Continuing the debate on the role of Quaternary environmental change for macroevolution

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The Quaternary has been a period of dramatic environmental change for the past 1.8 Myr, with major shifts in distributions and abundances of terrestrial and marine organisms. The evolutionary consequences of this have been debated since the nineteenth century. However, the lack of accurate relative and absolute time-scales for evolutions and environmental change inhibited progress. We do now have an understanding of time-scales. Palaeoecology has demonstrated the individualistic nature of species' response to environmental change, but lacks a means of determining ancestry. DNA characterization of modern populations in relation to their distributions nicely complements palaeoecological results by contributing ancestry. The chance to understand how species originate and the causal factors of speciation (environmental change or otherwise) may be within reach.

Keywords: Quaternary; evolution; environmental change

1. INTRODUCTION

The modern history of thinking about the origin of species has been dominated by links between environments (and changes in them) and the process of speciation. Darwin's original argument for evolution by means of natural selection (Darwin 1859) is an ecological argument: species 'adapt' to their physical and biotic environments. Those best adapted to their environment survive and leave more descendants than those that are less well adapted. Much ecological research has been undertaken into this theme (Endler 1986), notably the work on Darwin's finches by Grant (1986) and Grant & Grant (1989), demonstrating that, on decadal time-scales, the mechanism does work more or less as Darwin proposed.

But does it work on longer time-scales? Gould (1985) has described evolutionary time as a hierarchical system of distinct tiers: evolutionary events of the ecological moment (first tier), trends within lineages over geological time (millions of years) (second tier) and mass extinctions (third tier). In this terminology, the evolutionary processes that Darwin (1859) described operate at the first tier only. Gould has argued that:

> our failure to find any clear vector of fitfully accumulating progress, despite expectations that processes regulating the first tier should yield such advance, represents our greatest dilemma for the study of pattern in life's history. I shall call it the *paradox of the first tier.*
> (Gould 1985, p. 4)

He presented two possible solutions: processes of the first tier, such as competition, do indeed control macroevolution, but in ways that we do not currently understand; or else any progress that does accumulate is undone by processes of the second tier, which operate by quite different rules. Punctuated equilibria (Eldredge & Gould 1972) provides a partial solution to the paradox of the first tier. Features are spread through lineages because populations that carry them have a greater tendency to speciate, and thus the spread is non-adaptive. There is then no reason to expect that evolutionary trends would be progressive. The first tier does not regulate events at the second, resolving the paradox. Mass extinctions at the third tier complete the process: little, if any, accumulating progress passes this bottleneck.

I have argued elsewhere (Bennett 1990, 1997) that Gould's (1985) model is incomplete because global climatic changes on time-scales of 10–100 kyr (Milankovitch oscillations) also effectively block the accumulation of progress, because changes in physical and biotic environments at those time-scales prevent the continuous operation of selection pressures that might have been effective in generating microevolution on shorter (e.g. decadal) time-scales. I suggested that a fourth tier was needed to complete Gould's model (table 1). More generally, I proposed that the response of species to Milankovitch oscillations would normally be 'stasis', because of the continually changing directions of selection pressures, but would occasionally be 'speciation' through the geographical isolation mechanism of Mayr (1942).

Vrba (1985, 1992, 1993; Vrba & DeGusta 2004) has argued that speciation and extinction do not normally occur unless forced by changes in the physical environment. It follows that most lineage turnover in the history of life should have occurred in pulses, in tune with changes in the physical environment. Turnover pulses may be small peaks involving a few lineages and/or, may be restricted geographically. Others are massive and of global extent. This hypothesis is probably one of the stronger proposals for the linkage of evolution (speciation)

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Table 1. Temporal hierarchy of processes controlling evolutionary patterns.
(The changes of the second and fourth tiers undo any evolutionary changes accumulated at the first and third tiers, respectively. After Bennett (1997, table 8.2).)

tier	periodicity (years)	cause	evolutionary process
1	20 000	natural selection	microevolutionary change within species
2	20 000–100 000	orbital forcing	disruption of communities, loss of accumulated change
3	1–10 million	isolation	allopatric speciation
4	*ca.* 26 million	mass extinctions	sorting of species

to environmental change. On longer time-scales, Willis & McElwain (2002) have emphasized linkages between long-term trends in speciation and global environments, particularly those brought about by plate tectonics.

It is thus possible that the action of climate on species distributions is a genuine example of species acting as interactors (*sensu* Hull 1980), and the single most important factor in enabling speciation. Distributions are pushed and pulled, this way and that, again and again. Eventually, something gives. A bit of the distribution becomes separated, and the two pieces may then have different histories, including possible development as new species. How long this takes depends on the nature of the distribution, the pace of the response to climate change and the amplitude of change. Distributions of species are thus an emergent property of species (Jablonski *et al.* 1985), which can interact with climate in a way that individuals cannot.

But is there a relationship between speciation and Milankovitch-scale environmental change? Research in the area during the past 10 years (e.g. Taberlet & Bouvet 1994; Konnert & Bergmann 1995) has been dominated by the results of DNA characterizations revealing the relationships between populations and providing indications of the time-scales of divergence of populations, species and higher categories. In some cases, a relationship with Quaternary environmental change is seen, in others not. The molecular clock time-scales are not yet as precise as geological time-scales, but they are good enough to be revealing about the points in a temporal hierarchy (such as table 1) at which divergencies should be placed. The information about ancestry from DNA work, of course, far exceeds anything available from classical morphological or geological methods.

In this paper, I aim to revisit the original nineteenth century debate about the relationship between evolution and environmental change, and then to discuss recent advances from both palaeoecological and molecular viewpoints. Is there a relationship after all?

2. LYELL AND DARWIN

Debate on the origin of species began during the nineteenth century, and is nicely encapsulated by a question sent by one leading British scientist, Charles Lyell, to another, Charles Darwin.

(a) *Lyell's question*

Charles Lyell (1797–1875) was a British geologist who dominated geology for most of the nineteenth century. His classic text (Lyell 1830, 1832, 1833) described the geo-

logical record in terms of modern processes, and is one of the foundations of modern geology. Lyell's view on species and their origin was that they are created at a single spot, multiply, and spread, surviving certain environmental and biotic fluctuations, but without being transformed, and they eventually become extinct. Species, he believed, are stable units that come into existence at ecologically appropriate points in space and time, survive for a longer or shorter period in dynamic ecological equilibrium with other organisms and spread to some degree, but are eventually eliminated by the pressures of the ever-changing physical and biotic environment (Rudwick 1990). Lyell was not specific about how species come into being, but understanding of contemporary geological processes suggested to him that the surface of the Earth is in a state of constant change. Associations of plants and animals could not always have been maintained in exactly the same spots, but must have shifted continually over land and sea (Worster 1985). Lyell saw that shifting distributions was likely to be a more rapid response to environmental change than *in situ* transformation, because there would always be species nearby better suited to new conditions than the species on the spot originally. He pointed out that, following climatic change, some species would be preserved by shifting their distributions, but that same change would be 'fatal to many which can find no place of retreat, when their original habitations become unfit for them' (Lyell 1832, p. 170). He noted that

> if a tract of salt water becomes fresh by passing through every intermediate degree of brackishness, still the marine molluscs will never be permitted to be gradually metamorphosed into fluviatile species; because long before any such transformation can take place by slow and insensible degrees, other tribes, which delight in brackish or fresh water, will avail themselves of the change in the fluid, and will, each in their turn, monopolize the space.
>
> (Lyell 1832, p. 174)

Lyell learned of Darwin's ideas about evolution and natural selection before the publication of *On the origin of species* (Darwin 1859), and was not convinced, initially. Lyell worked extensively with Tertiary molluscs, many of which can be identified to living species, and he appreciated that they must have survived changing climates since the Tertiary (Lyell 1830, 1832, 1833), which appeared to conflict with Darwin's ideas. In a letter to Darwin dated 17 June 1856, Lyell wrote the following.

> And why do the shells which are the same as European or African species remain quite unaltered like the Crag

species which returned unchanged to the British seas after being expelled from them by Glacial cold, when 2 millions? of years had elapsed, and after such migration to milder seas. Be so good as to explain all this in your next letter.

(Burkhardt & Smith 1990, p. 146)

This question came at the end of a long letter about uplift of continents, and Darwin commented on that aspect of the letter (in a postscript on 18 June 1856 of a letter to Joseph Hooker, and in reply to Lyell on 25 June 1856 (Burkhardt & Smith 1990, pp. 147, 153–155). It appears that Darwin did not reply directly to Lyell's closing question, or comment on it anywhere else. Lyell, however, copied the main points of his question into his journal (Wilson 1970, pp. 104–105), which suggests that he thought it was important (Burkhardt & Smith 1990).

(b) *Darwin's answer*

Charles Darwin (1809–1882) was an English scientist who, after an early period travelling around the world as a naturalist on the *Beagle*, spent the rest of his life working and thinking about a wide range of biological and geological problems, including the first full development of a coherent theory of evolution that included the principle and a plausible explanation (natural selection). This work (Darwin 1859) is, of course, generally seen as the defining document of evolution.

Darwin presented natural selection as the conclusion of a strong deductive argument: if certain conditions hold, then natural selection is the result. The point has been emphasized, and the structure of the argument formalized by Huxley (1942) and Mayr (1993), among others. Darwin's argument dealt with species as temporary stages in continual, gradual change as a consequence of increasing minute adaptation to other species and the environment (Gould 1993), making ecological interactions the driving force for macroevolution, and hence giving them a dominant role in the course of the history of life on Earth.

In his Chapter 11, Darwin began discussion of geographical distribution, and included an extended commentary (18 pages) on the effects of 'the glacial period'. He suggested that plants and animals of the Northern Hemisphere would generally have spread southwards during time of increasing cold, and then spread back northwards during the following climatic warming.

> The arctic forms, during their long southern migration and re-migration northward, will have been exposed to nearly the same climate, and, as is especially to be noticed, they will have kept in a body together; consequently their mutual relations will not have been much disturbed, and, in accordance with the principles inculcated in this volume, they will not have been liable to much modification.
>
> (Darwin 1859, p. 368)

Thus, we have Darwin's view that modifications will occur when the environments of species are altered by changes such as those related to continental glaciation. Although he appears not to have answered Lyell's question directly, the passage quoted above probably indicates what his answer would have been like. The significant part is his assertion that major climatic changes (such as those associated with glaciations) will not have caused 'modification'

because, as species shifted their distributions, they will have remained in the same communities ('kept in a body together'). Much Quaternary palaeoecology has been directed at precisely this point.

3. SPECIES' RESPONSE TO MILANKOVITCH OSCILLATIONS

How do species respond in evolutionary terms to climate changes at the scale of Milankovitch oscillations? Three broad categories of response are recognizable, with some overlap.

(a) *Evolution*

For most fossil groups through most of the Quaternary, there is remarkably little evidence of evolutionary change. Work on groups as diverse as Quaternary beetles (Coope 1979) and plants (Willis & McElwain 2002) is dominated by the same taxa over periods of time that are long relative to the periodicity of climatic change. Potts (1983, 1984), for example, argued that reef-building corals in the Indo-Pacific region exhibit little evolutionary change during the Quaternary, despite a growth zone that is never stable for more than a few thousand years, because their generation times, measured in decades, are long compared with other reef organisms. There are few known examples of evolutionary change, at any level, operating through the Holocene, and none where cause can be ascribed with confidence (so none that would meet the criteria of Endler (1986) to pass muster as 'demonstrations' of natural selection). Genetic work on modern populations in relation to Holocene distribution changes indicates spread of these populations, but even at this level the appearance of new genotypes is not apparent. Davis & Shaw (2001) argue that, within species, genotype frequencies will shift during spread of species, constituting an adaptive response to climate change.

Two of the architects of the modern synthesis quoted geographical evidence that populations of a species may have diverged to at least subspecies level during the period since the last glacial, citing examples from, especially, vertebrates (Mayr 1942; Simpson 1944). Examples from other groups were added by Mayr (1963). These examples need treating with care, as they are based mostly on inference from modern distributions. Angus (1973) has shown that one beetle subspecies persisted over more than one glacial–interglacial oscillation, and Lister (1989) has described dwarfing of red deer during the last interglacial. Molluscan evidence, described in detail by Gould (1970), suggests some speciation takes place within single oscillations of Milankovitch time-scales.

Stanley (1979, 1985) presented data on mean species duration within groups by direct observation and by making estimates from curves of the percentage of species within fossil biota persisting to the present day (Lyellian percentages), plotted against the age of those biota. Both methods yield estimates for species durations of 1–30 Myr, depending on the taxonomic group. Species are thus observed to persist much longer than the period of orbitally forced climatic oscillations (Vrba 1985, 1993; Bartlein & Prentice 1989; Bennett 1990, 1997). This is true even for the current (Quaternary) series of oscillations with climatic changes enhanced to yield massive,

continental-scale glaciation in parts of the Northern Hemisphere.

On Galápagos, extreme weather events forced episodes of selection in Darwin's finches (Grant 1986; Grant & Grant 1989). These events recur on time-scales of about the longevity of the longest-lived individuals of Darwin's finches. But the periods of selection in one direction are followed by intervening periods of relaxed selection, or selection in a different direction. The net result is that populations of finches remain as recognizably the same species overall: there has been no speciation event within the period of study, and no species other than modern ones are known to have existed on Galápagos within the past few thousand years (Steadman 1986).

These long species durations are equivalent to *ca.* 10^5–10^7 generations, depending on group. Thus, as far as competent taxonomists can tell, there is so little net measurable morphological change over millions of generations that populations this far removed from each other are considered identical at specific level (Stanley 1985).

New genetic information is increasingly providing information on divergence times between populations, species and higher categories. These divergence times are based on so-called 'molecular clocks', and there are considerable uncertainties about their precision (Lambert *et al.* 2002). Results often indicate surprisingly long divergence times (Zink *et al.* 2004). For example, Shirihai *et al.* (2001) have shown that the bird genus *Sylvia* may be more than 12 Myr old. The main subgenera diversified 8–12 Ma, meaning that two of the most widespread species in northern Europe today, the blackcap *Sylvia atricapilla* and the garden warbler *Sylvia borin*, are probably of this antiquity. None of the *ca.* 28 species appear to have originated within the Quaternary (figure 1). However, Shirihai *et al.* (2001) argue that several Mediterranean species may have originated at 5.5–8.5 Ma, and their origin may be connected to long-term aridity then. Some intraspecific variation may have taken place within the Quaternary for *Sylvia* species, as for other birds (Avise & Walker 1998) and other vertebrates (Avise *et al.* 1998). However, there has been active speciation in groups such as the cichlid fishes of Lake Victoria, where a radiation of *ca.* 500 species has taken place within the past 100 kyr (Verheyen *et al.* 2003). The Quaternary seems to have been an active period for population separation, including speciation (e.g. Kadereit *et al.* 2004; Lister 2004), but the importance of this period relative to others is uncertain.

(b) *Extinction*

The frequency of extinctions within the Quaternary in response to orbitally forced climatic change is generally low, and clearly not a typical response (Leopold 1967; Kershaw 1984; Coope 1995), but has occurred (Jackson & Weng 1999). Among mammals and birds, a high proportion of Quaternary extinctions that have occurred took place during the late-Quaternary, and especially the Holocene, and were probably or certainly anthropogenic (e.g. Pimm *et al.* 1995). Among other groups, extinctions have been much rarer (e.g. plants: Kershaw 1984). Local extinctions, however, have been frequent and occur at spatial scales up to continental (Willis & McElwain 2002). One prominent example is the gradual loss of tree genera from Europe during the late

Cenozoic (Tallis 1991). For earlier periods we are not yet in a position to say whether extinction is typically brought about by environmental change or by some other factor, such as competition.

However, we can say that species survive most of the time, despite dramatic climatic oscillations.

(c) *Stasis*

If there is little speciation or extinction in response to Milankovitch oscillations, we are left with stasis as the typical response in evolutionary terms. It is interesting to consider what happened in terms of species' distributions and abundances, however, not least because of the Lyell–Darwin discussion on the matter. The question of whether species 'kept in a body together' or not is particularly interesting.

American plant ecologists working during the first part of the twentieth century saw vegetation formations and associations as climatically determined climaxes, or as being in the course of successional development towards such climaxes (Weaver & Clements 1929). An alternative approach, radical and derided at the time, was the 'individualistic' concept of species within plant associations (Gleason 1926), developed without the benefit of modern knowledge of time-scales of change. West (1964), through comparison of floras of different interglacials, also appreciated that communities are only 'temporary aggregations', and thus provided an early insight into the Quaternary palaeoecological discoveries of the following three decades. Palaeoecological results, notably the mapping efforts of Davis (1976, 1983) and Huntley & Birks (1983), are a major scientific development of those insights, developed crucially from the application of the radiocarbon method of age determination, mainly after the 1970s. The analysis of Quaternary fossil sequences has been expanded and improved considerably, but the method of obtaining ages for each sequence studied has enabled an appreciation of the rates of change of distribution and abundances. In particular, it is clear that the break-up of communities because of the individualistic response of species to orbitally forced climatic oscillations is a global phenomenon, involving tropical communities (Flenley 1979; Hooghiemstra & van der Hammen 2004) as well as temperate systems (Davis 1976; Davis & Shaw 2001), marine as well as terrestrial communities. The view of many ecologists (e.g. Wilson 1994) that the tropics have been a centre of community stability for millions of years is no longer tenable (see also Colinvaux *et al.* 2001).

Results from DNA characterization of populations are now accumulating fast, and generating new insights into the postglacial spread of populations (Lascoux *et al.* 2004). Such data nicely complement classical sources of information (fossils) by making it possible to work with groups of organisms that lack a fossil record, and to work at the level of populations, rather than species or higher categories. However, a time-scale is often poor or lacking. Genetic information may reveal patterns and directions of spread during the Holocene, for example, but may be unable to distinguish distribution shifts brought about by climate change at the beginning of the Holocene from shifts that occurred later, possibly in response to the late Holocene spread of agriculture and transformation of landscapes. The record may also be confused by recent
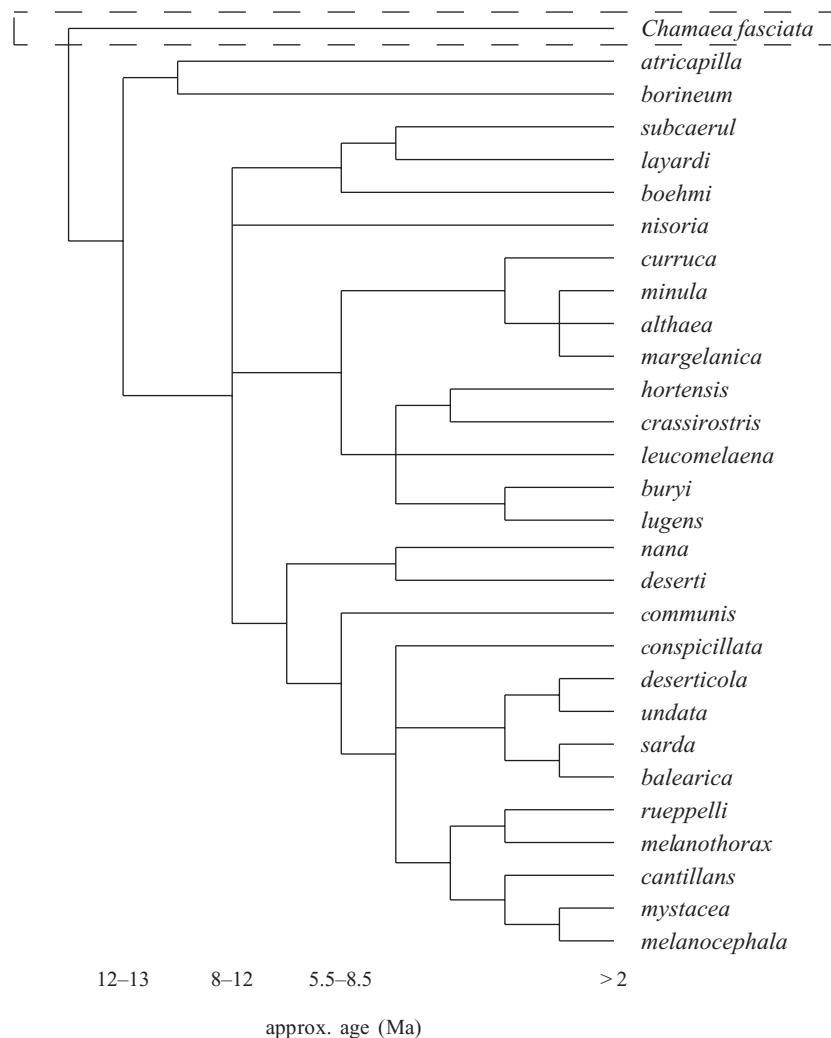
Figure 1. Phylogenetic relationships of the *Sylvia* warblers, representing a consensus phylogeny based on mitochondrial DNA sequences, DNA hybridization and phenotypic characters. *Chamaea fasciata* is a member of a related genus included in the analysis as an 'outgroup taxon' to identify those features present in all the *Sylvia* species that must be ancestral. Redrawn from Shirihai *et al.* (2001, fig. 4).

introduction and management of the populations of interest (Cottrell *et al.* 2002). Using DNA information, Petit *et al.* (2002) have been able to describe in detail the spread of oak into northern Europe. Synthesis involving both fossil pollen and modern genetic data offers considerable potential for the future (Lascoux *et al.* 2004).

Distribution change of species on subcontinental and continental scales involves, potentially, an enormous increase in the numbers of individuals constituting the species concerned. In Europe and eastern North America during the Holocene, for example, several tree species increased from low abundances in scattered sites within a small area of the south of either continent to become forest dominants across most of the region. The total numbers of individuals in these species should have increased by several orders of magnitude within the first few thousands of years of the Holocene, and such changes may have been typical through many earlier interglacials. Following a suggestion by Watts (1973), investigation at several individual sites shows that build-up of populations in any one area was, initially at least, geometric for Holocene forest taxa, in temperate and tropical regions and for interglacial temperate taxa (Bennett 1997, tables 5.1 and 5.2).

Doubling times for population increase were of the order of a few tens to a few hundred years, and are similar to those obtained from modern tree populations over much shorter periods of time (Bennett 1986; Prentice 1988; MacDonald 1993). These rates of increase were maintained for periods measured in hundreds or even thousands of years, and so involved massive increases in population size of many orders of magnitude. The transition into interglacial conditions seems to provide opportunities for species to increase in abundance geometrically, occupying and dominating considerable areas in the process. This unchecked population growth is just the situation that Elton (1927) envisaged as being necessary to enable the spread of non-adaptive characters through populations.

Species and lower categories have appeared and persisted for longer or shorter lengths of time during the Quaternary as well as during earlier periods. It is uncertain whether the frequency of speciation has changed or not relative to the Tertiary, but species clearly persist, unchanged (at least morphologically) over multiple glacial–interglacial oscillations. Thus, stasis exists despite considerable environmental change, and is thus, presumably,

dynamic behaviour (Gould & Eldredge 1993; Eldredge 1995). Speciation may take place by lineage splitting because environmental change enables establishment of new populations with a genetic make-up that is different from that of the organisms in the species originally. But that stasis is the most frequent evolutionary response to Quaternary climatic change, and the stability of species through these oscillations, are impressive (Gould 1992). Natural selection has been shown to have occurred (for example, among populations of Darwin's finches (Grant & Grant 1993)), but there is no evidence that it accumulates over longer periods of time to bring about speciation in the Darwinian sense.

Stasis turns out to be interesting behaviour, not for itself, but for the fact that it came about in circumstances where it might have been expected that there would be a speciation response to Milankovitch oscillations.

> 'Is there any point to which you wish to draw my attention?'
> 'To the curious incident of the dog in the night-time.'
> 'The dog did nothing in the night-time.'
> 'That was the curious incident,' remarked Sherlock Holmes.
> (from *Silver Blaze* (Conan Doyle 1981)).

4. ICE AGES RELATIVE TO THE REST OF EARTH HISTORY

It has been argued that the Quaternary is not typical of the rest of Earth history because of its extensive glaciation. Boucot (1990) identifies what he terms a 'Quaternary paradox': why is the pattern of biotic change as seen during the Quaternary different from that seen in the rest of geological time? He resolves it by arguing that the Quaternary record is a reflection of a 'high global climatic gradient, combined with the Milankovitch-cycle-generated, rapidly changing Quaternary environment that contrasts so markedly with the relatively unchanging Phanerozoic norm (when commonly sampled at million-year intervals or longer), plus the far more unchanging, buffered marine environment' (Boucot 1990, p. 555). Potts & Behrensmeyer (1992) discuss the response of organisms to climatic oscillations within the Quaternary, but question whether these responses are typical of the rest of the fossil record, hinting that the Quaternary may be a suitable model for those periods in Earth history that do have a glacial record, but not for the rest. In part this appears to result from the appearance of relative stability in pre-Quaternary periods, without consideration of the degree to which this is an artefact of the general coarsening of temporal resolution with increasing distance in time back from the present.

Climatic oscillations on time-scales of 10–100 kyr are caused by orbital forcing and thus should be permanent features of Earth history. Oxygen isotope analyses over the whole of the Cenozoic (65 Ma) indicate that long-term trends in climate are greater in amplitude than individual oscillations at the Milankovitch frequencies, and that the amplitude of oscillations is greater during glacial periods (especially the Quaternary) than at other times (Zachos *et al.* 2001). It should therefore be the case that species' responses to these oscillations in the Quaternary are similar in kind to species' responses in the rest of Earth history (see Willis & Niklas (2004) for a discussion of this question). This is the background to the structure of table 1. The chief problem with this argument is that everything is predicated on the assumption that major climatic changes should bring about speciation, though possibly at low frequencies. If those frequencies approach zero, the validity of the argument falls. However, long-term trends in climate exceed Milankovitch oscillations in amplitude. If evolution is linked to major climatic change, perhaps these longer-term trends are more important?

5. THE ORIGIN OF SPECIES

Several key components are now in place from which to begin a re-examination of the processes that lead to the origin of species.

(i) The Earth's climate oscillates on frequencies of 10–100 kyr, superimposed on longer-term trends brought about by processes such as plate tectonics.
(ii) Species longevities are generally much longer than this, typically in the range of 1–10 Myr.
(iii) The Quaternary, a period of high amplitude environmental change does not appear to be associated particularly with the origination of new species. Subspecific forms are known (Angus 1973; Lister 1989) or suspected (Shirihai *et al.* 2001) to have appeared and then persisted during one or more glacial–interglacial cycles (but see Gould (1970)).

If environmental change at Milankovitch time-scales forces speciation, or even enables it, we are finding it hard to find a 'smoking gun'. Even the part of the geological record for which we have most information, the best dating and some of the highest amplitude climatic oscillations known, is failing to yield evidence for speciation in tune with the known environmental change. The record is good enough to see plenty of change, in distributions and in abundances, both of which can be dramatic and encompass many orders of magnitude in area and numbers. It is clear that communities are largely temporary and that species behave individualistically. But we cannot see speciation as a response.

If environmental change does not even enable speciation, a complete reassessment of the processes of speciation is required. Those mechanisms that are coupled to some aspect of the environment become less plausible. Other mechanisms become more likely.

6. CONCLUSIONS

With the benefit of hindsight, the writings of Lyell and Darwin, quoted in § 2, make fascinating reading. Lyell, with a perspective rooted in Tertiary palaeobiology with a weak geological record and a time-scale that was only a guess, saw that species persisted unchanged through major climatic oscillations. Darwin was a good geologist, but took his perspective from natural history and observations of how organisms behave towards each other and their

environments. The approaches of these two men are mirrored today in much of the debate around the origin of species; ecologists working in the modern environment and palaeobiologists collecting fossils.

Darwin's view, however, is clearly testable. He is explicit that his migrating arctic species 'will have kept in a body together'. We now know that this does not happen and the rest of his argument therefore falls. On the contrary, it is likely that their 'mutual relations' were much disturbed. And this should mean, according to Darwin, that they would have been liable to much modification. But we can see that they were not. Consider the 10 Myr antiquity of the blackcap (*Sylvia atricapilla*), migrating to and from northern breeding grounds every year, while those same breeding grounds shift backwards and forwards every 40–100 kyr as ice sheets waxed and waned, without any speciation that we are aware of, either from palaeoecological or genetic evidence. Whether longer-term changes, such as plate tectonics, bring about phases of increased speciation (Willis & McElwain 2002) remains to be tested. The issue becomes complicated when finer scale change is added to the longer-term trends. If such phases of speciation are coupled to long-term (millions of years) trends, why is there so little apparent reaction to environmental change at shorter time-scales? Natural selection is a useful concept, and a valid hypothesis for the mechanism of evolution, but we may now be nearing a point where the hypothesis is testable (and should be tested) by a combination of palaeoecological and genetic approaches.

Lyell had a clear view of species as fixed stable entities, and this now seems to be much more in accord with what we can see from the fossil record. However, he made no suggestion of how these entities came into being, and this still needs to be done. The 'evolutionary legacy of the Ice Ages' may well be the crucial insight that evolution, after all, has rather little to do with environmental change.

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Discussion

A. M. Lister (*Department of Biology, University College London, London, UK*). I mentioned in my lecture that reindeer evolved specializations in response to the development of tundra habitats in the Quaternary, and that polar bears evolved in response to the expansion of ice floes. Why in the face of this evidence do you deny the likely involvement of natural selection? I also suggested that the high-amplitude climatic oscillations of the Quaternary may have effected a higher-level process of species sorting, leaving us with a legacy of species with characteristics like high fecundity and generalist adaptations.

K. D. Bennett. Natural selection is an important ecological and evolutionary process, but it is has not actually been shown that natural selection visible at ecological time-scales (decades, at best) builds up into the macroevolutionary patterns seen in the fossil record over millions of years. I am by no means clear that the Quaternary is different enough from the Tertiary to have made much difference in terms of evolutionary mechanisms, but it would certainly be interesting to know more about this. The late appearance of animals such as reindeer and polar bears at a time of particularly strong climatic oscillations is interesting, but not in itself conclusive.

R. I. M. Dunbar (*School of Biosciences, University of Liverpool, Liverpool, UK*). It is important to remember that 'environmental selection' is only one part of Darwin's theory of evolution by natural selection. The other part is his theory of sexual selection, which has come to be recognized as a major force in speciation in recent years. Sexual selection may have an environmental component, but equally it may be quite independent of environmental factors.

K. D. Bennett. I agree. Sexual selection may be very important among certain animal groups. Among plants, polyploidy provides a mechanism for rapid speciation independent of environmental change.

P. R. Sheldon (*Department of Earth Sciences, Open University, Milton Keynes, UK*). Rather than abandon the role of natural selection, we need to revise our expectation of the link between evolution and environmental change. As you clearly show, there is remarkably little evolution and extinction in the Quaternary. This is consistent with the '*plus ça change*' model (Sheldon 1996) in which stasis arises from the *in*stability of physical environments. Responses to environmental change will be contingent on long-term history: if a species has been subjected many times to large physical disturbances, yet another such disturbance may yield no evolutionary response at all (*or send the species over a threshold*). Conversely, it is smaller physical events, and especially biotic interactions, that tend to drive evolution, and such stimuli will be hard, if not impossible, to detect in the geological record. Punctuated equilibrium, with stasis as the norm, may be being perceived as the overwhelming pattern in the history of life because the settings where gradualism prevails, such as a tropical rainforest, are so rarely preserved. The last 10 000 years of relative climatic stability may be an order of magnitude too short to release species from the influences promoting stasis during the Pleistocene.

K. D. Bennett. I do not think that we should abandon natural selection, but I do think that we should reconsider its role and significance in relation to other processes driving evolution. The Quaternary provides a convenient geological backdrop to do this, with relatively accessible fossils of species that are still extant, and increasingly access to macromolecules such as DNA in those fossils. The key difficulty is still probably dating and time-scale, as it was for Lyell and Darwin. It is one matter to order events (such as the Quaternary ice ages), but it is another matter to correlate these directly with events dated by other means (such as molecular clock estimates for the age of species originations). We may not get much further on any of this until we can do that precisely, and locate evolutionarily significant events precisely within both space and the geological record of environmental change.

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