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Does climatic change drive mammalian evolution?*Donald R. Prothero, Department of Geology, Occidental College, Los Angeles, CA 90041, prothero@oxy.edu***ABSTRACT**

Neo-Darwinian evolutionary theory argues that species and faunas are exquisitely adapted to their environment and should respond when their habitat changes. To test this hypothesis, the mammalian response to four of the largest climatic events of the Cenozoic (as documented by the marine record, oxygen isotopes, land plants, and other climatically sensitive organisms) are examined. These events occurred during the global cooling at the end of the middle Eocene (37 Ma), the cooling and drying event in the earliest Oligocene (33 Ma), the spread of C4 grasslands in the late Miocene (7 Ma), and the rapid climatic fluctuations of the Pliocene-Pleistocene (2.5 Ma to present). In each case, there is relatively little short-term response of the mammalian fauna. Typically, there is greater turnover millions of years before and after the time of climatic change than during the climatic event itself. This pattern suggests that the climatic control on mammalian evolution is much more complex than previously supposed, or that intrinsic biotic controls may be more important than extrinsic environmental controls.

INTRODUCTION

One of the central tenets of neo-Darwinian evolutionary theory is the idea that organisms are highly responsive to changes in their environment caused by climate, and readily adapt to environmental selection pressures. Evolutionary biologists have documented many elegant (but small-scale and short-term) examples of organisms responding to environmental selection (Weiner, 1994). One explicitly testable hypothesis related to this idea was



Figure 1. Looking south at exposures of the Eocene-Oligocene White River Group south of Douglas, Wyoming (Laramie Range in the background). The prominent white ash layer in the middle of the cliff (Sa tuff of Evanoff et al., 1992) has been $^{40}\text{Ar}/^{39}\text{Ar}$ dated at 33.9 ± 0.13 Ma (Prothero and Swisher, 1992). Extinction of the brontotheres and most other faunal events at the end of the Chadronian occurred just before and after deposition of this ash. Yet the climatic change (as shown by the sedimentology and land snails—Evanoff et al., 1992) is reflected much higher in this same section.

Vrba's (1985, 1993) "turnover pulse" hypothesis, which suggests that most evolutionary turnover events are correlated with episodes of major climatic change. The turnover pulse idea has appeared in many recent books that purport to explain human evolution as a response to climatic change and instability (Stanley, 1996; Potts, 1996; Boaz, 1997).

However, a growing body of data conflicts with the notion that all organisms are highly sensitive to climatic changes, and respond by adaptation to environmental selection pressures. One of the surprising outcomes of the punctuated equilibrium model of Eldredge and Gould (1972) has been recognition of the prevalence of stasis among species through millions of years and many episodes of climatic change (Eldredge, 1995, p. 64). This is not to say that most organisms are insensitive to climate. For some groups of organisms, such as microplankton or land plants, the response to environmental change is well established. However,

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the environmental sensitivity of other organisms (especially marine invertebrates and terrestrial vertebrates) is less obvious.

In recent years, the potential to document and evaluate such patterns with excellent, detailed fossil records of certain organisms has greatly improved. The development of high-resolution chronostratigraphy with integrated biostratigraphy, magnetostratigraphy, and $^{40}\text{Ar}/^{39}\text{Ar}$ dating has allowed paleontologists to directly date and correlate patterns of faunal response in both the marine and terrestrial realms at a very fine scale. It is now possible to test aspects of the "turnover pulse" hypothesis with a much better data base than was available only a decade ago.

We now can ask whether turnover pulses are typical of the history of mammals. Broad, long-term changes in mammalian faunas (spanning tens of millions

of years) apparently correlate with the well-documented climatic changes of the Cenozoic (Webb, 1977; Webb and Opdyke, 1995; Janis, 1989, 1993), but do mammalian faunas respond to rapid, short-term climatic changes, as predicted by the turnover pulse model? Alroy (1995, 1997, 1998) showed that there was a very poor correlation between the turnover patterns of North American Cenozoic mammals and accepted proxies of climatic change, such as the global oxygen isotope record. Hill (1995) and Behrensmeyer et al. (1997) argued that the turnover pulses reported by Vrba (1985) for African Pliocene-Pleistocene mammals are not substantiated by the much larger database of Pliocene mammals from the Tugen Hills and Turkana Basin of Kenya. Thus, even the original data set that led to the turnover pulse hypothesis is under question.

TESTING THE HYPOTHESIS

What is the mammalian response to the major climatic events of the past 50 m.y.? The highly detailed climatic history now available for much of the Cenozoic allows us to pinpoint certain episodes of major environmental change (as recognized in marine faunas, oxygen isotopes, land plants, and other climatically sensitive organisms). With improved dating and correlation, we can examine any mammalian response to each of these global climatic events. If the turnover pulse hypothesis is generally valid for Cenozoic mammals, then there should be similar responses to the other great climatic crises of the Cenozoic. Four major climatic events stand out (see below). This study excludes turnover events such as those at the Paleocene-Eocene boundary, or the Grande Coupure in the European Oligocene, because those episodes include

significant immigrational turnover, which complicates the picture of in situ change.

Test 1—Middle Eocene Event

The first major step in the climate change of the Cretaceous through middle Eocene "greenhouse world" was the profound cooling event at the end of the middle Eocene, dated at 37.0 Ma (Berggren and Prothero, 1992; Berggren et al., 1995) (Fig. 1). Oxygen isotope records from benthic foraminifera show that the oceans cooled by about 4–5 °C at this time (Miller et al., 1987). Boersma et al. (1987) argued that there was a major cooling of oceanic bottom waters, which became decoupled from surface waters. In response to this rapid cooling and oceanographic change, there was a major extinction in the warm-water foraminifera (Boersma et al., 1987), a major extinction of many long-lived tropical nannoplankton (Aubry, 1992), and extinctions in the bivalves (84% of

species) and gastropods (89% of species) in the Gulf Coastal Plain (Hansen, 1987, 1992). By any standard, the end of the middle Eocene was a dramatic cooling and extinction event, especially in the marine realm.

The terrestrial paleoclimatic record of the middle-late Eocene transition is rather limited, but there are some important clues. Land plants from Alaska to the Gulf Coast indicate a reduction of mean annual temperature of about 14–16 °C (Wolfe, 1978, 1994). Late Duchesnean paleosols from the Big Badlands of South Dakota indicate dense tropical forests with more than 1 m of annual rainfall, while those of the overlying upper Eocene Chadron Formation received between 500 and 1000 mm and were less densely forested (Retallack, 1983).

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How did land mammals respond to these climatic changes? The middle-late Eocene boundary at 37.0 Ma is now correlated with the boundary between the Duchesnean and Chadronian North American land mammal "ages" (Prothero, 1995; Prothero and Emry, 1996). Most mammalian faunas can be correlated to this interval through a combination of magnetic stratigraphy and ⁴⁰Ar/³⁹Ar dates. In west Texas, the Duchesnean-Chadronian transition can be directly calibrated between ⁴⁰Ar/³⁹Ar dates of 36.7 ± 0.07 and 37.8 ± 0.15 Ma, and by correlation with other faunas, the overall pattern in North America can be determined.

All recent studies of this interval conclude that there was very little change in mammalian faunas between the Duchesnean and Chadronian. Large-scale compilations of species and generic diversity and turnover (Stucky, 1990, 1992; Alroy, 1998) show no significant diversity changes or unusual turnover rates between the late Duchesnean and early Chadronian; there was a stable equilibrium value of between 72 and 84 genera throughout this 5 m.y. (40–35 Ma) interval (Fig. 2). Turnover rates are about average for the late Paleogene. In fact, Emry (1981) and Wilson (1984, 1986) argued that the Duchesnean could be considered a "sub-age" of the Chadronian, because the differences were so slight. A much greater faunal change (Fig. 2) occurred between the early

Duchesnean and the late Duchesnean (Wilson, 1986; Lucas, 1992). This turnover occurred at 39 Ma, 2 m.y. before the climatic change in the oceanic realm (Prothero and Emry, 1996).

Test 2—Early Oligocene Event

On the basis of the oxygen isotope curve (Miller et al., 1987) or the land floras (Wolfe, 1978, 1994), the most significant climatic event in the Cenozoic was the global refrigeration that occurred in the earliest Oligocene (about 33.2 Ma). This event was marked by the first significant Antarctic glaciers, and about 5–6 °C of global cooling (Miller et al., 1987; Miller, 1992). The cooling was as drastic as that at the end of the middle Eocene, and extinctions in the marine realm were almost as severe. There were major extinctions in the calcareous nannoplankton (Aubry, 1992), diatoms (Baldauf, 1992), and benthic foraminifera (Gaskell, 1991). Gulf Coast molluscs were decimated again; 97% of gastropod species and 89% of bivalve species disappeared after their late Eocene recovery (Hansen, 1987, 1992). Echinoids dropped 50% in species diversity at this time (McKinney et al., 1992). Planktonic foraminifera underwent a minor extinction; most surviving early Oligocene species were small, low in diversity, and cold adapted (Boersma et al., 1987).

Numerous climatic indicators show that the earliest Oligocene was a time of rapid (less than a few thousand years) change in terrestrial habitats. Land plants from the Gulf Coast to Alaska indicate a decrease of 13 °C in mean annual temperature, a great increase in seasonality (mean annual range of temperatures increased dramatically from about 5 °C to almost 25 °C), and much drier climates (Wolfe, 1978, 1994). Floras indicate that most of North America changed from paratropical forests (like those of tropical Central America) to broad-leaved deciduous forests (like those of New England) in a very short period of time. Paleosols from the Big Badlands of South Dakota show that late Eocene forests, which received more than 1 m of rainfall, were replaced in the early Oligocene by open scrublands with less than 500 mm of annual precipitation (Retallack, 1983, 1992). In Douglas, Wyoming (Fig. 1), flood-plain deposits were replaced by eolian deposits, indicating even greater trends toward aridity (Evanoff et al., 1992). Late Chadronian land snails are large forms adapted to wet, subtropical habitats (like those of modern central Mexico). In the early Orellan they were replaced by smaller taxa with restricted apertures, typical of drier climates, like those of modern Baja California (Evanoff et al., 1992). Late Chadronian reptiles and amphibians were predominantly aquatic taxa, such as crocodylians, pond turtles, and salamanders, but only dry land tortoises are common in the Orellan (Hutchison, 1982, 1992).

How did land mammals respond to this dramatic change in their environment? As Prothero and Heaton (1996) have shown, there was almost no response (Fig. 2). The earliest Oligocene climatic event (middle early Orellan, Chron C13n) was almost ignored by land mammals. Of 70 species known from the earliest Orellan, 62 persisted unchanged into the late Orellan. Most of the modest faunal responses during the Chadronian-Orellan transition had already taken place more than 250 k.y. before the climatic crash of the early Orellan. But even these changes were unimpressive: A few archaic groups from the Chadronian, such as the brontotheres, oromerycid artiodactyls, and cylindrodont rodents disappeared, and the oreodont *Miniochoerus* underwent slight dwarfing, but most mammalian lineages showed no changes worth documenting. Compared to the 177 species now documented for this interval, this is a remarkably mild response to what all the other evidence indicates was a major climatic and floral change. This lack of change cannot be dismissed as an artifact of sampling or preservation, because the White River Group in eastern Wyoming is densely fossiliferous through all of the relevant interval (Prothero and Heaton, 1996; Evanoff et al., 1992).

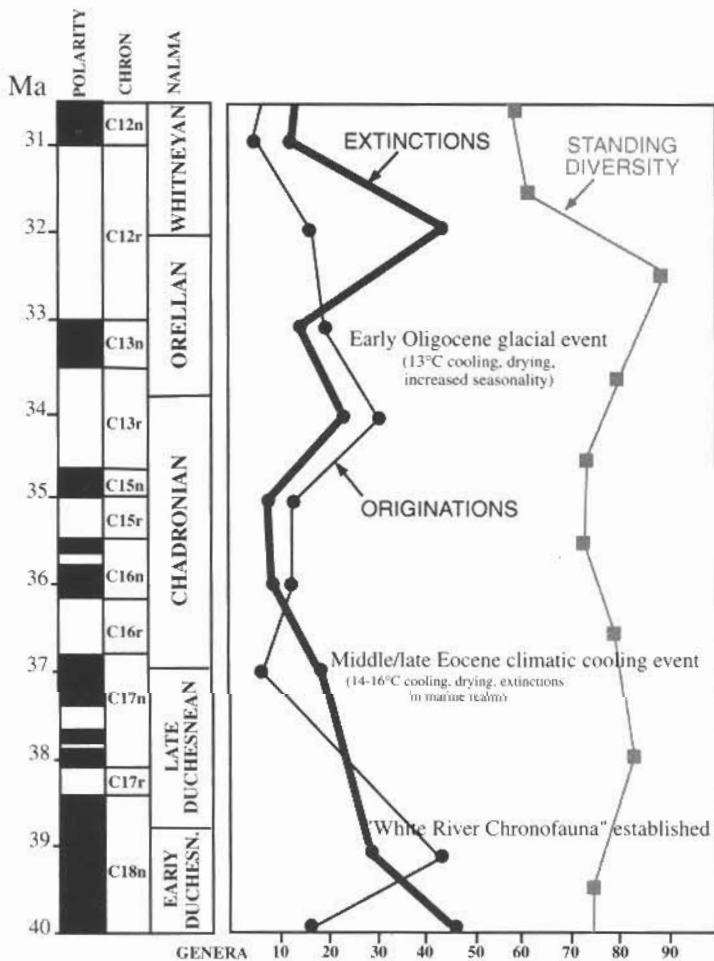


Figure 2. Mammalian diversity and turnover through the late middle Eocene (Duchesnean), late Eocene (Chadronian), and early Oligocene (Orellan and Whitneyan). Diversity data modified from Stucky (1992) for the Duchesnean, and Prothero and Heaton (1996) for the Chadronian through Whitneyan. Total generic diversity (green squares) shown in the middle of 1 m.y. increments; originations (blue circles) shown at the beginning of each 1 m.y. interval, and extinctions (red circles) at the end of each 1 m.y. interval. NALMA = North American land mammal "ages." Time scale after Berggren et al. (1995) and Prothero and Emry (1996).

Test 3—Late Miocene Carbon Isotopes and Grasslands

One of the classic cases of evolutionary response to climate is the well-known story of how some herbivorous mammals acquired high-crowned teeth for eating gritty grasses in the Miocene. This is most often noted in the evolution of horses, but it also occurred in camels, bovids, pronghorns, rhinoceroses, and other groups. Scientists have long pointed to this as a clear example of an evolutionary response to a climatic and vegetational change. There is a major problem with this scenario: the timing is all wrong. Hypsodont horses, camels, rhinos, and bovids all first developed their high-crowned teeth in the middle Miocene (about 15–16 Ma), but geochemical evidence of extensive C₄ grasslands (the grasses that now dominate most temperate and tropical latitudes) did not become widespread until the late Miocene (8–7 Ma), at least 7 m.y. later (Quade et al., 1989; Cerling, 1992; Cerling et al., 1997). Retalack (1997) has argued that there must have been an expansion of C₃ grasslands in the middle Miocene, but if this is so, we have no modern analogues for such a vegetation (Wang et al., 1994).

Regardless of how one tries to explain this mismatch between teeth and vegetation, the C₄ carbon isotope signal, which marks the great expansion of tropical and temperate grasslands and savannas at 8–7 Ma, produces another climatic-evolutionary enigma (Cerling et al., 1997). The carbon isotopic records of several areas (in North America, South America, East Africa, Pakistan) indicate a dramatic and abrupt global isotopic event at 7 Ma. C₄ grasslands must have rapidly taken over huge areas in lower and middle latitudes at this time (Fig. 3).

Such a dramatic vegetational change should have led to drastic changes in the mammalian faunas that ate the grasses, especially in their abundance, extinction, and diversification. Yet, a detailed examination of the mammalian record does not support this. In North America, the 7 Ma isotope event falls at the early-late Hemphillian boundary (Woodburne and Swisher, 1995). The change in carbon isotope values at this time was dramatic (Cerling et al., 1997). Before 7 Ma, the values range between -7‰ and -14‰ (all C₃ plants), but after 7 Ma, there are numerous values above -7‰ and some as high as +5‰ (mostly C₄ plants). At the end of the early Hemphillian, there was some extinction in the horses, browsing camels, and pronghorns (Webb, 1983; Webb et al., 1995), for a total of 9 genera of large ungulates, and 27 genera overall (Stucky, 1990). But only 33 new genera (Stucky, 1990) appeared as the grasslands expanded in the late Hemphillian, and there was no great increase in grazing taxa. No new grazing ungulate genera were added, and the percentage of grazing taxa actually declines from 87% in the late Clarendonian-early Hemphillian to 80% in the late Hemphillian Coffee Ranch Quarry, Texas (Webb, 1983). Janis et al. (1999) found no increases in grazing ungulate taxa in this interval.

In addition, much greater turnover (45 new early Hemphillian genera, 36 Clarendonian genera extinct) marked the beginning of the Hemphillian (9.0 Ma), which was 2 million years before the C₄ grasslands appeared. The most significant turnover event (37 new genera, 63 genera extinct) of the entire Miocene occurred 2.5 million years later, at the end of the Hemphillian (4.5 Ma), when most of the savanna fauna of North America (especially among the horses, camels, pronghorns, proceratids, dromomerycids, rhinoceroses, gomphotheres, and mylagaulids) disappeared (Webb, 1983).

In Asia, isotopic data (Cerling et al., 1997) show an abrupt and dramatic increase in grasslands at 7 Ma (Fig. 3). Before 7 Ma, the $\delta^{13}\text{C}$ values are between -5 and -14‰, but after 7 Ma, the values range from 0 to +5‰. Barry (1995) showed the detailed history of faunal change (mostly bovids and rodents) in the well-studied Siwalik deposits of Pakistan. There was a major turnover event between 9.0 and 8.5 Ma, but none at 7 Ma (Fig. 3). In fact, turnover rates (both first and last occurrences) declined dramati-

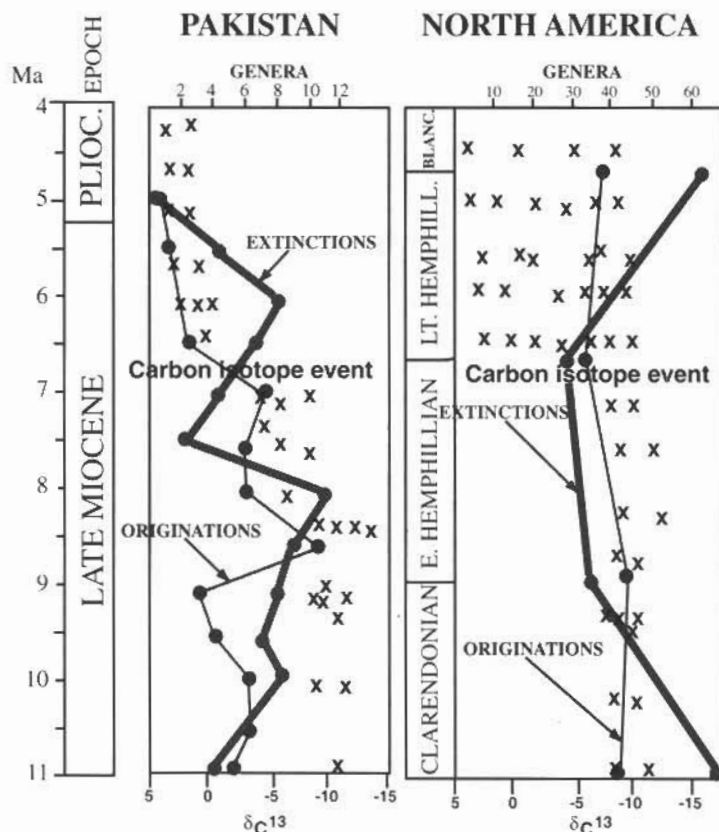


Figure 3. Comparison between carbon isotope values and changes in late Miocene mammalian diversity in Pakistan and North America. Symbols for origination and extinction curves as in Figure 2. Carbon isotopic values (X's) modified from Cerling et al. (1997, Fig. 2). Mammalian diversity statistics for North America after Stucky (1990), and for Pakistan after Barry (1995). Time scale after Woodburne and Swisher (1995) and Barry (1995).

cally after 8.0 Ma (Barry, 1995). Cerling et al. (1997) suggested that there were some faunal replacement events between 8 and 7 Ma, but this change in dominance is not reflected in the overall taxonomic turnover. In addition, there are many pulses of turnover throughout the Miocene of Pakistan that do not seem to be correlated with any known climatic event. Researchers have argued that these data are evidence of climatically driven turnover, but much of the turnover has no apparent climatic explanation (Barry et al., 1985). Even if higher-resolution studies should show more turnover at 7 Ma, the salient fact remains that turnover was higher before and after the C₄ event.

In western Europe, the pattern is similar. Köhler et al. (1998) showed that there were two major faunal turnover events in the Neogene mammals of Spain, one at 10–9 Ma, and the other at 6.5 Ma, but none at 7.0–7.5 Ma. This is consistent with the episodes of maximum turnover in Pakistan. Köhler et al. (1998) suggested that the synchronous turnover across Western Eurasia uncorrelated with the C₄ grasslands (which developed in Pakistan but not in Spain) supports a model of protracted faunal change that is caused by more complex forcing factors than a single climatic change.

Isotopic studies from East Africa (Cerling et al., 1997) document a significant carbon isotope event between 9 and 7 Ma. Yet Hill (1987, 1995) argued that the faunas of East Africa show little evidence of grassland dominance until Pliocene-Pleistocene time. Leakey et al. (1996) also found little faunal change in the 9–7 Ma interval. South America also shows the 7 Ma carbon isotope event (MacFadden et al., 1994, 1996; Cerling et al., 1997; Latorre et al., 1997), yet there was no obvious response in turnover or hyp-

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sodontology of South American mammals (MacFadden et al., 1994, 1996).

Test 4—Pleistocene Climatic Changes

The most rapid climatic fluctuations of the entire Cenozoic have occurred in the past 2 m.y.a., when climate has been controlled by 120 ka glacial-interglacial cycles. In the classic neo-Darwinian model that postulates species adapting to each climatic change, we would expect that such climatic variability would trigger much adaptation and speciation in Pleistocene mammals. Yet Barnosky (1987, 1994) and Barnosky et al. (1996) have shown that the response is much more complicated than this. Most Pleistocene mammals persist through many climatic cycles. They usually respond to climate change not by evolving new adaptations and producing new species, but simply by migrating north or south as climatic belts shift in latitude. Relatively few evolutionary changes (other than size changes) can be directly attributed to climatic change. The same evolutionary stability has been documented in Pleistocene reptiles and amphibians (Holman, 1995).

CONCLUSIONS

Paleontologists and evolutionary biologists have long sought to explain the excellent fossil record of land mammals, with its many dramatic faunal changes, and examples of adaptations (such as high-crowned teeth or long limbs) in terms of the Cenozoic changes in vegetation and climate. As our understanding of the fossil record of mammals improves, and the dating of the relevant deposits reaches higher levels of resolution and precision, it is possible to test hypotheses of climatic causes for evolutionary changes in much greater detail. In each of these four examples of independently established climatic change (as documented by the marine record, terrestrial isotopes, and terrestrial soils, plants, and climatically sensitive organisms), there are very few instances of direct response of the mammalian fauna to a specific, temporally limited climatic stimulus. Instead, the striking feature of each of these abrupt climatic changes is the *lack* of response of land mammals, even though in each example, it is clear that land plants and other elements of the terrestrial biota are responding. Clearly, the response of mammalian faunas to climatic stimuli is much more complicated than we have previously suspected. As previous studies of species and faunal stasis have shown, many organisms are much more stable in face of environmental change than classic neo-Darwinian models have previously supposed.

In past studies of excellent faunal records through long periods of time, scientists tried to explain each pulse of turnover by a specific external environmental event. Yet as the quality of the dating and of external records of climate improves, the emerging picture is not one of each pulse of turnover having a direct climatic cause. Instead, we are finding that many faunal events occur with no obvious extrinsic trigger, and many other climatic changes seem to cause no mammalian faunal change. On the longer-term scale, this is similar to the conclusions reached by Alroy (1995, 1997, 1998), who found that few of the major global climatic events (as represented by changes in marine oxygen isotopes) were correlated with peaks of mammalian turnover in North America, and vice versa. This noncorrelation seems to reveal an inherent bias toward focusing on possible instances of climatic causation of faunal change, and ignoring all the other unexplained turnover events. Instead, an objective (and statistically valid; Alroy, 1998) view of the mammalian faunal record in the Cenozoic leads to the conclusion that few turnover events can be directly tied to specific climatic changes.

This suggests that scientists should be more skeptical and more rigorous when they wish to suggest a cause-and-effect relationship between short-term climatic and faunal change. Such relationships may exist, but scientists must establish correlation

on a very highly resolved chronostratigraphic basis before these hypotheses can be evaluated. To date, when such detailed correlations have been established between global climatic signals and terrestrial faunal change, the response has been contrary to expectations.

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