern African regions inhabited today by *Panthera leo*, potentially suitable habitat for this species not only includes its historic range in the Middle East, Arabian Peninisula, and the Indian subcontinent, but a large part of coastal Europe, including nearly the whole of Spain, France and Britain (**Figure 4H**).

3.3.9. Reindeer (Rangifer tarandus)

Perhaps surprisingly, the climate envelope for *Rangifer tarandus* extends today across eastern and central Europe, into the Altai and Himalayas, and forms isolated patches in mountainous Spain, France, Italy and Britain (**Figure 4I**).

3.3.10. Wild boar (Sus scrofa)

This most geographically widespread of the ten extant species also has the most extensive suitable habitat (**Figure 4J**). There is nowhere in Eurasia or Africa that does not have bioclimatic conditions compatible with *Sus scrofa*; all of Britain would make highly suitable habitat for the boar, where it was native historically and has since been reintroduced (Yalden, 1999).

3.3.11. Summary

Of the ten species in this study, only the water vole, red deer and wild boar currently reside in Britain. Six species, including the vole, would find suitable bioclimatic conditions somewhere in Britain today: arctic fox, water vole, red deer, lion, reindeer, and wild boar. The remaining four species – spotted hyena, hippo, Norway lemming, and musk-ox – do not have even marginally suitable climate conditions in today's Britain.

3.4. Non-analogue associations in British Quaternary sites

In total, 22 British fossil mammal faunas were identified as having three or more of our ten species (**Figure 5**). The following results are derived from those sites. Note that the taxonomic considerations sometimes influenced whether a site was considered. We lumped *Arvicola terrestris* with the archaic form *A. t. cantiana*, *Panthera leo* with *P. l. spelaea*, and *Crocuta crocuta* with *C. c. spelea*, even though some authors consider the Pleistocene forms to belong to separate subspecies or even species (see discussion in section 4.2.3). Following current convention, all large lion-like cats in the British Pleistocene have been considered to be lions rather than tigers, even though the distinction has been debated in the past (discussed in 4.2.3).

Of the 22 faunas, 18 (82%) were geographically non-analogous (**Figure 5, Table 3**). Hyena and red deer were the most common geographically non-analogue species pair, and reindeer and either hyena or lion (or both) was the next most common. The

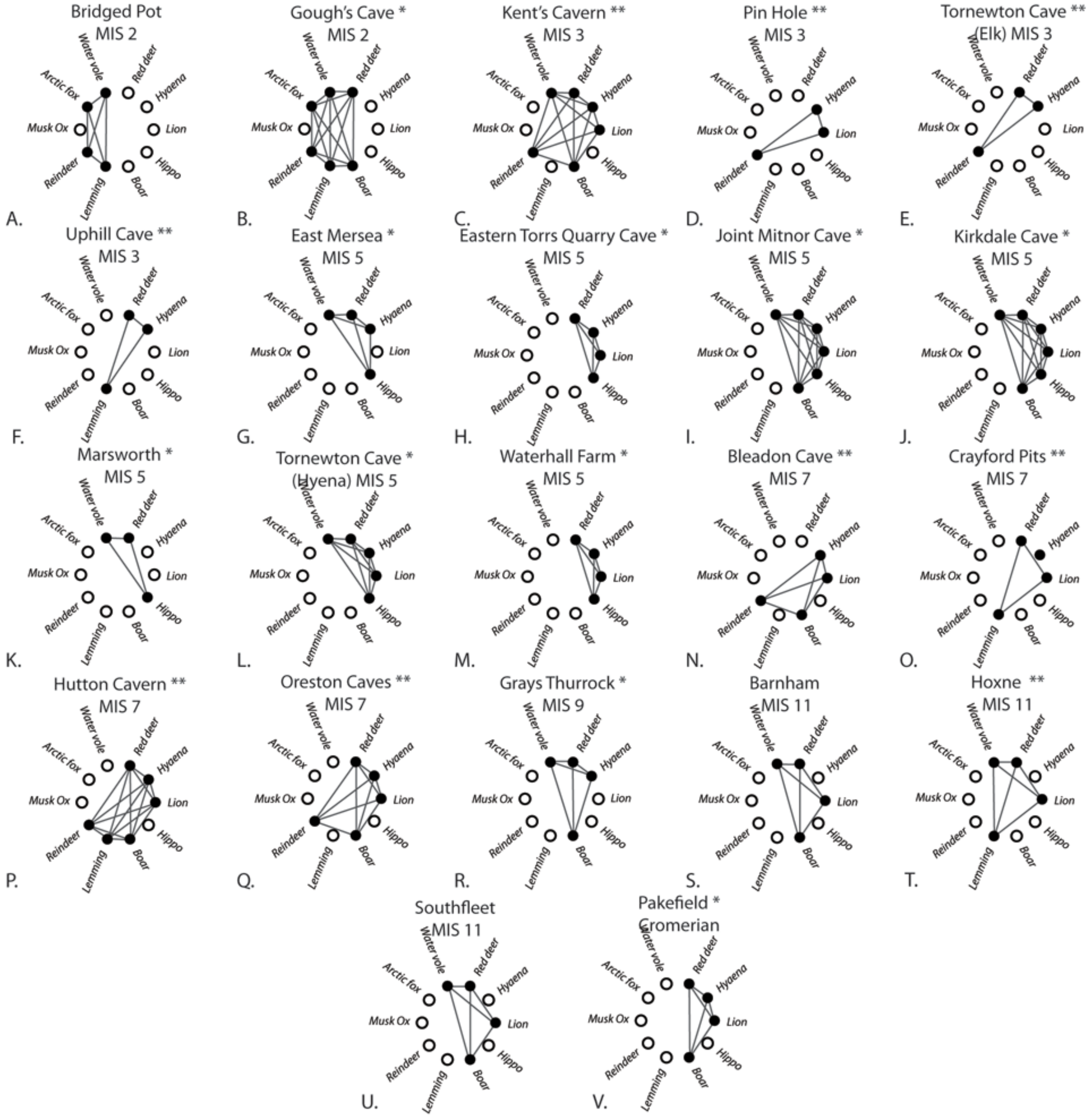

Figure 5. Associations of species at British Quaternary fossil sites. Filled circles connected by lines show which species are present at the site. * = sites that are geographically non-analogous; ** = sites that are both geographically and climatically non-analogous.

Table 3. Summary of climatic and geographic non-analogue faunas. MIS, Marine Isotope Stage; C_H, number of analogue species pairs, C_D number of non-analogue species pairs; C_E, rescaling factor; I_D, unscaled index of disharmony; I_R, rescaled index of disharmony.

Site Name	MIS	Non-analogue?		Species	Geographic Disharmony					Climatic Disharmony				
		Geographic	Climatic		C_H	C_D	I_D	C_E	I_R	C_H	C_D	I_D	C_E	I_R
Bridged Pot	2	No	No	4	6	0	0.00	0.0	0.00	6	0	0.00	0.0	0.00
Gough's Cave	2	No	No	6	15	0	0.00	0.1	0.00	15	0	0.00	0.1	0.00
Kent's Cavern	3	Yes	Yes	6	10	5	0.33	0.1	0.33	13	2	0.13	0.1	0.13
Pin Hole	3	Yes	Yes	3	1	2	0.67	0.0	0.67	1	2	0.67	0.0	0.67
Tornewton Cave (Elk)	3	Yes	Yes	3	1	2	0.67	0.0	0.67	2	1	0.33	0.0	0.33
Uphill Cave	3	Yes	Yes	3	1	2	0.67	0.0	0.67	2	1	0.33	0.0	0.33
East Mersea	5	Yes	No	4	2	4	0.67	0.0	0.67	6	0	0.00	0.0	0.00
Eastern Torrs Quarry Cave	5	Yes	No	4	4	2	0.33	0.0	0.33	6	0	0.00	0.0	0.00
Joint Mitnor Cave	5	Yes	No	6	9	6	0.40	0.1	0.40	15	0	0.00	0.1	0.00
Kirkdale Caverns	5	Yes	No	6	9	6	0.40	0.1	0.40	15	0	0.00	0.1	0.00
Marsworth	5	Yes	No	3	1	2	0.67	0.0	0.67	3	0	0.00	0.0	0.00
Tornewton Cave (Hyena)	5	Yes	No	5	5	5	0.50	0.0	0.50	10	0	0.00	0.0	0.00
Waterhall Farm	5	Yes	No	4	4	2	0.33	0.0	0.33	6	0	0.00	0.0	0.00
Bleadon Cave	7	Yes	Yes	4	4	2	0.33	0.0	0.33	4	2	0.33	0.0	0.33
Crayford Pits	7	Yes	Yes	4	3	3	0.50	0.0	0.50	5	1	0.17	0.0	0.17
Hutton Cavern	7	Yes	Yes	6	9	6	0.40	0.1	0.40	11	4	0.27	0.1	0.27
Oreston Caves	7	Yes	Yes	5	6	4	0.40	0.0	0.40	8	2	0.20	0.0	0.20
Grays Thurrock	9	Yes	No	4	3	3	0.50	0.0	0.50	6	0	0.00	0.0	0.00
Barnham	11	No	No	4	6	0	0.00	0.0	0.00	6	0	0.00	0.0	0.00
Hoxne	11	Yes	Yes	4	4	2	0.33	0.0	0.33	5	1	0.17	0.0	0.17
Southfleet	11	No	No	4	6	0	0.00	0.0	0.00	6	0	0.00	0.0	0.00
Pakefield	Pre-Crom	Yes	No	4	4	2	0.33	0.0	0.33	6	0	0.00	0.0	0.00
						Mean	0.38		0.38		**Mean**	0.12		0.12

mean index of geographic disharmony, I_D, was 0.38 and the mean rescaled index, I_R, was 0.47.

Nine of the 22 faunas (41%) had bioclimatically non-analogue pairs of species (**Figure 5, Table 3**). Reindeer with either hyena or lion was the most common climatically non-analogous pair (Kent's Cavern, Pin Hole, Tornewton Cave Elk Stratum, Bleadon Cave, Hutton Caverns, and Oreston Caves) and Norway lemming with one of the same two carnivores was second most common (Uphill Cave, Crayford Pits, Hutton Cavern, and Hoxne). The indices of climatic disharmony (I_D = 0.12 and I_R = 0.14) were much lower than the ones for geographic disharmony.

3.5 *Palaeoclimate estimates*

Maximum-likelihood estimates for the climate of each site **Table 4**. These results can be interpreted as the best estimate of the climate at these sites based on the 10 mammal species used in this study, if (and only if) those species were distributed in past environments with the same climatic range as they have today and if climate is and was a limiting factor on their geographic distribution.

4. Discussion

4.1 *Non-analogue faunas: geographic versus climatic disjunction*

Non-analogous faunas are often considered to be indicators of past environments that have no modern counterpart. This conclusion is logical if the geographic ranges of species are determined by particular climatic and environmental parameters; a different combination of species would then imply a different combination of climate parameters (Lundelius *et al.*, 1983; Webb and Barnosky, 1989; Graham *et al.*, 1996; Jackson and Overpeck 2000; Graham, 2005).

Table 4. Maximum-likelihood estimates of the 19 bioclimatic variables for each fossil site.

	MIS	Annual Mean Temp (C)	Mean Diurnal Range (C)	Isothermality	Temp Seasonality	Max Temp of Warmest Month (C)	Min Temp of Coldest Month (C)	Temp Annual Range (C)	Mean Temp Wettest Quarter (C)	Mean Temp of Driest Quarter (C)
Bridged Pot	2	4.3	9.5	27.5	1006.3	23.7	-14.0	37.6	15.7	-5.1
Gough's Cave	2	5.0	9.5	28.4	946.0	23.7	-12.4	36.0	15.2	-3.6
Kent's Cavern	3	6.1	11.0	33.1	952.7	25.4	-12.2	37.7	12.6	1.5
Pin Hole	3	4.7	8.7	28.3	881.7	22.4	-11.4	33.8	13.6	-2.0
Tornewton Cave (Elk)	3	7.6	11.9	37.7	953.1	27.2	-11.4	38.6	15.3	1.2
Uphill Cave	3	3.9	9.1	28.2	947.4	22.7	-13.2	35.8	14.2	-4.1
East Mersea	5	8.6	11.7	37.8	884.1	27.0	-9.8	36.8	16.7	1.0
Eastern Torrs Quarry Cave	5	10.5	13.1	44.4	762.3	27.8	-7.4	35.2	18.6	3.0
Joint Mitnor Cave	5	10.2	12.3	40.0	822.5	28.0	-7.8	35.8	17.3	3.7
Kirkdale Caverns	5	10.2	12.3	40.0	822.5	28.0	-7.8	35.8	17.3	3.7
Marsworth	5	7.6	11.5	38.0	887.0	26.3	-10.3	36.5	14.5	1.9
Tornewton Cave (Hyena)	5	9.4	12.4	42.9	823.9	27.4	-8.7	36.1	18.2	0.6
Waterhall Farm	5	10.5	13.1	44.4	762.3	27.8	-7.4	35.2	18.6	3.0
Bleadon Cave	7	9.0	11.8	36.8	882.9	27.4	-9.5	36.9	16.6	3.2
Crayford Pits	7	5.5	9.2	30.1	881.8	23.0	-11.1	34.1	14.8	-2.1
Hutton Cavern	7	4.5	9.4	28.3	945.9	22.8	-13.1	36.0	15.0	-4.3
Oreston Caves	7	8.3	11.2	35.9	887.2	26.8	-9.5	36.2	13.9	4.1
Grays Thurrock	9	6.3	11.1	33.8	952.8	25.7	-12.0	37.7	12.8	1.8
Barnham	11	6.2	11.0	33.1	952.7	25.5	-12.2	37.6	12.6	1.5
Hoxne	11	4.5	9.3	28.3	947.5	23.2	-12.6	35.9	14.5	-3.3
Southfleet	11	6.2	11.0	33.1	952.7	25.5	-12.2	37.6	12.6	1.5
Pakefield	Crom	10.2	11.8	37.0	822.5	27.8	-7.5	35.3	15.9	5.3

Table 4. (Cont.) Maximum-likelihood estimates of the 19 bioclimatic variables for each fossil site.

	MIS	Mean Temp of Warmest Quarter (C)	Mean Temp of Coldest Quarter (C)	Annual Precip (mm)	Precip of Wettest Month (mm)	Precip of Driest Month (mm)	Precip Season-ality	Precip of Wettest Quarter (mm)	Precip of Driest Quarter (mm)	Precip of Warmest Quarter (mm)	Precip of Coldest Quarter (mm)
Bridged Pot	2	16.5	-8.2	568.0	83.0	20.7	45.8	216.5	71.9	224.0	64.6
Gough's Cave	2	16.6	-6.7	523.1	75.2	19.1	44.1	196.2	66.3	205.4	58.3
Kent's Cavern	3	17.7	-5.5	508.0	99.1	9.0	60.2	250.7	34.0	155.3	73.5
Pin Hole	3	15.7	-6.1	594.7	81.2	22.5	41.5	212.9	78.2	201.3	104.9
Tornewton Cave (Elk)	3	19.1	-4.3	508.5	99.0	9.7	67.6	249.8	36.8	154.9	73.3
Uphill Cave	3	15.6	-7.8	530.8	68.8	21.7	39.8	181.2	75.1	186.9	93.3
East Mersea	5	19.2	-2.5	556.4	123.6	4.7	70.4	312.8	20.1	206.5	15.2
Eastern Torrs Quarry Cave	5	19.7	0.9	459.5	110.3	-0.1	81.3	287.7	3.5	187.4	-32.6
Joint Mitnor Cave	5	20.1	-0.1	504.2	122.3	0.9	77.9	306.7	7.1	206.2	0.0
Kirkdale Caverns	5	20.1	-0.1	504.2	122.3	0.9	77.9	306.7	7.1	206.2	0.0
Marsworth	5	18.3	-3.4	571.6	110.9	9.8	60.2	283.1	37.6	169.6	85.1
Tornewton Cave (Hyena)	5	19.3	-0.8	511.7	115.3	3.5	72.7	292.2	16.2	187.7	8.7
Waterhall Farm	5	19.7	0.9	459.5	110.3	-0.1	81.3	287.7	3.5	187.4	-32.6
Bleadon Cave	7	19.6	-2.0	550.9	129.0	0.9	81.7	324.8	7.6	224.8	-19.9
Crayford Pits	7	16.3	-5.5	594.5	81.0	22.5	40.4	213.2	78.4	201.3	104.9
Hutton Cavern	7	16.1	-7.3	523.2	75.1	19.1	44.9	196.1	66.3	205.4	58.3
Oreston Caves	7	19.1	-2.7	572.1	111.5	10.2	64.9	282.0	38.6	169.5	85.0
Grays Thurrock	9	17.9	-5.4	509.5	97.7	7.4	61.0	248.9	29.3	155.3	73.6
Barnham	11	17.7	-5.6	508.0	99.1	9.0	60.2	250.7	34.0	155.3	73.5
Hoxne	11	16.2	-7.2	530.7	68.9	21.6	39.0	181.3	75.1	187.0	93.3
Southfleet	11	17.7	-5.6	508.0	99.1	9.0	60.2	250.7	34.0	155.3	73.5
Pakefield	Crom	20.1	-0.1	504.4	122.7	0.9	78.5	306.3	6.8	206.3	-26.3

But climate may not completely determine the geographic ranges of mammalian species. A species may have climatic limits, but factors such as interspecific competition, resource availability, geographic barriers or past local extinctions may prevent a species from living everywhere climate would permit (Hutchinson, 1957; Soberón and Peterson, 2005; Soberón, 2007). Comparison of the bioclimatic niche models in **Figure 4** with the actual ranges showing in **Figure 1** show that many of our species are not distributed everywhere they are climatically capable of living. Only the Norway lemming is distributed close to the geographic limits of its modern climate envelope, though the arctic fox, water vole, and reindeer are close. The musk-ox is blocked by ocean barriers from suitable climates in northern Europe and Siberia, the red deer is blocked by environmental barriers from suitable climates in southern Africa.

A species may thus not inhabit all the geographic areas that are compatible with its climate envelope which means that there may be geographic areas where two geographically disjunct species might live sympatrically without either experiencing different climate than in their existing ranges. For example, the red deer is geographically disjunct from the lion, hyena and hippo, but its climate envelope includes areas in Africa that are sympatric with these three African species. Thus, a geographically non-analogue fauna need not imply a combination of climate parameters that does not exist in the modern world. The issue is complicated, however, because the uninhabited areas that are compatible with a species' climate envelope may, in fact, have a different combination of climate parameters than areas where the species actually lives (**Figure 6**; see further discussion in 4.2.1). For example, the uninhabited region may have a climate that has temperatures toward the higher tolerance of a species and precipitation toward the lower tolerance, whereas the inhabited regions may have lower temperatures and higher precipitation. In such cases, an analogous environment may or may not exist today, but the species does not live in it if it does.

We found that many species have overlapping climate envelopes even though they do not live sympatrically today. Only half as many species pairs are climatically disjunct than are geographically disjunct (**Figure 3**). Consequently, 9 of the 18 geographically non-analogue sites (50%) are, in fact, climatically compatible with the species found there.

Nevertheless, a large number of sites had climatically non-analogue faunas. Nine out of 22 faunas (41%) contained species whose modern climate envelopes do not overlap. Those sites ranged in age from the Middle Pleistocene (Hoxne, MIS [Marine Oxygen Isotope Stage] 11, approximately 400,000 ybp [years before present]) down to the later part of the Late Pleistocene (MIS 3, approximately 50,000 ybp). It should be noted that we did not consider sites younger than 20,000 or older than 750,000, so our findings do not imply that sites older or younger than that do not have climatically non-analogue faunas.

British sites appear to have many more geographically non-analogue species pairs than do contemporary North American sites. Mean geographic I_D for the British sites was 0.38 (**Table 3**), compared to the much lower values found by Alroy (1999) across North America as a whole: I_D = 0.12 for the Late Wisconsinan (MIS 2-3), I_D = 0.02 for the Sangamonian (MIS 5), and I_D = 0.02 for Early to Middle Pleistocene (equivalent to the rest of our sites). The discrepancy between our British findings and Alroy's North American ones may come from biases in the two data sets rather than real biological or climate differences. As pointed out by Graham (2005), Alroy used the co-occurrence of species in a single biome as a proxy for their geographic sympatry, thus overestimating the number of species that are geographically analogous today. This tactic may have artificially reduced the average values of I_D that he found compared to ours because our geographic data had finer resolution, which means fewer of our modern taxa would be identified as sympatric, thus increasing the chance of past species pairs being non-analogue. Another possible bias is that our samples were smaller and fewer than Alroy's. The rescaled disharmony index, I_R, adjusts for this bias, but it made no difference to our results because mean geographic I_R was still 0.38 for our sites, compared to 0.12, 0.09, and 0.10 respectively for the Late Wisconsinan, Sangamonian, and Early/Middle Pleistocene of North America.

Climatic disharmony was lower in Britain than geographic disharmony when measured using Alroy's index. Mean climatic I_D = 0.12 and mean I_R was the same (**Table 3**).

4.2 Why do we find so many non-analogue species co-occurring?

Theoretical and empirical research both strongly suggest that a species' niche does not change quickly. Natural selection is normally thought to stabilise niches because only a tiny proportion of individuals live outside a species' fundamental niche giving selection little power to push it in a new direction (Brown and Pavlovic, 1992; Holt and Gaines, 1992; Houston and MacNamara, 1992; Kawecki and Stearns, 1993). Even speciation events may not favour change in the fundamental niche because allopatric or vicariant speciation, which are the most common modes (Coyne and Orr, 2004), may merely split a species that is already adapted to its environment into two reproductively isolated populations which retain the same climatic tolerances. Empirical evidence that a significant number of sister-species pairs have mutually compatible (and predictable) bioclimatic tolerances has been found in birds (Peterson *et al.*, 1999), but a similar study of mammals found that climate niches often differed significantly between sister-species (Dormann *et al.*, 2009). Bioclimatically non-analogue species frequently occur together in the British Pleistocene, supporting the finding that climate envelopes do change in mammals. Nevertheless, Martínez-Meyer *et al.* (2004) found that ecological niche models from modern mammal species predicted Pleistocene occurrences of the same species when projected onto palaeoclimate reconstructions.

If climate envelopes do actually limit species' geographic distribution, then non-analogue pairs should, in principle, never co-occur; yet half of our sites had them. There are several possible reasons why (Stewart *et al.*, 2003): (1) climate envelopes have been incorrectly estimated and the fauna is really climatically compatible; (2) the non-analogue species did not actually coexist, either because they were seasonal migrants and inhabited the site at different times of year or because their remains have been subsequently mixed prior to deposition. at the time of excavation or subsequently; (3) climate envelopes have changed, either because the fundamental niche of the species has changed or because bioclimatic variables do not limit the species' geographic distribution and are thus not part of its fundamental niche; or (4) fossil material has been misidentified and harmonious species confused for non-analogue ones.

4.2.1 Are the climate envelopes accurate?

One aspect of accuracy is the mathematical model used to construct the climate envelopes. We used rectilinear envelopes whose boundaries are defined by the minimum and maximum value of the species on each climatic variable (**Figure 6**). These envelopes are susceptible to error in particular ways and they are controversial in the niche modelling literature. Because rectilinear envelopes are based on the full range of climate variation, they are highly influenced by outlying data points (Farber and Kadmon, 2003). Our species do indeed have outlier points that increase the volumes of their climate envelopes considerable. We took this into consideration by dropping the outermost 0.1% of the climate points and recalculating the envelopes. The reduced envelopes are, on average, 0.8 units smaller than the full envelopes (**Table 2**), but dropping the outliers did not make much of a practical difference because most non-analogue species pairs were still non-analogue with the smaller envelopes. The exception was the lion, whose reduced envelope no longer overlapped with the arctic fox, reindeer and lemming (**Table 2**; **Figure 3**). Consequently, we treated the lion as if it were climatically disjunct from these species, even though they are marginally compatible at the extremes of their climatic ranges.

Related to the same issue, overestimation of the geographic range of a species may inadvertently increase the size of its climate envelope. The geographic ranges in our study are known to be over-estimations because they are derived from

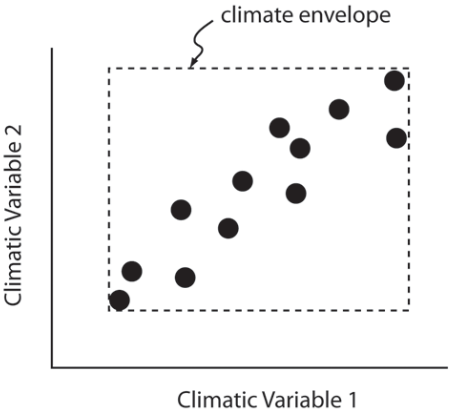

Figure 6. The relationship of a rectilinear climate envelope to its climatic variables. When climate variables are correlated, the empty corners of the envelope describe combinations of the climate variables that do not exist within the modern range of the species. It is these parts of the envelope that might represent "non-analogous" or "disharmonious" palaeoenvironments.

ecoregion species lists rather than actual point occurrence records. For example, range we used for *Alopex lagopus* (**Figure 1A**) extends further south in Scandinavia than other published accounts of its range (*e.g.*, Audet *et al.*, 2002; Mitchell-Olds *et al.*, 1999). We believe that such overextensions of range data do not substantially affect our climate envelopes because the ecoregions themselves defined by having similar climate conditions, particularly temperature and precipitation (Bailey, 1998; Olson *et al.*, 2001), so the geographic overestimation of their range does not entail a climatic overestimation.

Potential bias from estimations of geographic ranges is not unique to our study. The geographic range attributed to a species is always extrapolated from field sightings and museum voucher localities (*e.g.*, Hall, 1981); the range of bioclimatic conditions across a species' range is thus also an extrapolation. Some methods estimate the range and distribution of bioclimatic variables statistically from point localities where species were actually observed or voucher specimens collected (*e.g.*, Lindenmayer *et al.*, 1991; Stockwell and Peters, 1999), while others, including ours, derived the bioclimatic distribution from the full geographic range. The disadvantage of deriving the bioclimatic distribution from voucher localities is that they may not sample the full range of bioclimatic conditions, especially if those points are not randomly distributed across the full range of the species; the disadvantage of deriving the bioclimatic distribution from across the entire range is that error in the extrapolation of the geographic range will translate into error in the bioclimatic envelope.

Rectilinear range-based envelopes are the subject of current debate, with some authors advocating different conceptual kinds of envelopes over the rectilinear one. Rectilinear envelopes always have unoccupied corners if the climate variables are geographically or mathematically correlated, as they usually are (**Figure 6;** Farber and Kadmon, 2003). In our data, the 19 bioclimatic variables were so intercorrelated that the first four principal components explained 99% of the variance in the climate data. Even though rectilinear envelopes have a lot of unoccupied space and can thus result in overpredicted actual ranges in ecological niche modelling exercises (Heikkinen *et al.*, 2006; Kadmon *et al.* 2003), the rectilinear envelope is best for our purposes because we are interested in the maximum environmental tolerances of species and because we want to make no assumptions that correlations among climatic variables today were the same in the past (Jackson and Overpeck, 2000). In other words, the rectilinear envelope is potentially a better representation of a species' Grinnellian fundamental niche (for those cases where climate is, in fact, the factor that limits the species' range), than are other kinds of envelopes, even though other envelopes may better model the "realized niche" of a species (Peterson, 2001; Heikkinen *et al.*, 2006; Kadmon *et al.* 2003). It is the Grinellian fundamental niche, not the realised niche, that is critical to many interpretations of palaeoclimate that are based on species occurrences, including the use of non-analogue faunas as indicators of non-analogue environments.

Climate envelopes can be poorly estimated for biological reasons as well. For example, migration patterns or microhabitats may make the real envelope of a species smaller than its full geographic range implies. Water voles may restrict themselves to more temperate lowlands and river valleys in Siberia, but the ranges we used and our sampling scheme derives climate values that include habitats with potentially harsher climates. (Microhabitat use is especially characteristic of small mammals that have small home ranges. These mammals are more adapted to the microhabitats in which they live than to broad-scale regional habitats.) Similarly, seasonal migration in species like the reindeer may mean that the species is not exposed to the winter extremes of their summer habitats, even though our sampling scheme does not make this distinction. Finally, a species range may be limited by climate or environmental factors, but not the ones we used to construct the envelope. Vegetation cover, snow cover, and insolation are examples (Stewart *et al.*, 2003; Stenseth *et al.*, 2004), though they too are highly correlated with the climate variables that we used here.

4.2.2 Are non-analogue faunas temporally mixed?

Another possible reason non-analogue species pairs may be found together is temporal mixing of the fauna or the misdating of specimens (Stewart *et al.*, 2003). If remains from warm and cold stages have been inadvertently combined, they may appear to be non-analogue when they are not. We have taken care to only include faunas that were truly found in association at the same site in the same stratigraphic level. Still, unrecognized mixing is always possible. For example, the material from Oreston Caves may also be mixed based on the observation that the matrix on the voucher specimens differs among the taxa as though they came from different layers: the hyena and reindeer have one kind of matrix, while the red deer, lion, and boar have another. The possibility that the non-analogue species found at these sites did not actually coexist should not be forgotten. But several of our climatically non-analogue faunas are almost certainly unmixed. The Lower Cave Earth of Pin Hole has been the subject of careful reinvestigation and its fauna serves as the type of the Pin Hole British mammal-assemblage zone (MAZ) (Currant and Jacobi, 2001). Likewise, the fauna from Hoxne has been carefully excavated and its stratigraphic structure is well-recorded (West, 1956; Singer *et al.*, 1993; Ashton *et al.*, 2001, 2002, 2003, 2004). As far as can be determined, these sites preserve geographically and bioclimatically disjunct species in temporal and geographic association.

4.2.3 Are past climate envelopes the same as present ones?

The existence of climatically non-analogue faunas in the British Quaternary suggests that some species may have lived in different climates in the past than they do today. Nearly all the non-analogue faunas involved reindeer being found in combination with hyenas (5 out of 9) or lions (also 5 out of 9). Are reindeer, on the one hand, or hyenas and lions on the other, restricted to a narrower range of climates today than they were in the past? Or is their geographic distribution determined by factors other than the bioclimatic variables we considered in our study?

The modern climate envelope for reindeer probably does not misrepresent the climates inhabited by them in the Quaternary. Our climate envelope is mostly likely over-estimated for reindeer, minimizing the chance that the disharmonious associations are due to the reindeer having inhabited a wider climatic range than in our study. Not only is the modern geographic range of the reindeer overestimated, as discussed above, but reindeer migrate seasonally from more southerly sheltered areas in the winter to more northerly open areas in the summer (*e.g.,* Ferguson and Elkie, 2004) and thus avoid the cold extremes characteristic of open tundra in the winter. Thus the true envelope reindeer is probably smaller than we used. Furthermore, the range of reindeer probably is closely linked to climate, even for domesticated herds (which live freely within the large areas, for example in the whole northern Finland): reindeer are closely tied to their food, especially ground and arboreal lichen, whose distribution is climatically controlled (Johnson *et al.*, 2001; Lundqvist *et al.*, 2007); snow cover and ice crusts are also known to be important distributional and selective factors on reindeer (Klein *et al.*, 1987; Lundqvist *et al.*, 2007), phenomena that are directly related to temperature, precipitation, isothermy and seasonality, which are among the bioclimatic variables used to construct our climate envelopes; and the widespread Pleistocene distribution of reindeer far to the south of their modern range (Kurten, 1968; Churcher *et al.*, 1988; Kahlke, 1994) is consistent with their current climatic envelope projected onto cold-stage climates, such as the one at the last glacial maximum (Banks *et al.*, 2008). One might be concerned that the restricted modern range of reindeer due to hunting and domestication has artificially reduced their climate envelope and, thus, created the appearance that the species is climatically disharmonious when it is not; their bioclimatic niche model (**Figure 4I**) suggests this is not the case because the niche model encompasses the historical range and more indicating that the regions from which reindeer were extirpated did not have different climates than where they live today. Many lines of evidence thus suggest that the range of climate in which the reindeer lives today are similar to climates where it lived in the past.

The spotted hyena, however, probably has a modern climatic range that is not representative of its tolerances. The past distribution of hyenas is incongruous with its current climate envelope: hyenas were widespread through Europe and Asia in the Pleistocene, ranging as far north as northern England, southern Denmark, and mid-latitude Siberia (Werdelin and Solounias, 1991). For the hyena to have lived in Britain and still been restricted by its modern climate envelope the climate would have had to have been much than today. It was warmer at times, such as MIS 5e (Joint Mitnor Cave mammal assemblage-zone, Currant and Jacobi, 2001), but hyenas lived in Britain during cooler, more continental, and more climatically variable times, such as MIS 3 (Pin Hole mammal assemblage-zone, Currant and Jacobi, 2001) when

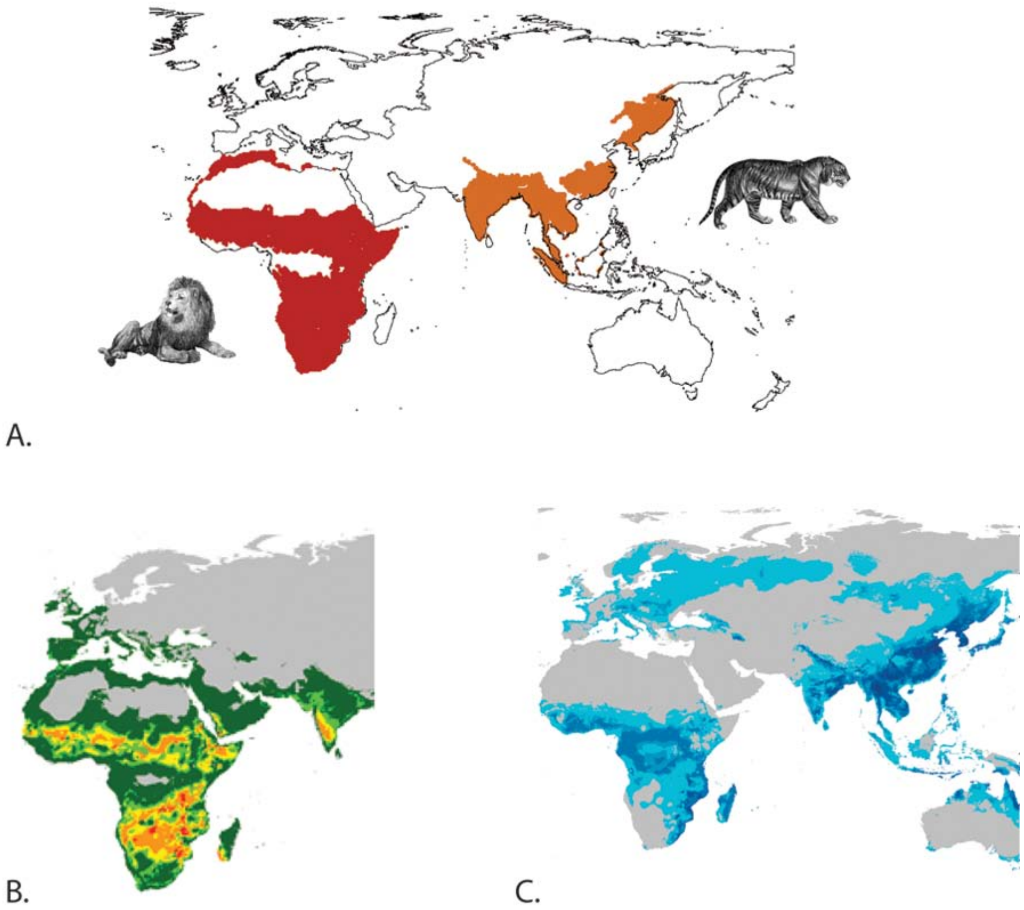

Figure 7. Comparison between current geographic ranges and bioclimatic niche models for lion and tiger. **A.** Modern geographic range of *Panthera leo* (red) and *P. tigris* (orange). **B.** The lion's modern climate envelope is restricted to warm, equible climates as indicated by its bioclimatic niche model. **C.** The heterogenous modern environment of the tiger results in its niche model including both warm and cold regions.

the British climate would not have been compatible with its modern climate envelope. The argument could be made that fossil hyenas were a different species and that they had different climate specializations. In fact, fossil European hyenas are often split into their own species, *Crocuta spelea* (Goldfuss, 1832) based on their larger size and more robust skulls. But morphological analyis and ancient mtDNA gene trees suggest that these Eurasian fossil hyenas are not a distinct clade from the living African groups (Kurten, 1957; Turner, 1984; Rohland *et al.*, 2005). Even if the fossil forms were a distinct species, they would be a closely related, recently diverged sister-species of the living spotted hyena (Werdelin and Solounias, 1991) and so are expected, on theoretical grounds, to be no more different ecologically than if the two were conspecific (but see Dormann *et al.*, 2009). Something other than climate probably restricts spotted hyenas to Africa today, most likely their dietary dependence on large to medium sized mammals (Mills, 1989). The Eurasian extinction of megafaunal herbivores during MIS 3 coincides with the last appearance of hyenas in Europe (Koch and Barnosky, 2006).

The association of lion with reindeer is less problematic than hyena and reindeer, but only a little less. Lion and reindeer have climate envelopes that marginally overlap (**Table 2**) and their modern bioclimatic niche models (e.g., their modern climate ranges) overlap geographically in Anatolia, the Balkans, and other parts of Europe, suggesting that conditions exist where the two species could live together without either experiencing different a climate than it tolerates today. But when only 0.1% of the outlying climatic distribution points are dropped, lion and reindeer become climatically disharmonious. Is the lion's current geographic distribution representative of the climates it inhabited in the past? Like the hyena, the lion's European fossils have been considered by some authors to belong to a separate species, *Panthera spelea* Goldfuss, 1810. While many palaeontologists consider *P. spelea* to be conspecific with the living *P. leo* (*e.g.,* Kurten, 1968; Turner, 1997), others continue to argue the two are distinct (Sotnikova and Nikolskiy, 2006), the latter opinion supported by mtDNA evidence that places lion fossils in a sister-clade to living lions (Burger *et al.*, 2004; Barnett *et al.*, 2009). While the evidence is stronger that Pleistocene lions may have been a distinct species from the modern lion, nevertheless the two would still be sister-species and not expected to have dramatically different climatic tolerances depending on how ancient the speciation event between the two (but see Dormann *et al.*, 2009). Thus, evidence for whether the lion's current climate is representative of the range of climates it inhabited in the past is more equivocal than for the hyena; nevertheless, it is likely that this large carnivore is also more dependent on the presence of prey species than on climate *per se*. Like with the hyena, sites with fossils lions may have had considerably different climates than the ones in which the lion lives today.

Connection to with the environmental variables may not be the same for all species. The constant, warm body temperature of mammals enables them to live in a wide range of climates and their complex, intelligent behaviours allow them to shield themselves from exposure to local extremes. Factors like the presence of running water the trophic relationship of the species to others maybe cause different species to have different relationships to local climate. Herbivores, for example, may be more closely tied to local environment than carnivores because the vegetation on which they specialise may be tightly linked to precipitation, temperature, and day length, whereas the animal prey of carnivores may not be.

4.2.4 Are the fossil species identified correctly?

Any palaeontological study operates under the presumption that the species being analysed have been identified correctly (Stewart *et al.*, 2003). The species identifications of the faunas used in this study have all been revisited by other workers as part of the Ancient Human Occupation of Britain Project. Nevertheless, there is always room for error, especially with fragmentary material. The risk of misidentification of most of the ten species is slim because they are comparatively distinctive and any species with which they might be confused are closely related and unlikely to have major differences in geographic or climatic range.

An exception is the lion. Lions and tigers can be difficult to distinguish, especially based on fragmentary fossil remains. Since the work of Kurtén (1968), fossil remains found in Europe have been regarded as lions, not tigers, despite the doubts of some authors that at least some material referred to *Panthera leo* might be referred to *P. tigris* (Harington, 1969; Groiss, 1996). Indeed, early fossil remains in Britain, such as the material from Hutton Cavern, were first referred to *P. tigris* (Rutter and Rowbotham, 1829). Morphological (Sonikova and Nikolskiy, 2006) and molecular (Burger *et al.*, 2004) analyses indicate that at least some European material, notably skeletons from Austria, eastern Europe and Siberia, really are closer to lions than to tigers, nevertheless it is conceivable that both species have inhabited Europe during the Pleistocene. On purely climatic grounds, both lion and tiger are compatible with modern European climates, the lion in the more southerly Mediterranean habitats and the tiger in the cooler, more northerly habitats (**Figure 7**). Statistically speaking, if the modern climate envelopes of the two species were the same in the past, it is more likely that the lion would have inhabited Europe during warm stages and the tiger in cold stages – the reindeer and tiger are more climatically compatible than reindeer and lion.

4.3 What do mammal associations say about climate?

Mammals faunas are often indicators of climate, especially species that are from a characteristically narrow environment. The species in a fauna say a lot about whether the environment was cold-weather or temperate, moist or dry, open grassland or closed forest, usually by analogy to the environments those species inhabit today (Graham and Semken, 1987; Currant and Jacobi, 2001; Koenigswald, 2003; Graham, 2005). We have extended and formalized this approach to palaeoclimate interpretation by

Table 5. Comparison of climate estimates from mammal faunas with estimates made from pollen, beetles and other data (Aalbersberg and Litt, 1998), palaeoclimate models (Barron and Pollard, 2002; Barron *et al.*, 2003), and beetles (Parfitt *et al.*, 2005). Each mammal estimate is categorized as being too high, too low, or correct with respect to the independent estimate.

Age	Locality	Mammal Estimate	Comparison	Comparison Source	High / Corr / Low
Annual Temperature Range (C)					
MIS 5	East Mersea	36.8	15 - 22	Pollen, Beetles and other	High
MIS 5	Marsworth	36.5	15 - 22	Pollen, Beetles and other	High
MIS 5	Waterhall Farm / Eastern Torrs	35.1	15 - 22	Pollen, Beetles and other	High
Maximum Temperature the Warmest Month (C)					
MIS 2	Gough's Cave	23.7	> 4 - 8 (*avg temp)	Palaeoclimate Model	? High
MIS 3	Kent's Cavern	25.4	> 8 - 18 (*avg temp)	Palaeoclimate Model	? High
MIS 3	Pin Hole	22.4	> 8 - 18 (*avg temp)	Palaeoclimate Model	? Corr
MIS 3	Uphill Cave	22.7	> 8 - 18 (*avg temp)	Palaeoclimate Model	? Corr
MIS 5	East Mersea	27.0	16 - 20 (*min temp)	Pollen, Beetles and other	? Corr
MIS 5	Marsworth	26.3	16 - 20 (*min temp)	Pollen, Beetles and other	? Corr
MIS 5	Waterhall Farm / Eastern Torrs	27.8	16 - 20 (*min temp)	Pollen, Beetles and other	? Corr
Mean Temperature of the Warmest Quarter (C)					
MIS 11	Pakefield	20.1	18 - 23	Beetles	Corr
Minimum Temperature the Coldest Month (C)					
MIS 2	Gough's Cave	-12.4	-20 - -4 (*avg temp)	Palaeoclimate Model	Corr
MIS 3	Kent's Cavern	-12.2	-8 - 0 (*avg temp)	Palaeoclimate Model	Corr
MIS 3	Pin Hole	-11.4	-8 - 0 (*avg temp)	Palaeoclimate Model	?Corr
MIS 3	Uphill Cave	-13.2	-8 - 0 (*avg temp)	Palaeoclimate Model	?Corr
MIS 5	East Mersea	-9.8	-2 - 1	Pollen, Beetles and other	Low
MIS 5	Marsworth	-10.3	-2 - 1	Pollen, Beetles and other	Low
MIS 5	Waterhall Farm / Eastern Torrs	-7.4	-2 - 1	Pollen, Beetles and other	Low
Precipitation the Warmest Quarter (mm)					
MIS 2	Gough's Cave	205.4	0 - 306	Palaeoclimate Model	Corr
MIS 3	Kent's Cavern	155.3	0 - 360	Palaeoclimate Model	Corr
MIS 3	Pin Hole	201.3	0 - 360	Palaeoclimate Model	Corr
MIS 3	Uphill Cave	186.9	0 - 360	Palaeoclimate Model	Corr
Precipitation Coldest Quarter (mm)					
MIS 2	Gough's Cave	58.3	126 - 360	Palaeoclimate Model	Low
MIS 3	Kent's Cavern	73.5	162 - 432	Palaeoclimate Model	Low
MIS 3	Pin Hole	104.9	162 - 432	Palaeoclimate Model	Low
MIS 3	Uphill Cave	93.3	162 - 432	Palaeoclimate Model	Low

quantitatively representing the modern environments of ten species and applying a probabilistic maximum-likelihood approach to combining the information from the species found at a site to arrive at a best estimate of the climate they co-inhabited (**Figure 2**, **Table 4)**. Our method resembles the pioneering work of Hokr (1951), and has some similarity to the approach adopted by Stewart *et al*. (2003), but we draw on more extensive climate information for modern species and a more statistically explicit method for combining the climate distributions from fossil faunas than either of these authors. Our method can be viewed as an extension of the mutual climatic range method (MCR; Atkinson *et al.*, 1987), which uses the intersection of the climatic ranges of the species in a palaeofauna as an estimate of the palaeoclimate. Analytically our method differs from MCR in using the probability density of climate values across the geographic ranges of modern species rather than just the limiting values (it is arguable which approach is more valuable in this regard) and our method differs in using a likelihood support function to combine data from different species, which allows even non-analogue associations to be included (since non-analogue species do not have overlapping climate ranges the MCR method cannot be applied to them). Our approach offers a possible new tool for studying palaeoenvironment. Several tools are already available for estimating actual palaeotemperature, palaeorainfall, and other palaeoclimatic values: stable isotope proxies, pollen frequencies, plant morphology, mammalian ungulate hypsodonty, beetle faunas, reptilian body size, and climate modelling. Temperatures and rainfall amounts predicted quantitatively from the assemblage of species in mammal faunas provides another independent estimate for palaeoclimate that will complement already existing methods.

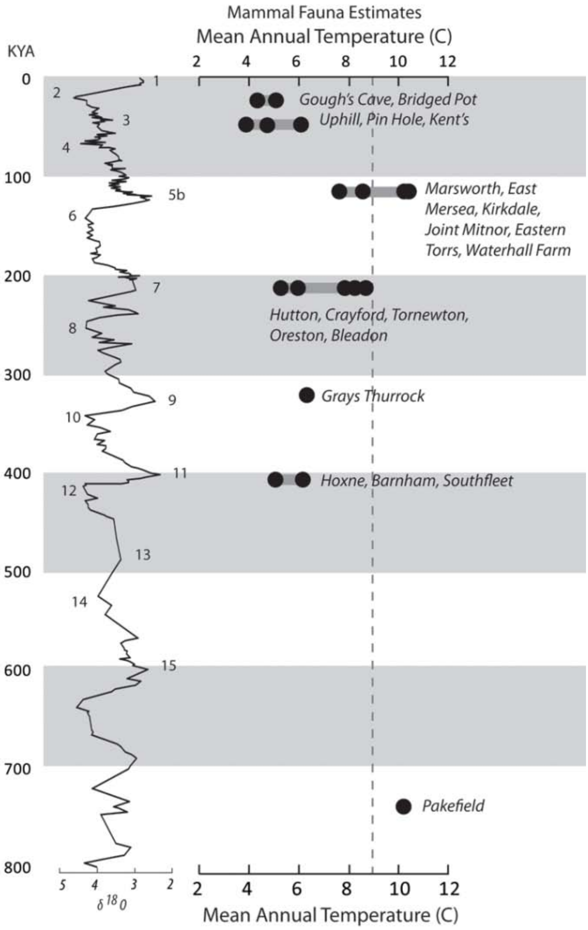

Figure 8. Temporal plot of mean annual temperature (C) as estimated from the mammal faunas. Black circles indicate the estimate for each site, sites are grouped by marine isotope stage (MIS), site labels refer to the points in each group from left to right. MISs are labelled on the oxygen isotope curve on the left, which is for the northern hemisphere (Raymo and Ruddiman, 2004). The broken vertical line shows mean annual temperature today for south-east England outside the Thames valley (Met Office data, 1961-1990 average).

But how meaningful are the palaeoclimate estimates made from the mammal faunas? **Figure 8** shows mean annual temperature as estimated from the faunas plotted by marine isotope stage (MIS) alongside an oxygen isotope curve for the northern hemisphere (data from DSDP Site 607, Raymo and Ruddiman, 2004). The mammal estimates correspond reasonably well in a relative sense to the oxygen istope ratios, and hence to global temperatures: MIS 2 and 3 faunas give the coldest estimates, MIS 5 and the pre-Cromerian fauna from Pakefield give the warmest estimates, and the other interglacial faunas give intermediate estimates. Despite the good relative correspondence, the estimates from the mammal faunas are perhaps too cool, most of them below today's mean annual temperature southern England (vertical broken line shows mean annual temperature for south-east England outside the Thames Valley, 1961-1990 average, UK Met Office data).

Direct comparisons between mammal fauna estimates and the other proxies are made in **Table 5** for those variables that were identical with or similar to the ones we used. For MIS 3, the mammal estimates are compared to the results of a mesoscale palaeoclimate model that drew its boundary conditions from geological and palaeobotanical data to predict winter and summer temperatures and daily precipitation patterns on a 60-km grid scale across Europe during warm and cold phases of MIS 3 (Barron and Pollard, 2002; Barron *et al.*, 2003). For MIS 5, the mammal estimates are compared to a multiproxy climate reconstruction that used pollen and beetle data, along with geological data to estimate temperatures across Europe for several warmer and cooler stages of MIS 5 (Aalbersberg and Litt, 1998). For Pakefield, the mammal estimates are compared to ones made from the beetle fauna (Parfitt *et al.*, 2005). The annual temperature ranges estimated from the mammal faunas in MIS 5 were always much higher than the multiproxy estimates. The summer maximum temperatures estimated from the mammal faunas at MIS 2 and 3 sites were higher than those predicted by palaeoclimate modelling (bearing in mind that the climate model predicted average temperature for the warmest month rather than maximum temperature), but the mammal estimates for MIS 5 were similar to ones estimated by multiproxy data (especially considering that the multiproxy data were used to estimate the minimum temperature of the warmest month rather thanthe maximum temperature). The winter minimum temperatures predicted from the mammal faunas agreed well with the palaeoclimate model for the MIS 2 and 3 sites, but the mammal estimates for MIS 5 were colder than the multiproxy estimates. Summer precipitation estimates from the mammal faunas agreed well with the palaeoclimate model, but winter precipitation estimates from the mammals were low.

5. Conclusions

Our understanding of the interaction between climate and species is enhanced when the interactions can be studied in both the present and the past. Concerns about anthropogenic climate change make such an enhanced understanding urgent. Paradigms like ecological niche modelling (ENM), which use existing relationships between geographic range and climate to predict the fate of species in the face of future climate changes and to prioritize conservation efforts, depend on firm knowledge of whether climate limits the geographic range of a species. Likewise, paradigms for reconstructing palaeoclimates based on palaeocommunities also depend on such knowledge. We found that most of our ten extant species currently live in climates that are consistent with their geographic ranges and community associations in the past. Two species stood out as having a different past association with climate than they do today: *Crocuta crocuta*, the spotted hyena, and *Panthera leo*, the lion. Both of these species appear to be restricted to a narrower, warmer climate range today than they were in the past when they were regularly found living with colder-climate species, notably *Rangifer tarandus*, the reindeer. Most likely these large bodied carnivores are probably not restricted directly by climate, but by the presence of medium to large bodied prey species, which themselves are probably more directly dependent on local vegetation and, thus, climate. Such past associations between species that appear to be climatically incompatible in the modern world contribute to an enhanced understanding of the dynamics of changing environments, climates and biotas.

We found that non-analogue community assemblages were common in Quaternary Britain. Of the ten modern mammal species we surveyed, nearly half of the 45 possible pairs now have geographic ranges that do not overlap (49%) and more than a quarter have climate envelopes that do not overlap (27%). When we looked at palaeofaunas that had more than three of these species, we found that 82% of them had geographically non-analogue faunas and 41% had bioclimatically non-analogue faunas. Mammalian communities have, thus, not responded to climate cycles as unified wholes: at least some species have responded differently than others, otherwise such non-analogue combinations would not be found in palaeocommunities. Differential response in mammals is not surprising since plant communities also do not response to changes as whole communities (e.g., Jackson & Overpeck 2000).

We confirmed that some Quaternary mammal species are likely to make better palaeoenvironmental predictors than others. The Norway lemming, *Lemmus lemmus*, is a good predictor of palaeoclimate because of its very small climate envelope. Large carnivores appear to be poor estimators, probably because they are further removed from climate ecologically speaking, than herbivores and small mammals. The omnivorous wild boar, *Sus scrofa*, is also a poor indicator because it has an especially broad climate envelope, one more than four orders of magnitude larger than the Norway lemming, giving it the potential to live in almost any climate currently found in the old world. Non-carnivore species with small climate envelopes are likely to make the best predictors, especially if they are dependent on the macroscale habitats that are representative of regional climates rather than on microhabitats that vary with topography, water sources or other such factors.

We have shown how the geographic distribution of climate variables from modern mammal species can be used to make quantitative palaeoclimate estimates. Species-specific climate distributions can be thought of as probability distributions for how likely the species is to be found in areas with a particular climate. The probability distributions for the species in a palaeofauna can be combined using maximum-likelihood to estimate the most probable climate for a site given the fauna found there. Most of the palaeoclimate estimates we made from British Quaternary faunas were reasonable, but they were not without discrepancies. We have suggested ways that this method can be refined to provide better estimates of palaeoclimate, namely utilizing a larger number of species, and weighting the contribution of large herbivores and small mammals over large carnivores. Such quantitative reconstructions based on mammalian faunas provide a potentially valuable and independent tool for studying palaeoclimate.

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8. Appendix

The following summaries of the sites included in this study are arranged stratigraphically from youngest to oldest.

8.1 Sites from MIS 2

8.1.1. Gough's Cave

Somerset. (UK National Grid Reference: ST4754). Gough's Cave, a show cave located in Cheddar Gorge in the Mendip Hills, was first excavated, extensively by Richard Gough in the last decade of the 19th Century and has yielded one of the largest collections of artefacts and faunal remains of any Upper Palaeolithic cave in Britain. Recent excavations in the 1980s uncovered new material and improved understanding of the cave's stratigraphy (Currant, 1986; Currant et al., 1989; Stringer, 1990). The fauna comes from a clastic wedge that filled the mouth of the cave, apparently gathered there by humans because of the cut marks and associated flint artefacts. Radiometric dates place the majority of the fauna slightly older than 12,000 years before present, in the Lateglacial Interstadial of MIS 2 (Currant, 1986; Stringer, 1990). The reindeer remains are human-fashioned artefacts that may not have been of local origin (Currant, 1986). The fauna is the type of the Gough's Cave mammal assemblage zone (Currant and Jacobi, 2001).

8.1.2. Bridged Pot Shelter

Somerset. (UK National Grid Reference: ST5349). The Bridged Pot Shelter (also known as Bridgend Pot Shelter) is a cave in Ebbor Gorge that has a Late Devensian (MIS 2) fauna dominated by tundra species, including reindeer and arctic fox (Price, 2003).

8.2 Sites from MIS 3

8.2.1. Kent's Cavern

Torbay. (UK National Grid Reference: SX9364). Kent's Cavern is a coastal cave near Torquay that was first excavated in 1825 by John MacEnery and later, between 1846 and 1858, by William Pengelly. The site notably contains an Early Upper Palaeolithic human mandible (Dowie and Ogilvie, 1927). Our fauna comes from the lower deposits of the cave and has been assigned to the Pin Hole MAZ of MIS 3 (Currant and Jacobi, 2001). The reindeer and lion from this fauna have been dated radiometrically, the lion at 43,600 (±3,600) radiocarbon years bp and the reindeer at 37,900 (±1000), 40,000 (±700), and 49,600 (±2,200) respectively (Jacobi et al., 2006).

8.2.2. Pin Hole

Derbyshire. (UK National Grid Reference: SK5374). Pin Hole is a cave in the Creswell Crags with Palaeolithic archaeology first excavated in 1875. Our fauna comes from the lower cave earth, which is the type of the Pin Hole MAZ of MIS 3 (Currant and Jacobi, 2001). The reindeer remains have been radiometrically dated to 44,200 (±800), 40,650 (±500), 30,940 (±490), and 37,760 (±340) radiocarbon years bp (Jacobi et al, 2006).

8.2.3. Tornewton Cave (Elk Stratum)

Devon. (UK National Grid Reference: SX8167). One of the Torbryan Caves, Tornewton Cave has one of the longest Pleistocene sequences in Britain, including at least two major interglacial periods. Tornewton was first excavated in 1877 by J. L. Widger, and later from 1944 through the 1960s by A. J.Sutcliffe and others. The cave contained a series of warm and cold stage mammal faunas now known to span from MIS 7 up through MIS 3. The Elk Stratum forms part of the talus slope outside the cave entrance and includes evidence of human occupation (Sutcliffe and Zeuner, 1962). The Elk Stratum fauna is considered to be mid-Devensian in age (MIS 3) (Currant, 1998). (The Hyena Stratum fauna from MIS 5e is discussed in section 8.4.6).

8.2.4. Uphill Cave

North Somerset. (UK National Grid Reference: ST3258). This hyena den site was discovered in 1826. The cave contained a many animal remains and human artefacts, most of which were quarried away in the late 19th century. The fauna has been referred to the Pin Hole MAZ of MIS 3 (Currant and Jacobi, 2001, 2002). Radiocarbon dates on bone knives associated with the fauna are 28,080 (±360) and 31,730 (±250) radiocarbon years bp (Jacobi, et al, 2006).

8.4 Sites from MIS 5

8.4.1. East Mersea

Essex. (UK National Grid Reference: TM0515) The hippo fauna from the 'East Mersea Restaurant Site' on Mersea Island is a classic and diverse MIS 5 fauna of the Joint Mitnor Cave MAZ (Bridgland and Sutcliffe, 1995; Bridgland *et al.*, 1995; Roe et al., 2009).

8.4.2. Eastern Torrs Quarry Cave

Devon. (UK National Grid Reference: SX5851). Our fauna was discovered in a cave opened in Eastern Torrs Quarry, near Yealmpton in 1954 (Sutcliffe, 1959, 1985). The fauna belongs to the Joint Mitnor Cave MAZ of MIS 5. Other caves at Yealmpton, such as Kitley Cave, which was discovered by quarrying in the 18th century, have yielded similar faunas (Pengelly, 1870).

8.4.3. Joint Mitnor Cave

Devon. (UK National Grid Reference: SX7466). This cave near Buckfastleigh (Sutcliffe, 1960) has a diverse hippopotamus fauna that serves as the type of the Joint Mitnor Cave MAZ of MIS 5e (Currant and Jacobi, 2001).

8.4.4. Kirkdale Caverns

North Yorkshire. (UK National Grid Reference: SE6886). The bones of Kirkdale Cave in Yorkshire were discovered by quarrymen who used them as trackway mettle. William Buckland recognized the bones not to be those of cattle, as the quarry workers had thought, but of deer, elephant, hyena, lion, and hippopotamus. The site had been a hyaena den and the scavengers had accumulated the bones in their foul-smelling den, as Buckland (1823) demonstrated using the excrements of his pet hyaena, Billy. The site is referred to the Joint Mitnor Cave MAZ of MIS 5e (Currant and Jacobi, 2001).

8.4.5. Marsworth

Buckinghamshire. (UK National Grid Reference: SP9314). Two fluvial channels are emplaced at Marsworth in what is now the College Lake Wildlife Centre, formerly Quarry No. 3 of Pitstone Tunnel Cement, Ltd. (Green et al., 1984; Murton et al., 2001). Our fauna comes from the upper channel, which is a hippopotamus fauna of the Joint Mitnor Cave MAZ (MIS 5e).

8.4.6. Tornewton Cave (Hyena Stratum)

Devon. (UK National Grid Reference: SX8167). The Hyena Stratum is a massive bone bed from Tornewton Cave (described above in section 8.2.3) that represents a long period of hyena occupation, including the remains of more than 80 individual hyenas (Sutcliffe and Zeuner, 1962). The fauna, which questionably includes *Hippopotamus*, is considered to belong to the Joint Mitnor Cave MAZ of MIS 5e (Currant, 1998; Currant and Jacobi, 2001).

8.4.7. Waterhall Farm

Hertfordshire. (UK National Grid Reference: TL1821). River terrace deposits of the River Lea at Waterhall Farm have yielded a hippopotamus fauna (Stuart, 1976; Sutcliffe and Kowalski, 1976) that is part of the Joint Mitnor Cave MAZ of MIS 5e (Currant and Jacobi, 2001).

8.5 Sites from MIS 7

8.5.1. Bleadon Bone Cave

North Somerset. (UK National Grid Reference: ST3457). Bleadon Bone Cave was a network of passages in a quarry at the western end of Bleadon Hill, most of which are now gone. Much of the surviving fossil material, which includes a rare British occurrence of leopard, *Panthera pardus*, is held in the museums at Weston-Supra-Mare, Taunton, and Wells (Schreve, 1997; Currant, 2004). The fauna has been attributed to the Sandy Lane MAZ, MIS 7 (Schreve, 2001).

8.5.2. Crayford Pits

Kent. (UK National Grid Reference: TQ5276) This series of brickearth pits, including includes Soneham's, Rutter's, Norris's, Furner's Old, Furner's New, and Talbot's Pits, have been worked commercially since the early 19th century and have produced an important Pleistocene fauna in association with Levallois 'working floors' (Kennard, 1944; Wymer, 1968). The site is on the third of the four terraces of the lower Thames and the fauna belongs to the Sandy Lane MAZ (MIS 7) (Schreve, 2001).

8.5.3. Hutton Cavern

Somerset. (UK National Grid Reference: ST3658). Hutton Cavern was found by Mendip miners in the late eighteenth century. Essentially a wolf den, the site was periodically used by other predators. The caves are believed to be physically quite to Bleadon Cavern, but the precise location has not yet been positively relocated. Fossil material was collected by William Beard and others, much of which survives at the Somerset County Museum of Taunton (Currant, 2004). The fauna belongs to the Sandy Lane MAZ (MIS 7) (Schreve, 2001).

8.5.4. Oreston Caves

Plymouth. (UK National Grid Reference: SX5053). Fossils, including rhinoceros, from the caves at Oreston were first found by an engineer working on the Plymouth breakwater, who passed them to the Royal Society in 1817 (Dawkins, 1874). The fauna belongs to the Sandy Lane MAZ (MIS 7) (Schreve, 2001).

8.6 Sites from MIS 9

8.6.1. Grays Thurrock

Essex (UK National Grid Reference: TQ5679). The brickearths between Grays station and Little Thurrock has produced a spectacular vertebrate fauna and Clactonian flint artefacts, especially at Globe Pit (King and Oakley, 1936; Wymer, 1968). The deposits there were equivalent to those explosed at Botany Pit at Purfleet, but despite designation of Globe Pit as one of special scientific interest, the last remnants of the fossilferous deposits were removed in the 1980s. The fauna belongs to the Sandy Lane MAZ (MIS 7) (Schreve, 2001).

8.7 Sites from MIS 11

8.7.1 Barnham

Suffolk. (UK National Grid Reference: TL8778). East Farm Pit at Barnham St. Gregory has been known as a palaeontological site since the late 19th century and, later, was noted for its succession of lithic industries. The site was reinvestigated by Wymer in 1979 and again by a team from the British Museum in 1989-1994 (Ashton *et al.*, 1998). The site contains a complete glacial-interglacial sequence, including a large fauna from channel deposits in the lower part of the pit that has been referred to the Hoxnian interglacial (Swanscombe MAZ, MIS 11) (Parfitt, 1998, Schreve, 2001).

8.7.2. Hoxne

Suffolk. (UK National Grid Reference: TM1877). The small Suffolk village of Hoxne was the site of John Frere's discovery in 1797 of hand axes in association with extinct animals, which he speculated might have belonged 'to a very remote period indeed' (Frere, 1800). Twentieth-century excavations made Hoxne one of the best documented sites of early human occupation of Britain during the clement period following the Anglian glaciations (Wymer, 1968; Singer, 1993; Ashton *et al.*, 2001, 2002, 2003, 2004). A diverse mammalian fauna has been recovered from Stratum C which belongs to the Swanscombe MAZ (MIS 11), probably early in the interglacial (Schreve, 2000).

8.7.3. Southfleet Road

Kent. (UK National Grid Reference: TQ6173). This Clactonian elephant butchery site was discovered during excavations for the Channel Tunnel Rail Link. Excavation in 2004 produced an elephant skeleton associated with lithic artefacts, apparently manufactured on the spot for butchery, and a mammalian fauna that belongs to the Swanscombe MAZ (MIS 11) (Wenban-Smith et al., 2006).

8.8 Sites from the pre-Cromerian

8.1. Pakefield

Suffolk. (UK National Grid Reference: TM5489). The cliffs of Pakefield, whose fossils have been known for a century, rose to new prominence when human-worked flint flakes were found at a site perhaps more than 700,000 years old, long before humans were thought to have been in northern Europe (Parfitt et al., 2005). The Pakefield findings pushed the earliest known human occupation back to more than 750,000 years (MIS still debated) from the previous 450,000 year old record at Boxgrove. The fauna was from a mild lowland environment, including elephants, hippos, lions, giant deer, bison, and scimitar-toothed cats.