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Slowly changing boundary conditions can sometimes cause discontinuous responses in climate models and result in relatively rapid transitions between different climate states. Such terrestrially induced abrupt climate transitions could have contributed to biotic crises in earth history. Ancillary events associated with transitions could disperse unstable climate behavior over a longer but still geologically brief interval and account for the stepwise nature of some extinction events. There is a growing body of theoretical and empirical support for the concept of abrupt climate change, and a comparison of paleoclimate data with the Phanerozoic extinction record indicates that climate and biotic transitions often coincide. However, more stratigraphic information is needed to precisely assess phase relations between the two types of transitions. The climate-life comparison also suggests that, if climate change is significantly contributing to biotic turnover, ecosystems may be more sensitive to forcing during the early stages of evolution from an ice-free to a glaciated state. Our analysis suggests that a terrestrially induced climate instability is a viable mechanism for causing rapid environmental change and biotic turnover in earth history, but the relation is not so strong that other sources of variance can be excluded.

THE STUDY OF EXTINCTION EVENTS DURING EARTH HISTORY was given considerable impetus by the hypothesis of an asteroid impact at the end of the Cretaceous (*1*). Further work suggested that extinctions may also be periodic and related to cycles of comet impacts (*2*). Although these hypotheses have been challenged (*3*), extraterrestrial impacts remain a plausible possibility as a mechanism for causing environmental disruptions (*4*). However, in this article we consider whether abrupt environmental change and extinction events may also result from a discontinuous climate response to slowly varying terrestrial boundary conditions; that is, under certain conditions, instabilities in the climate system can be triggered by small changes in forcing. We believe it is appropriate to examine this mechanism more closely, because there is a growing body of theoretical and empirical support for such responses in the climate system. Furthermore, the impact-extinction correlation at other extinction boundaries, although sometimes present (*5*), is not as strong as it is for the end of the Cretaceous. These results suggest the need for other mechanisms that cause abrupt environmental change.

The hypothesis of extinctions resulting from terrestrially induced climate variations, sometimes with threshold effects, has often been discussed previously as a factor that could have contributed to biotic turnover (*6*). Most of these conjectures have been from the vantage point of a geologist (*7*). We believe it is useful to examine the problem from the climate modeling perspective. Our contribution to the problem involves several new features. There is a more complete description of climate models with abrupt transitions, with some special emphasis on conditions occurring during transition periods. We also review geological evidence indicative of abrupt climate change. Finally, we compare times of extinction with climate change.

Models of Abrupt Climate Change

Theoretical support for the hypothesis of abrupt climate change is based on climate model results that suggest the presence of multiple equilibrium climate states for a given level of forcing. Transitions between states at "critical points" can be rather sudden and can be caused by small changes in forcing. Such features have been known to exist in simple climate models for some time (*8*), and there has

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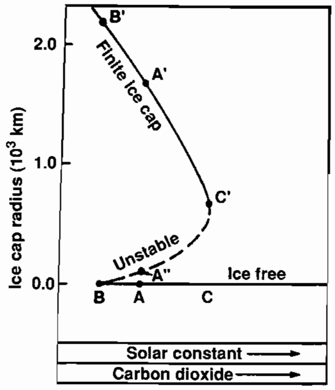
Fig. 1. Schematic of equilibrium solutions of ice feedback models for different levels of forcing. The dependent variable is the ice cap radius and the independent variable is the solar constant (or CO_2) increasing to the right. See text for additional discussion. [From (*18*); reproduced by permission of the Geological Society and *The Journal of the Geological Society (London)*]



been considerable debate whether such features are artifacts of model assumptions. The phenomenon may be a real feature of the climate system, because it also occurs in a more complex atmospheric general circulation model (*9*), an ocean general circulation model (*10*), and a thermohaline model of deep-water circulation (*11*). Abrupt transitions can occur in other types of climate models (*12*) and are a fairly common feature in complex physical systems.

Abrupt transitions can be of several types and affect the environment in different ways. There can be a transition from ice-free conditions to a climate with polar caps. Incremental changes in precipitation or evaporation could affect surface salinity (and density) of ocean surface waters, thereby affecting production rates of deep water. Changes in deep-water circulation could alter heat transport and affect carbon storage and oxygen levels, both in deep waters and in the atmosphere. Abrupt transitions also occur in the planetary circulation and affect such phenomena as onset and seasonal migration of the Asian monsoon (*13*) and changes in the jet stream (blocking) that can result in anomalous weather patterns (*14*). Changes in some of these atmospheric circulation patterns have already been linked to climate patterns during the Little Ice Age [1480 to 1890 (*15*)].

There is increasing evidence for abrupt climate change in the geologic record (*16*). A seasonal energy balance climate model (*17*) has already been used to interpret some climate steps in the Cenozoic in terms of a discontinuous response to slowly varying boundary conditions (*18*). For these reasons, the applicability of abrupt climate change to the problem of biotic crises must be contemplated more seriously. We will primarily discuss one type of multiple equilibrium solution by more fully developing ideas discussed earlier (*18*). We recognize that this is only an example of a larger class of models, and that there is a need for a fuller exploration of such behavior in climate models.

A typical solution (Fig. 1) for an energy balance climate model (*19*) illustrates the equilibrium solutions for ice cap area versus some controlling parameter, such as the solar constant or carbon dioxide (CO_2). Changes in summer temperatures on high-latitude land masses, due to changing land-sea distribution, could also affect the distribution of ice (*20*). Although there has been a large increase in solar luminosity throughout earth history (*21*), solar luminosity is plotted here because the sensitivity to solar constant fluctuations is a standard method of classifying climate model behavior. However, there have probably been significant fluctuations in CO_2 through earth history (*22*).

More than one equilibrium solution (for example, A, A′) may exist for the same external boundary condition, with intermediate solutions (A″) that are not stable (*23*). For energy balance climate models with diffusive heat transport, the multiple equilibria are related to discontinuous changes in surface albedo between ice-covered and ice-free regions. The feature has sometimes been called "the small ice cap instability," since ice caps smaller than C′ are unstable. Geologists have postulated on intuitive grounds that this mechanism may be important for glacial inception during the Pleistocene (*24*). One equilibrium solution in the model (A) may correspond to an ice-free earth; the other equilibrium solution (A′) may correspond to a glaciated earth (finite ice cap). Although the real climate system may contain more than two branches, for example, polar ice caps and mid-latitude glaciation, the basic concept of discontinuous steps remains the same.

An important feature of these solutions involves the response to altered boundary conditions. The response depends on initial conditions. For example, suppose the initial climate state was at A, a solution representing an ice-free state. Now suppose that the solar constant (or CO_2) is varied. Lowering the solar constant moves the equilibrium solution for the earth along the lower line to point B. The earth is still ice-free up to this stage. However, decreasing the solar constant by a small increment forces the equilibrium point to jump to the upper solution curve at point B″, representing a glaciated state. Reversing the forcing may not necessarily reverse the results. To return to the ice-free state, the solar constant (or CO_2) may have to increase greatly until another critical point (C′) is reached. The solution state might then dramatically return to the original ice-free branch at point C.

Figure 2 is a simple cartoon illustrating the underlying reasons for the critical-point phenomenon in diffusive energy balance climate models. The interested reader is referred to North (*25*) for a more rigorous discussion of the problem. First, consider a situation analogous to conditions on an ice-free earth (Fig. 2A), for example, point A of Fig. 1. For a given level of forcing, temperatures will increase with distance from the pole. If the heating decreases, the shape of the temperature curve will remain the same but will shift downward along the *y*-axis until some critical temperature is reached that might represent, for example, the mean annual temperature below which ice is permanently present. By convention, we choose $-10°C$ as this critical temperature (*8*).

The presence of a small patch of ice at the pole effectively produces a steady heat sink because of its higher albedo. The linear response of the climate model to this sink of heat can be found. The result is a sizable thermal depression over a large distance from the sink (Fig. 2B), with the length scale dependent on a balance between transport and the adjustment time scale for the radiative perturbation. Adding the curves in Fig. 2, A and B, leads to the temperature curve in Fig. 2C. For parameter values representative of the earth's transport and radiation, the effective range of the

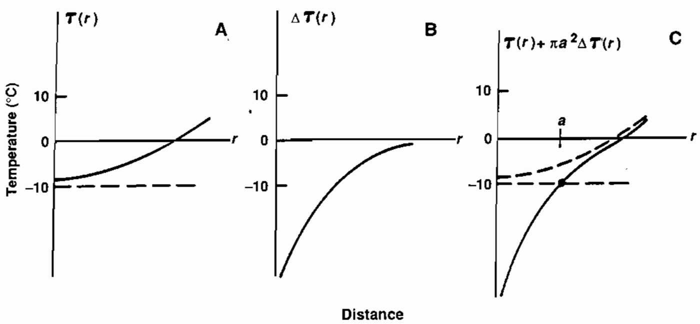


Fig. 2. Temperature solutions versus distance from the pole for (**A**) the temperature for a climate state corresponding to point A in Fig. 1; (**B**) the depression of temperature due to a point sink of heat at the pole corresponding to a small patch of highly reflective ice. The depression is everywhere approximately proportional to the ice disk area; (**C**) the sum of curves in (A) and (B), where the size of the ice disk has been chosen to be of radius *a*; this value is also the correct equilibrium value for an ice cap corresponding to point A in Fig. 1. [From (*18*); reproduced by permission of the Geological Society and *The Journal of the Geological Society (London)*]

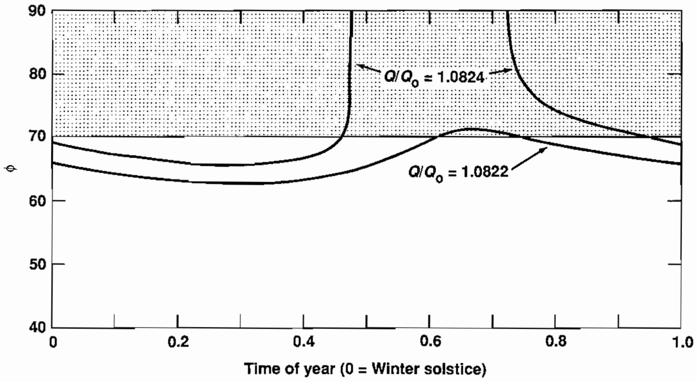


Fig. 3. Calculation illustrating that the transition between a seasonally ice-free state and permanent snow cover can occur for a very small change in forcing. Example based on results from a highly idealized seasonal climate model with land poleward of 70° (*27*). Ordinate is latitude; forcing represents changes in the solar constant (Q), normalized to present values. [From (*27*); reproduced by permission of Springer-Verlag and *Climate Dynamics*]

influence function is about 20° on a great circle. Thus a strong localized heat sink will have a nonnegligible effect as far as 2000 km away, potentially depressing temperatures below −10°C over a wide area. A second equilibrium solution with glaciation is implied. Ice-age experiments with general circulation models (*26*) and glacial-maximum ice positions suggest approximately the same horizontal range to the influence function, as does the simple climate model.

Sensitivity experiments (Fig. 3) with a highly idealized seasonal energy balance climate model (*27*) suggest that a discontinuous transition from a glaciated to an ice-free state could occur for very small perturbations in forcing (0.0002 percent change in the solar constant). The change in forcing (0.0007 W/m^2) is more than four orders of magnitude less than seasonal insolation changes associated with Pleistocene glacial cycles (*28*).

Environmental Instability Near Singularities

In addition to the change in ice cover associated with the climate model discussed above, environmental stability may decrease near a singularity. For example, Fig. 4 illustrates fluctuations for a simple energy balance model of global average temperature, which is forced by a heating term whose time dependence is white noise (*29*). These simplifications, which may seem extreme, are necessary in order to generate a time series long enough to illustrate the concept of instability near a bifurcation point. The model has ice-albedo feedback and is known to have a solution that plunges to an ice-covered earth if the solar constant decreases below a certain level (*19*). As the slope of the operating curve increases near a bifurcation, the fluctuations are larger for a given level of noise (natural fluctuations such as weather), and the autocorrelation time is longer. This feature may also occur in more complicated general circulation models (*30*). If this environmental destabilization has occurred in the past, it could have affected populations and further contributed to biotic overturn.

Duration of Abrupt Climate Transitions

On geological time scales, there are relative degrees of abruptness. Although an asteroid impact may reasonably be considered abrupt by any measure of the word, the events being discussed may be abrupt geologically but may still require thousands or tens of thousands of years, and perhaps even longer, to transpire. Crossing a critical point for even a few years by a natural fluctuation will not ensure complete transition to another equilibrium climate. Furthermore, thousands of years may be required for the buildup of ice volume associated with glaciation. Finally, we have no good theoretical basis for predicting the length of time the system will waver on a singularity before crossing over to a new state. Recent evidence of unstable behavior at the postulated time of West Antarctic Ice Sheet development suggests that the transition period could be as long as a million years (*31*).

Other factors may act to disperse the effect of an "abrupt" climate change over a longer time interval. As discussed above, environmental stability may decrease even before the transition is made to a glaciated state. Increased rates of deep-water formation may precede ice sheet growth. All of these factors should increase selection pressure and contribute to biotic turnover. The finite transition time required for such "abrupt" climate events may be important in explaining some of the "stepwise" features of extinctions near major transitional boundaries; that is, extinction events often consist of a sequence of abrupt steps and may occur over geologically brief but not instantaneous intervals (*32*).

Evidence for Abrupt Climate Change

There are some particularly good examples of abrupt climate change in records from the Quaternary—the terminations of Pleistocene glaciations (*33*), the "Younger Dryas" cool oscillation during the last deglaciation (*34*), evidence for rapid climate swings in the interstadial preceding the last glacial maximum (*35*), the abrupt initiation of glaciation during the early stages of a glacial cycle (*36*), and a relatively abrupt transition in the dominant period of glaciations during the mid-Pleistocene (*37*).

There is also evidence for significant steps in the evolution of climate for the last 100 million years (Ma) (Fig. 5). The long-term trend involves the evolution of climate from an ice-free earth in the mid-Cretaceous (100 Ma) to a bipolar glacial state with periodic glacial expansion into northern mid-latitudes (*38*). There have also been significant increases in aridity during the last 30 Ma (*39*). Each step in the isotopic curve presumably involves one stage in the evolution of this process—for example, the development of a cold deep-water circulation, separate development of the East and West Antarctic Ice Sheets, initiation of Arctic Ocean ice cover and glaciation on Greenland, and onset of significant mid-latitude Northern Hemisphere glaciation. The timing and interpretation of some of these transitions require more work.

High-resolution studies of the above climate shifts indicate that they can occur in as geologically short a time as 5,000 to 10,000 years (*33, 36, 40*), and in some cases in less than 1,000 years (*34, 35*). Very high resolution studies of the last glacial-interglacial transition in the Dye 3 Greenland ice core suggest that the atmospheric circulation may have shifted states in less than 100 years (*41*). Similarly, Antarctic sea ice cover changed from glacial to interglacial states in about 200 years (*42*) and the Little Ice Age may have ended in less than a decade (*43*). The sample resolution and time control on these studies are as good as or superior to any found in older geological deposits, and the records often appear abrupt even under high-resolution examination. The above results suggest that it might be difficult to distinguish these finite but geologically brief transitions from truly "instantaneous" events, such as an asteroid or comet impact.

There is some evidence for increased system variability near some of the climate steps (*31, 44*). Some of this evidence has subsequently been questioned (*45*), and the interpretation of system variability is often beset with problems associated with sample aliasing (*46*). It is our impression that the phenomenon of increased variability requires better documentation before its existence can be established.

Climate model experiments with a linear, seasonal energy balance climate model (*20*) suggest that the long-term trend over the last 100 Ma may be largely controlled by plate tectonic–induced changes in climate (Fig. 5, inset). In addition to variations in the seasonal cycle of temperature over key land masses, changes in atmospheric CO_2 and in ocean circulation have probably occurred (*47*). Although such forcing may explain the long-term trend, climate steps may involve threshold phenomena such as those outlined above.

As ice may have existed for only the most recent 40 Ma (*48*), and steps exist prior to that time (Fig. 5), more than one type of mechanism may be involved in terrestrially driven instabilities. Variations in the production of warm, saline bottom water (*49*) may explain some of the steps in Fig. 5. Experiments with thermohaline models indicate that the deep-water circulation may be susceptible to instabilities as a result of salinity variations in source regions of deep-water productions (*10, 11*). Variations in warm, saline bottom water production may be sensitive to the extent of shallow seas (*49*) or marginal basins (*50*) in the subtropics, the region of excess evaporation over precipitation. Shallow, epicontinental seas were much more extensive during the first 60 Ma of the record illustrated in Fig. 5 (*49*).

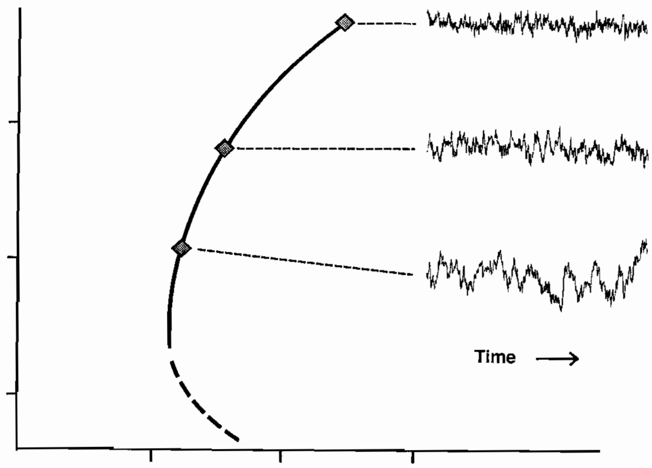


Fig. 4. Schematic depiction of the time series of temperature fluctuations about three different equilibrium climates near a bifurcation point. Operating curve is for an energy balance model of global average temperature. Different time series represent solutions to stochastic forcing of the model. Time and temperature scales are arbitrary, but the relative magnitude of different temperature amplitudes represents actual model output. For reference, the smallest temperature fluctuations may be considered representative of a system in equilibrium. Analysis of the instrumental record of surface temperature fluctuations over the last 120 years suggests that the natural variability of such a system is about ±0.5°C (*91*).

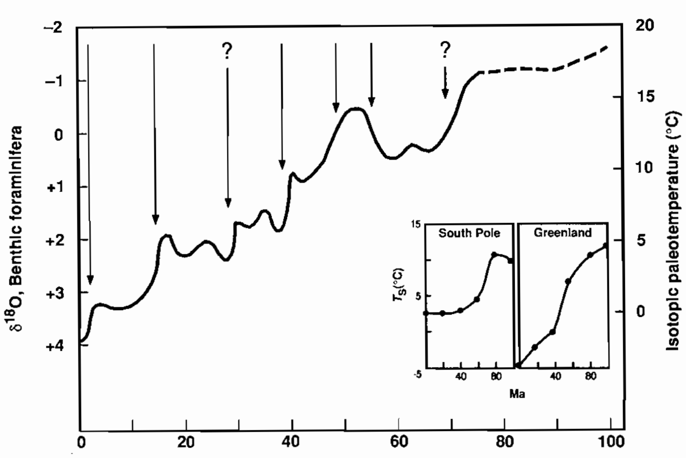


Fig. 5. Climate steps during the last 100 Ma in the oxygen isotope record, along with climate model simulations (inset) suggesting that the long-term trend in climate in key areas is strongly influenced by plate tectonic–induced changes (T_s = summer temperature). Oxygen isotope record from (*92*), modified by information from (*37, 48, 81*); climate simulations from (*20*).

Comparison of Major Phanerozoic Extinction Events with the Climate Record

Given the growing body of evidence for abrupt climate change, it is instructive to compare the major extinction events of the Phanerozoic (*51*) (Fig. 6) with the climate record. Although detailed information is lacking about high-resolution aspects of the evolution of climate over much of this time, some information is available that enables a climate-extinction comparison. In order for a climate change to be a candidate for an abrupt event, it must meet the requirement that the climate state prior to an extinction event is significantly different than the climate state for some extended period of time after the event; in other words, that the before and after states resemble different branches of the operating curve in Fig. 1.

If the above criterion is used, two climate-extinction events are well correlated—the Late Ordovician (440 Ma) and Late Devonian (365 Ma) extinctions coincide with glacial periods that follow long intervals of ice-free conditions (*52*). The Ordovician extinction has long been associated with the glaciation at that time (*53*); interpretations are more varied for the Devonian (*54, 55*). Although the Late Permian (250 Ma) extinction has often been related to changes in sea level (*56*), there has been a persistent current of suggestions linking the extinctions with glaciation (*55*) or more often with salinity changes associated with extensive evaporite formation (*57*). The latter association may implicate thermohaline instabilities as a contributing mechanism. There is some geochemical evidence for abrupt transitions in the Late Permian (*58*) and indications that biotic changes at the Permian-Triassic boundary may be rapid (*59*). There is little evidence for ice in the Mesozoic (*60*), but the Late Triassic extinctions occurred during a geologic period in which there was a peak in Phanerozoic evaporite formation (*61*). Instabilities related to changes in ocean salinity might also be involved in this extinction. A significant evolution event, the expansion of soft-bodied metazoans in the Late Precambrian (after 670 Ma), postdates the most widespread phase of Late Precambrian glaciation (*62*).

When compared to the long-term paleoclimate record, the Cretaceous-Tertiary (K-T) extinction stands out as somewhat different than the other extinctions. The background oxygen isotope record is relatively stable over a 10- to 15-Ma interval bracketing the event (Fig. 5), so there is no step-function change in the climate. There was a general fall in sea level between the Late Cretaceous and early Tertiary (*63*), but little geological evidence that it may have been associated with an ice-growth event (*60*). There is also little evidence for any ocean evaporite or anoxic event that might link the changes to variations in bottom-water production rates. Some extinction scenarios (*3*) have suggested that a rapid sea level change at the K-T boundary (*63*) may have affected seasonality. Although there have been significant changes in seasonality over the last 100 Ma (*20*), it is unlikely that such a mechanism would cause a sudden environmental shift. In the absence of ice sheets, changes in seasonality appear to be linearly related to changes in the land-sea distribution

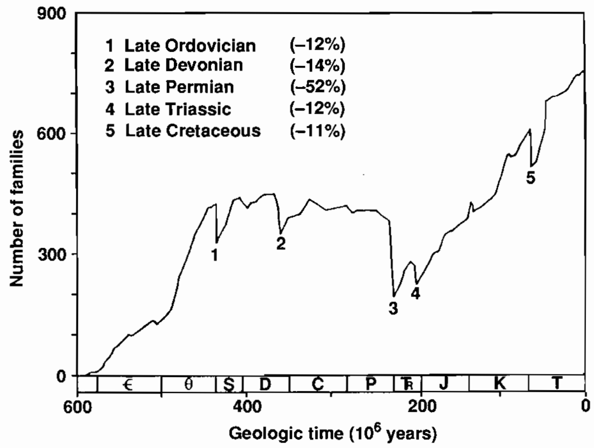


Fig. 6. Standing diversity through time for families of marine invertebrates. Numbered intervals refer to significant extinction events over the last 600 Ma [from (*51*)].

(*47*). Furthermore, the effects on pelagic biota would be almost negligible. We therefore find less justification for positing a terrestrially induced climate instability at the K-T boundary than we do for the other major extinction events of the Phanerozoic (*64*).

There are some significant disagreements between the climate and evolutionary records. The magnitude of the Late Permian extinctions seems much too large for the area of land affected by glaciation. Additionally, no major extinction event occurs during the widespread Late Carboniferous (330 Ma) glaciations. However, there were significant reductions in some faunal groups (*65*). The relatively low extinction rates during the Carboniferous glaciation may reflect the fact that the ecosystem had not fully recovered from the Late Devonian extinctions (*55*). It may also of course suggest that the climate-life connection is intermittent and sometimes quite weak.

Progress has been made in understanding the origin of some of the Paleozoic climate events. For example, plate tectonic–induced changes in the seasonal cycle may have triggered the Ordovician and Carboniferous glaciations (*66*). Onset of Ordovician glaciation may even have been possible in a CO_2-enriched world (*66*). The transition from a glaciated to an ice-free state in the Late Precambrian is not well understood from the climate modeling perspective, but it may reflect a C-C′ type transition (Fig. 1). The climate change coincided with the breakup of a postulated Precambrian supercontinent (*67*). By analogy with the Mesozoic breakup of Pangaea (*22*), such a development may have been associated with an increase in atmospheric CO_2 due to enhanced seafloor-spreading rates (*68, 69*).

Comparison of Climate Steps and Extinction Events for the Last 100 Million Years

The effect of abrupt climate change on organisms can be evaluated in more detail by comparing the oxygen isotope record of the last 100 Ma (Fig. 5) with extinction events in marine invertebrates (*70*) over the same interval (Fig. 7). Some information is also available for changes in terrestrial plant and vertebrate populations over this interval. However, the discontinuous nature of the terrestrial stratigraphic record places some limits on its use as a tight constraint on theory.

Several points are of interest. First, three of the extinction events coincide to some degree with the three major steps in the evolution of Cenozoic climate—the onset of mid-latitude Northern Hemisphere glaciation at about 2.4 to 3.0 Ma (*71*), expansion of ice on Antarctica between about 10 and 14 Ma (*72*), and major cooling between about 31 and 40 Ma (*40, 73*). A fourth extinction event at about 90 Ma coincides with a major environmental change not manifested in the oxygen isotope record—an ocean anoxic event (*74*) that correlates with the highest sea level of the last 200 Ma (*63*) and with an abrupt change in carbon isotopes in pelagic carbonates (*74*). Changes in organic carbon burial may have significantly affected atmospheric pCO_2 levels at this time (*75*). This last event is therefore also a candidate for an abrupt environmental change due to slowly changing boundary conditions. Some of the second-order trends in the oxygen isotope record also correlate with smaller extinction events (*76*).

Although there is good evidence that extinction events occur approximately at the same time as major changes in the environment, the evidence is more variable when we compare how abrupt and coincident the events were. The cooling between 2.4 and 3.0 Ma correlates with a regional reduction in mollusks (*77*) and an increase of grazing vertebrates in low latitudes (*78*). The first appearance of the genus *Homo* also occurred near this time (*79*). There may have been more than one major environmental change in the mid-Miocene—one dominated by cooling of bottom waters around 14 Ma (*48*) and a major ice growth event about 10 to 11 Ma (*48, 63*). The estimated age for the Miocene marine extinction is 11 Ma (*70*), very close in time to the very large sea level fall thought to indicate major expansion of Antarctic ice (*63*). There is also some evidence for an increase in the number of grazing herbivores in low latitudes at this time (*80*).

Some previous discussions on the climate-life connection in the mid-Cenozoic have focused primarily on comparison of events at the Eocene-Oligocene boundary (36 Ma) and concluded that the connection was not strong (*81*). However, the ^{18}O event at 36 Ma (Fig. 5) represents only one of at least three stages of climate change that resulted in an overall transition from the warm climates of the Early Tertiary to the cool climates of the Late Tertiary: Late Eocene cooling (36 to 40 Ma), abrupt bottom water cooling with some ice growth at about 36 Ma, and a major sea level fall and presumed ice growth event at about 31 Ma. Stanley (*55*) has recently reemphasized that the most significant turnover in Cenozoic biota also occurred during this same interval, a coincidence indicative of a strong climate-life connection. The most severe mid-Cenozoic ex-

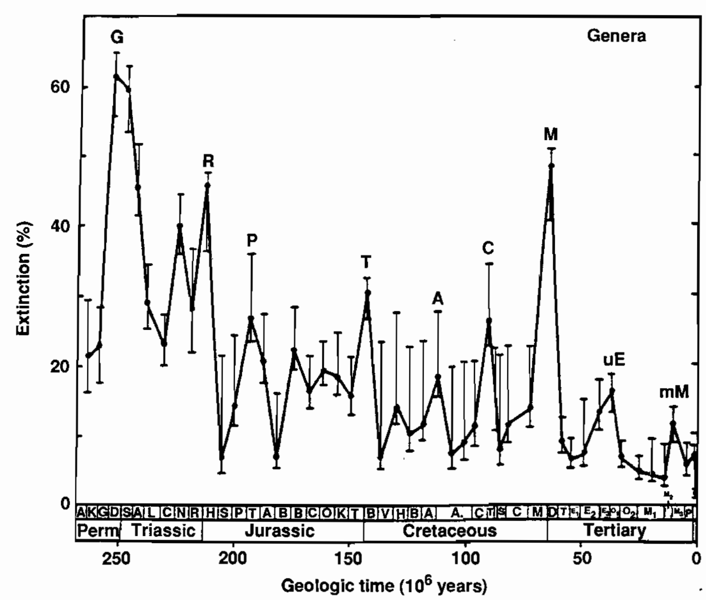


Fig. 7. Percentage of extinction of marine animal genera in stratigraphic intervals between the mid-Permian and the Recent [from (*70*)].

tinctions occur prior to the sharp change in the ^{18}O record at 36 Ma (*82*). However, changes in the deep-ocean circulation began as early as 40 Ma (*83*) and coincide approximately with the Late Eocene extinction peak and with less intense cooling events (*84*). There is also evidence that two of the earlier steps coincide with microtektite layers and iridium anomalies (*84*). The major sea level fall in the mid-Oligocene at about 31 Ma (*63, 85, 86*) also coincides with a turnover in planktonic foraminifera (*87*) and in plants and terrestrial vertebrates of North America (*88*). Lack of continuous stratigraphic control in the land record does not allow for a more precise comparison of times of transition with the paleoclimatic record, however.

Based on the above summary, we conclude that overall there is a reasonably good climate-life connection in the Late Eocene–Oligocene. However, the connection is not so strong that other sources of forcing can be precluded. The climate-life comparison for the mid-Cenozoic also reveals an important relation. If climate is significantly influencing life, the biotic response is not always proportional to the forcing regardless of whether the forcing is gradual or abrupt. Many extinctions occur during the early stages of climate cooling, for example, the 6°C cooling from about 50 to 40 Ma (Fig. 5). The more severe climate changes of the Plio-Pleistocene correlate with much smaller extinction events. Stanley (*55*) has suggested that the cooling events of the prior 20 to 30 Ma had essentially removed most of the vulnerable species from the ecosystem, so that the remaining forms were more robust and able to tolerate the extreme environmental swings of the last 2 Ma.

Concluding Remarks

To summarize, abrupt transitions occur in several types of climate models and in the geologic record. Abrupt environmental changes can involve formation of polar ice caps, but they may also occur in ice-free climates because of thermohaline instabilities in the ocean circulation. There is a frequent correspondence between times of environmental change and biotic turnover, and some support for the coincidence of abrupt transitions. However, more stratigraphic information is needed to evaluate the phase relations more closely.

If our analysis is valid, it suggests that different components of the climate system may be responsible for different environmental transitions. There are methods to test the multiple mechanism hypothesis. For example, different climate events may have different regional manifestations, which may be reflected by different regional patterns of extinctions. Thermohaline instabilities may affect different types of organisms (for example, salinity-sensitive groups). Extinction trends in conodonts already support the conjecture of multiple mechanisms (*89*). Other criteria will probably have to be established in order to make this explanation more robust.

There is also some evidence that if climate change is significantly contributing to biotic turnover, then ecosystems may be more sensitive to forcing during the early stages of evolution from an ice-free to a glaciated state (for example, mid-Cenozoic and mid-Paleozoic); that is, during the initial stages of environmental change. Later, more extensive glaciations had a lesser effect on biota. This analysis suggests that a more complete understanding of the climate-life connection requires modeling potential instabilities in the ecosystem that can be triggered by slowly varying climate change.

We do not claim that abrupt climate change due to terrestrially driven instabilities represents the sole explanation for past biotic turnovers, only that it may be applicable to some events, and that it represents a viable alternate to catastrophic changes due only to catastrophic forcing. However, our analysis is not intended to suggest that we discount extraterrestrial impacts as a possible source for some environmental changes. In fact, the one interval where evidence for a terrestrially induced instability is weakest (the K-T boundary) is the same interval where evidence for an extraterrestrial impact is strongest. Along with others (*90*), we suspect there may be multiple explanations for extinction events, including some that may be related to climate in only a minor way. Even if some specifics of our analysis are modified by future studies, we believe the general approach has merits, because it focuses on the need for a more explicit incorporation of results from climate theory into the discussion of factors influencing biotic events in earth history.

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