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Speciation, extinction and climatic change in hominid evolution

The temporal association of hominid evolution with a period of global climatic instability and cooling is suggestive of a causal relationship. A number of authors have proposed a climatic forcing model for the timing and nature of evolutionary changes in human evolution during the Pliocene and Pleistocene (5–0 Mya), such as the appearance of new taxa, and by inference only a limited role for continuous evolutionary change in response to inter- and intra-specific competition at the local level. A major problem with such models is that both climatic change and hominid evolution are now recognised as complex with numerous events. By splitting climatic change as revealed in deep sea cores into a number of distinct attributes (temperature, stability and variability) and examining the relationship of each to the appearance, diversity and disappearance of hominid taxa it is possible to investigate more closely the effect of climatic change on hominid evolution. It is shown that the effect of climatic change can be observed in relation to extinction events, but that there is no significant relationship with the first appearance of hominid taxa. This implies that the mechanism by which climate influences evolution is primarily through extinction, and that further factors dependent upon local competitive conditions play a significant part in the appearance of new taxa.

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Introduction

The fact that human evolution occurred at the same time as the major climatic deterioration associated with glaciation and global cooling has prompted considerable speculation about the extent to which these two events are causally related. In recent years a number of authors (Vrba, 1980, 1985*a*,*b*, 1988; Grine, 1985; Prentice & Denton, 1988) have linked the major events of hominid evolution—divergence of *Australopithecus* and *Homo* and the origins of *Homo sapiens*—with climatic cooling. This has led to some specific theories about the driving forces in hominid evolution, especially for key events of *Homo-Australopithecus* divergence and the appearance of *Homo sapiens*.

In this paper I attempt to develop some methods for exploring quantitatively the relationship between evolutionary and climatic patterns. It also sets out to provide an empirical basis for discussing the causes of change in the course of hominid evolution. Furthermore, by carrying out these analyses at the species level an attempt is made to study human evolution in terms of general palaeobiological parameters such as speciation and extinction, rather than continuous anagenetic change.

Climate and human evolution

The most elegant analyses of the effects of climate on human evolution have been those of Vrba (1980, 1985*a*,*b*, 1988). She has explored a three-way relationship. Firstly, she has shown that there is a relationship between African bovid speciation and the pattern of climatic change as represented by the oxygen isotope curves taken from deep sea drilling projects. Bursts of speciation occur when there is a marked decline in temperature, particularly in the period between 2·0 and 2·4 Myr ago. Secondly, there appears to be a broad similarity in timing between the emergence of the genus *Homo* (and the species *Homo sapiens*) and

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speciation amongst the bovids. By implication, therefore, there is a relationship between hominid evolution and climatic change. From this analysis Vrba sees "the correlation between different habitats and different species as likely to indicate causation: a widespread change in temperature, rainfall and vegetation caused the evolution of hominid phenotypes" (Vrba, 1985*a*, p. 67). This position has been qualified, and Vrba has indicated that the "model does not imply the total environmental determinism of speciation. Physical change is *necessary for turnover pulses, but is not sufficient*" (Vrba, 1985*c*, p. 234). Climate is therefore the primary rather than the exclusive factor. Nonetheless, it is a clear implication of the model that the appearance of new taxa should be measurably related to patterns of climatic change.

This model has become known as the climatic forcing model. It is a powerful model for a number of reasons. It is explicit, it is based on empirical evidence and draws in comparative data from other lineages, and it is linked into a general theory of speciation, one that views evolutionary events as being driven by environmental change. Such a model can also be contrasted with others, such as that of the Red Queen (Van Valen, 1973; Foley, 1984), which would see evolutionary change occurring as a response to the internal dynamics of competitive relationships among sympatric populations. Models such as the Red Queen would not predict a tight relationship between major climatic change and evolutionary events, but would instead expect evolutionary change to continue even during periods of relative stability. The climatic forcing model, therefore, plays down the importance of competitive interactions as an evolutionary mechanism, and Grine (1985) has argued that there is no evidence for inter-specific competition as a significant factor in early hominid evolution.

There are, though, a number of problems that arise out of the climatic forcing model, and it is these that provide the stimulus for the approach adopted here. First, climatic change is not a simple phenomenon, and therefore does not impinge upon evolution in a straightforward manner. For example, it is possible for the actual direction of the climatic change to be significant, i.e. whether the temperature increases or decreases. On the other hand, it may be that it is simply the magnitude of the change, regardless of direction that is significant. Equally, it could be that the nature of the climatic change is immaterial, and that the rate of change or the degree of variation or the level of stability is what has most influence on evolutionary events. Furthermore, data derived from oxygen isotope analysis of foraminifera collected from deep sea drilling projects have shown that there may be as many as 20 major climatic oscillations during the last two million years, and even more minor ones. Any development of the climatic forcing model should therefore both take into account this complexity and attempt to detail the mechanical links between climate and evolutionary events.

A second problem lies in the equally complex nature of the hominid fossil record. Obviously there are general problems, such as the reliability of dating methods that are essential for calibrating evolutionary and climatic change, and the tendency for the framework to shift with the discovery of new finds. Equally important, though, is the question of interpretation. For example, Vrba (1985*a*) suggests that the divergence of *Homo* and the robust australopithecines occurred after *A. africanus*. This would make the period 2–2·4 Myr the critical phase for speciation. However, others would argue that *Homo* had already diverged prior to the evolution of *A. africanus* (Johanson & White, 1979), which would push the significant period back considerably. A further problem lies in determining what is a significant event in hominid evolution. According to some views, the shift from *H. erectus* to archaic *H. sapiens* in the late middle Pleistocene is the critical change, where others would suggest that it is the appearance of modern forms between 150 Kyr and 100 Kyr that represents a major evolutionary change (Stringer & Andrews, 1988). Such an interpretation would radically alter the relationship between hominid evolution and climatic change. And finally, the last five years have seen a tendency among some palaeoanthropologists to recognise more species within the Hominidae, and consequently there are a greater number of events to be accounted for than the divergence of *Homo-Australopithecus* and the emergence of *Homo sapiens*.

Materials and methods

Here the problem is approached from a statistical perspective. To pursue the relationship between climate and hominid evolution we need to establish a set of comparable data. To this end it is necessary to compile several measures for both climatic and evolutionary events by chronological period. Two chronological frameworks are used:

1. 500 Kyr Units: the period 5·0 Myr to the present was divided into ten chronological units of half a million years each. This unit has the advantage of providing a larger number of climatic and evolutionary events per unit, although chronological resolution is clearly lost.
2. 100 Kyr Units: the period 2·6 Myr to the present was divided into 26 chronological units of 100 Kyr each. This provides a more finely resolved picture of both climatic and evolutionary events, although the latter are clearly more sparsely scattered. The limit of 2·6 Myr was imposed by the availability of good palaeoclimatic data.

For each period within each chronological framework the following data were used.

Climatic data

The best record of climatic change is derived from the oxygen isotope record from deep sea cores. The isotopic curves presented by Prentice & Denton (1988) and Shackleton *et al.* (1990) were used to compile the following variables, in the two time units described above.

1. Number of climatic cycles
2. Maximum δ^{18} (= minimum temperature)
3. Minimum δ^{18} (= maximum temperature)
4. Modal temperature (500 Kyr time units only)
5. Magnitude of climatic variation (maximum temperature – minimum temperature)
6. Magnitude of climatic change (modal temperature of one period less modal temperature from preceding period)

For the 100 Kyr dataset both planktonic and benthic δ^{18} values were used, but the modal values were not estimated. Table 1 shows the climatic data for the period 5·0 to 0 Myr, in 500 Kyr units. Table 2 shows the climatic data for the last 2·6 Myr in 100 Kyr units.

Palaeontological data

For each time unit data were compiled on various evolutionary events (see notes to Table 3 for discussion of some of the associated problems with defining hominid taxa).

1. Number of hominid species present in fossil record.
2. Number of first appearances of hominid taxa.
3. Number of last appearances of hominid taxa.

Table 1 **Climatic data for last 5·0 million years. See text for discussion of sources and methods**

Time (Myr)	Number of climatic cycles	Maximum δ18	Minimum δ18	Modal δ18	Climatic variation	Magnitude of change
0·0–0·5	6	4·40	2·40	3·40	2·00	0·10
0·5–1·0	7	4·50	2·70	3·50	1·80	0·25
1·0–1·5	8	4·60	2·20	3·25	2·40	0·00
1·5–2·0	9	3·70	2·80	3·25	0·90	0·25
2·0–2·5	8	4·70	2·10	3·00	2·60	0·20
2·5–3·0	11	3·10	2·40	2·80	0·70	0·40
3·0–3·5	7	3·30	2·00	2·40	1·30	0·10
3·5–4·0	8	3·00	1·70	2·30	1·30	0·10
4·0–4·5	4	2·65	1·90	2·40	0·75	0·10
4·5–5·0	5	2·95	2·30	2·50	0·65	0·10

Table 2 **Climatic variables for the period 0–2·6 Myr in 0·1 Kyr intervals**

Time (Kyr)	Number of cycles (P)	Number of cycles (B)	Max. Delta 18 (P)	Min. Delta 18 (P)	Max. Delta 18 (B)	Min. Delta 18 (B)	Climatic variation (P)	Climatic variation (B)
0·0	3·0	3·5	−0·6	−2·1	5·1	3·8	1·53	1·29
0·1	2·5	2·5	−0·5	−2·1	5·1	3·5	1·61	1·57
0·2	3·5	2·5	−0·8	−2·1	4·9	3·7	1·25	1·19
0·3	1·5	1·5	−0·5	−2·5	5·1	3·3	1·96	1·78
0·4	1·5	2·0	−0·5	−2·6	4·9	3·4	2·12	1·47
0·5	3·0	3·5	−1·1	−2·2	4·6	3·5	1·06	1·08
0·6	1·5	2·5	−0·4	−2·1	5·0	3·7	1·72	1·30
0·7	3·0	3·5	−0·7	−2·0	4·9	3·7	1·31	1·21
0·8	3·5	1·5	−0·4	−1·8	4·9	3·6	1·43	1·30
0·9	3·0	2·0	−0·9	−2·0	4·5	3·5	1·15	1·08
1·0	3·5	2·5	−1·0	−1·9	4·5	3·4	0·92	1·14
1·2	3·0	2·5	−0·9	−1·9	4·6	3·7	1·06	0·88
1·3	3·0	2·5	−0·7	−1·8	4·5	3·3	1·07	1·22
1·4	3·5	2·5	−1·0	−1·9	4·4	3·5	0·86	0·91
1·5	3·5	2·5	−1·1	−1·9	4·2	3·2	0·84	0·99
1·6	3·5	2·5	−1·1	−1·8	4·4	3·4	0·77	1·04
1·7	2·5	2·5	−0·8	−1·9	4·4	3·4	1·07	1·01
1·8	4·5	3·0	−0·8	−1·8	4·4	3·4	1·01	1·04
1·9	3·5	4·5	−1·1	−1·8	4·4	3·6	0·79	0·83
2·0	3·0	2·5	−1·1	−1·7	4·2	3·4	0·65	0·80
2·1	2·0	2·5	−1·2	−1·7	4·4	3·4	0·51	1·01
2·2	2·5	2·5	−0·9	−1·9	4·4	3·3	0·94	1·11
2·3	3·5	2·5	−1·3	−1·9	4·1	3·4	0·66	0·66
2·4	2·5	3·5	−1·4	−2·0	3·9	3·0	0·64	0·87
2·5	2·0	2·0	−1·3	−1·8	4·4	3·4	0·56	1·05
2·6	2·5	3·0	−1·2	−1·9	4·3	3·2	0·73	1·13

For the 500 Kyr data similar data were compiled on baboons, divided into *Papio*/*Parapapio* and *Theropithecus* (Foley, 1993) and overall measures of diversity for all species (the African Terrestrial Primates) were also calculated. Clearly the main problem in compiling such data is the lack of consensus among researchers as to what constitutes a hominid species. Estimates would vary from a minimum of three or four (Wolpoff, 1992) to a maximum of 17 (Groves, 1989). To avoid these problems the data was compiled using various degrees of lumping and splitting. The main areas of variation lie in terms of (a) whether *Homo sapiens* refers to anatomically modern humans only, or to all later middle Pleistocene hominids displaying brain enlargement relative to *Homo erectus*; (b) whether the various types of archaic *H. sapiens* from the late Middle Pleistocene should be put into separate species, as has been proposed by Tattersall (1986) and Howell (in press); (c) whether *Homo erectus* refers to all the material from both Africa and Asia covering the period from over 1·5 Myr to less than 400 Myr, or whether it refers specifically to the Asian specimens; (d) whether the various robust australopithecines (or *Paranthropus*) are lumped together or successively divided into as many as four taxa (*A. robustus, A. crassidens, A. boisei* and *A. aethiopicus*). For overall number of species present three models were used:

Model 1, which has a relatively high level of splitting;
Model 2, which has a reduced level of splitting;
Model 3, which has a minimal number of taxa.

Only Models 1 and 2 were used for first and last appearances as Model 3 virtually assumes that all evolution is anagenetic and therefore the number of events that can be measured is too small. Table 3 shows the hominid taxa used in these analyses. Table 4 shows the distribution of evolutionary events among the Hominidae and the Papionini over the last 5·0 Myr, at 500 Kyr units. Table 5 shows the distribution of evolutionary events among the Hominidae for the period 2·6 Myr to the present.

These datasets were analysed using SPSS PC+ to determine the strength of association between climatic and evolutionary events.

Analysis and results

For the most part the data do not depart significantly from a normal distribution, but in testing for associations both parametric and non-parametric correlation coefficients were calculated.

500 Kyr units: climatic patterns

Table 6 shows a matrix of correlation coefficients between the climatic variables. The climate of the last 5·0 Myr showed progressive cooling. Significant relationships were found between time and modal temperature for each period. A close association was found between maximum, minimum and modal temperatures as measured through δ^{18} values. Furthermore, although temperature variables are closely related to each other, the magnitude of change, the variability in climate and climatic stability are not significantly correlated. This confirms the view that climatic change is not a simple phenomenon, and different patterns of climatic-evolutionary interactions would be expected depending upon what climatic variables are used.

500 Kyr units: relationship between climatic and evolutionary events

According to the climatic forcing model it would be expected that significant statistical relationships should occur between climatic and evolutionary events, especially speciation

Table 3 **Dates of first and last appearances of fossil hominid taxa used in these analyses**

Taxon	First appearance	Last appearance	Notes
A. afarensis	5·1	2·89	1
A. africanus	3·55	2·05	2
A. aethiopicus	2·69	2·29	3
A. boisei	2·11	0·81	4
A. crassidens	1·55	0·65	5
A. robustus	2·11	1·91	5
H. habilis	2·35	1·61	6
H. rudolfensis	1·91	1·61	6
H. ergaster	1·61	1·15	7
H. erectus	1·21	0·25	7
H. heidelbergensis	0·45	0·15	8
H. rhodesiensis	0·49	0·15	8
H. mapaensis	0·25	0·05	8
H. neanderthalensis	0·125	0·03	8
H. sapiens	0·14	0·0	8

Further lumping and splitting of the data is based on these dates. The level of accuracy shown is spurious, but used to force the taxa into the chronological units used.

Notes

1. *A. afarensis* is taken here to include the material from Hadar and Laetoli, as well as earlier and more fragmentary material from Lothagam, Tabarin, Koobi Algi, Kanapoi and Middle Awash (Hill *et al.*, 1992). Lothagam represents the earliest and Hadar the latest.

2. *A. africanus* comprises specimens from Sterkfontein and Makapansgat. Dates from Delson (1988).

3. *A. aethiopicus* is included by some authorities in *A. boisei*, (lumped here in "Minimal" model), and is represented by specimens from West Turkana and Omo (see Grine, 1988).

4. *A. boisei* (Klein, 1989; Grine, 1988).

5. *A. crassidens* is recognised by some authors (Grine, 1988) as a distinct taxa, but is lumped with *A. robustus* in the "Minimal" model. *A. robustus* consists of material from Kromdraai (Delson, 1988).

6. Early *Homo* has been reported from Baringo by Hill *et al.* (1992). Following Wood (1992) early Homo is divided into two groups, referred to here as *H. habilis* and *H. rudolfensis*, the former being the Olduvai material plus specimens from Koobi Fora such as KNM-ER1813, the latter including the larger Koobi Fora material such as KNM-ER 1470. In the "Minimal" model these are lumped together.

7. For the purposes of the analyses here a distinction is made between the early African material that has been ascribed to *H. erectus* (e.g. KNM-ER 3733, 3883, WT-15000) (=*H. ergaster*) and the later African material (e.g. OH9) and the Asian material. In the "Minimal" model these are lumped together (see Wood, 1992).

8. In the "Minimal" model all non-*erectus* material is lumped firstly into *H. sapiens* as a whole and secondly into three categories: "archaic *sapiens*", neanderthals; and anatomically modern humans. In the "Maximal" model the following groups are recognised: (a) European "archaic *sapiens*" (=*H. heidelbergensis*); (b) African "archaic *sapiens*" (=*H. rhodesiensis*); (c) neanderthals from Europe and the Middle East (=*H. neanderthalensis*); (d) *H. mapaensis* from eastern Europe and (e) anatomically modern humans (=*H. sapiens*). (See Groves, 1989, Howell, in press, Tattersall, 1986).

Table 4 Temporal distribution of evolutionary events among the Hominidae (500 Kyr data), based on the chronological ranges shown in Table 3. See Table 3 for differences between the models

Time (Myr)	Number of species present (Model 1)	Number of species present (Model 2)	Number of species present (Model 3)	Number of first appearances (Model 1)	Number of first appearances (Model 2)	Number of last appearances (Model 1)	Number of last appearances (Model 2)
0·0–0·5	6	4	2	5	3	5	3
0·5–1·0	3	3	3	0	0	2	2
1·0–1·5	4	3	3	1	0	1	0
1·5–2·0	6	4	4	2	1	3	1
2·0–2·5	5	5	5	3	3	2	2
2·5–3·0	3	3	3	1	1	1	1
3·0–3·5	2	2	2	0	0	0	0
3·5–4·0	1	1	1	1	1	0	0
4·0–4·5	1	1	1	0	0	0	0
4·5–5·0	1	1	1	0	0	0	0

as represented by the first appearance of taxa. However, correlation coefficients between climatic events and hominid evolution were largely not significant (Table 7). No significant relationships were found between the appearance of hominid taxa and any climatic variable. Hominid extinction, measured by the last appearance of a taxon in the fossil record, showed a significant relationship with minimum and modal temperature. Significant correlations were also found between species diversity (minimal and modal models of hominid diversity) and the number of climatic cycles (lagged relationship); between hominid diversity (modal) and minimum temperature; and between hominid diversity (minimal model) and modal temperature.

These results suggest that the proposed effect of climatic change on the appearance of new taxa in hominid evolution cannot be supported. To investigate this further, correlation coefficients were also calculated between the climatic variables and papionine taxa and the South African bovids. Correlations were also produced for evolutionary events and the climatic variables for the preceding 0·5 Myr time period to allow for time lag effects. The results were striking (Table 7). While climatic instability correlated with overall primate diversity, especially baboons, and to a lesser extent hominids, all the other significant relationships were again with last appearance (extinction) rather than first appearance (speciation). The only exception was the appearance of new bovid taxa, as shown also by Vrba (1985*a*).

100 Kyr units

It might well be argued that the chronological level used here is too coarse grained to identify the associations. To test for this the same analyses were run on the 100 Kyr dataset. A number of interesting patterns emerged at this level, although again, there was no relationship between first appearances and climatic change (Table 8). In this set of analyses *Homo* and *Australopithecus* were treated separately, and they yielded differing results. For example, the number of australopithecine species showed a negative relationship with minimum temperature and a positive one with maximum temperature. *Homo* on the other hand showed a slightly positive relationship with minimum temperature, and also with the degree of climatic variation.

Table 5 **Temporal distribution of evolutionary events among the Hominidae (100 Kyr data), based on the chronological ranges shown in Table 3. See Table 3 for differences between the models**

Time (Kyr)	Number of species present (Model 1)	Number of australopithecine species present (Model 1)	Number of *Homo* species present (Model 1)	Number of species present (Model 2)	Number of species present (Model 3)	Number of first appearances (Model 1)	Number of first appearances (Model 2)	Number of last appearances (Model 1)	Number of last appearances (Model 2)
0·1	3	0	3	1	3	0	0	2	0
0·2	5	0	5	1	3	2	0	2	0
0·3	4	0	4	1	2	1	0	1	1
0·4	3	0	3	1	2	0	0	0	0
0·5	3	0	3	1	2	2	1	0	0
0·6	1	0	1	1	1	0	0	0	0
0·7	2	1	1	2	2	0	0	1	1
0·8	2	1	1	2	2	0	0	0	0
0·9	3	2	1	3	3	0	0	1	1
1·0	3	2	1	3	3	0	0	0	0
1·1	3	2	1	3	3	0	0	0	0
1·2	4	2	2	3	3	0	0	1	0
1·3	3	2	1	3	3	1	0	0	0
1·4	3	2	1	3	3	0	0	0	0
1·5	3	2	1	3	3	0	0	0	0
1·6	3	2	1	3	3	1	0	0	0
1·7	4	1	3	3	3	0	1	2	1
1·8	3	1	2	2	2	0	0	0	0
1·9	3	1	2	2	2	0	0	0	0
2·0	4	2	2	3	3	0	0	1	0
2·1	4	2	2	4	4	0	0	1	1
2·2	5	4	1	4	4	1	2	1	1
2·3	3	2	1	3	3	0	0	0	0
2·4	3	2	1	3	3	1	1	0	0
2·5	2	2	0	2	2	0	0	0	0
2·6	2	2	0	2	2	0	0	0	0

Table 6 Correlation coefficients between climatic variables for the 500 Kyr dataset

	TIME	NCYCLE	MAXD	MIND	MODED	CLIMVAR
TIME	1					
NCYCLE	−0·30235	1				
MAXD	−0·85498*	0·195279	1			
MIND	−0·59209	0·282234	0·406923	1		
MODED	−0·93272**	0·243275	0·843402*	0·775126*	1	
CLIMVAR	−0·65334	0·076167	0·900268**	−0·03132	0·553441	1
MAGCHG	−0·12766	0·636864	−0·05383	0·519665	0·209751	−0·30656

Key: * = $p<0{\cdot}01$; ** = $p<0{\cdot}001$; TIME = time unit in 0·5 million year periods; NCYCLE = number of climatic cycles per unit of time; MAXD = maximum delta^{18} value; MIND = minimum delta^{18} value; MODED = modal delta^{18} value; CLIMVAR = the amount of climatic variability (MIND–MAXD); and MAGCHG = the magnitude of climatic change from one time period to another (MODED(1)–MODED(2)).

Table 7 Statistically significant (* = $p<0{\cdot}01$; ** = $p<0{\cdot}001$) relationships between climatic variables and evolutionary events among the hominids and the papionines at the 500 Kyr level. These include lagged data

	Number of species present (species diversity)	Number of first appearances (speciation)	Number of last appearances (extinction)
Number of cycles	*Papio* (0·775)* *Theropithecus* (0·908)** Papionini (0·743)* Hominids 2 (0·8171)* and 3 (0·8833)* (lagged)		Papionini (0·8156)* (lagged)
Max. delta 18	Hominids 2 (0·7729)*		Hominids 1 (0·7968)* (lagged) *Papio* (0·797)* Papionini (0·870)** ATP (0·8559)*
Min. delta 18			
Mode delta 18	Hominids 1 (0·7897)*		Hominids 1 (0·7884)* (0·7971)* (lagged) ATP (0·8751)* (0·8070)* (lagged)
Climatic variation			Papionini (0·757)*
Magnitude of change		Bovids (0·762)*	

Causality in hominid evolution

It is a truism to say that correlation shows association, not causality, and equally it must be remembered that a lack of correlation does not necessarily mean that there is no inter-linking of variables. Undoubtedly the evolution of the Hominidae during the last five million years

Table 8 Significant correlation coefficients between hominid evolutionary events and 100 Kyr climatic variables

	Number of species present (species diversity)	Number of first appearances (speciation)	Number of last appearances (extinction)
Number of cycles			
Max. delta 18	Australopithecines (−0·4586)* (P) (−0·630)** (B) *Homo* (0·460)* (P) (0·530)* (B) Hominids 2 (−0·551)** (B)		
Min. delta 18	Australopithecines (0·661)** (P) Hominids 2 (0·698)** (P)		Hominids 1 (0·458)* (B)
Climatic variation	Australopithecines (−0·534)* (B) (−0·642)** (P) *Homo* (0·528)* (P) Hominids 2 (−0·630)** (P)		
Magnitude of change			

* = $p<0{\cdot}01$; ** = $p<0{\cdot}001$. P = planktonic data, B = benthic.

occurs against the background of major climatic change and instability, and that context is bound to be significant. What is at issue is less whether climate and evolutionary events are related to each other, but to determine the nature of the effects and mechanisms involved. What these analyses show is that the relationship is not a simple one, and that climatic change is not the direct and only cause of the rate and pattern of change in hominid evolution. It certainly cannot be claimed that climate takes primacy over other explanations of hominid evolutionary change.

Temperature effects: speciation

Although the association between the first appearance of taxa in the fossil record and evolutionary speciation must be treated with some caution, the most significant result to emerge is that there appears to be no statistically significant relationship between first appearance, and by implication speciation, and changes in temperature. This suggests that a simple climatic forcing model of evolutionary change should be treated with caution. The African terrestrial primates as a whole do not show a speciation response to either increases or decreases in the temperature, despite the fact that this is the most progressive change that occurs during the period under investigation. This is true whether the scale of analysis is 100 Kyr or 500 Kyr. Such a relationship, though, does hold for the bovids, supporting the hypothesis that different taxa will respond differently to the same environmental changes.

Temperature effects: extinction

In contrast, a number of close relationships occur between patterns of extinction, as measured through last appearances in the fossil record, and changes in temperature. At the 500 Kyr scale, the lower the minimum or modal temperatures, the higher the probability of extinction of hominids. The same is true of the baboons. At the 100 Kyr level the same pattern can be observed weakly, as the last appearance of hominid species is negatively correlated with changes in maximum temperature, although the effect can only be seen in the more speciose model of hominid taxa. The most important conclusion to be drawn is that the data presented here seem to show a stronger relationship between extinction and climatic change than between speciation and climate. The implication would be that climatic change leads to habitat loss, which in turn leads to extinction of populations, but that other factors are involved in the subsequent appearance of new taxa to exploit the new environments.

Temperature effects: species diversity

The third parameter of evolutionary change employed in these analyses is the number of species present at any one time. In this case baboon diversity showed no relationship with the temperature variables. At the 500 Kyr level some effect was found for hominids, which were more diverse when minimum and modal temperatures were lower. However, the effect is not strong as it is sensitive to which set of hominid data is used. At the 100 Kyr level species diversity varied both positively and negatively with different measures of temperature. This was sensitive to both the hominid dataset used and the climatic datasets (planktonic versus benthic), suggesting that the relationship is not a robust one. An interesting contrast appears between *Homo* and *Australopithecus*, in that the former vary negatively with minimum temperature, whereas the latter vary positively. Overall it appears that the australopithecines are more temperature sensitive than *Homo*. However, it may also be the case that phylogenetic systems, both at the species and the generic level, can play a part in how evolutionary patterns are interpreted. Furthermore it may be argued that species diversity is a measure that shows how ecological changes determine the way in which speciation and extinction interact (i.e. whether speciation and extinction are in equilibrium and if so, at what level). If this is the case then species diversity might both be very sensitive and rich in ecological information and also be extremely complex.

Climatic stability and speciation

The discussion so far has focused on the actual changes in climate as measured through temperature. However, it may be the case that the temperature itself is not the critical variable, but the degree of stability. It is possible to hypothesise that regardless of the direction of change, a decrease in environmental stability is likely to have an effect on species distribution and abundance, and therefore on speciation, diversity and extinction.

Climatic stability was measured in these analyses in terms of the number of major oscillations or cycles per unit of time (500 Kyr and 100 Kyr), the amount of variation in temperature per unit of time (the difference between maximum and minimum δ^{18} values), and the magnitude of change. In no case, though, did the first appearance of either hominids or baboons show a significant relationship with these climatic variables. In contrast the first appearance of bovid species did seem to occur when there had been a marked climatic change, as has been suggested by Vrba (1985*a*). This contrast between ecologically distinct lineages may be significant, and it could be argued that the herbivores, being more speciose than primates, are more sensitive to change, or that the resources and habitats in which they live are more liable to change. If this is the case then it may be argued that primates, as more eurytopic species, evolve new species in response to different climatic and environmental parameters than do the bovids in general, and as the stenotopic bovids relative to the eurytopic ones (Vrba, 1985*a*).

Climatic stability and species diversity

When species diversity is examined in relation to climatic stability a number of relationships occur, especially among the baboons. The strongest association was found between *Theropithecus* and the number of climatic cycles ($r = 0{\cdot}908, p < 0{\cdot}001$), suggesting that this very specialised lineage was sensitive to changes in distribution of habitat caused by fluctuating temperatures. *Papio* showed a similar but less strong association. Amongst the hominids a relationship was found between the more conservative datasets and the number of climatic cycles, but only using values lagged by one time unit, at the 500 Kyr level. This particular association could not be found at the 100 Kyr level, although for the more conservative dataset the number of hominid species did show a significant relationship with the amount of climatic variation. In this case the association was negative, that is, the more stable the climate, the more hominid species. Interestingly, when the hominid species are divided into australopithecines and *Homo*, the former maintained this negative association, while *Homo* showed a positive one. The behaviour of *Homo* in relation to climatic change through the Pleistocene is likely to be very sensitive to the longevity given to *H. erectus*.

Climatic stability and extinction

Finally, when last appearance or extinction patterns are examined in relation to climatic stability, the baboons showed a stronger set of relationships than did the hominids.

Evolutionary response and climate

In summary the effect of climate on evolutionary patterns among the hominids and other terrestrial African primates can be said to be complex and certainly not overwhelming. In the entire set of correlation coefficients calculated not a single statistically significant result was obtained between the first apppearance of taxa (speciation) and a climatic variable, at either the 100 Kyr or the 500 Kyr level. The only group to show a relationship between speciation and climate were the bovids. Number of species present, or species diversity, showed a number of significant relationships, primarily with temperature rather than stability. Extinction (last appearances) also showed a number of associations. However, in all these cases it is clear that the associations are sensitive to the degree of lumping and splitting of the hominid taxa, and therefore conclusions should be drawn with caution. Altering the response time by lagging the effects of climatic change also yielded some positive results that were different from the immediate ones.

Relationship between speciation and extinction

Given the weak relationship between climate and evolutionary events, especially extinction, it is worth looking at the internal relationships between speciation and extinction. At the 500 Kyr level speciation and extinction appear to be strongly related to each other ($r = 0{\cdot}8577$, $p < 0{\cdot}001$). This relationship holds whatever the level of hominid diversity employed. In other words, speciation and extinction tend to occur within the same time frame, regardless of climatic patterns. However, this statistical relationship is lost when considered at the finer 100 Kyr level of analysis, although from the perspective of the sequence of events in hominid evolution there is clearly an interesting pattern to explain. Lagged correlations at either 100 Kyr or 500 Kyr levels, i.e. correlating extinction rate with speciation rate in the subsequent time period, fail to show a significant relationship.

Climate and competition

Climate is likely both on *a priori* and empirical grounds to be an important element in any model of evolutionary change. Another such element is competition, both within and between species. The data presented here are most consistent not with a simple climatic model, but with one in which it is the interaction between climatic patterns and local competitive conditions that is critical. It is probably the case that where climatic change is an important factor, it operates through competition. Climatic change will alter the nature, abundance and distribution of environments and resources within those environments. This will lead to changes in competitive relationships between and within species, and it is these altered competitive relationships that are likely to lead to evolutionary consequences. The consequences might be extinction of populations as the most direct effect, or speciation as a less direct one arising either out of reduced intra-community competition or the opening up of new ecological opportunities. Competition, therefore, is always likely to be the immediate cause of evolutionary change, played out within a framework determined by, among other factors, the climate.

However, the data presented here suggest that even allowing for this interpretation of the relationship between climate and competition, climatic change alone is not sufficient to explain the patterns of speciation and extinction we see amongst hominids and other terrestrial African primates. Clearly competitive relationships can change independent of climate, or alternatively, the impact of climate change will vary markedly with geographical factors. In other words, it is probable that species appear and disappear as a result of local competitive conditions rather than broad global patterns of climatic change. To test this hypothesis would obviously require an immense improvement in the available data, but should necessarily be the next step in exploring the causal factors underlying hominid evolution.

Methodological limitations

The data presented here indicate clearly that other factors must be involved in speciation, even if they have not been identified, and that climatic forcing is not necessarily the most significant factor. It is apparent, however, that a number of methodological problems can be identified which make it hard to be conclusive about the role of climate in both evolutionary events in general, and human evolution in particular. As pointers to future research, these can be briefly mentioned here.

First, an association is generally made between the process of speciation and the first appearance of taxa. It is certainly the case that this is an oversimplification that can be misleading. By definition the appearance of new species is bound to be geographically variable, and it may be all too easy to conflate speciation with geographical dispersal. While this is a serious problem, it does perhaps point to the fact that what we should be looking for in relation to climate are ecologically significant events, and these may not be the same as the genetically significant event of speciation. For example, the dispersal of hominids out of Africa may be the most significant evolutionary event, but not associated with speciation at least in its early stages. This event, however, which on current evidence lies between one and two million years ago, does not coincide with any particular climatic event.

Second, it may be that the phylogenetic range of species considered here is too narrow to pick up pulses that are spread in complex ways across whole biota. Only extension to other taxa can solve this particular problem. Turner & Wood (1993) have recently presented data on the first and last appearances in East and South Africa of a whole range of large mammals over the last 4·0 million years. When these data were correlated with the 500 Kyr climatic dataset presented here it was found that there were no significant relationships at all. This result should be treated with caution, however, as the number of temporal periods used is smaller than in the analyses presented here. Nonetheless, these preliminary results do suggest that even with a greater taxonomic sample the pulse effect is not strong.

This conclusion, though, should be qualified by one further consideration. The assumption underlying the analyses presented here is that the climatic effects on evolution are essentially linear—small climatic change may have small effects, large climatic change will have large effects. It may be the case, but has yet to be shown, that there is a threshold effect in operation; only the most climatically significant events, such as the 2·4–2·1 Myr climatic change, will be of sufficient magnitude. If this is the case, then testing the climatic forcing model becomes harder still. More importantly, though, it implies that some other factors are setting the threshold, which returns the problem yet again to the nature of local competitive interactions and community structure.

Conclusions

Climate does have an effect on hominid and other primate evolution, but this is not directly related to speciation or the appearance of new taxa. Climatic forcing alone cannot explain the pattern of evolutionary novelty. The data presented here suggest that the primary effect of climatic change is on levels of diversity and extinction patterns. However, the appearance of new species following these extinction events is independent of climate. A case can be made that climatic change leads to fragmentation and loss of habitats, leading to an increase in the probability of extinction. The rate at which new species will then evolve is likely to be dependent upon local competitive conditions and the specific characteristics of the taxa involved. There is no evidence to support the contention that the direction taken in human evolution is determined by climatic change rather than competition between and within species. These results have implications for understanding the mechanisms and dynamics of evolutionary change in relation to large scale environmental change and the patterns of evolutionary rates in hominids and other taxa. There are interesting avenues to pursue by extending the taxonomic range of this approach, as it is striking that patterns that are confirmed for the bovids fail to show so clearly for primate taxa. How different species respond to the changing competitive conditions in which they find themselves should turn out to be one of the key elements in the development of evolutionary theory.

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