All is flux: the predictive power of fluctuating Quaternary mammalian faunal-climate scenarios

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**Abstract**

The long-term impact of Middle and Late Pleistocene glacial-interglacial change led to the major reorganisation of mammalian faunal communities in northern Europe through species origination, extinction, evolutionary change and distributional shifts. A Bray-Curtis cluster analysis with single linkage to examine relative faunal similarity was performed on mammalian assemblages from five successively older interglacials (MIS 1, 5e, 7c-a, 9 and 11) in Britain, a region with an exceptionally well-resolved faunal record for this time period. The results indicate a degree of continuity in terms of common interglacial elements occurring across all periods but also reveal that the particular climatic and environmental parameters of each interglacial resulted in the generation of very different faunal assemblages, depending on the length, intensity and structure of the interglacial. Of particular note are the comparability of the mammalian assemblages from warm interglacials MIS 5e and 9, and the high species diversity seen in MIS 7c-a, linked to relatively cool temperate conditions and the spread of dry grasslands. Together, these results offer insight into the overall ‘predictability’ of Quaternary mammalian interglacial community composition and what might be expected in the natural evolution of a Holocene interglacial freed of anthropogenic interference.

**1. Introduction**

The Quaternary period (last 2.6 million years) occupies a place of arguably unparalleled importance in palaeoecological studies since it includes the present day and therefore offers a unique perspective on contemporary ecological and conservation biology questions.In particular, the direct comparability of the position of the continental landmasses, the analogous configuration of atmospheric and oceanic systems, the presence of many mammals still living today (or their very close relatives) and the fine-scale resolution made possible through the application of diverse geochronological and analytical techniques to a rich palaeontological record makes the Quaternary of special relevance amongst geological periods. Indeed, even a quick glance at the 100 “fundamental ecological questions” put forward on the centenary of the British Ecological Society (Sutherland *et al*., 2013) reveals that Quaternary palaeoecological data have the ability to provide significant information on a myriad of issues, including species responses to rapid environmental change (taken here as sub-millennial rates in the Quaternary record), community restructuring and the rate of distributional shifts, amongst many others. Nevertheless, despite recognition amongst conservation practitioners and policy makers of the need to develop biodiversity ‘baselines’ that extend over a longer period than just the last 50 years (Willis *et al*., 2005) – not even the lifespan of an African elephant today – the integration of palaeoecological information into conservation strategies is still in its relative infancy (Gillson and Marchant, 2014). Although the level of past ecosystem variability caused by Quaternary climatic oscillations has been seen as problematic by some ecologists (e.g. Pahl-Wostl, 1996), it is precisely this degree of disturbance that should be embraced if we are to understand the full range of biotic responses to long-term and abrupt climatic and environmental change.

Britain is particularly sensitive to long-term and abrupt climatic oscillations on account of its geographical position adjacent to the North Atlantic. It also preserves rich, multiproxy evidence from past interglacials, which were periods lasting several thousand years when the climate was as warm or sometimes warmer than the present day, global sea levels were high and continental ice volume was relatively reduced. In particular, since interglacials vary in duration, intensity and structure (Tzedakis *et al*., 2009), examination of the different boundary conditions of these diverse warm-climate periods may offer new insight into the factors governing mammalian community structure and allow evaluation of the degree of predictability (or otherwise) in interglacial faunas. Various definitions of interglacials have been discussed in recent years (eg. Tzedakis *et al*., 2009; Yin and Berger, 2010, 2012) but the definition adopted here follows that of Berger *et al*. (2015), where an interglacial is defined as any period shown in the LR04 benthic isotope stack (Lisiecki and Raymo, 2005) with benthic δ18O values above a threshold of 3.5-3.73‰. This method generates an interglacial roster of eleven major temperate-climate episodes back to 800,000 years ago, correlated with odd-numbered Marine Oxygen Isotope Stages (MIS) or sub-stages therein. These comprise (most recent first) MIS 1 (Holocene), 5e (Last Interglacial), 7c-7a, 7e, 9e, 11c (Hoxnian), 13a, 15a, 15e, 17c, and 19c (**Figure 1**).

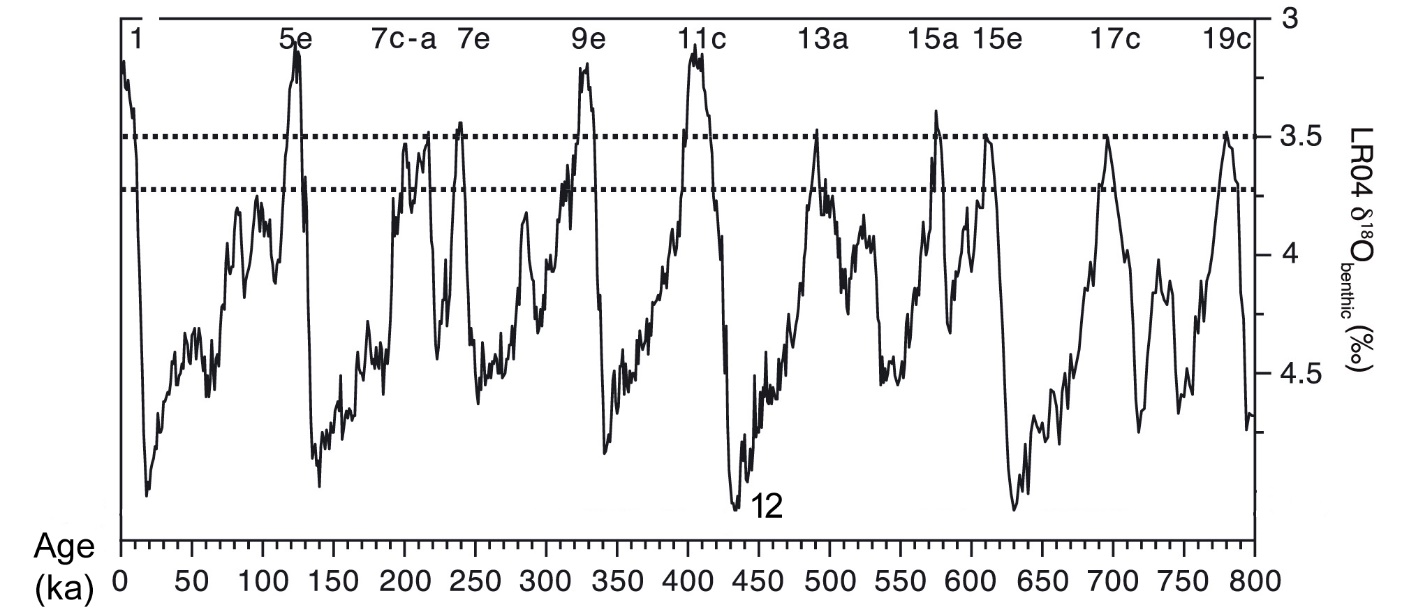


Figure 1: Interglacials of the last 800,000 years based on δ18O composition of benthic foraminifera; interglacial threshold set at >3.5-3.73‰ (Berger *et al*., 2015). Odd-numbered stages indicate interglacials. The position of the Anglian glaciation, correlated with Marine Oxygen Isotope Stage (MIS) 12, is indicated.

The focus for this study is, however, the suite of late Middle and Late Pleistocene interglacials that post-date the Anglian glaciation in Britain (correlated with MIS 12, Shackleton, 1987), ie. MIS 11c, 9e, 7, 5e and 1. The advent of the Anglian glaciation caused a major re-structuring in the British mammalian fauna, with local or complete extinctions or replacements in many mammalian families, including soricids, microtine rodents, rhinoceroses, giant deer and large bovids. Climatic deterioration in MIS 12 was clearly a major factor in precipitating this degree of faunal turnover but the subsequent distinctiveness of each successive interglacial mammalian assemblage was further enhanced by the severing (by catastrophic overspill from an ice-dammed lake in the southern North Sea basin) of the Chalk landbridge that had previously permanently connected Britain to the continental European mainland (Gibbard, 1985, 1988). Thus, after each subsequent period of climatic deterioration (accompanied by a fall in sea level that exposed a temporary terrestrial connection to the continent), a window of opportunity existed in each interglacial for mammalian species to (re)immigrate into Britain before sea-level rise caused island isolation (Schreve, 2001a). These factors have contributed to the recognition of well-established, biostratigraphically-diagnostic suites of mammals for each post-Anglian interglacial (Schreve, 2001a; Currant and Jacobi, 2011), characterized by different presence and absence data, supplemented by patterns of evolutionary development in certain lineages and/or body size variation that are equally of age significance. Additional climatic complexity, apparently corresponding to smaller-scale climatic change at the isotopic substage level, is also suggested by variation in the mammalian assemblages from some of these interglacials (Schreve, 2001b).

In Britain, the attribution of these distinctive faunal assemblages to particular interglacials correlated with the marine oxygen isotope record is underpinned by absolute dating, e.g. Gascoyne *et al*. (1981) for MIS 5e, Candy and Schreve (2007) for MIS 7, Bridgland *et al*., (2013) for MIS 9 and Rowe *et al*. (1999),Preece *et al*. (2007), Ashton *et al*. (2008) and Grün and Schwarcz (2000) for MIS 11, and by terrace stratigraphy (e.g. Bridgland, 1994), other biostratigraphical proxy date (e.g. Keen, 2001; Roe *et al*., 2009; White *et al*., 2013) and amino acid racemisation (AAR) stratigraphy (Penkman *et al*., 2011). Mammalian assemblages can be confidently correlated with MIS 5e (Currant and Jacobi, 2011) and the different parts of MIS 7 (Candy and Schreve, 2007). Although MIS 9 is more poorly known in Britain, the stratigraphical position of vertebrate assemblages in the Lower Thames valley in close association with deposits yielding evidence for high sea levels (Schreve *et al*., 2002) and palaeoecological evidence for elevated summer temperatures (Roe *et al*., 2009) suggest that they should be correlated with MIS 9e, the climatic optimum of this interglacial. For MIS 11 in Britain, nothing is currently known of the mammalian fauna from MIS 11a and all assemblages are now considered to come from the main interglacial peak, MIS 11c (*contra* Schreve, 2001b; see Candy *et al*., 2014 for a full review).

**2. Diversity of Interglacials**

Interglacials vary considerably in terms of characteristics that may have impacted on mammalian representation in Britain, for example the question of whether warmer interglacials were accompanied by higher species diversity. Recent multiproxy terrestrial, marine and ice core compilations and comparisons of interglacial intensity (eg. Lang and Wolff, 2011; Berger *et al*., 2015) have revealed that several globally-significant palaeoclimatic measures (benthic oxygen isotopes, deepwater temperature and atmospheric CO2) consistently identify the strongest interglacials as MIS 1, 5e, 9e and 11c, albeit with some variation in rank order depending on the proxy involved. In the LR04 benthic oxygen isotope stack, for example, the strongest interglacial is MIS 5e, followed by 11c, 1 and 9e in that order, whereas MIS 7 is weak throughout (Lisiecki and Raymo, 2005). Deepwater temperature reconstructions based on data from Elderfield *et al*. (2012) indicate that MIS 11c, 7e, 5e, 1, and 9e have significantly warmer values than MIS 7c-a, while the same interglacials also show the highest levels of atmospheric CO2, although the ranking is different, with MIS 9e showing the highest value at 291 ppm. MIS 1, 5e, 7e, 9e, and 11c all exceed 275 ppm, while MIS 7c-a is lowest at 257ppm (Berger *et al*., 2015). By all representative measures, MIS 7c-a is therefore a relatively cool temperate episode relative to MIS 1, 5e, 9 and 11 (Ruddiman *et al*., 1989; EPICA, 2004; Candy *et al*., 2010).

These global measures chime well with regional palaeotemperature reconstructions from Britain based on the thermal tolerances of Coleoptera, ostracods, herpetofauna, plant macrofossils and pollen. It should be noted that palaeotemperature reconstructions are presented as a range of values, with the true value falling anywhere in that range. The two warmest interglacials were MIS 5e, where the mean temperature of the warmest month (TMAX) has been reconstructed as +20 to +21°C, i.e. 3-5°C warmer than the present day, and that of the coldest month (TMIN) as +1.5 to +3°C (Candy *et al*., 2016) and MIS 9, where TMAX was +18 to +22°C and TMIN was -7 to +4°C (Green *et al*., 2006; Roe *et al*., 2009). Although MIS 7c-a is not as warm as either of these two interglacials, the presence of thermophilous reptiles, molluscs and aquatic plants with predominantly southern and eastern European core distributions today (e.g. Green *et al*., 1996) implies warm summer temperatures of 18°C (Stuart, 1979; Candy *et al*., 2010), comparable to or slightly lower than those encountered in southern England today. Mutual climatic range estimates from beetle assemblages from MIS 7 age sites indicate TMAX values of +15 to +16°C (comparable to central England today) and TMIN values between 0 and -5°C (e.g. de Rouffignac *et al*., 1995; Murton *et al*., 2001). Palaeotemperature reconstructions for MIS 11c TMAX are +15 to +22°C, broadly comparable with, or indeed slightly warmer than, the present day (Coope, 1993; Coope and Kenward, 2007).

Differences in interglacial structure are also apparent. In MIS 5e, 9, 11, the warmest part of the interglacial is clearly represented by the first temperate peak, followed by more subdued interstadials, whereas in MIS 7, the three interglacial peaks (MIS 7e, 7c and 7a) are of broadly comparable magnitude, with no clear main peak (e.g. McManus *et al*., 1999). In other records, and depending on geographical location, the warmest peak (in what is already a muted interglacial) varies from MIS 7e, 7c or even 7a (Imbrie *et al*., 1984; EPICA, 2004; Lisiecki and Raymo, 2005; Jouzel *et al*., 2007). Whereas MIS 1 and 11 in particular are relatively stable interglacials, MIS 7 reveals a unique pattern of climate forcing, driven by coincidence with the most extreme peak in orbital eccentricity seen over the last 800ka and thus, higher magnitude insolation variability than any other warm stage of the Middle and Late Pleistocene (Hays *et al*., 1976; Droxler *et al*., 2003; Berger and Loutre, 2002, 2003). Furthermore, two key modes of interglacial warming are apparent. The first group (MIS 5e, 7e and 9e) displays a pattern of climatic warming where the peak, accompanied by a sea level maximum, is reached close to the start of the interglacial (i.e. soon after the glacial termination). The second group (MIS 11c), in contrast, demonstrates a gradual increase towards maximum values late in the interglacial, accompanied by a slow rise in sea level (Berger *et al*., 2015). MIS 7c-a, however, apparently shows different trends in key parameters and cannot unfortunately be classified in the same way (Berger *et al*., 2015). The nature and rapidity of warming into the interglacial is significant for mammalian immigration into Britain during these interglacials, since it should determine whether access into Britain is relatively extended for terrestrial mammals (eg. during MIS 11c), or whether the route was more rapidly cut off by abrupt sea level rise (eg. MIS 9e, 7e, 5e).

Finally, the duration of past interglacials was also highly variable. There is no single, globally-applicable definition for calculating interglacial length and therefore, a range of methods were employed using data from the benthic isotope stack, atmospheric CO2 concentrations from Antarctic ice cores and δ‐deuterium for the EPICA Dome C ice core in order to calculate interglacial duration (see Berger *et al*. [2015] for a full explanation of methods). These generate the following estimates for interglacial duration, with mean, median and range values given for the methods applied: MIS 11c (mean 27.7ka, median 26.9ka, range 13-42.2ka), MIS 9e (mean 15.7ka, median 14.4ka, range 7.5-29.1ka), MIS 7e (mean 6.5ka, median 5.1ka, range 0.5-14.9ka), MIS 7c-a (mean 11.1ka, median 19.5ka, range 1.2-28ka), MIS 5e (mean 17.4ka, median 15.8ka, range 11-38.2ka) and MIS 1 (mean 12.1ka, median 12ka) (Berger *et al*., 2015). Using these measures, MIS 11 is the longest interglacial (as has been established by previous workers, e.g. Shackleton and Turner, 1967; Turner, 1975, although see Nitychoruk *et al*., 2005 and Koutsodendris *et al*., 2010), followed by MIS 9e and 5e, 7c-a and with MIS 7e as the shortest episode of temperate-climate conditions. Again, the length of the interglacial might be expected to have ramifications for the mammalian fauna of Britain, with longer interglacials potentially showing a greater degree of faunal change through time.

**3. Materials and methods**

In order to test the different potential impacts of interglacial variability, a database was compiled of mammalian species in Britain for the five interglacials of interest over the last c.400,000 years (MIS 11c, 9e, 7e, 7c-a, 5e and 1), excluding Chiroptera (for which the fossil record is generally very poor) and marine mammals. In the case of MIS 1, the list of Holocene mammals is taken from Stewart (2008) and comprises the native, ‘natural’ fauna of Britain, including species that have been historically extirpated such as Eurasian beaver (*Castor fiber)*,wolf (*Canis lupus*), brown bear (*Ursus arctos*) and wild boar (*Sus scrofa*), but excluding anthropogenic introductions such as grey squirrel (*Sciurus carolinensis*), fallow deer (*Dama dama*), brown hare (*Lepus europaeus*) and rabbit (*Oryctolagus cuniculus*). For MIS 5e, data were obtained from Currant and Jacobi (2011) and Coxon *et al*. (1980). For MIS 11, 9 and 7, data were obtained from Schreve (1997) and any species for which specimens could not be verified in an exhaustive search was excluded. The list for MIS 11 is supplemented by information in Parfitt (1998) and Turner (2009). Because of taxonomic uncertainty in the soricids, water shrews are assigned to *Neomys* sp. and white-toothed shrews to *Crocidura* sp. Furthermore, *Microtus agrestis* and *Microtus arvalis* are frequently conflated in published species lists because of difficulties in separating their first lower molars using traditional morphometrics (although *M. agrestis* can be confidently identified on the basis of the morphology of the upper second molar). The decision was therefore taken to leave *M. arvalis* out of the lists; although this species was undoubtedly present in Britain in the past, its exclusion here has been applied to all sites equally. Any record of hominin (almost always based on the presence of stone tools as opposed to physical remains) is attributed to *Homo* sp. The list of species and total number of species per interglacial are shown in **Table 1**.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | MIS 11c | MIS 9e | MIS 7c-a | MIS 5e | MIS 1 |
| Taxon |  |  |  |  |  |
| *Erinaceus* *europaeus* |  |  | X |  | X |
| *Sorex araneus* | X | X | X | X | X |
| *Sorex minutus* | X | X |  | X | X |
| *Neomys* sp. | X | X | X |  | X |
| *Crocidura* sp. Ɣ | X | X |  | X |  |
| *Desmana moschata* Ɣ | X |  |  |  |  |
| *Talpa europaea* | X |  |  |  | X |
| *Talpa minor\** | X |  |  |  |  |
| *Macaca sylvanus* Ɣ | X | X |  |  |  |
| *Homo* sp. | X | X | X |  | X |
| *Sciurus vulgaris* |  | X | X |  | X |
| *Spermophilus citellus* Ɣ |  |  | X |  |  |
| *Oryctolagus cuniculus* | X |  |  |  |  |
| *Ochotona pusilla* Ɣ |  |  | X |  |  |
| *Lepus timidus* |  |  | X | X | X |
| *Castor fiber* Ɣ | X | X | X | X | X |
| *Trogontherium cuvieri\** | X |  |  |  |  |
| *Lemmus lemmus* Ɣ | X |  | X |  |  |
| *Dicrostonyx torquatus* Ɣ |  |  | X |  |  |
| *Cricetus cricetus* Ɣ |  |  | X |  |  |
| *Allocricetus bursae\** |  |  | X |  |  |
| *Myodes glareolus* | X | X | X | X | X |
| *Arvicola terrestris* |  |  |  | X | X |
| *Arvicola cantiana\** | X | X | X |  |  |
| *Microtus agrestis* | X | X | X | X | X |
| *Microtus oeconomus* Ɣ | X | X | X | X |  |
| *Microtus subterraneus* Ɣ | X |  |  |  |  |
| *Apodemus sylvaticus* | X | X | X | X | X |
| *Apodemus maastrichtiensis\** | X |  | X |  |  |
| *Apodemus flavicollis* |  |  |  |  | X |
| *Muscardinus avellanarius* |  |  |  |  | X |
| *Canis lupus* Ɣ | X | X | X | X | X |
| *Vulpes vulpes* |  | X | X | X | X |
| *Ursus spelaeus\** | X |  |  |  |  |
| *Ursus arctos* Ɣ |  | X | X | X | X |
| *Mustela erminea* | X |  |  |  | X |
| *Mustela nivalis* |  |  | X |  | X |
| *Mustela putorius* | X | X | X |  |  |
| *Martes martes* | X |  |  |  | X |
| *Lutra lutra* | X | X |  |  | X |
| *Meles meles* |  | X | X | X | X |
| *Cyrnaonyx antiqua\** |  |  | X |  |  |
| *Crocuta crocuta* Ɣ |  | X | X | X |  |
| *Felis chaus* Ɣ |  |  | X |  |  |
| *Lynx lynx* Ɣ | X |  |  |  | X |
| *Felis silvestris* | X |  | X | X | X |
| *Panthera leo* (*spelaea*) Ɣ | X |  | X | X |  |
| *Panthera pardus* Ɣ |  |  | X |  |  |
| *Homotherium latidens\** | X |  |  |  |  |
| *Palaeoloxodon antiquus\** | X | X | X | X |  |
| *Mammuthus trogontherii\** |  |  | X |  |  |
| *Mammuthus primigenius\** |  |  | X |  |  |
| *Equus ferus* Ɣ | X | X | X |  |  |
| *Equus hydruntinus\** | X |  | X |  |  |
| *Stephanorhinus hemitoechus\** | X | X | X | X |  |
| *Stephanorhinus kirchbergensis\** | X | X | X |  |  |
| *Coelodonta antiquitatis\** |  |  | X |  |  |
| *Sus scrofa* Ɣ | X | X | X | X | X |
| *Hippopotamus amphibius* Ɣ |  | X |  | X |  |
| *Cervus elaphus* | X | X | X | X | X |
| *Dama dama clactoniana\** | X |  |  |  |  |
| *Dama* sp. |  | X |  | X |  |
| *Capreolus capreolus* | X | X | X |  | X |
| *Megaloceros giganteus\** | X | X | X | X |  |
| *Alces alces* Ɣ |  | X |  |  | X |
| *Bison priscus\** | X | X | X | X |  |
| *Bos primigenius\** | X | X | X | X | X |
| *Ovibos moschatus* Ɣ |  |  | X |  |  |
| TOTAL NUMBER OF TAXA | 41 | 33 | 46 | 25 | 31 |
| NO. OF EXTINCT SPECIES | 14 | 7 | 14 | 5 | 0 |
| NO. OF EXTIRPATED SPECIES | 12 | 11 | 16 | 9 | 6 |

Table 1: Mammalian taxa from British interglacials in the last 400,000 years: MIS 1, 5e, 7c-a, 9e and 11c, also showing total number of taxa and numbers of extinct and extirpated species. X = confirmed presence, \* = extinct, Ɣ = extirpated in Britain.

Two potential confounding factors have been accounted for, in as far as the limitations of the fossil record permit. The first relates to the taphonomic origins of the individual assemblages, since those from cave sites are expected to be subject to different depositional and/or preservational processes to those from open sites, for example the impact of predator-derived accumulations in the former. Thus, in order to mitigate against potential bias and to ensure as wide a representation of taxa as possible, species lists have been drawn from a range of depositional environments, including cave, fluvial and raised beach contexts. The second relates to the number of sites known for each interglacial stage. This is highly variable and depends on a variety of factors, including the impacts of past glaciations in creating accommodation space for interglacial sedimentation and/or destruction of interglacial sites by subsequent ice advances, the discovery of sites through industrial exploitation (for example of sand and gravel quarries or brickpits) and historical chance. The data in **Table 1** are compiled from nine sites for MIS 11c, six sites for MIS 9e, two sites for MIS 7e, 23 sites for MIS 7c-a and 34 sites for MIS 5e (data from Schreve, 1997 and D.C. Schreve unpublished data 2018; Lewis *et al*. 2011; Currant and Jacobi, 2011). However, although the numbers of localities may appear small in some cases, the MIS 11c and MIS 9e groupings both have over 3500 specimens each (Schreve, 1997), whereas those from MIS 7c-a and MIS 5e both have over 11,500 specimens each (Schreve, 1997 and D.C. Schreve personal observation 2019). All chronological periods include sites where sieving for microvertebrate remains has been carried out, in order to mitigate against the historical lack of small mammal data for sites discovered in the more distant past. Sample size is therefore considered to be fully appropriate for the study undertaken. The exception to this is MIS 7e, for which only two sites with <250 specimens are known; this interglacial was therefore excluded from subsequent analyses. The faunal lists for each interglacial ‘bin’ were then broken down into the following mammalian Orders: Eulipotyphla, Primates, Lagomorpha, Rodentia, Carnivora, Proboscidea, Perissodactyla and Artiodactyla (**Figure 2**).

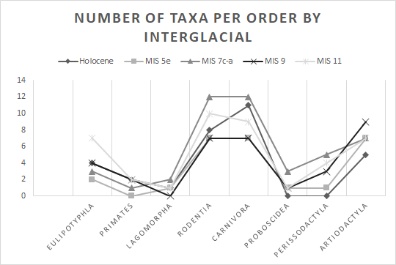


Figure 2: Number of taxa per mammalian Order for interglacials Holocene (MIS 1), 5e, 7c-a, 9e and 11.

In order to establish ecological distances between taxonomic groupings, a cluster analysis using the Bray-Curtis metric with single linkage was then performed on these data, using the BioDiversity Pro software package to create a tree (**Figure 3**). The Bray-Curtis analysis was chosen so as to provide comparability with previously published studies such as Stewart (2008). The Bray-Curtis dissimilarity is a number between 0 and 1, ie. if two assemblages share all the same species, the score is 0, whereas it is 1 if there are no species in common. These values are multiplied by 100 and then treated as a percentage. In order to calculate similarity, the Bray-Curtis dissimilarity is subtracted from 1 and then multiplied by 100 to obtain a percentage similarity. Identical assemblages therefore have a Bray Curtis dissimilarity of 0, or 0%, and a Bray Curtis index of 100%. Sites which share no species would have a Bray Curtis dissimilarity of 1 (100%), and a Bray Curtis index of 0. The percentage Bray-Curtis similarity of each grouping to one another is shown in **Table 2**.

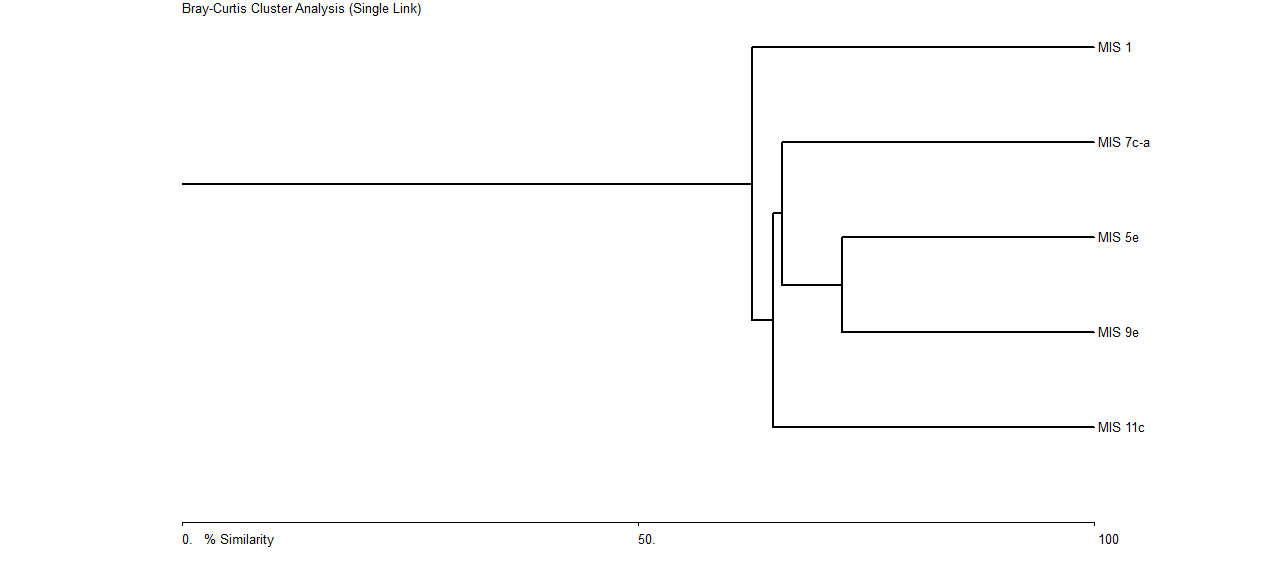


Figure 3: Bray-Curtis cluster analysis of % similarity in British mammalian assemblages from the Holocene (MIS 1) and past interglacials (MIS 11c, 9e, 7c-a and 5e).

**4. Results**

As can be seen in **Table 1**, the number of species varies between the late Middle and Late Pleistocene interglacials with MIS 7c-a the highest (46), followed by MIS 11c (41), MIS 9e (33) and MIS 5e (26). The Holocene (MIS 1) records 31 species. One soricid (*S. araneus*), four rodents (*C. fiber*, *M. glareolus*, *M. agrestis* and *A. sylvaticus*), one carnivore (*C. lupus*), one suid (*S. scrofa*), one cervid (*C. elaphus*) and one bovid (*B. primigenius*) occur in every interglacial, including the Holocene. The water vole genus, *Arvicola*, also occurs in every interglacial, albeit as two chronospecies, *A. cantiana* and *A. terrestris*. Several species are present in all interglacials except the Holocene, including *M. oeconomus*, *P. antiquus*, *S. hemitoechus*, *M. giganteus* and *B. priscus*. Three carnivore taxa, *V. vulpes*, *U. arctos* and *M. meles,* are present in the last four interglacials.

Figure 2 provides a breakdown of taxa according to mammalian Order by interglacial. Rodentia and Carnivora are the two most species-diverse groups (both showing a minimum of 7 and maximum of 12 species depending on the interglacial), followed by Artiodactyla (minimum 5, maximum 9). MIS 11 has a particularly good record for Eulipotyphla (7 species) and MIS 9 for Artiodactyla (9 species). The number of primates (2) remains constant across the three oldest interglacials. However, MIS 7c-a is otherwise remarkable in showing the highest numbers of taxa in all other Orders: Lagomorpha (2), Rodentia (12), Carnivora (12), Proboscidea (3) and Perissodactyla (5), with 7 artiodactyls.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **MIS 11c** | **MIS 9e** | **MIS 7c-a** | **MIS 5e** | **MIS 1** |
| **MIS 11c** | \* | 64.8649 | 57.4713 | 51.5152 | 52.7778 |
| **MIS 9e** | \* | \* | 65.8228 | 72.4138 | 62.5 |
| **MIS 7c-a** | \* | \* | \* | 59.1549 | 54.5455 |
| **MIS 5e** | \* | \* | \* | \* | 57.1429 |
| **MIS 1** | \* | \* | \* | \* | \* |

Table 2: Percentage Similarity Matrix comparing MIS 1, 5e, 7c-a, 9e and 11.

The results of the Bray-Curtis analysis in **Figure 3** and the similarity matrix in **Table 2** reveal that the mammalian fauna of MIS 11 is most different to other interglacials, in particular the Holocene (MIS 1) and the Last Interglacial (MIS 5e), with which it shares only 52.77% and 51.51% species in common respectively. Older interglacials generally follow a pattern of being most similar to their nearest neighbour in time, with the notable exception of MIS 9e and MIS 5e, which have a 72.41% similarity.

**5. Discussion**

In terms of species composition and notwithstanding the taphonomic issues presented above, there are clearly some consistent and predictable elements across all interglacials. Several species seen in all major warm-climate episodes (*C. fiber*, *S. scrofa* and *B. primigenius*) are restricted to temperate-climate occurrences in the British Pleistocene (Stuart, 1982); the others (*S. araneus*, *M. glareolus*, *M. agrestis*, *A. sylvaticus*, *C. lupus*, *C. elaphus*)are more catholic in their distribution, although a co-abundance of bank vole and wood mouse was noted by Currant (1989) as an indicator of interglacial conditions. In addition, *M. oeconomus*, *P. antiquus*, *S. hemitoechus*, *M. giganteus* and *B. priscus* are present in all interglacials except the Holocene (MIS 1) and can therefore also be considered predictable elements of British Pleistocene interglacials. Of these, only the former is extant (although no longer native to Britain), whereas the remainder all went extinct during the Late Pleistocene. After MIS 11, elements of the native Holocene British carnivore guild, such as red fox, Eurasian badger and brown bear become permanently established on the roster of interglacial taxa.

The distinctiveness of MIS 11 (**Figure 3**) in comparison to the Holocene (MIS 1) is to be anticipated, given that it contains 14 extinct species and 12 taxa now extirpated from Britain. The correlation of increasing distinctiveness with age was noted by Stewart (2008), who attributed this to individualistic (ie. Gleasonian) species responses to climate change. The close correspondence of MIS 9e and MIS 5e is also noteworthy, since these two interglacials are separated in time by approximately 200,000 years. The MIS 9 group is more species-rich (33), compared to MIS 5e (25), despite the latter having many more known localities (34 sites compared to 6) and containing both cave and open localities, compared to the exclusively open sites known for MIS 9 (Schreve, 2001a). Nevertheless, the 72.41% similarity score underlines important commonalities in species composition, here proposed to be the result of shared interglacial characteristics, notably elevated summer temperatures (warmer than the present day) and mild winters (Candy *et al*., 2010) and extensive deciduous woodland, denoted by high percentages of arboreal pollen (e.g. Green *et al*., 2006; Roe *et al*., 2009). Both interglacials are characterised by the presence of hippopotamus, which requires winter temperatures above freezing, thereby constraining the winter values predicted by the coleopteran assemblages (Candy *et al*., 2010), and the fallow deer, which is restricted to interglacial occurrences and deciduous-mixed mature woodland in the Pleistocene in Britain (Stuart, 1982).

However, neither MIS 5e nor MIS 9 is the most species-rich interglacial assemblage in Britain. That distinction goes to MIS 7c-a with 46 taxa (almost double the number from the Last Interglacial, MIS 5e, despite fewer sites – 23 compared to 34), of which 14 species are extinct and 16 are extirpated from Britain. One possible explanation might be the length of the interglacial, since the second most species-diverse interglacial recorded is also the longest - MIS 11c, with a calculated mean duration of over 27,000 years. However, this is not the case for MIS 7c-a; with a calculated mean duration of 11,100 years, it is the shortest of all the interglacials considered here. A more persuasive explanation for the high overall diversity and notable richness in (particularly) rodents, perissodactyls and proboscideans in MIS 7c-a lies in its palaeoclimatic and palaeoenvironmental characters.

As noted above, MIS 7c-a is a relatively cool interglacial, with mean summer temperatures of +15 to +16°C, no warmer than southern Britain today, and is characterised by higher magnitude insolation variability than any other interglacial of the Middle and Late Pleistocene. These characteristics produce a distinctive landscape of dry, predominantly open grassland conditions, highlighted by abundant pollen spectra of non-arboreal taxa, particularly grasses, sedges and dry ground herbs (e.g. West, 1969; Green *et al*., 1996; Murton *et al*., 2001). Where tree pollen is present, it occurs in reduced proportions and is suggestive of patches of open woodland (e.g. Green *et al*., 1996). Modern large herbivores are able to maintain and even enhance their environment through grazing (McNaughton, 1985), leading to increased evapotranspiration and reduced surface water infiltration; there is no reason to suppose that Pleistocene herbivores behaved differently (see Guthrie, 1990). These open environments favoured a proliferation of rodents that are today distributed in dry grasslands, steppes and semi-deserts (Kryštufek *et al*., 2008a,b; Shar and Lkhagvasuren, 2008) including *C. cricetus*, *A. bursae* (possibly conspecific with the living grey dwarf hamster, *Cricetulus migratorius*) and *S. citellus* (probably conspecific with the living long-tailed ground squirrel, *Spermophilus undulatus*).

MIS 7c-a is also characterised by a distinctive suite of open-ground large grazers, including a late morphotype of steppe mammoth (*M. trogontherii*), first co-existing with, and then being replaced by woolly mammoth (*M. primigenius*) (Lister and Sher, 2001), in association with two equids, *E. ferus* and *E. hydruntinus*. Three species of rhinoceros are present: *S. kirchbergensis*, *S. hemitoechus* and *C. antiquitatis*, the lastsuited to dry and open habitats, irrespective of temperature (Kahlke, 1999). An unusual component is present in the form of *O. moschatus*, an otherwise cold-adapted species but one that was found at the site of Crayford (Kent) in association with Mediterranean plant remains, temperate-climate vertebrates and molluscs (Kennard, 1944). Together with the presence of two lemming species and *M. oeconomus*, a continental climate with hot summer and cold winters is implied during this interglacial (Schreve, 1997). The high species diversity in MIS 7c-a is therefore apparently unrelated to either the number of sites known, or to interglacial length, elevated temperatures or woodland development but instead is a function of high insolation variability, moderate temperatures and dry, open landscapes. In this respect, it is interesting to note that MIS 7c-a holds the same number of taxa (46; Stewart, 2008) as the early Middle Pleistocene interglacial correlated with MIS 13 (c.500ka), as recorded at the site of Boxgrove (Roberts and Parfitt, 1999). Since MIS 13 pre-dates the breaching of the Strait of Dover and MIS 7c-a post-dates it, high species diversity is thus seemingly not constrained by the availability of a permanent landbridge. MIS 13 has been posited as the coolest interglacial of the past 800 000 years (Lang and Wolff, 2011), although this has been challenged by the detailed multiproxy terrestrial evidence in Britain (see Candy *et al*., 2015 for a review). Rather more significant may be the observation that most of the Boxgrove sequence apparently post-dates the MIS 13 interglacial peak, an interpretation supported by the development of the fossiliferous sequence on top of a raised beach landform, after sea level began to fall in the later part of the interglacial–glacial cycle. This underlines the assertion made here that the warmest part of interglacials is apparently not the most species-rich.

What is more difficult to determine is the possible influence of interglacial structure on mammalian diversity and representation. MIS 11c and MIS 7c-a are the most species-rich interglacials of the suite examined here. The former is characterised by a gradual rise to the thermal optimum late in the interglacial, accompanied by a slower sea-level rise that may have extended the length of access into Britain for terrestrial mammals before the landbridge became obliterated. This in itself may have enhanced the number of species present in Britain, when compared to interglacials such as MIS 5e, where temperatures (and sea level) rose rapidly after the onset of climatic amelioration. However, as mentioned above, it cannot currently be determined whether MIS 7c-a displayed the same characteristics. With reference to MIS 11c, the exceptionally long duration of the interglacial may have played a defining role in the degree of faunal community evolution apparent, with an early interglacial woodland-dominated mammalian assemblage being succeeded by an open grassland-dominated assemblage late in the interglacial (Schreve, 2001b). Since MIS 11 has been put forward the most appropriate analogue for the Holocene (MIS 1) (EPICA community members, 2004; Tzedakis, 2010), although not without controversy (summarised in Candy *et al*., 2014), the natural mammalian succession in the Holocene in Britain might have been expected to follow a similar pattern of development, were it not for the impacts of humans.

**6. Conclusions**

The study of Quaternary interglacials provides a window on some of the principal factors governing mammalian species community structure and turnover in the past. Examination of the fossil record from Britain, which preserves one of the best archives of late Middle and Late Pleistocene mammalian faunal succession in the world, reveals that individual characteristics such as interglacial intensity, duration and structure and changing biogeographical barriers had varying predictable impacts on species diversity. British interglacials are underpinned by a core group of taxa common to all periods, including *C. fiber*, *S. araneus*, *M. glareolus*, *M. agrestis*, *A. sylvaticus, C. lupus*, *S. scrofa*, *C. elaphus* and *B. primigenius*, demonstrating the particular resilience of these taxa to Quaternary climatic oscillations. Interglacials prior to MIS 1 highlight the consistent presence of *M. oeconomus*, *P. antiquus*, *S. hemitoechus*, *M. giganteus* and *B. priscus* as regular components of the British interglacial scene.

While interglacial duration and structure may have played an important role in allowing the natural succession of mammalian communities throughout the course of an interglacial to be revealed (for example the transition from woodland-dominated to grassland-dominated faunas seen in the long interglacial of MIS 11c), this is not the prime factor in governing species representation in Britain. Similarly, interglacials characterised by enhanced summer warmth compared to the present day (MIS 5e, MIS 9e) and dense deciduous-mixed woodland produce very comparable suites of mammals but are not the highest in species numbers. Instead, the highest species diversity is found in relatively cool interglacials such as MIS 7c-a, characterised by high insolation variability and in association with predominantly dry, open grassland habitats. This highlights the fact that the disappearance of the permanent landbridge to the European continent during MIS 12 did not cause a significant decline in numbers of taxa reaching Britain in subsequent interglacials. This underlines the exceptional ability of mammals to disperse rapidly into Britain from refugia during periods of climatic amelioration.

What of mammalian responses to climatic and environmental changes over the remainder of the Holocene in Britain and more widely in northern Europe? As can be observed from the level of faunal change seen in Table 1, species have responded to past changes on an individualistic basis, rather than as communities, although replication of certain environmental conditions naturally leads to a core group of common taxa appearing in Britain during every warm stage. It is therefore critical to view each species in the context of its own individual trajectory when considering (particularly) the matter of range shifts. As discussed above, if MIS 11 is indeed the most appropriate analogue for the current interglacial, an extended period of temperate-climate conditions should be anticipated, perhaps another 16,000 years, based on the mean and median estimations of MIS 11 duration. While a long interglacial can be demonstrated to have a positive effect on species diversity by allowing greater turnover in the fauna, a key difference between MIS 11 and the Holocene is the more rapid rise in sea level in the latter, which eliminated the landbridge to the continent and therefore limited access for terrestrial taxa. This, combined with human persecution and other anthropogenic impacts, means that opportunities for (re)colonization are now effectively zero unless achieved by artificial means such as deliberate translocation. The Quaternary fossil record does, however, bear an important message in terms of the extent and nature of species distribution and coexistence in the recent geological past. The natural environmental succession of MIS 11 in Britain saw early interglacial woodland giving way to late interglacial grassland habitats, the latter known to be important in past episodes of temperate climate for species diversity; this type of phasing should equally be expected in the Holocene but may now have diverged markedly from the predicted path because of anthropogenic disturbance. Based on the evidence from past interglacials, climate warming leading to increased summer temperatures is unlikely to promote enhanced species diversity, as is afforestation or reforestation.

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