REVIEW

The evolutionary consequence of the individualistic response to climate change

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Abstract

The Quaternary fossil record has abundant evidence for ecologically non-analogue communities made up of combinations of modern taxa not seen in sympatry today. A brief review of the literature detailing these nonanalogue communities is given with a discussion of their various proposed causes. The individualistic, Gleasonian, response of species to climate and environmental change is favoured by many. The degree to which communities are nonanalogue appears to increase with greater time depth, and this progressive process is a necessary outcome of the individualistic response of species to climate change through time. In addition, it is noted that populations within species, as well as the species as a whole, respond individualistically. This paper proposes that many elements of nonanalogue communities are extinct populations, which may explain their environmentally anomalous combinations. These extinct populations are, by definition, lineages without descendents. It is further proposed that the differential extinction of populations, as a result of continuous ecological reassembly, could amount to a significant evolutionary phenomenon.

Introduction

The role of ecology in species evolution has been viewed as critical since the time of Darwin and Wallace (Lack, 1944; Schluter, 2000, 2001; Day & Young, 2004; McKinnon *et al.*, 2004). Studies of the evolutionary ecology of extant live organisms are ongoing and cover a great range of taxa (e.g. Grant, 1986; Losos, 1990; Schluter, 1996). However, most studies are temporally limited, looking at processes that are generally only visible during the lifetime of researchers, such as that of the *Geospiza* finches of the Galapagos over the last few decades (Grant & Grant, 2007). In addition, most studies only look at subspecific processes with the unresolved question as to whether they can be extrapolated to the species level. The emerging field of evolutionary palae-oecology (Jablonski & Sepkoski, 1996; Stewart & Cooper, 2008) can provide a partial antidote to this, giving a

greater time depth to the study of the evolution of organisms in relation to their changing ecologies.

The Quaternary, the last 2.6 millions years, with its regular and extreme climatic oscillations at different amplitudes and the accompanying ecological variation would appear to be a likely time for species evolution (Willis & Niklas, 2004). Despite this, it has been claimed that Quaternary climate change has acted in such a way as to decrease the opportunities for species formation rather than be the principle driver of modern species evolution (Coope, 1978; Bennett, 1990, 1997, 2004). This is because the differentiation that occurs because of endemism in allopatry during glacials would be undone in subsequent interglacials by the interbreeding of the formerly allopatric populations (Coope, 1978; Bennett, 1990, 1997, 2004; Klicka & Zink, 1997). While this argument appears sound, and not withstanding alternative arguments from molecular studies claiming Pleistocene species evolution (e.g. Avise & Walker, 1998; Johnson & Cicero, 2004; Weir & Schluter, 2004), it is not consistent with observations showing that new mammal and bird species have evolved during the

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Pleistocene (Kurtén, 1959, 1968; Mourer-Chauviré, 1993; Lister, 2004; Stewart, 2002, 2007). However, it is acknowledged that there is a great deal of variation in the taxonomic interpretation of fossils (Erwin & Anstey, 1995; Stewart, 2002; Lister, 2004).

Nevertheless, there is one generally accepted phenomenon in the Quaternary that may provide a solution to the lack of observed speciation in many organisms. That is the phenomenon known as nonanalogue communities which has been recorded in most organisms with fossil records (Graham, 1985a,b; Williams & Jackson, 2007) and may provide evidence as to the actual amount of species evolution taking place (Jablonski & Sepkoski, 1996). Nonanalogue communities are those that include a combination of species whose ranges today do not overlap (Graham, 1985a,b). This is because nonanalogue communities are thought to have existed because of the individualistic response of species to climate change. This is the process whereby populations of species rather than ecological communities respond to climate change. Furthermore, the degree to which communities are nonanalogue has been shown to become progressively greater with increasing age (Stewart, 2008), as had already been suggested by the ever-changing composition of biotas (Hengeveld, 1994). Therefore, it is clear that in each subsequent oscillation the environment will not return to the state it was in at the equivalent stage of the preceding oscillation. This is partly because of the likelihood that populations within species, in addition to the species as a whole, operate individualistically (Bennett & Provan, 2008; Stewart, 2008). This further signifies that species compositions may not be represented by the same population or lineage over time. So, in addition to the phenomenon recognized for some time, that the proportion of extinct to extant species increases with greater age (e.g. Harmer, 1900a,b; Jablonski & Sepkoski, 1996), the combinations of those taxa will also have changed. As suggested by Jablonski & Sepkoski (1996): 'A portrait is beginning to emerge of how these major attributes of ecological associations have themselves changed through time and how this has been driven not only by climate but also by the evolution of constituent taxa'.

Hewitt (1996, 2000, 2001) considered the significance of recombining organisms in each subsequent climatic oscillation of the Pleistocene, he called it the 'new neighbour hypothesis'. The following quote summarizes Hewitt's thinking: '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 latter emphasizes another phenomenon, that of refugia, and suggests that geographical speciation modes are most important. Therefore, Hewitt combines allopatric (geographical) process with a level of sympatry (ecological) in a more holistic view of speciation. The quote of Hewitt also mentions different condi-

tions in various refugia by which he was presumably referred to various physical variables encountered. Clearly these will also be important although the present paper is restricting its attention to the effects of the recombination of species.

The present paper draws on the evidence for non-analogue communities in the past, which are the inevitable consequence of the individualistic process which caused the new neighbours. A brief review of nonanalogue communities and their progressive nature is given with a description of their likely cause, followed by a discussion of their likely significance to the evolution of organisms. What shall be argued here is that the phenomenon of progressive, or ever-changing, nonanalogue communities is a proxy for the evolution that is often, but not entirely, invisible in the fossil record. This is because it seems likely that the explanation for the nonanalogue ecological associations of taxa in the past is that key components, individualistic populations or lineages of the anomalous species, are now extinct. The evidence that these lineages may be extinct comes from the pattern emerging from ancient DNA studies of Late Pleistocene populations of extant mammals where many have been shown to undergo intraspecific genetic turnover (Hofreiter & Stewart, 2009). If component populations of nonanalogue communities are extinct lineages, this might suggest that their ecological adaptations were not identical to those of surviving lineages of those species. This loss of part of the ecological range of species is an evolutionary process. Finally, an attempt is also made to integrate this ongoing process into the science of evolutionary ecology (Schluter, 2001) and so to contribute a greater time dimension to that science (Stewart & Cooper, 2008). Here, I argue that the reorganization of species through time enhances the opportunities for evolution rather than decreases them, as suggested by others.

Nonanalogue ecological communities in the fossil record

Nonanalogue ecological communities, also sometimes called disharmonious communities or intermingled biotas (Graham, 1985b) are the rule, rather than the exception in Pleistocene palaeontology (Davis, 1976, 1981, 1983, 1986; Anderson et al., 1989; Huntley, 1991; Roy et al., 1995; Jackson & Overpeck, 2000; Williams et al., 2001; Jackson & Williams, 2004; Lyons, 2005; Edwards et al., 2005; Williams & Jackson, 2007; but see Pandolfi & Jackson, 2006 for stability in coral reef ecology). The phenomenon has been recognized across a large spectrum of organisms in the Pleistocene (Graham, 1985b), including vascular plants (Bell, 1969; Huntley, 1990, 1991; Kullman, 1998, 2002; Williams et al., 2001; Williams & Jackson, 2007), diatoms (Gasse et al., 1997), birds (Bramwell, 1984; Emslie, 1986; Brasso & Emslie, 2006), beetles (Coope & Angus, 1975; Coope, 2000), terrestrial molluscs (Kerney, 1963; Preece &

Bridgland, 1998), marine molluscs (Roy *et al.*, 1995), ostracods (Whittaker in Bates *et al.*, 2000), polychaetes (Sanfilippo, 1998), dinoflagellates (Head, 1998) and mammals (Graham & Grimm, 1990; Faunmap Working Group, 1996; Stafford *et al.*, 1999; Stewart *et al.*, 2003; Stewart, 2005; Price, 2004). Different explanations for these nonanalogue communities have been offered by various authors (Kerney, 1963; Coope & Angus, 1975; Bramwell, 1984; Graham & Grimm, 1990; Faunmap Working Group, 1996; Stafford *et al.*, 1999), although the most generally accepted cause is thought to be that species respond individually to environmental change [the Gleasonian model (Gleason, 1926)] and not as part of communities [the Clementsian model (Clements, 1904)] (Graham, 1985a,b; Faunmap Working Group, 1996). The individualistic response of species has long been used to explain the different plant taxa that come together during the successive climatic episodes of the Quaternary (West, 1980; Webb, 1986; Prentice, 1986). The latter is probably because of the individualistic response of populations of those tree species which change differently according to changing physical conditions over successive climatic oscillations (Bennett & Provan, 2008; Stewart, 2008). Jackson & Williams (2004) summarized the proposed mechanisms behind the individualistic response of plant species, which include migration lags, geographical barriers, soil development and differing centres of distribution during the Last Glacial Maximum (LGM). More recently, phylogeographers have recognized the same polarized hypotheses and have called these the concerted (community) vs. independent (individual species) responses to environmental fluctuations (Sullivan *et al.*, 2000). Taberlet *et al.* (1998), for example, gives firm support to the independent (individualistic) response of species. The fact that different species are believed to be in their contractive refugial phases during different parts of the Milankovitch oscillations is a consequence of this. Therefore, cold adapted taxa are generally in refugium during interglacials rather than during glacials when temperate taxa are in refugia (Stewart & Dalén, 2008). The potential existence of cryptic northern refugia for some temperate taxa during glacials (Stewart & Lister, 2001; Provan & Bennett, 2008) is also a consequence of the individualistic response of species, and their constituent populations, to environmental change (Stewart, 2008).

The Faunmap project used a thorough analysis of Quaternary mammals from the United States to look at changes in species distribution through time (Faunmap Working Group, 1996). The results showed that mammal species respond to climate change individualistically. The timing, rates and directions of the different species responses varied, producing nonanalogue communities. Despite the composition varying from that of today, the mammals formed ecological provinces with similar biogeographical distributions to the provinces today (Faunmap Working Group, 1996). These results were paralleled by a similar analysis for MIS 3 (Marine Oxygen isotope Stage 3), ca. 60–25 000 years ago, in Europe (Stewart *et al.*, 2003; Stewart, 2005). However, the results of the Faunmap database analysis, with almost 3000 late Quaternary sites, has been questioned by Alroy (1999). He argued that such nonanalogues are very rare and not restricted to the Pleistocene as they were also present in the Holocene. Alroy (1999) did acknowledge that differences between glacial and interglacial faunas had been noted and attributed these to differences in seasonal climates and that this partly lay behind the nonanalogue phenomenon. However, he suggested that most mammals 'maintained ecologically stable and predictable distribution that only gradually contracted in the face of Holocene environmental change' (Alroy, 1999). Subsequently, Graham (2006) vigorously rejected what Alroy has said about nonanalogue communities suggesting that Alroy used a nontraditional definition of nonanalogues which artificially decreased the number of observed examples of such biotas. Most recently Lyons (2005) re-examined the Faunmap data and came to an intermediary conclusion. Her analysis suggested that although there were nonanalogue communities in the United States in the Pleistocene there was also a greater degree of consistency of association between species than previously claimed. The three studies using the Faunmap database agree on one point that nonanalogue communities existed in the past although they disagree about the degree to which this was the case. It should be noted, however, that individualism does not predict that species congruence can never occur more than once. Instead it suggests that if analogues to the present do occur in the past it is because the conditions required for the different species to exist are present and not because of the presence of other apparently similar ecological species (Smith & Smith, 1998).

The most important, and potentially problematic, alternative explanation of the nonanalogue ecological data patterns seen among Pleistocene biotas is that they represent mixtures of organisms from different time frames with different climates. This argument has been proposed by Coope (2000) to explain Late Pleistocene (MIS 3) nonanalogue beetle assemblages in localities such as Earith in Southern England. The possibility that mixtures of temperate and more northern species came from two distinct climatic time frames would be a viable explanation for the anomaly. However, the site of Earith has a plant macrofossil record (Bell, 1969) which is very similar to the beetle fauna in its temperate and arctic climatic indicators with the addition of steppic and even halophytic species. The mixture of temperate and northern plants could be taken as further evidence of Coope's explanation although it can be argued that for two distinct types of organism, with different routes into the fossil record, to show the same pattern may suggest that it is a genuine contemporary mixture. So either Earith has sediments with organisms with different climatic

tolerances because the fossils were physically mixed together and they represent different time episodes (Coope's explanation) or the assemblage is a genuine nonanalogue mixture (Bell's explanation). It is significant that fossil mammal and bird assemblages from the same time frame in Britain and north-west Europe show very much the same patterns, particularly the mixture of steppic and cold species (Jacobi *et al.*, 1998; Stewart & Jacobi, unpublished data). In response to similar stratigraphical mixing explanations Graham & Lundelius (1984) cited that pollen analyses often show nonanalogue communities but that because they often involve lake sediments it is unlikely that they are because of reworking or time averaging. In fact palynologists largely accept the existence of nonanalogue ecologies in the Late Pleistocene (Jackson & Williams, 2004; Williams & Jackson, 2007; see below).

It is with mammalian nonanalogue assemblages that accelerator mass spectometry ^{14}C dating has proved the contemporaneity of Late Pleistocene species in America and Russia that are today allopatric (Stafford *et al.*, 1999). Single bones of nonanalogue small mammals with stratigraphical associations were dated showing that many modern biological community assemblages are younger than 12 000 years old. This further suggests that the nonanalogue nature of the ecology of the mid-latitudes of the northern hemisphere in the Late Pleistocene were genuine. The nonanalogue nature of mammalian taxa can also be quantified, as has been done recently for Europe during MIS 3 (60–20 000 years ago) (Stewart *et al.*, 2003; Stewart, 2005). In this instance the past distributions of different species of small mammal were mapped onto climate model output maps giving climate variable values with which they were associated in the past. These values were then compared with the temperatures and precipitation values with which those taxa are associated with today, showing discrepancies in both climatic variables. Taxa such as *Spermophilus* sp., the ground squirrel, with continental climatic associations today, were associated in the past with colder temperatures than their European counterparts today. Conversely, the northern taxa such as the arctic fox *Alopex lagopus* and the lemming *Lemmus* sp. were associated with MIS 3 model output values that were too warm in relation to their modern climate associations. Clearly the climate model simulations could not be predicting temperatures that were too cold and too warm at the same time. These discrepancies give a sense of the degree to which the faunas are nonanalogue during MIS 3 (Stewart *et al.*, 2003; Stewart, 2005). Jackson & Overpeck (2000) applied ecological niche theory to late Quaternary plant communities and defined the fundamental niche of species as being a subset of the environmental space available which was determined by the suite of combinations of variables that permit survival and reproduction of individuals. However, they also said that in reality only a subset of the fundamental niche of species was generally occupied, the

realized niche. In so doing they demonstrated that in many instances species could survive in conditions with different sets of environmental variables to those that they occupied today. Therefore, it follows that given different conditions, the realized niche of a species can move as novel environmental space within the fundamental niche becomes available. Jackson & Overpeck (2000) also considered the possibility that species may evolve maintaining a fundamental niche that is broad enough to keep track with a viable realized niche. They stated that generally the evidence for this is poor.

The nature of the past environmental space itself has been shown to have changed over time (since the late-glacial). This has led to the notion that nonanalogue climates existed in the past which in turn supported the nonanalogue ecologies (Jackson & Williams, 2004; Williams & Jackson, 2007). Environmental factors that are thought to have particularly contributed to this are the increased seasonality of insolation, lowered CO_2 levels and the persistence of continental ice sheets. The idea that nonanalogue communities were the result of nonanalogue climates maybe at odds with the conclusion of Stewart *et al.* (2003) and Stewart (2005) where the organisms are believed to have changed by extinction of populations with broader environmental tolerances.

The phenomenon of nonanalogue communities is not restricted to terrestrial assemblages. The marine environment also seems to have been characterized by non-analogue associations of taxa during the Pleistocene although workers on marine assemblages are not convinced that nonanalogue assemblages are genuine. The most extensively studied region is the Eastern Pacific coast of North America (Roy *et al.*, 1995, 1996). In this case the term used to describe the phenomenon is that of 'thermally anomalous assemblages'. The explanation for these faunas is that the assemblages are caused by short-term, high-amplitude climatic 'flickers' (Roy *et al.*, 1996). The reason given that such 'flickers' cause apparent genuine assemblages is that the different mollusc species responded close to the resolution limits of the fossil record and hence the assemblages are actually mixes of organisms that are responding fast to short climatic fluctuations. Roy *et al.* (1996) also suggested that because Pleistocene climatic changes are not known to be accompanied by significant speciation or extinction events, the thermally anomalous assemblages are likely to be mixtures rather than genuine ecological associations. Other explanations, including that by Zinsmeister (1974), suggest that temporary ocean currents not present today were introducing tropical mollusc larvae, which survived to adulthood, to areas with cooler waters. However, the alternative explanation, that the thermally anomalous mollusc associations represent genuine ecological communities has not been given a great deal of weight. Furthermore, it is interesting that a different use of the phenomenon of rapid climatic fluctuations was made by Lister & Sher (1995) who controversially

suggested that they promoted the existence of the variable ecology of the Late Pleistocene, the steppe-tundra, by creating a mosaic like mix of ecologies as opposed to the banded ones seen today when climates are temporally more stable.

It is implicit in the work of various authors that biotas are likely to be progressively different with increasing age because biotas are continually being mixed and are unlikely to reoccur in successive climatic episodes (West, 1980; Webb, 1986; Prentice, 1986; Tzedakis & Bennett, 1995). An analysis of mammalian assemblages from the British Isles has shown that this is indeed the case (Stewart, 2008). Faunas from the Holocene were compared with those from the last glaciation (MIS 3) and four progressively older interglacials (MIS 5e, 11, 13 and 17) using a Bray-Curtis cluster analysis with a single link. The result of the analysis was that there is a progressive difference of mammalian faunas with increasing age. The pattern was not regular, however, as the last cold stage fauna was more different to that of the Holocene than to any of the interglacials. Figure 1 shows the percentage pairwise similarity values for the progressively older faunas plotted against time with a trend line showing the decrease in similarity of interglacial faunas with time and the hypothesized decrease in similarity of glacial faunas. It is likely that the trend of similarity index of glacial faunas will converge on the values for interglacial faunas (Fig. 1). This is because the difference between the glacial and interglacial faunas has increased with time. This suggests that glacial faunas have evolved relatively recently and their constituent species are likely to have evolved from interglacial taxa (Stewart, 2008). For example, the genus *Mammuthus* is represented in MIS 3 by the woolly mammoth *Mammuthus primigenius* and in MIS 17 by the interglacial phylogenetic ancestor *M. trogontheri* (Lister & Sher, 2001).

The evolutionary consequences of progressive individualistic responses

Eldredge (1995) suggested that there are two main ways in which organisms respond to changes in their envi-
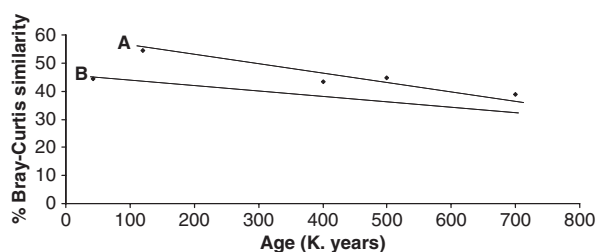

Fig. 1 Hypothesized different, but converging, trend lines of percentage Bray-Curtis similarity indices (to the Holocene mammalian fauna) were available for glacial and interglacial mammalian faunas. A – interglacial trend line; B – glacial trend line (after Stewart, 2008).

ronment. The first is to move and hence change their geographical distribution, while the second is to evolve. These can be augmented by other responses, such as changes in behaviour, through phenotypic plasticity (often called ecophenotypic effects) as well as extinction (Lister, 1996). However, when the phenomenon of nonanalogue ecological communities is taken as genuine it becomes apparent that the reality is more complex. The two basic forms of long term response (distribution shifts and/or evolution) are not as different and unconnected as might originally seem. If, as it has been shown, individual taxa (and populations of taxa) respond separately (in an individualistic manner), and hence differently, to environmental change then nonanalogue communities are inevitable. Furthermore, since the species making up ecological communities are themselves part of the environment, then the existence of different combinations of these taxa (nonanalogues) will have consequences to the evolution of the component species. As mentioned above, this has been called the new neighbour hypothesis (Hewitt, 1996, 2000, 2001) and if it is combined with the existence of the non-analogue communities it is likely that evolutionary processes such as character displacement, because of competitive diversification (Brown & Wilson, 1956) or facilitative diversification (Day & Young, 2004) as well as diffuse coevolution (Janzen, 1980) will become relevant. All the aforementioned processes have been considered coevolutionary processes by some authors (Strickberger, 1990). Character displacement is a process which has been observed, since its first description, in a variety of organisms, such as Darwin's finches (Grant, 1972), hydrobid gastropods (Fenchel, 1975) and shrews (Malmquist, 1985). It has also been demonstrated that character displacement need not result from the interaction between two closely related organisms, as exemplified by the bees and finches in the Galapagos Islands, which simply amplifies the degree to which this can be significant (Schluter, 1986). Other ecological phenomena may also be important in promoting speciation such as facilitative diversification which is a relatively newly identified process and has also been implicated in evolutionary divergence of species in theoretical and empirical studies (Day & Young, 2004). Another process, diffuse coevolution, as distinct from pairwise coevolution, involves nonobligate coevolving partners. It theoretically occurs when loose evolutionary associations occur where natural selective pressures are imposed by more than one species (Janzen, 1980). Examples of diffuse coevolution include the relationship between herbivores and their plant foods (Iwao & Rausher, 1997). These evolutionary ecological processes have been implicated in species formation (e.g. Schluter, 2000) and in turn imply that mixing of taxa as a result of different individualistic responses will have consequences to their evolution.

The role of ecology in macroevolution has some support from palaeontology (Conway Morris, 1998)

although not without scepticism (Benton, 1996). However, various authors (Graham & Grimm, 1990; Huntley *et al.*, 1997) have argued that the individualistic response suggests that no evolution involving interactions between taxa such as coevolution can occur. The reasoning is that the reorganization of biological communities is likely to draw apart some of the taxa deemed to have coevolved in one set of Quaternary associations during subsequent associations. Huntley *et al.* (1997) therefore question the coevolution paradigm because many of the species associations that exist today arose at the beginning of the Holocene and are therefore only approximately 10 000 years old. This was described as the coevolutionary disequilibrium, and first applied to help explain megaherbivore extinction at the end of the Pleistocene (Graham & Lundelius, 1984) and suggests that such coevolutionary scenarios may be exceptional evolutionary circumstances. Although this reasoning appears sound, coevolution has been demonstrated for pairwise mutualists over considerable time spans such as figs (*Ficus*) and wasps (Agaonidae) (Rønsted *et al.*, 2005), pocket gophers (Geomyidae) and their chewing lice (Phthiraptera) (Hafner *et al.*, 2003) and *Glochidion* trees and *Epicephala* moths (Kato *et al.*, 2003) although such examples might be rare (Iwao & Rausher, 1997). Diffuse coevolution, involving more than a pair of species in an obligate relationship, has been described as likely to be more common (Iwao & Rausher, 1997) and it is these types of mutualistic evolutionary scenarios that are probably more difficult to reconcile with the existence of the individualistic response of species to climate change. While there may be some theoretical difficulty reconciling their diffuse coevolutionary histories with the individualistic response, the fact that they generally involve more than a pair of species interacting allows for greater variation in the specific species imposing selection on the other. Coevolutionary disequilibrium as a process which encourages extinction (Graham & Lundelius, 1984) is also likely to result in evolution. As species associations break down, other new associations, and hence new diffuse coevolutionary relationships, become possible.

The other point is that not all evolutionary divergence that occurs during one Quaternary climatic phase, and hence through one set of species associations, is likely to become extinct during the following phase. As discussed above, suggestions that speciation is generally discouraged by Millankovitch scale climatic oscillations rather than promoted have been made by a number of authors such as Coope (1978), Bennett (1990, 1997) and Klicka & Zink (1997). The arguments made are that the cyclicity causes mixing of populations at regular intervals which counters any isolation and divergence that may take place (Bennett, 1990, 1997). This is an important perspective as it is related to the arguments of microevolution around a mean used by Eldredge & Gould (1972) to explain evolutionary stasis. Clearly the problem

highlighted cannot be ignored. However, it leaves a paradox which is that allopatric speciation is generally favoured by biologists today and that a convincing general causal mechanism for speciation in prequaternary times is lacking. The existence of nonanalogue communities which probably involve extinct constituent populations, may be an indication that evolution is proceeding through the Quaternary, although it may not be easily discerned from the fossil record without aDNA studies.

Hellberg *et al.* (2001) have shown that morphological evolution occurred in a marine gastropod because of climatically induced range expansion. This is contrary to some expectations as evolution is usually expected in isolation (e.g. Bilton *et al.*, 1998). The morphological results of Hellberg *et al.* (2001) correlate with a lack of sequence variation in the northern expansive populations. This shows that morphological evidence may be misleading and that it should, where possible, be backed up by molecular studies. Nevertheless, ecological factors have been shown to cause phenotypic and genotypic diversification and there is increasing evidence that speciation may be a possible outcome (Schluter, 2001). The latter is shown by factors such as the low hybrid fitness in the offspring of individuals from two populations that have come from different ecological conditions with perhaps different ecomorphological characterstics (Orr, 1995). Other observations such as the correlations of mate choice with morphology and habitat and that premating isolation can evolve independently in similar environments also give greater credence to a role of ecology in evolution (Schluter, 2001).

The outcome that may result from the individualistic process described is one where periods of differently mixed ecological communities yield differently adapted populations of taxa. Many of these are likely to go extinct, as has been shown recently in the Late Pleistocene arctic fox populations of Belgium and Germany which have also been shown to have distinct adaptation to local conditions distinct from those of modern populations (e.g. Dalén *et al.*, 2007). However, the likelihood that the process of colonization from, and retreat to, glacial refugia may be more complex than often portrayed at present (Valdiosera *et al.*, 2008) and may imply that some parts of these populations survive. If such populations survive to come into contact (sympatry) with their allopatric sister taxa this may lead to speciation through reinforcement.

In their discussion of late Quaternary plant ecologies using niche theory Jackson & Overpeck (2000) suggest that evolution of species might occur so as to track the environment by changing their fundamental niche. They indicate that there was little evidence for this but they did not fully consider intraspecific genetic variation and how changes in the total range of populations of a species through local extinctions are very likely to occur. The

arctic fox study by Dalén *et al.* (2007) could be an example illustrating this process.

Hewitt's (1993, 1996, 2000, 2001) new neighbour hypothesis recognizes the potential evolutionary significance of ecological mixing and although Hewitt returned to this issue a number of times he never expanded upon it except to say that meeting new competitors, host plants, etc. would doubtless lead to new adaptations (Hewitt, 1993). This highlights the importance of a thorough consideration of nonanalogue ecologies to the adaptive speciation of organisms. Hewitt (1993) was specifically making reference to work by palynological palaeoecologists such as West (1980) and Webb (1986) who showed that in successive interglacials, separate plant taxa had colonized at different times from different ice age refugia.

Returning to the fact that many of the lineages making up nonanalogue communities are probably extinct, and that therefore the phenomenon has an evolutionary consequence, one can consider the constituent taxa in greater depth. Examples include the Noway lemming (*Lemmus lemmus*) and the arctic fox (*Alopex lagopus*) during the Late Pleistocene of Europe. During this time the Norway lemming and arctic fox's distribution extended from its modern range in Fennoscandia to as far south as the Belgian Ardennes, central France and beyond (Stewart *et al.*, 2003; Sommer & Benecke, 2005). The existence of populations of these species in Fenno-scandia itself during the Late Pleistocene is attested by the fossil record (Larsen *et al.*, 1987; Frafjord & Hufthammer, 1994; van Valen *et al.*, 1996) and inferred from mtDNA work (Fedorov & Stenseth, 2001). This signifies that the late Pleistocene populations of more southern reaches of Europe are unlikely to have contributed to the modern gene pool in Fennoscandia (Stewart *et al.*, 2003). The more southern populations were ones living in nonanalogue associations with temperate and steppic taxa and subsequently probably went extinct (Stewart *et al.*, 2003). In fact, as already mentioned, the arctic fox populations of the lower latitudes of the Late Pleistocene are known to be to be extinct (Dalén *et al.*, 2007). Furthermore, these southerly distributed arctic foxes have smaller paws than contemporary arctic foxes, which represents an adaptation to local conditions (Dalén *et al.*, 2007), presumably because of a relative lack of snow fall. Examples of such nonanalogue communities are common in the mid-latitudes of Europe during the Late Pleistocene with arctic fox and Norway lemming accompanied by collared lemming *Dicrostonyx torquatus*, bank vole *Clethionomys glareolus*, mole *Talpa europea*, pika *Ochotona pusila*, common hamster *Cricetus cricetus* and ground squirrel *Citelus* spp. (Stewart *et al.*, 2003). These species include ones that today are found in northern cold, more southern temperate and eastern continental climates. Similar small mammal nonanalogue associations are known in North America (Graham, 1985b, 1997).

The regional extinctions represented by certain populations of these nonanalogue communities rarely receive attention. This is no doubt because they are not easily recognized in the morphology of fossils and even if they are, because they are subspecific, they are not often considered to be greatly significant, either taxonomically or ecologically, in Pleistocene palaeontology. An exception to this is that of the Northern European water vole *Arvicola terrestris* during the Middle Pleistocene. In this instance there is an apparent reversal in the lineages' evolutionary trends. *Arvicola terrestris* apparently undergoes an evolutionary reversal in the morphology of the molars which is probably explained by an immigration of a population with a more 'primitive' state from southern Europe (van Kolfschoten, 1990; Lister, 1993). The population preceding the apparent reversal is likely to have been replaced either because they became extinct or because they moved. It may be that extinction is more likely because whole populations do not generally become displaced; instead they retreat by population extirpation *in situ* (Hewitt, 1999; Bennett *et al.*, 1991). This demonstrates that extinction is not a completely separate phenomenon from distribution change. A similar scenario is observed in mammoth evolution in the Middle Pleistocene of Europe (Lister & Sher, 2001).

There is a growing awareness of population level extinctions accompanying geographical range contractions from work on ancient DNA such as that by Barnes *et al.* (2002) on brown bear *Ursus arctos*, Shapiro *et al.* (2004) on bison *Bison bison*, Burger *et al.* (2004) on lions *Panthera leo*, Rohland *et al.* (2005) on Eurasian cave hyenas *Crocuta crocuta spelaea*, MacPhee *et al.* (2005) on musk ox *Ovibos moschatus* and by Leonard *et al.* (2007) on Beringian wolves *Canis lupus*. In fact most of the studies to date treating extant mammals have revealed a similar pattern. These studies showed that the genetic diversity in these species was hugely reduced because of climatic events such as the LGM or the termination of the Pleistocene. This was probably because of the environmental change that accompanied these extreme global cooling and warming events and further demonstrates, in a direct manner, the importance of climate and environment on genetic diversity through local extinction. One could also add the new molecular findings from work on Neanderthals during MIS 5 showing that the extreme cold phase, during MIS 4, caused a gradual extinction of haplotypes prior to their eventual complete demise in MIS 3 (Orlando *et al.*, 2006).

Therefore, local population level extinctions cause apparent punctuations in the fossil record. Ancestral taxa become extinct because of an environmental event that in turn leads to the immigration of an allopatric descendant which makes the fossil record to appear punctuated. The example of the Beringian wolf population extinction illustrates the process well because these wolves were distinct genetically as well as ecomorphologically (Leonard *et al.*, 2007). It appears that they were adapted

to hunting and/or scavenging megafaunal animals on the steppe-tundra and went extinct at the end of the Pleistocene following the demise of that biota (Leonard *et al.*, 2007). Wolves today in the area described as Beringia are a more gracile type and concentrate on smaller prey. This demonstrates that the coevolutionary disequilibrium process is an evolutionary process as the Pleistocene hypercarnivorous wolves had evolved in response to the existence of the megafauna in Beringia.

Conclusion

The individualistic mixing of species within communities appears to have progressed through Quaternary time, suggesting that evolution is moving at a relatively significant pace. Many populations of animals living in progressively different combinations are likely to have become extinct because of environmental change. Therefore, the phenomenon of nonanalogue communities may be used as a proxy for a cryptic evolutionary process in the fossil record. This is because such local extinctions differ from species extinctions in possibly representing the selection of populations of individuals in favour of others. The subspecific extinctions are only reliably demonstrated by use of ancient DNA studies such as those pioneered by Barnes *et al.* (2002). This should act in part as a reply to Coope (1978), Bennett (1990, 1997) and Klicka & Zink (1997) who have questioned the importance of ice ages to the process of speciation during the Pleistocene. Their suggestion was that climate fluctuations are short and thus cause allopatric populations to be assimilated back into the whole parent population once climate completes a glacial-interglacial oscillation and sympatry reoccurs. The process evoked by those authors would cause stability while the process implicated by the individualistic mixing with extinction described here is one of ecological and genetic change.

If fossils are as ambiguous taxonomically, or at least phylogenetically, as some suggest (Erwin & Anstey, 1995; Stewart, 2002), then it is little wonder that the fossil record has proved relatively unfruitful in documenting evolution in many organisms. Taxa such as plants and beetles may be more phenotypically conservative in the Quaternary than mammals and the evidence for evolution is simply not there as speciation may be cryptic in those taxa. Mammals have teeth which is why there is more evolution visible in their fossil record than in that of birds, for example, although it may be unlikely that these two vertebrates did not have similar levels of species evolution during the Quaternary (Stewart, 2002). This perspective has been given renewed attention recently by revised calibrations of estimates of divergence times for some bird sister species suggesting that divergence times fall within the past 250 000 years (Ho *et al.*, 2008).

As mentioned above, losses of genetic diversity are only now being revealed by ancient DNA analyses (Barnes *et al.*, 2002; Shapiro *et al.*, 2004; Burger *et al.*, 2004; MacPhee *et al.*, 2005; Rohland *et al.*, 2005; Orlando *et al.*, 2006; Leonard *et al.*, 2007; Dalén *et al.*, 2007). They confirm that more local extinctions took place across Quaternary climate oscillations than has been formerly been recognized. These studies imply that gene pools are undergoing natural selection by environmental change and that hence this is an evolutionary process that requires more consideration. It is also clear, as has been demonstrated recently by Dalén *et al.* (2007) for arctic fox, that the dominance of the individualistic response to climate change implies that the habitat tracking explanation for the stasis required in the punctuated equilibrium model (Eldredge & Gould, 1972; Gould & Eldredge, 1993) may no longer be tenable. Whilst definitive evidence for this process is so far restricted to mammals, because of the aDNA work performed to date, it is thought that similar evidence will eventually be forthcoming for invertebrates and plants, particularly in the permafrost regions (Willerslev *et al.*, 2004; Hofreiter & Stewart, 2009).

It is also difficult to demonstrate this process definitively in more southern latitudes with tropical biotas because of the inherent lack of aDNA preservation in these regions. There are, however, signs that nonanalogue communities existed at more southern locations in for example marsupials in Australia (Price, 2004). This suggests that other organisms, including animals (vertebrates and invertebrates) and plants, also responded to the climate changes of the past by geographical range shifts which resulted in changes in ecological associations with corresponding population level changes to component taxa. The process is envisaged to have taken place in tropical climes as a result of changes in relative aridity that took place which mirrored the changes in relative temperature (and aridity) towards the poles.

Ackerly (2003) has shown that the fundamental niche breadth may shift in response to changes climatic conditions by adaptation. While climatic variables are likely to lead to an adaptive response, the ecological community composition is also likely to have an effect. Many adaptations are ones involving the means of acquiring resources, which immediately suggests that there are limits to some resources, such as food availability or canopy space. This will in turn invoke processes involving interspecies competition. Therefore, the diagram of Ackerly (2003) whereby adaptation takes place in response to temperature and precipitation could be transformed to include changes in ecological community composition (Fig. 2).

It is envisaged that the process described will have been progressing throughout geological time, during the Pleistocene certainly, but that because of modern analogues in discerning its existence may be less visible in deeper time. If it is to be recognized at earlier times it will have to be inferred from the recognition of the individualistic responses of species to climate and environmental
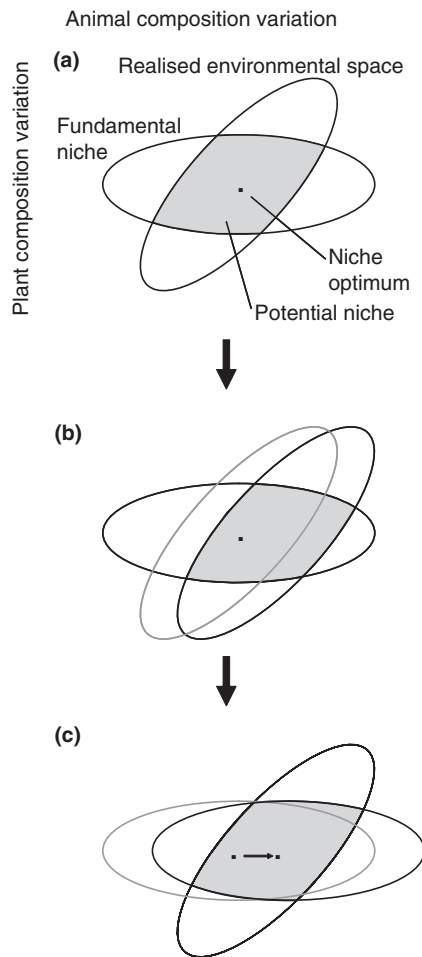
Animal composition variation

Fig. 2 Diagram indicating response of species niche space defined by accompanying plant and animal species composition. (a) Potential niche of species before change, based on the intersection of its fundamental niche with the realized environmental states along a hypothetical accompanying animal and plant species composition gradients. (b) Change in potential niche space due to change in accompanying animal species composition. (c) Adaptive response by change in fundamental niche space due to new animal species composition. Same can occur due to a change in plant species composition. Modified from Ackerly (2003).

changes. A possible example of this was described recently from the Palaeozoic where elements of plant communities were shown to be responding individualistically to climate change (DiMichele *et al.*, 2001).

In conclusion, the significance of the progressively individualistic response of species is that it imposes limits on the arguments of Coope and others. The completion of a Milankovitch cycle does not bring ecologies and individual species full circle and unchanged. Populations separated by climate change, environmental disruption and distribution change can be ecologically different as well as genetically distinct and therefore unable to hybridize. The progressive individualistic response of

species populations to environmental change has important implications to processes of species evolution if ecology is important in such processes. This process, whereby populations of species undergo differential extinction, is reminiscent of the group selection hypotheses described by Vrba (1984). The full implications of the phenomenon will doubtlessly emerge with time.

Acknowledgments

References

Ackerly, D.D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int. J. Plant Sci.* **164**(Suppl. 3): S165–S184.

Alroy, J. 1999. Putting North America's end-Pleistocene megafaunal extinction in context. Large-scale analyses of spatial patterns, extinction rates and size distributions. In: *Extinction in Near Time. Causes, Contexts, and Consequences* (R.D.E. MacPhee, ed.), pp. 105–143. Kluwer Academic/Plenum Publishers, New York.

Anderson, P.M., Bartlein, P.J., Brubaker, L.B., Gajewski, K. & Ritchie, J.C. 1989. Modern analogues of late-Quaternary pollen spectra from the western interior of North America. *J. Biogeogr.* **16**: 573–596.

Avise, J.C. & Walker, D. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. *Proc. R. Soc. Lond. B. Biol. Sci.* **265**: 457–463.

Barnes, I., Matheus, P., Shapiro, B., Jensen, B. & Cooper, A. 2002. Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* **295**: 2267–2270.

Bates, M.R., Bates, C.R., Gibbard, P.L., Macphail, R.I., Owen, F.J., Parfitt, S.A., Preece, R.C., Roberts, M.B., Robinson, J.E., Whittaker, J.E. & Wilkinson, K.N. 2000. Late Middle Pleistocene deposits at Norton Farm on the West Sussex coastal plain, southern England. *J. Quat. Sci.* **15**: 61–89.

Bell, G.F. 1969. The occurrence of southern, steppe and halophytic elements in the Weichselian (Last Glacial) floras of southern Britain. *New Phytol.* **68**: 913–922.

Bennett, K.D. 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology* **16**: 11–21.

Bennett, K.D. 1997. *Evolution and Ecology: The Pace of Life.* Cambridge studies in Ecology, Cambridge University Press, Cambridge.

Bennett, K.D. 2004. Continuing the debate on the role of Quaternary environmental change for macroevolution. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **359**: 295–303.

Bennett, K.D. & Provan, J. 2008. What do we mean by 'refugia'? *Quat. Sci. Rev.* **27**: 2449–2455.

Bennett, K.D., Tzedakis, P.C. & Willis, K.J. 1991. Quaternary Refugia of North European Trees. *J. Biogeogr.* **18**: 103–115.

Benton, M.J. 1996. On the non-prevalence of competitive replacement in the evolution of tetrapods. In: *Evolutionary Palaeobiology: In Honor of James W. Valentine* (D. Jablonski, D.H. Erwin & J.H. Lipps, eds), pp. 185–210. University of Chicago, Chicago.

Bilton, D.T., Mirol, P.M., Mascheretti, S., Fredga, K., Zima, J. & Searle, J.B. 1998. Mediterranean Europe as an area of endemism for small mammals rather than a source for northwards postglacial colonisation. *Proc. R. Soc. Lond. B Biol. Sci.* **265**: 1219–1226.

Bramwell, D. 1984. The birds of Britain: when did they arrive? In: *In the Shadow of Extinction: A Quaternary Archaeology and Palaeoecology of the Lake, Fissures and smaller Caves at Cresswell Crags SSSI* (D.D. Gilbertson & R.D.S. Jenkinson, eds), pp. 89–99. University of Sheffield, John Collis Publisher, Sheffield.

Brasso, R.L. & Emslie, S.D. 2006. Two new Late Pleistocene Avifaunas from New Mexico. *The Condor* **108**: 721–730.

Brown, W.L. Jr & Wilson, E.O. 1956. Character displacement. *Syst. Zool.* **5**: 49–64.

Burger, J., Rosendahl, W., Loreille, O., Hemmer, H., Eriksson, T., Götherström, A., Hiller, J., Collins, M.J., Wess, T. & Alt, K.W. 2004. Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. *Mol. Phylogenet. Evol.* **30**: 841–849.

Clements, F.E. 1904. *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institute, Washington.

Conway Morris, S. 1998. The evolution of diversity in ancient ecosystems: a review. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **353**: 327–345.

Coope, G.R. 1978. Constancy of species versus inconstancy of Quaternary environments. In: *Diversity of Insect Faunas* (L.A. Mound & N. Waloff, eds), pp. 176–187. Blackwell Science, London.

Coope, G.R. 2000. Middle Devensian (Weichselian) coleopteran assemblages from Earith, Cambridge (UK) and their bearing on the interpretation of 'Full glacial' floras and faunas. *J. Quat. Sci.* **15**: 779–788.

Coope, G.R. & Angus, R.B. 1975. An ecological study of a temperate interlude in the middle of the last glaciation, based on fossil Coleoptera from Isleworth, Middlesex. *J. Anim. Ecol.* **44**: 365–391.

Dalén, L., Nyström, V., Valdiosera, C., Germonpré, M., Sablin, M., Turner, E., Angerbjörn, A., Arsuaga, J.L. & Götherström, A. 2007. Ancient DNA reveals lack of postglacial habitat tracking in the arctic fox. *Proc. Natl. Acad. Sci. USA* **104**: 6726–6729.

Davis, M.B. 1976. Pleistocene biogeography of temperate deciduous forests. *Geosci. Man* **13**: 13–26.

Davis, M.B. 1981. Quaternary history and the stability of forest communities. In: *Forest Succession: Concepts and Application* (D.C. West, H.H. Shugart & D.B. Botkin, eds), pp. 132–153. Springer, New York.

Davis, M.B. 1983. Quaternary history of deciduous forests of eastern North America and Europe. *Ann. MO Bot. Gard.* **70**: 550–563.

Davis, M.B. 1986. Climatic instability, time lags, and community disequilibrium. In: *Community Ecology* (J. Diamond & T.J. Case, eds), pp. 269–284. Harper & Row, New York.

Day, T. & Young, K.A. 2004. Competitive and facilitative evolutionary diversification. *Bioscience* **54**: 101–109.

DiMichele, W.A., Pfefferkorn, H.W. & Gastaldo, R.A. 2001. Response of Late Carboniferous and Early Permian plant communities to climate change. *Annu. Rev. Earth Planet. Sci.* **29**: 461–487.

Edwards, M.E., Brubaker, L.B., Lozhkin, A.V. & Anderson, P.M. 2005. Structurally novel biomes: a response to past warming Beringia. *Ecology* **86**: 1696–1703.

Eldredge, N. 1995. *Reinventing Darwin: The Great Evolutionary Debate*. Weidenfeld & Nicholson, London.

Eldredge, N. & Gould, S.J. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: *Models in Paleobiology* (T.J. Schopf, ed.), pp. 82–115. Freeman, Cooper, San Francisco.

Emslie, S.D. 1986. The late Pleistocene (Rancholabrean) avifauna of Little Box Elder Cave, Wyoming. *Contr. Geol. Univ. Wyo.* **23**: 63–82.

Erwin, D.H. & Anstey, R.L. 1995. *New Approaches to Speciation in the Fossil Record*. Columbia University Press, New York.

Faunmap Working Group 1996. Spatial response of mammals to Late Quaternary environmental fluctuations. *Science* **272**: 1601–1606.

Fedorov, V.B. & Stenseth, N.C. 2001. Glacial survival of the Norwegian lemming (*Lemmus lemmus*) in Scandinavia: inference from mitochondrial DNA variation. *Proc. R. Soc. Lond. B Biol. Sci.* **268**: 809–814.

Fenchel, T. 1975. Character displacement and coexistence in mud snails (Hydrobiidae). *Oecologia (Berl.)* **20**: 19–32.

Frafjord, K. & Hufthammer, K. 1994. Subfossil records of the Arctic fox (*Alopex lagopus*) compared to its present distribution in Norway. *Arctic* **47**: 65–68.

Gasse, F., Barker, P., Gell, P.A., Fritz, S.C. & Chalié, F. 1997. Diatom-inferred salinity in palaeolakes: an indirect tracer of climate change. *Quat. Sci. Rev.* **16**: 547–563.

Gleason, H.A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* **53**: 1–20.

Gould, S.J. & Eldredge, N. 1993. Punctuated equilibrium comes of age. *Nature* **366**: 223–227.

Graham, R.W. 1985a. Diversity and community structure of the late Pleistocene mammal fauna of North America. *Acta Zool. Fenn.* **170**: 181–192.

Graham, R.W. 1985b. Response of mammalian communities to environmental changes during the Late Quaternary. In: *Community Ecology* (J. Diamond & T.J. Case, eds), pp. 300–313. Harper & Row Publishers, New York.

Graham, R.W. 1997. The special response of mammals to Quaternary climate changes. In: *Past and Future Rapid Environmental Change: The spatial and Evolutionary Responses of Terrestrial Biota* (B. Huntley, W. Cramer, A.V. Prentice & J.R.M. Allen, eds), pp. 153–162. Springer, Berlin.

Graham, R.W. 2006. Fallacies of the disharmonious index and relevance of Quaternary non-analogue mammal faunas for future environment change. Biotic Response to Global Environmental Change: Analogs for the Future of Life on Earth, Philadelphia Annual Meeting (22–25 October 2006). *Geol. Soc. Am.* (Abstracts with Programs) **38**: 118.

Graham, R.W. & Grimm, E.C. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *Trends Ecol. Evol.* **5**: 289–292.

Graham, R.W. & Lundelius, E.L. 1984. Coevolutionary disequilibrium and Pleistocene extinctions. In: *Quaternary Extinctions:*

A Prehistoric Revolution (P.S. Martin & R.G. Klein, eds), pp. 223–249. University of Arizona Press, Tucson.

Grant, P.R. 1972. Convergent and divergent character displacement. *Biol. J. Linn. Soc.* **4**: 39–68.

Grant, P.R. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton.

Grant, P.R. & Grant, B.R. 2007. *How and Why Species Multiply: The Radiation of Darwin's Finches*. Princeton University Press, Princeton.

Hafner, M.S., Demastes, J.W., Spradling, T.A. & Reed, D.L. 2003. Cophylogeny between pocket gophers and chewing lice. In: *Tangled Trees: Phylogeny, Cospeciation and Coevolution* (R.D.M. Page, ed.), pp. 195–220. The University of Chicago Press, Chicago.

Harmer, F.W. 1900a. The Pliocene deposits of the East of England– Part II: the crag of Essex (Waltonian) and its relation to that of Suffolk and Norfolk. *Quart. J. Geol. Soc. Lond.* **56**: 705–738.

Harmer, F.W. 1900b. On a proposed new classification of the Pliocene deposits of the East of England. *Rep. Brit. Assoc. Adv. Sci.* (for 1899) 751–753.

Head, M.J. 1998. Marine environmental change in the Pliocene and early Pleistocene of eastern England: the dinoflagellate evidence reviewed. *Meded. Nederl. Instit. Toeg. Geowet. TNO* **60**: 199–226.

Hellberg, M., Balch, D.P. & Roy, K. 2001. Climate-driven range expansion and morphological evolution in marine gastropods. *Science* **292**: 1707–1710.

Hengeveld, R. 1994. Biogeographical ecology. *J. Biogeog.* **21**: 341–351.

Hewitt, G. 1993. Postglacial distribution and species substructure: lessons from pollen, insects and hybrid zones. In: *Evolutionary Patterns and Processes* (D.R. Lees & D. Edwards, eds), pp. 97–123. Academic Press, London.

Hewitt, G. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc.* **58**: 247–276.

Hewitt, G. 1999. Post-glacial recolonisation of European biota. *Biol. J. Linn. Soc.* **68**: 87–112.

Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* **405**: 907–913.

Hewitt, G.M. 2001. Speciation, hybrid zones and phylogeography – or seeing genes in space and time. *Mol. Ecol.* **10**: 537–549.

Ho, S.Y.W., Saarma, U., Barnett, R., Haile, J. & Shapiro, B. 2008. The effect of inappropriate calibration in molecular ecological studies: evidence from three case studies. *PLoS ONE* **3**: e1615.

Hofreiter, M. & Stewart, J.R. 2009. Ecological change, range fluctuations and population dynamics during the Pleistocene. *Curr. Biol.* **19**: R584–R594.

Huntley, B. 1990. European post-glacial forests: compositional changes in response to climatic change. *J. Veg. Sci.* **1**: 507–518.

Huntley, B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Ann. Bot.* **67**(Suppl. 1): 15–22.

Huntley, B., Cramer, W., Morgan, A.V., Prentice, H.C. & Allen, J.R.M. 1997. Predicting the response of terrestrial biota to future environmental changes. In: *Past and Future Rapid Environmental Change: The spacial and Evolutionary Responses of Terrestrial Biota* (B. Huntley, W. Cramer, A.V. Prentice & J.R.M. Allen, eds), pp. 487–504. Springer, Berlin.

Iwao, K. & Rausher, M.D. 1997. Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *Am. Nat.* **149**: 316–335.

Jablonski, D. & Sepkoski, J.J. Jr 1996. Paleobiology, community ecology and scales of ecological pattern. *Ecology* **77**: 1367–1378.

Jackson, S.T. & Overpeck, J.T. 2000. Responses of plant communities to environmental changes of the late Quaternary. *Paleobiology* **26**(Suppl. 4): 194–220.

Jackson, S.T. & Williams, J.W. 2004. Modern Analogs in Quaternary Paleoecology: here today, gone yesterday, gone tomorrow? *Annu. Rev. Earth Sci.* **32**: 495–537.

Jacobi, R.M., Rowe, P.J., Gilmour, M.A., Grün, R. & Atkinson, T.C. 1998. Radiometric dating of the Middle Palaeolithic tool industry and associated fauna of Pin Hole Cave, Creswell Crags, England. *J. Quat. Sci.* **13**: 29–42.

Janzen, D.H. 1980. When is it coevolution? *Evolution* **34**: 611–612.

Johnson, N.K. & Cicero, C. 2004. New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. *Evolution* **58**: 1122–1130.

Kato, M., Takimura, A. & Kawakita, A. 2003. An obligate pollination mutualism and reciprocal diversification in the tree genus Glochidion (Euphorbiaceae). *Proc. Natl. Acad. Sci. USA* **100**: 5264–5267.

Kerney, M.P. 1963. Late-glacial deposits on the chalk of South-East England. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **246**: 203–254.

Klicka, J. & Zink, R.M. 1997. The importance of recent ice ages in speciation: a failed paradigm. *Science* **277**: 1666–1669.

van Kolfschoten, T. 1990. The evolution of the mammal fauna in the Netherlands and the middle Rhine area (West Germany) during the Late Middle Pleistocene. *Meded. Rijk. Geol. Dienst* **43**: 1–69.

Kullman, L. 1998. Non-analogous tree flora in the Scandes Mountains, Sweden, during the early Holocene – macrofossil evidence of rapid geographic spread and response to palaeoclimate. *Boreas* **27**: 153–161.

Kullman, L. 2002. Boreal tree taxa in the central Scandes during the Late-Glacial: implications for Late-Quaternary forest history. *J. Biogeog.* **29**: 1117–1124.

Kurtén, B. 1959. On the longevity of mammalian species in the Tertiary. *Comment. Biol.* **21**: 1–14.

Kurtén, B. 1968. *Pleistocene Mammals of Europe*. Weindenfeld & Nicholson, London.

Lack, D. 1944. Ecological aspects of species formation in Passerine birds. *Ibis* **86**: 260–286.

Larsen, E., Gullisken, S., Lauritzen, S.E., Lie, R., Løvlie, R. & Mangerud, J. 1987. Cave stratigraphy in western Norway; multiple Weichselian glaciations and interstadial vertebrate fauna. *Boreas* **16**: 267–292.

Leonard, J.A., Vilá, C., Fox-Dobbs, K., Koch, P.L., Wayne, R.K. & Van Valkenberg, B. 2007. Megafaunal extinctions and the disappearance of a specialized wolf ecomorph. *Curr. Biol.* **17**: 1146–1150.

Lister, A.M. 1993. Patterns of evolution in Quaternary mammal lineages. In: *Evolutionary Patterns and Processes* (D.R. Lees & D. Edwards, eds), pp. 71–93. Academic Press, London.

Lister, A.M. 1996. The evolutionary response of vertebrates to Quaternary environmental change. In: *Past and Future Rapid Environmental Change: The Spatial and Evolutionary Responses of Terrestrial Biota* (B. Huntley, W. Cramer, A.V. Prentice & J.R.M. Allen, eds), pp. 287–302. Springer, Berlin.

Lister, A.M. 2004. The impact of Quaternary ice ages on mammalian evolution. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **359**: 221–241.

Lister, A.M. & Sher, A.V. 1995. Ice cores and mammoth extinction. *Nature* **378**: 23–24.

Lister, A.M. & Sher, A.V. 2001. The origins and evolution of the woolly mammoth. *Science* **294**: 1094–1097.

Losos, J.B. 1990. Ecomorphology, performace capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr.* **60**: 369–388.

Lyons, S.K. 2005. A quantitative model for assessing community dynamics of Pleistocene mammals. *Am. Nat.* **165**: 168–185.

MacPhee, R.D.E., Tikhonov, A.N., Mol, D. & Greenwood, A.D. 2005. Late Quaternary loss of genetic diversity in muskox (*Ovibos*). *BMC Evol. Biol.* **5**: 49.

Malmquist, M.G. 1985. Character displacement and biogeography of the pygmy shrew in Northern Europe. *Ecology* **66**: 372–377.

McKinnon, J.S., Mori, S., Blackman, B.K., David, L., Kingsley, D.M., Jamieson, L., Chou, J. & Schluter, D. 2004. Evidence for the role of ecology's role in speciation. *Nature* **429**: 294–298.

Mourer-Chauviré, C. 1993. The Pleistocene avifaunas of Europe. *Archaeofauna* **2**: 53–66.

Orlando, L., Darlu, P., Toussaint, D., Bonjean, D., Otte, M. & Hänni, C. 2006. Revisiting Neanderthal diversity with a 100,000 year old mtDNA sequence. *Curr. Biol.* **16**: 400–401.

Orr, H.A. 1995. The population genetics of speciation: the evolution of hybrid incompatibilities. *Genetics* **139**: 1805–1813.

Pandolfi, J.M. & Jackson, J.B.C. 2006. Ecological persistence interrupted in Caribbean coral reefs. *Ecol. Lett.* **9**: 818–826.

Preece, R.C. & Bridgland, D.R. eds 1998. *Late Quaternary Environmental Change in North-West Europe: Excavations at Holywell Coombe, South-East England*. Chapman & Hall, London.

Prentice, I.C. 1986. Vegetation response to past climate changes. *Vegetatio* **67**: 131–141.

Price, G.J. 2004. Fossil bandicoots (Marsupialia, Peramelidae) and environmental change during the Pleistocene on the Darling Downs, Southeastern Queensland, Australia. *J. Syst. Palaeontol.* **2**: 347–356.

Provan, J. & Bennett, K.D. 2008. Phylogeographic insights into cryptic glacial refugia. *Trends Ecol. Evol.* **23**: 564–571.

Rohland, N., Pollack, J.L., Nagel, D., Beauval, C., Airvaux, J., Pääbo, S. & Hofreiter, M. 2005. The population history of extant and extinct hyenas. *Mol. Biol. Evol.* **22**: 2435–2443.

Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A. & Savolainen, V. 2005. 60 million years of co-divergence in the fig–wasp symbiosis. *Proc. R. Soc. Lond. B Biol. Sci.* **272**: 2593–2599.

Roy, K., Jablonski, D. & Valantine, J.W. 1995. Thermally anomalous assemblages revisited: patterns in the extraprovincial latitudinal range shift of Pleistocene marine mollusks. *Geology* **23**: 1071–1074.

Roy, K., Valantine, J.W., Jablonski, D. & Kidwell, S.M. 1996. Scales of climate variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends Ecol. Evol.* **11**: 458–463.

Sanfilippo, R. 1998. Spirorbid polychaetes as Boreal guests in the Mediterranean Pleistocene. *Riv. Ital. Paleo. Strat.* **104**: 279–286.

Schluter, D. 1986. Character displacement between distantly related taxa? Finches and bees in the Galapagos. *Am. Nat.* **127**: 95–102.

Schluter, D. 1996. Ecological speciation in postglacial fishes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **351**: 807–814.

Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.

Schluter, D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.* **16**: 372–380.

Shapiro, E., Drummond, A.J., Rambaut, A., Wilson, M.C., Matheus, P.E., Sher, A.V., Pybus, O.G., Gilbert, M.T.P., Barnes, I., Binladen, J., Willerslev, E., Hansen, J.A., Baryshnikov, G.F., Burns, J.A., Davydov, S., Driver, J.C., Froese, D.G., Harington, C.R., Keddie, G., Kosintsev, P., Kunz, M.L., Martin, L.D., Stephenson, R.O., Storer, J., Tedford, R., Zimov, S. & Cooper, A. 2004. Rise and fall of the Beringian steppe Bison. *Science* **306**: 1561–1565.

Smith, R.L. & Smith, T.H. 1998. *Elements of Ecology*, 4th edn. The Benjamin/Cummings Publishing Company, California.

Sommer, R. & Benecke, N. 2005. Late-Pleistocene and early Holocene history of the canid fauna of Europe (Canidae). *Mamm. Biol.* **70**: 227–241.

Stafford, T.M. Jr, Semken, H.A. Jr, Graham, R.W., Klipel, W.F., Markova, A., Smirnov, N. & Southon, J. 1999. First accelerator mass spectrometry ^{14}C dates documenting contemporaneity of nonanalogue species in late Pleistocene mammal communities. *Geology* **27**: 903–906.

Stewart, J.R. 2002. The evidence for the timing of speciation of modern continental birds and the taxonomic ambiguity of the Quaternary fossil record. In: *Proceeding of the 5th Symposium of the Society of Avian Paleontology and Evolution* (Z. Zhou & F. Zhang, eds), pp. 261–282. China Science Press, Beijing.

Stewart, J.R. 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3. *Quat. Int.* **137**: 35–46.

Stewart, J.R. 2007. *An Evolutionary study of some Archaeologically Significant Avian Taxa in the Quaternary of the Western Palaearctic*. BAR International Series 1653. Hadrian Books Ltd, Oxford.

Stewart, J.R. 2008. The progressive effect of the individualistic response of species to Quaternary climate change: an analysis of British mammalian faunas. *Quat. Sci. Rev.* **27**: 2499–2508.

Stewart, J.R. & Cooper, A. 2008. Ice age refugia and Quaternary extinctions: an issue of evolutionary palaeoecology. *Quat. Sci. Rev.* **27**: 2443–2448.

Stewart, J.R. & Dalén, L. 2008. Is the glacial refugium concept relevant for northern species? *Clim. Change* **86**: 19–22.

Stewart, J.R. & Lister, A.M. 2001. Cryptic northern refugia and the origins of modern biota. *Trends Ecol. Evol.* **16**: 608–613.

Stewart, J.R., van Kolfschoten, M., Markova, A. & Musil, R. 2003. The Mammalian Faunas of Europe during Oxygen Isotope Stage Three. In: *Neanderthals and Modern Humans During the Last Glaciation, 60,000 to 20,000 Years Ago: Archaeological Results of the Stage 3 Project* (T.H. van Andel & W. Davies, eds), pp. 103–129. MacDonald Institute Monograph Series, Cambridge.

Strickberger, M.W. 1990. *Evolution*, 2nd edn. Jones & Bartlett Publishers, London.

Sullivan, J., Arellano, E. & Rogers, D.S. 2000. Comparative phylogeography of Mesoamerican highland rodents: concerted versus independent response to past climatic fluctuations. *Am. Nat.* **155**: 755–768.

Taberlet, P., Fumagalli, L., Wust-Saucy, A. & Cosson, J. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Mol. Ecol.* **8**: 1923–1934.

Tzedakis, P.C. & Bennett, K.D. 1995. Interglacial vegetation succession: a view from southern Europe. *Quat. Sci Rev.* **14**: 967–982.

Valdiosera, C.E., Garcia-Garitagoitia, J.L., Garcia, N., Doadrio, I., Thomas, M.G., Hänni, C., Arsuaga, J.L., Barnes, I., Hofreiter, M., Orlando, L. & Götherström, A. 2008. Surprising migration and population size dynamics in ancient Iberian brown bears (*Ursus arctos*). *Proc. Natl Acad. Sci. USA* **105**: 5123–5128.

van Valen, L., Magerud, J., Larsen, E. & Hufthammer, A.K. 1996. Sedimentology and stratigraphy in the cave Hamnsundhelleren, western Norway. *J. Quat. Sci.* **11**: 185–210.

Vrba, E.S. 1984. What is species selection? *Syst. Zool.* **33**: 318–328.

Webb, T. 1986. Is vegetation in equilibrium with climate? How to interpret late Quaternary pollen data. *Vegetatio* **67**: 75–91.

Weir, J.T. & Schluter, D. 2004. Ice sheets promote speciation in boreal birds. *Proc. R. Soc. Lond. B Biol. Sci.* **271**: 1881–1887.

West, R.G. 1980. Pleistocene forest history in East Anglia. *New Phytol.* **85**: 571–622.

Willerslev, E., Hansen, A.J., Binladen, J., Brand, T.B., Gilbert, M.T.P., Shapiro, B., Bunce, M., Wiuf, C., Gilichinsky, D.A. & Cooper, A. 2004. Diverse plant and animal genetic records from Holocene and Pleistocene sediments. *Science* **300**: 791–795.

Williams, J.W. & Jackson, S.T. 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5**: 475–482.

Williams, J.W., Shuman, B.N. & Webb, T. III 2001. Dissimilarity analyses of late-Quaternary vegetation in Eastern North America. *Ecology* **82**: 3346–3362.

Willis, K.J. & Niklas, K.J. 2004. The role of Quaternary environmental change in plant macroevolution: the exception or the rule? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **359**: 159–172.

Zinsmeister, W.J. 1974. A new interpretation of thermally anomalous molluscan assemblages of the California Pleistocene. *J. Paleontol.* **48**: 74–94.