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The progressive effect of the individualistic response of species to Quaternary climate change: an analysis of British mammalian faunas

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ABSTRACT

The individualistic response of species to climate change is accepted by many although how this process works across several climate oscillations has not been widely considered. A cluster analysis using the Bray–Curtis metric with single linkage to show relative faunal similarity was performed on successively older British mammalian faunas to investigate whether they become progressively different compared to the present day (Holocene). British mammalian faunas from MIS 3, 5, 11, 13 and 17 were compared with the Holocene revealing that the last glaciation (MIS 3) is more different than are any of the interglacials (MIS 5, 11, 13, 17). Furthermore, the interglacials generally become more distinct from the Holocene with age. This difference relates to the fact that interglacial faunas have greater proportions of extinct and extirpated species with increased age. The increase in extirpated taxa in turn relates to faunas becoming more non-analogue with greater age. The increase in extirpated elements with age probably relates to the individualistic response to climate change which appears to be progressing with time. The implications of this progressive process are considered in relation to refugia, extinction and evolution.

1. Introduction

It is widely accepted that species, and not ecological communities, respond to climate change. This has become known as the individualistic, or Gleasonian (Gleason, 1926), response to climate change (Graham, 1985a, b; Faunmap Working Group, 1996; Jablonski and Sepkoski, 1996; Williams et al., 2001; Williams and Jackson, 2007) and is the counterpart to the Clementsian (Clements, 1904), community response. It is also believed by many that the individualistic response lies behind the phenomenon whereby ecological communities in the Quaternary are often composed of taxa that today have allopatric distributions (Graham, 1985a; Huntley, 1991; Roy et al., 1995; Jablonski and Sepkoski, 1996; Williams et al., 2001). Indeed such non-analogue communities have been widely documented amongst almost the complete spectrum of organisms with Quaternary fossil records. Examples are known amongst both vascular plants (Bell, 1969; Huntley, 1990, 1991; Kullman, 1998, 2002; Williams et al., 2001) and diatoms (Gasse et al., 1997). In animals, examples include birds (Bramwell, 1984; Emslie, 1986; Brasso and Emslie, 2006), beetles (Coope and Angus, 1975; Coope, 2000), terrestrial molluscs (Kerney, 1963; Preece and Bridgland, 1998), marine molluscs (Roy et al., 1995), foraminifera (Whittaker in Bates et al., 2000), polychaetes (Sanfilippo, 1998), dinoflagellates (Head, 1998) and mammals (Graham, 1985a, b; Graham and Grimm, 1990; Guthrie,1990a,b; Faunmap Working Group, 1996; Stafford et al., 1999; Tankersley, 1999; Stewart et al., 2003; Stewart, 2005). Different explanations for non-analogue communities have been offered by various authors (Kerney, 1963; Bramwell, 1984, Graham and Grimm, 1990; Faunmap Working Group, 1996; Stafford et al., 1999) although the main alternative explanation for non-analogue assemblages is that they are mixtures of fossil taxa of different ages. For example, the non-analogue coleopteran assemblages from the Late Pleistocene have been explained as a mixture of material dating from distinct intervals with different climates during the Late Pleistocene (Coope, 2000). Mammalian researchers have however successfully proved the contemporaneity of species not expected in sympatry by using AMS ^{14}C dating (Stafford et al., 1999).

The individualistic response of species has long been used to explain the different vegetational elements that recombine during the successive climatic episodes of the Quaternary (West, 1980; Webb, 1986; Prentice, 1986). Phylogeographers have also recognised the same polarised hypotheses and have called these the concerted (community) versus independent (individual species) responses to environmental fluctuations (Sullivan et al., 2000). Taberlet et al. (1998) in their paper on comparative phylogeography in Europe give firm support to the individualistic response of species.

Furthermore, the individualistic response of species over several climatic cycles is likely to lead to a progressive effect. With

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increasing age there should be an increase in the degree to which ecologies deviate from modern analogues. This effect has been demonstrated by the ever changing composition of biotas though time (Hengeveld, 1994). A similar ecological phenomenon has been recognised for some time, in the increasing proportion of extinct to extant species that occur through time (e.g. Harmer, 1900a, b; Jablonski and Sepkoski, 1996). This paper presents an analysis of the degree to which mammalian species in Britain can be shown to respond individualistically to climate change in a progressive way. The ecological and evolutionary implications of this progressive individualistic response are then explored.

2. Materials and methods

To test the hypothesis that ecologies in the past were progressively less analogous to those of the Holocene with increasing age, an analysis was conducted on the mammalian faunas of Britain (in practise England and Wales) during the last 700,000 years.

The faunas of Britain are relatively well known and the data used in this analysis is from six progressively older faunas. An area the size of Britain is considered here to be large enough to contain a degree of regional ecological diversity without crossing climatic boundaries and faunal provinces. The youngest fauna analysed was that which existed in Britain during the Holocene (10,000 years–present) and is here considered to be the “natural” present day fauna. It is the Holocene fauna that is used here as the analogue with which older faunas are compared. The fauna is essentially the present day British species list although it includes taxa now locally extinct (extirpated) in Britain such as wolf *Canis lupus*, wild boar *Sus scrofa*, brown bear *Ursus arctos* and beaver *Castor fiber*, which have disappeared due largely to anthropogenic reasons (Stuart, 1995). Conversely, it also excludes the species that have been introduced by humans including grey squirrel *Sciurus carolinensis*, fallow deer *Dama dama*, brown hare *Lepus europaeus* and rabbit *Oryctolagus cuniculus* (Lever, 1977; Yalden, 1999). It was recently claimed that harvest mouse *Micromys minutus* and birch mouse *Sicista* are extinct Holocene natives to Britain (Kitchener and Yalden, 2008) although they have been omitted here due to concerns over the reliability of their ages. New claims, such as these, need to be verified, ideally with radiocarbon dates on the remains themselves, to remove the possibility that stratigraphic mixing is involved. Another perspective of the Holocene fauna in the present analysis is that certain taxa like the hedgehog and squirrel have been described as *Erinaceus* sp. and *Sciurus* sp. respectively. This is because the Pleistocene fossil records of these two taxa have not been identified to species. This in turn signifies that if the full species names for the Holocene records (i.e. *E. europaeus* and *S. vulgarius*) are used in the analysis it might artificially enhance the difference between the Holocene and older faunas with those taxa.

The analysis presented here is restricted to faunas whose ages are conservatively reliable. Therefore, faunas that are likely to date to MIS 7 (Marine Isotope Stage 7) and 9 are omitted because their ages are determined using the mammalian faunal compositions of the relevant sites (biostratigraphy) (Schreve, 2001) and to use these same compositions in this analysis would be circular.

The first fauna with which the Holocene is compared is that from MIS 3, the period between 60 and 25 thousand radiocarbon years before present (BP). These MIS 3 faunas derive from a number of sites which have a degree of reliability as to age based on associated ^{14}C dating and formed part of the Stage 3 Project database (Stewart et al., 2001). [The dates for some of the MIS 3 faunas included here have been questioned recently (Gilmour et al., 2007) although it is felt that all the taxa taken here as being found in Britain during MIS 3 (Appendix) were genuinely present. The distinctions seen by Gilmour et al. (2007) are in the dominance of specific taxa rather than in presence versus absence.]

The rest of the faunas analysed are believed to be from the peaks of interglacials. The next oldest fauna, from MIS 5e (the last interglacial), comes from a number of sites whose taxa are listed by Stuart (1995) (Shropham and Swanton Morley, Norfolk; Barrington, Cambridgeshire; Joint Mitnor, Devon; Victoria Cave, Yorkshire). They are relatively well dated and have a uranium series date of around 120,000 years from Victoria Cave in Yorkshire (Gascoyne et al., 1981). The other four MIS 5e sites are traditionally correlated with the Victoria Cave date by their faunas, which are often called the “hippopotamus fauna”, as they appear to be the only later Pleistocene faunas with hippos and a relative lack of extinct taxa in Britain. MIS 11 (an earlier interglacial) has been represented by three sites whose ages can be reasonably correlated because two independent sources of age exist. They are the Lower Loam and Lower Gravels at Swanscombe in Kent, and Beeches Pit and Barnham in Suffolk. Their similar age is suggested by their distinctive molluscan fauna and associated amino acid racemisation dates (Preece et al., 2000, 2007). Their faunas are described by Parfitt (1998) and Preece et al. (2007). The inclusion of Swanscombe on the one hand, and Beeches Pit and Barnham on the other, allows for a better consideration of both large and small mammals respectively.

Boxgrove is the next oldest fauna in the analysis, and is believed by many to represent MIS 13, giving it an age of approximately 500,000 years old (Parfitt, 1999). The site has been extensively excavated over several years and has one of the richest faunas in the British Pleistocene, including Britain’s oldest human remains (Roberts and Parfitt, 1999). Finally, West Runton is used which falls in an earlier part of the Cromerian Complex and has recently been correlated with MIS 17 (Maul and Parfitt, in press). The data for West Runton has been taken from Maul and Parfitt (in press), Preece and Parfitt (2000) and Stuart (1995). The use of individual sites in the analysis as achieved here with Boxgrove and West Runton used to represent MIS 13 and 17 respectively can circumvent the problems of potentially lumping sites of different ages under a single age category. The latter can only happen if sites exist with extensive faunas resulting from significant ongoing collection campaigns of both large and small mammals.

In an analysis of similarity of the fauna it is possible that factors influence the difference in their composition other than increased age. The taphonomic origin of a fauna is perhaps the most important confounding factor here. This has guided the choice of sites and hence where possible sites with the same taphonomic origins were used in the analysis. For example faunal assemblages from cave sites usually have a different taphonomic history to those from open air sites. In caves the origins of the faunal material is often from predator accumulations, whether it be owls depositing small mammals or hyaenas and wolves accumulating larger mammals. In open air sites, on the other hand, a broader range of processes are often involved with relative resistance to mechanical erosion and weathering and speed of burial often dominating the resultant assemblage composition. It is also imperative that the sites in question have been sieved adequately to promote the recovery of small mammals. The three oldest faunas (MIS 11, 13 and 17) have received significant attention in this regard and are all open air sites with reasonable small mammal lists. The MIS 5e and 3 faunas are based on more sites which is partly to acknowledge the fact that sieving appears to have been less systematic and partly to overcome the greater number of the site types as both faunas include cave and open sites. It is hoped that inclusion of open air sites will counter the ecological effect of the cave sites among both the MIS 5e and MIS 3 sites. The faunas used in the analysis include the best available sites and short of further field work the potential biases above can only be acknowledged.

Another factor which could be partially affecting the composition of British mammalian faunas is the variable island to peninsular status of the area (e.g. Stuart, 1995). While this clearly plays a role it can be considered to be part of the individualistic response as different taxa are likely to move to Britain at different rates relative to the area becoming isolated.

The presence/absence of mammalian taxa from the above age categories is shown in the Appendix. A cluster analysis using the Bray–Curtis metric with single linkage was conducted on this data using BioDiversity Pro software package and the results of this analysis are shown in a tree (Fig. 1). The Bray–Curtis metric allows the analyses of taxonomic datasets to establish ecological distance and is often used to do so with palaeoecological datasets (e.g. Park and Downing, 2001). In addition to the tree the percentage pair wise similarity values to (the Holocene fauna) are presented in Table 1. This analysis was performed using the faunas expressed as species (Appendix 1) present through time (Table 1). Also shown in Table 1 is the percentage of extinct, extant and extirpated taxa. Finally, in order to graphically demonstrate the decreasing degree of similarity values with time the percentage pair wise similarity, using the Bray–Curtis metric (to the Holocene fauna), for species were plotted against the approximate ages of each fauna (Fig. 2).

3. Results of analysis of progressive independence

The Bray–Curtis cluster analysis reveals (Fig. 1) that the past interglacials are all more different from the Holocene than they are from each other. Therefore, the tree in Fig. 1 shows the Holocene fauna forming a sister group to all the interglacial faunas (MIS 5e, 11, 13, 17). In addition, the past interglacials generally become progressively more distinct from each other as they get older as indicated by their percentage Bray–Curtis similarity indices (Table 1, Fig. 2). The exception is that the fauna from MIS 13 is more similar to that of the Holocene than is that from the younger MIS 11. This may be partly due to sampling because MIS 13 has a larger faunal list, with 46 species, than MIS 11, with 39 species. The larger faunal list has contributed to the greater number of taxa in MIS 13 that are still present in Britain (Table 2). They include the hedgehog *Erinaceus* sp., the mole *Talpa europaea*, the mountain hare *Lepus timidus*, the hazel dormouse *Muscardinus avellanarius*, the weasel and/or stoat *Mustela nivalis/M. erminea* and the badger *Meles meles*.

The glacial fauna of MIS 3 does not follow the progressive difference and falls outside the cluster that includes all the interglacial faunas (Fig. 1). This suggests that glacial faunas are probably generally more different from interglacial ones than interglacials are from each other. Table1 helps explain the tree in Fig. 1, showing the British mammalian faunas from progressively older time episodes broken down into the percentage extant, extinct and extirpated as well as the percentage pair-wise similarity values to the Holocene fauna. This analysis confirms that there is a progressive change in the mammalian fauna of the British Isles. Therefore, the fauna from MIS 5e is more similar to that of the Holocene in terms of both extinct and extirpated taxa than is the fauna from MIS 11. This change appears to be due to both an increase in extinct and extirpated (locally extinct) species with a corresponding decrease in extant taxa. However, while the percentage of extinct taxa increases with each older interglacial, the percentage of extirpated taxa increases and then greatly decreases between MIS 13 and MIS 17. The decrease in extirpated species between MIS 13 and 17 may be due to a threshold which is reached whereby morphological differences are no longer considered subspecific locally extinct populations and instead require classifying as extinct species. Regardless of this, it is clear that there is an increase in difference with increasing age of British interglacial faunas and the Last Glacial (MIS 3) fauna is particularly different in terms of extirpated taxa. This implies a great deal of faunal change that involves distribution change of an individualistic nature.

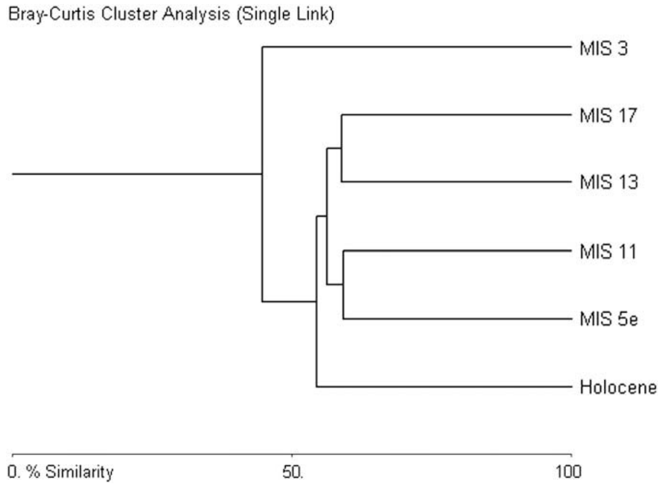

Fig. 1. Bray–Curtis cluster analysis of British faunas from the Holocene, former interglacials (MIS 5e, 11, 13 and, 17) and part of the Last Glacial (MIS 3).

The analysis was also performed on the data after removing the extinct taxa from the presence/absence matrix of the different faunas (Appendix). The result of this is to produce a significantly less steep trend into the past demonstrating the importance of the influence of the extinct taxa in the analysis. There is, however, a trend, among the interglacial faunas, of decreasing similarity to that from the Holocene, with increasing age. The most realistic analysis result is probably somewhere between the results of the two analyses, with and without extinct taxa, because a significant proportion of the extinct interglacial taxa are phylogenetically ancestral, or closely related, to extant taxa. Therefore, it is more reasonable to consider the results including the extinct taxa.

4. Discussion—consequence of progressive individualistic response

The progressive individualistic response of species through time has been demonstrated here for mammals in Britain although it seems likely that this process exists in other organisms in the Quaternary. Certainly, Hengeveld (1994) suggests as much in a review of the state of biogeographical ecology: "local community ecology composition deviate from a particular one, the greater the distance both in time—non-analogue vegetations—and space". It is also implied by many other studies even if it is not described as such. For example much of the work done by palynologists in Europe and elsewhere have this phenomenon at their core (e.g. Tzedakis and Bennett, 1996). It also lay behind the use of palynology as a relative dating method (e.g. West, 1970) although the use of pollen spectra in age determination has been criticised, certainly in Britain, due to demonstrations that comparable pollen spectra can occur during separate interglacials (Sutcliffe and Kowalski, 1976). The latter could indicate that the individualistic response of plant taxa to climate change may not always result in progressively different floras although there are problems with the interpretation of pollen in reconstructing plant migration rates (Reid's Paradox—Clark et al, 1998). More recently a similar biostratigraphic use has been made of mammals in Britain (Schreve, 2001). Here again the different interglacials are characterised as having similar but distinct faunas. These uses of biological remains in biostratigraphy both rely on the ever changing combinations of taxa which in turn are presumably formed by the individualistic response of species. Non-analogue communities are the most extreme manifestation of such re-combinations.

The fact that these re-combinations occur has implications for other phenomena and processes in the population biology of organisms through time and space. These shall be discussed in turn.

Table 1
Details of percentages of extant, extinct and extirpated mammalian taxa in Britain over the last 700 thousand years. Also shown are the percentage Bray–Curtis pair wise similarities to the Holocene mammalian faunas of progressively older faunas

	Interglacial	Glacial	Interglacials			
	Holocene (0–10 Ka)	MIS 3 (60–25 Ka)	MIS 5e (*ca* 120 Ka)	MIS 11 (*ca* 400 Ka)	MIS 13 (*ca* 500 Ka)	MIS 17 (*ca* 700 Ka)
Total no. of species	30	33	25	39	46	42
Percentage extant in Britain (No. extant)	100 (30)	42.42 (14)	60 (15)	38.46 (15)	36.96 (17)	33.33 (14)
Percentage extinct (No. extinct)	0	18.18 (6)	16 (4)	30.77 (12)	32.61 (15)	45.24 (19)
Percentage extirpated in Britain (No. extirpated)	0	39.39 (13)	24 (6)	30.77 (12)	30.43 (14)	21.42 (9)
Percentage Bray–Curtis similarity to Holocene (Species)	-	44.44	54.55	43.48	44.74	38.36
Percentage Bray–Curtis similarity to Holocene (Species) excluding the extinct taxa	-	49.12	58.82	52.63	55.74	52.83

4.1. *Refugia*

Refugia exist when species are in the contraction phase of their populations. Unlike extinctions, however, refugial populations are viable and can subsequently expand when optimal conditions broaden again. The individualistic response of species implies that refugia for different species need not coincide completely in area or time. If they do it is because the physical conditions required for the species exist and not because of the presence of other apparently similar ecological species (Smith and Smith, 1998). The progressive nature of the individualistic response further implies that refugia for a given species are likely to vary with the climate space that exists at any one time. Certain areas may re-occur as refugia in subsequent, similar climates although this is mostly dictated by the climates themselves and to a lesser extent on variations in land areas and topography.

The clearest example of the effect of the individualistic response to climate change is the difference between species found today in cold northern areas when compared to those from more southern temperate parts of the Palaearctic and Nearctic. Temperate species respond by contracting southwards and/or into cryptic northern refugia during glaciations (Hewitt, 1996, 2000, 2001; Taberlet et al, 1998; Stewart and Lister, 2001). Northern species, however, are generally in their expansive phases in cold stages and in refugia during interglacials such as that today (Stewart and Lister, 2001; Dalén et al., 2005; Stewart and Dalén, 2008). Various authors working on the phylogeography of a number of arctic taxa (Tremblay and Schoen, 1999; Holder et al., 1999; Fedorov and Stenseth, 2002; Loehr et al., 2005; Pruett and Winker, 2005; Anderson et al., 2006) have suggested that such taxa are in a population contraction phase during glacials. While this may be true for the glacial maxima, it is not the case for the whole glacials, as these are the times during which such species are generally in their expansive phases (Mourer-Chauviré, 1979; Musil, 1985; Tyrberg, 1991, 1995; Markova et al., 2002; Stewart, 1999; Stewart et al., 2003). The glacial refugium concept should therefore be complemented by an interglacial equivalent (see Bennett and Provan, 2008). It is also clear that taxa whose ecological and climatic adaptations appear to be defined by continental versus oceanic characteristics will need to be considered separately.

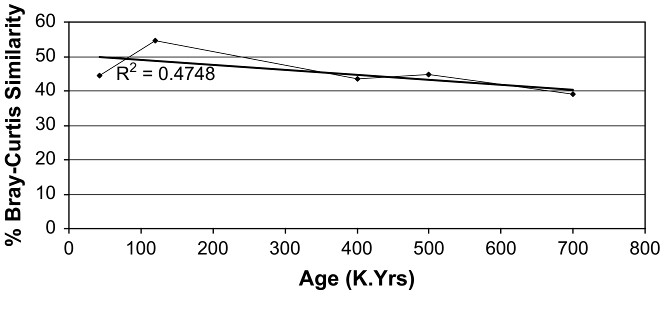

Fig. 2. Percentage Bray–Curtis similarity to the Holocene mammalian fauna of progressively older faunas plotted against their estimated ages. Also shown is trend line with R^2 value derived from all similarity indices.

4.2. *Extinction*

The subject of extinction (whether extinction of populations or species) is related to that of refugia as both involve the contraction phase of species. In extinctions the contraction phase of species (or populations) is complete while in refugia small remnants of a population survive.

The relationship between non-analogue communities, and by analogy the individualistic response, and extinction has been described by various authors. These authors suggest that the disappearance of “disharmonious” communities at the same time as the megafaunal extinctions, including that of the Neanderthals, indicates that climate, rather than modern human predation or competition, is the main cause their demise (Graham and Lundelius 1984; Guthrie, 1990a; Stewart, 2005). This is because the loss of large mammals of the Late Pleistocene were simply considered to be part of a ‘faunal revolution’ involving many changes including the major reorganisations of ecological communities (Guthrie, 1990a; Faunmap, 1996). This point of view was rejected by Alroy (1999) who criticised the link that has been made between the megafaunal extinctions of the Late Pleistocene and the loss of non-analogue assemblages. He argued that such non-analogues are very rare and were not restricted to the Pleistocene. He did acknowledge (Alroy, 1999) that differences between glacial and interglacial faunas had been noted and attributed these to differences in seasonal climates (e.g. Graham, 1986) and suggested that this partly lay behind the non-analogue phenomenon. However, he asserted that most mammals “maintained ecologically stable and predictable distribution that only gradually contracted in the face of Holocene environmental change” (Alroy, 1999). Graham (2006) vigorously rejected Alroy’s stance on non-analogue communities suggesting that Alroy used a non-traditional definition of non-analogues which artificially decreased the number of observed examples of such biotas.

It is clear, however, that the individualistic response implies that we should not expect species extinctions to be completely synchronous or, for the last populations of species, to be in precisely the same place. Also, the progressive nature of the individualistic response may suggest a further level of complexity to the extinction process as populations are likely to go extinct or become locally adapted in an unpredictable, stochastic way. The progressive individualistic phenomenon only affects species at a population level through time because once the species is extinct it can no longer respond, differently or otherwise. Populations are likely to have responded differently, according to the species involved, which is a predictable outcome of the progressive individualistic response. It is also likely that different populations of a single species could respond differently to the same environmental change.

Table 2
Extant, extinct and extirpated mammalian taxa in Britain over the last 700 thousand years

	Interglacial	Glacial	Interglacials			
	Holocene (0–10 Ka)	MIS 3 (60–25 Ka)	MIS 5e (*ca* 120 Ka)	MIS 11 (*ca* 400 Ka)	MIS 13 (*ca* 500 Ka)	MIS 17 (*ca* 700 Ka)
Total no. of species	30	33	25	39	46	43
Extant	*Erinaceus* sp. *Sorex araneus* *Sorex minutus* *Neomys fodiens* *Talpa europaea* *Homo sapiens* *Lepus timidus* *Sciurus* sp. *Castor fiber* *Clethrionomys glareolus* *Arvicola t. terrestris* *Microtus agrestis* *Apodemus flavicollis* *Apodemus sylvaticus* *Muscardinus avellanarius* *Canis lupus* *Vulpes vulpes* *Ursus arctos* *Mustela nivalis/erminea* *Mustela putorius* *Meles meles* *Martes martes* *Lutra lutra* *Felis sylvestris* *Lynx lynx* *Sus scrofa* *Cervus elaphus* *Capreolus capreolus* *Alces alces* *Bos primigenius*	*Neomys fodiens* *Homo sapiens* *Lepus timidus* *Arvicola t. terrestris* *M. agrestis* *Canis lupus* *Vulpes vulpes* *Ursus arctos* *Mustela nivalis /erminea* *Mustela putorius* *Felis sylvestris* *Cervus elaphus* *Alces alces* *Bos primigenius*	*Sorex araneus* *Sorex minutus* *Neomys fodiens* *Castor fiber* *Clethrionomys glareolus* *Microtus agrestis* *Apodemus sylvaticus* *Canis lupus* *Vulpes vulpes* *Ursus arctos* *Meles meles* *Felis sylvestris* *Sus scrofa* *Cervus elaphus* *Bos primigenius*	*Sorex minutus* *Neomys fodiens* *Sciurus* sp. *Castor fiber* *Clethrionomys glareolus* *Microtus agrestis* *Apodemus sylvaticus* *Canis lupus* *Mustela putorius* *Martes martes* *Felis sylvestris* *Sus scrofa* *Cervus elaphus* *Capreolus capreolus* *Bos primigenius*	*Erinaceus* sp. *Sorex minutus* *Neomys fodiens* *Talpa europaea* *Lepus timidus* *Sciurus vulgaris* *Castor fiber* *Clethrionomys glareolus* *Microtus agrestis* *Apodemus sylvaticus* *Muscardinus avellanarius* *Mustela nivalis/erminea* *Meles meles* *Felis sylvestris* *Sus scrofa* *Cervus elaphus* *Capreolus capreolus*	*Erinaceus* sp. *Sorex minutus* *Talpa europaea* *Lepus timidus* *Castor fiber* *Clethrionomys glareolus* *Apodemus sylvaticus* *Mustela nivalis /erminea* *Martes martes* *Lutra lutra* *Felis sylvestris* *Sus scrofa* *Cervus elaphus* *Capreolus capreolus*
Extinct		*Homo* cf. *neanderthalensis* *Ursus spelaeus* *Mustela putorius robusta* *Mammuthus primigenius* *Coelodonta antiquitatis* *Megaloceros giganteus*	*Arvicola terrestris cantiana* *Palaeoloxodon antiquus* *S. hemitoechus* *Megaloceros giganteus*	*Sorex runtonensis* *Talpa minor* *Homo* cf. *neanderthalensis* *Trogontherium cuvieri* *Arvicola t. cantiana* *Apodemus maastrichtiensis* *Ursus spelaeus* *Palaeoloxodon antiquus* *Equus hydruntinus* *Stephanorhinus hemitoechus* *S. kirchbirgensis* *Megaloceros giganteus*	*Sorex runtonensis* *Sorex savini* *Talpa minor* *Homo* cf. *heidelbergensis* *Pliomys episcopalis* *Arvicola terrestris cantiana* *Apodemus maastrichtiensis* *Canis lupus mosbachensis* *Ursus deningeri* *P.* cf. *gombaszoegensis* *Stephanorhinus* sp. A. *S. hundsheimensis* *Megaloceros verticornis* *Megaloceros dawkinsi* *Caprinae*	*Sorex runtonensis* *Sorex savini* *Neomys newtoni* *Macroneomys brachygnathus* *Talpa minor* *Trogontherium cuvieri* *Pliomys episcopalis* *Mimomys savini* *Pitymys gregaloides* *Canis lupus mosbachensis* *Ursus deningeri* *Pannonictis* sp. *P.* cf. *gombaszoegensis* *Mammuthus trogontherii* *S. hundsheimensis* *Megaloceros dawkinsi* *Megaloceros savini* *Alces latifrons* *Bison schoentensacki*
Extirpated		*Ochotona pusilla* *Citellus* sp. *Dicrostonyx torquatus* *Microtus gregalis* *Microtus arvalis* *Microtus oeconomus* *Alopex lagopus* *Gulo gulo* *Crocuta crocuta* *Panthera leo* *Equus ferus* *Rangifer tarandus* *Bison priscus*	*Microtus oeconomus* *Crocuta crocuta* *Panthera leo* *Hippopotamus amphibius* *Dama dama* *Bison priscus*	*Crocidura* sp. *Desmana moschata* *Macaca sylvanus* *Oryctolagus cuniculus* *Microtus subterraneus* *Microtus arvalis* *Microtus oeconomus* *Eliomys quercinus* *Panthera leo* *Equus ferus* *Dama dama* *Bison priscus*	*Oryctolagus cuniculus* *Myopus schisticolor* *Microtus subterraneus* *Microtus gregalis* *Microtus arvalis* *Microtus oeconomus* *Sicista* cf. *betulina* *Eliomys quercinus* *Mustela lutreola* *Crocuta crocuta* *Panthera leo* *Equus ferus* *Dama dama* *Bison priscus*	*Desmana moschata* *Macaca sylvanus* *Cricetus cricetus* *Cricetulus migratorius* *Microtus subterraneus* *Microtus oeconomus* *Crocuta crocuta* *Equus ferus* *Dama dama*

4.3. Evolution

> "Perhaps the effects of ice age range changes that are most likely to lead to adaptive novelty and divergence are the different conditions and organisms that a species may meet in its various refugia." (Hewitt, 1996).

The fact that the individualistic response has led to the mixing of biota, and appears to have progressed through time, suggests that evolution is moving at a significant pace in the Quaternary (Hewitt, 1996, 2000). This is because in addition to the evolutionary response of taxa to environmental change there is likely to have been changes to the populations in response to novel interactions between new neighbour species (see above quote). This hypothesis has some support because many populations of animals living in these different combinations are likely to have become extinct as range contractions occurred. The latter are only reliably demonstrated by use of ancient DNA studies such as those pioneered by Barnes et al. (2002). Evidence for extinct populations, living in non-analogue associations, has been found in the aDNA of arctic fox remains from the lower latitudes of the Late Pleistocene (in North West Europe) (Dalén et al., 2007). These populations have been shown to have become extinct as their ranges contracted at the end of the Pleistocene (Dalén et al., 2007) as hypothesised by Stewart et al. (2003). Interestingly, these southerly distributed arctic foxes had smaller paws than modern arctic foxes, representing an adaptation to the more southerly local conditions, presumably due to a relative lack of snow fall. This signifies that this non-analogue element of the late Pleistocene, the southern arctic fox population, were different genetically and ecomorphologically from modern counterparts. The range contraction at the end of the Pleistocene represents the extinction of this distinct arctic fox population that had evolved to live in the cold climates at lower latitudes during the later Pleistocene.

Therefore, the individualistic response of species may suggest that a cryptic evolutionary process is disguised in the fossil record. This should act in part as a response to those who have questioned the importance of ice ages to the process of speciation during the Pleistocene (Coope, 1978; Bennett, 1990, 1997; Klicka and Zink, 1997). It has been suggested that climate fluctuations are relatively short and thus cause differently derived populations to be assimilated back into the whole parent population once climate completes a glacial-interglacial cycle. The process evoked would cause stability while the process implicated by the progressive individualistic mixing of species, with extinction, described here, is one of constant ecological and genetic change.

If fossils are as ambiguous taxonomically, as suggested by the taxonomic level to which certain categories of remains are identified or perhaps should be (Moore et al., 1991; Stewart, 2002), it is little wonder that the fossil record has proved relatively unfruitful in documenting evolution in many organisms. The losses of gene pool diversity are only now being revealed by ancient DNA analyses (Barnes et al., 2002; Burger et al., 2004; Shapiro et al., 2004; MacPhee et al., 2005; Orlando et al., 2006; Dalén et al., 2007; Leonard et al, 2007). They confirm that more extinctions at a population level took place across Quaternary climate cycles than has been formerly been recognised. One example of a distinct population loss is that of the wolves of Beringia that went extinct at the end of the Pleistocene, probably following the demise of the megafauna in the area (Leonard et al., 2007). These wolves represent an extinct genotype and ecomorph with adaptations suggesting that they concentrated on hunting and scavenging the animals of the steppe-tundra (Leonard et al., 2007). Such studies imply that gene pools are undergoing selection by environmental change and that this is an evolutionary process that requires more consideration. It is envisaged that the process described will have been progressing throughout geological time, during the Pleistocene certainly, but that because of the use of modern analogues in discerning its existence may be less visible in deeper time. If it is to be recognised at earlier times it will have to be inferred from the recognition of individualistic responses of species to climate and environmental changes rather than in the recognition of non-analogue communities. The degree to which the modern analogue is used to identify the individualistic response may hamper the recognition of this process in deeper time. A possible example has been described from the Carboniferous where plant communities were shown to be responding individualistically during a time of significant climate change (DiMichele et al., 2001).

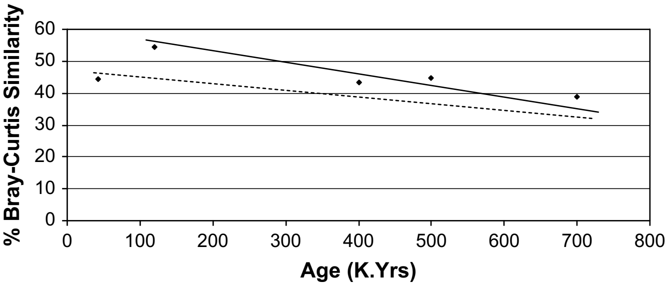

Fig. 3. Hypothesised different, but converging, trend lines of percentage Bray–Curtis similarity indices (to the Holocene mammalian fauna) were available for glacial and interglacial faunas. Key: Solid Line–interglacial trend line; Dashed Line–glacial trend line.

5. Conclusion

Guthrie (1990a), in his paper on the Late Pleistocene 'faunal revolution', believed that too much focus on the extinctions has obscured the fact that other processes were operating during the time of the Late Pleistocene megafaunal extinctions. Listed amongst the phenomena which took place during the end of the Pleistocene were rapid evolutionary changes, fractionation of biotic communities and enormous reductions in distributional ranges. It can be argued that many, or all, of these changes reflect population size changes. For example geographical distribution reductions often involve a retreat through local population extinctions. Community fractionations are a more complex version of distribution change involving the reorganisation of non-analogue communities and hence are also likely to involve local extinction. Meanwhile rapid evolution often involves extinction followed by immigration of allopatrically distributed, distinct, but congeneric, populations.

Similarly it is important to an understanding of the evolution of organisms during the Quaternary as a whole that other processes were taking place. An analysis of British Pleistocene mammalian faunas has shown that the individualistic response of species to climate change is a progressive phenomenon which causes ecological communities to become increasingly different, compared to the Holocene, with age. This phenomenon is not a simple one as variations exist according to whether faunas lived in interglacial or glacial times. The interglacial faunas become progressively different with age. The single glacial fauna examined in the analysis, from MIS 3, was more different from all the interglacials than they were from each other. It is predicted that the glacial faunas will also become less similar to the Holocene fauna with age on their own trajectory (Fig. 3). Unfortunately this cannot be demonstrated because the history of glacial faunas is much less complete than interglacial ones. It is also possible that the two trajectories will converge back through time (Fig. 3) as the glacially adapted taxa are believed to have evolved more recently (Lister, 2004). For example, the mammoth, *Mammuthus trogonterii*, from the interglacial MIS 17 site of West Runton, is believed to be ancestral to the late Pleistocene woolly mammoth *M. primigenius* of the MIS 3 glacial phase, although the evolution appears to have taken place outside Europe (Lister et al., 2004). Therefore, it is to be expected that glacial and interglacial faunas will be less distinguishable in the past. It is also probable that glacials are likely to be more impoverished in taxonomic diversity with increasing age. The colonisation of colder climates is a more recent phenomenon (Lister, 2004) and the evolution of cold-adapted organisms in these climates, which were more expansive in glacials, must have taken at least one glacial-interglacial cycle to take place.

The pattern described here, with an increase in extirpated and hence non-analogue combinations of organisms with increasing age, is similar to that known for some time where the proportion of extinct taxa increases with age. Indeed they are probably related phenomena as many of the non-analogue elements are likely to be extinct populations, adapted to environments and ecologies that are extinct.

Finally, it seems likely that the progressive process (the individualistic response of species) causing the pattern of increasing ecological difference with age has important implications for other related processes taking place in the Quaternary. The location and nature of refugia for species, the pattern and process of extinction of species and populations of species, and the evolution of the species will be affected by the progressively different, recombining, faunas of the Pleistocene. The individualistic response of species is recognised by most palaeoecologists working in the Quaternary but perhaps its evolutionary implications are not. The full implications of the phenomenon will doubtlessly emerge with time.

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Appendix

British Mammalian faunas from progressively older Quaternary stages expressed as presence–absence data

Taxa	Holocene[a]	MIS 3 (60–25 K yrs)[b]	MIS 5e[c]	MIS 11 (Swanscombe, Barnham and Beeches Pit)[d]	MIS 13 (Boxgrove)[e]	MIS 17 (West Runton)[f]
Erinaceus sp. and *E. europaeus*	1	0	0	0	1	1
Sorex araneus	1	0	1	0	0	0
Sorex minutus	1	0	1	1	1	1
Sorex runtonensis	0	0	0	1	1	1
Sorex savini	0	0	0	0	1	1
Neomys sp. and *N. fodiens*	1	1	1	1	1	0
Neomys newtoni	0	0	0	0	0	1
Macroneomys brachygnathus	0	0	0	0	0	1
Crocidura sp.	0	0	0	1	0	0
Talpa europaea	1	0	0	0	1	1
Talpa minor	0	0	0	1	1	1
Desmana moschata	0	0	0	1	0	1
Homo sapiens	1	1	0	0	0	0
Homo cf. *neanderthalensis*	0	1	0	1	0	0
Homo cf. *heidelbergensis*	0	0	0	0	1	0
Macaca sylvanus	0	0	0	1	0	1
Lepus sp. and *Lepus timidus*	1	1	0	0	1	1
Oryctolagus cuniculus	0	0	0	1	1	0
Ochotona pusilla	0	1	0	0	0	0
Sciurus sp. and *S. vulgaris*	1	0	0	1	1	0
Citellus sp.	0	1	0	0	0	0
Trogontherium cuvieri	0	0	0	1	0	1
Castor fiber	1	0	1	1	1	1
Cricetus cricetus	0	0	0	0	0	1
Cricetulus migratorius	0	0	0	0	0	1
Dicrostonyx torquatus	0	1	0	0	0	0
Myopus schisticolor	0	0	0	0	1	0
Clethrionomys glareolus	1	0	1	1	1	1
Pliomys episcopalis	0	0	0	0	1	1
Arvicola terrestris terrestris	1	1	0	0	0	0
Arvicola terrestris cantiana	0	0	1	1	1	0
Mimomys savini	0	0	0	0	0	1
Pitymys gregaloides	0	0	0	0	0	1
Microtus (*Terricola*) *subterraneus* and *M.* cf. *subterraneus*	0	0	0	1	1	1
Microtus gregalis	0	1	0	0	1	0
Microtus arvalis	0	1	0	1	1	0
Microtus agrestis	1	1	1	1	1	0
Microtus oeconomus	0	1	1	1	1	1
Apodemus flavicollis	1	0	0	0	0	0
Apodemus sylvaticus	1	0	1	1	1	1

(*continued on next page*)

Appendix (*continued*)

Taxa	Holocene[a]	MIS 3 (60–25 K yrs)[b]	MIS 5e[c]	MIS 11 (Swanscombe, Barnham and Beeches Pit)[d]	MIS 13 (Boxgrove)[e]	MIS 17 (West Runton)[f]
Apodemus maastrichtiensis	0	0	0	1	1	0
Sicista cf. betulina	0	0	0	0	1	0
Eliomys quercinus	0	0	0	1	1	0
Muscardinus avellanarius	1	0	0	0	1	0
Canis lupus	1	1	1	1	0	0
Canis lupus mosbachensis	0	0	0	0	1	1
Vulpes vulpes	1	1	1	0	0	0
Alopex lagopus	0	1	0	0	0	0
Ursus arctos	1	1	1	0	0	0
Ursus spelaeus	0	1	0	1	0	0
Ursus deningeri	0	0	0	0	1	1
Mustela nivalis and *M. erminea*	1	1	0	0	1	1
Mustela lutreola	0	0	0	0	1	0
Mustela putorius and *M.* cf. *putorius*	1	1	0	1	0	0
Mustela putorius robusta	0	1	0	0	0	0
Meles sp. and *Meles meles*	1	0	1	0	1	0
Gulo gulo	0	1	0	0	0	0
Martes sp. and *M. martes*	1	0	0	1	0	1
Pannonictis sp.	0	0	0	0	0	1
Lutra sp. and *L. lutra*	1	0	0	0	0	1
Crocuta crocuta	0	1	1	0	1	1
Panthera leo	0	1	1	1	1	0
Panthera cf. *gombaszoegensis*	0	0	0	0	1	1
Felis sylvestris and *Felis* sp.	1	1	1	1	1	1
Lynx lynx	1	0	0	0	0	0
Mammuthus primigenius	0	1	0	0	0	0
Mammuthus trogontherii	0	0	0	0	0	1
Palaeoloxodon antiquus	0	0	1	1	0	0
Equus sp. and *Equus ferus*	0	1	0	1	1	1
Equus hydruntinus	0	0	0	1	0	0
Stephanorhinus sp. A.	0	0	0	0	1	0
Stephanorhinus hundsheimensis	0	0	0	0	1	1
Stephanorhinus kirchbirgensis	0	0	0	1	0	0
Stephanorhinus hemitoechus	0	0	1	1	0	0
Coelodonta antiquitatis	0	1	0	0	0	0
Sus scrofa	1	0	1	1	1	1
Hippopotamus amphibius	0	0	1	0	0	0
Megaloceros giganteus	0	1	1	1	0	0
Megaloceros verticornis	0	0	0	0	1	1
Megaloceros dawkinsi	0	0	0	0	1	0
Megaloceros savini	0	0	0	0	0	1
Dama dama	0	0	1	1	1	1
Cervus elaphus	1	1	1	1	1	1
Capreolus capreolus	1	0	0	1	1	1
Alces alces	1	1	0	0	0	0
Alces latifrons	0	0	0	0	0	1
Rangifer tarandus	0	1	0	0	0	0
Bos primigenius	1	1	1	1	0	0
Bison priscus	0	1	1	1	1	0
Bison schoentensacki	0	0	0	0	0	1
Caprinae	0	0	0	0	1	0

[a] Stuart (1995), Lever (1977), Yalden (1999).

[b] Stewart et al. (2003).

[c] Stuart (1995), Currant and Jacobi (2001).

[d] Parfitt (1998).

[e] Parfitt (1999), Parfitt (pers. comm.).

[f] Stuart (1988), Preece and Parfitt (2000), Maul and Parfitt (in press).

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