
Chapter 12

**THE LATE PLEISTOCENE
EVENT AS A PARADIGM FOR
WIDESPREAD MAMMAL
EXTINCTION**

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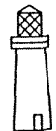
Mass extinctions:
Processes and evidence

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INTRODUCTION

Extinction is a fact of life. For living species, the question generally is not if extinction will occur, rather, the question is when. For many extinct species, we know when extinction took place, at least in general terms, and we are left with a different paradox: why did (and does) extinction occur? One chapter in Earth history, the Quaternary, casts a uniquely focused light on this question. Including the Pleistocene (around 1.8 million to 10 000 years BP) and Recent, or Holocene (10 000 years BP to the present), epochs, this snapshot of time reveals a major extinction event that took place at the terminal Pleistocene, within the time radiocarbon dating is effective (since 50 000 years BP). Moreover, the extinction affected primarily mammal species whose ecological requirements can be inferred with a clarity unattainable in earlier geologic epochs. Hence, both the speed of the extinction and likely reasons—climate change and the entry of human predators on the scene—are known in some detail (Martin and Klein, 1984; Barnosky, 1986; Owen-Smith, 1987).

Because of the well-dated time-scale and the possible role of humans, Pleistocene extinctions are commonly regarded as somehow atypical compared to previous extinction events. Here I take a different point of view. What can the finer focus of the terminal Pleistocene event, particularly in North America, tell us about the rules that govern extinction? I will attempt to answer this question by first discussing why the Pleistocene event should not be considered unique, then by reviewing what the enhanced detail of the Pleistocene demonstrates about causes of widespread mammal extinction. Finally, I will use the Pleistocene example to



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derive some 'rules of widespread extinction' that are testable with data from the Tertiary mammal record.

MAGNITUDE OF PLEISTOCENE EXTINCTION

The terminal Pleistocene extinction affected mainly large mammals in North America where 43 genera died. Approximately 91% of these were large-bodied (weighing over 5 kg including 73% of the megafauna (weighing over 44 kg). Also affected was South America (at least 46 extinct genera, including approximately 80% of the megafauna) and Australia (21 extinct genera, including 86% of the megafauna) (Webb, 1984; Martin, 1984a; Murray, 1984). Europe, Africa, and probably Asia endured only a few true extinctions (but many extirpations). Besides mammals, at least 19 genera of birds also vanished in North America (Steadman and Martin, 1984). In addition, a myriad of taxa survived. Nevertheless, many of these survivors, both animals and plants, responded to the extinction-causing event by markedly changing their geographic range (Guilday, 1984) and reassembling into new communities (Graham and Lundelius, 1984; Guthrie, 1984a; Owen-Smith, 1987; Webb *et al.*, 1987). In these ways terminal Pleistocene extinction affected much of the world's terrestrial biota. Marine extinctions, however, were insignificant (Stanley, 1984).

Thus, it seems clear that in general magnitude, the terminal Pleistocene extinction was not as severe as, say, the end Cretaceous extinction, when entire classes of vertebrates and many marine invertebrates breathed their last (Martin, 1984b; Hallam, 1987). Also, it follows that the terminal Pleistocene event was different in kind or magnitude from the events that caused numerous extinction episodes in the marine realm.

MAMMAL EXTINCTION

A cause for confusion, however, is how the Pleistocene event relates to other episodes of mammal extinction. Faunal turnover, that is, the sum of extinction plus origination (by immigration and evolution) has resulted in at least 18 temporally superposed, distinct mammal faunas in North America since the beginning of the Palaeocene. These faunas form the basis for dividing the Cenozoic into the North American Land Mammal Ages (NALMAs), which themselves can be further subdivided on the basis of faunal turnover (Woodburne, 1987).

Within these faunal turnovers are periods of extinction when at least 30 genera of North American mammals disappeared from earth within a time-span of at most 3 million years. (The actual time spanned by extinction might be shorter, but in most cases cannot be precisely resolved.) Such extinction episodes I arbitrarily call 'widespread mammal extinction'. They affect entire continents, if not the entire world. Besides the Pleistocene

extinction, widespread mammal extinction took place at least during the late Uintan (late Eocene, 42–44 million years BP), possibly Barstovian (middle Miocene, 11.5–16.5 million years BP), Clarendonian (late-middle Miocene, 9–11 million years BP), late Hemphillian (late Miocene, 4.5–6 million years BP), and late Blancan (late Pliocene, 1.8–3 million years BP) NALMAs (Webb, 1984; Stucky, 1989). Does the Pleistocene extinction differ from these enough to require a special explanation? Or does it express general principles that explain how and why widespread mammalian extinction takes place?

Rate of faunal turnover

One feature that makes the Pleistocene episode look special at face value is the extinction rate. Extinction rates, calculated as genera becoming extinct per million years, show that the Pleistocene rate of extinction approached 200, whereas Tertiary rates never exceeded 50 (Gingerich, 1984; 1987). But this is a misleading way to calculate rates. First, the shorter the time interval over which the rate is averaged, the faster the rate appears (Gingerich, 1987, p. 1059). Pleistocene rates are generally averaged over 1 million years or less, whereas other rates are averaged over more than 1 million years. Second, generic diversity increases through geologic time, possibly exponentially (Gingerich, 1987, p. 1055). Whether this represents a real increase in the diversity of life or simply reflects better representation of geologically young strata is unclear, but in either case the effect on calculating turnover rates is the same. Pleistocene rates are artificially inflated simply because there are more Pleistocene genera known. To avoid this sample bias, Gingerich (1984; 1987) calculated extinction rates as genera extinct per total genera available for extinction in a given time interval (Figure 12.1(a); redrawn from Gingerich, 1984, Figure 10.2(b)). By this method, Pleistocene extinctions are not any more pronounced than those that occurred at the following times: early Eocene, middle Eocene, late Eocene, early Oligocene, middle Oligocene, late Oligocene, early Miocene, 'Pliocene', and late Pliocene (*sensu* Gingerich, 1984; 1987; whose data are from Romer, 1966; his early 'Pliocene' is late Miocene in modern usage). In fact Pleistocene extinctions are about average for those that occur throughout the Cenozoic.

Extinction rates cannot be considered independent of origination rates. When rates are calculated as genera extinct (or originating) per total genera for given time intervals, Gingerich's analyses suggest that origination rates peaked at the same time as extinction rates peaked for all Tertiary extinction episodes (Figure 12.1(a)). In the middle Palaeocene, origination rate far exceeded extinction rate, but there was a progressive decline in the difference between the two until the middle Oligocene, when the two rates nearly met. Thereafter in the Tertiary, origination peaks continued to correspond with extinction peaks, but were only slightly

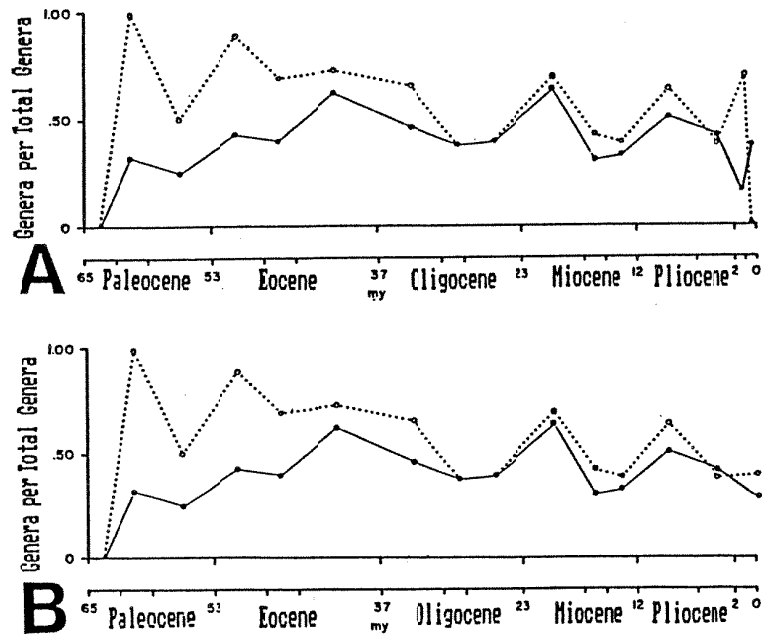


Figure 12.1. Origination (dotted line) and extinction (solid line) rates for genera of rodents, artiodactyls and fissiped carnivores. (a) Pleistocene considered as two 1-million-year intervals. (b) Pleistocene considered as one 2-million-year interval to make it more comparable to pre-Pleistocene intervals. Data are from Gingerich (1984, p. 214), who compiled it from Romer (1966); hence the time-scale is out of date. For example, Romer's 'early Pliocene' is now considered late Miocene. However, as Gingerich (1984; 1987) noted, this makes little difference for recognizing general trends.

higher. At the beginning of the Pleistocene, however, extinction rates dropped to an all-time low for the Cenozoic, at the same time as origination rates increased dramatically.

The origination rate in the Pleistocene was fed largely by immigration. Immigration rates for the Blancan, Irvingtonian and Rancholabrean NALMAs exceeded the average rate for any earlier Neogene immigration episode (Webb, 1984; Webb and Barnosky, 1939). Rapid evolution also took place in some groups, for example, the arvicoline rodents (Repenning, 1987).

Viewed as genera extinct or originating per total genera, the Pleistocene faunal turnover was special not for its extinction rate, which did not even exceed average values, but for its high origination rates, which increased faunal diversity to exceptionally high levels (Gingerich, 1984; 1987). So-

called disharmonious communities, which mix extant taxa (both animals and plants) that today are allopatric, bolster the view of at least locally increased biotic diversity during the Pleistocene (Graham and Lundelius, 1984; Graham and Mead, 1987; Webb *et al.*, 1987). If the exponential increase in number of genera noted by Gingerich (1987) is not a sampling artefact, global diversity may have increased as well. The landscape may have been able to support increased diversity because of the 'fragmentation and diversification of habitats accompanying successive Pleistocene glaciations', which increased spatial heterogeneity (Gingerich, 1984, p. 16).

Was the lag between Pleistocene originations and extinctions special at all? Figure 12.1(a) averages all of the Tertiary extinction and origination peaks over time-intervals of 2 million years in the best case (middle Oligocene) and 8 million years in the worst case (middle Eocene). Most of the Tertiary time intervals range from 3 to 6 million years in duration (data from Gingerich, 1984, Table 10.3). In contrast, the Pleistocene peaks and valleys in Figure 12.1(a) are based on 1-million-year time intervals. When the two Pleistocene intervals are lumped together to make them more comparable to the Tertiary intervals, the lag between the immigration peak and extinction peak disappears (Fig. 12.1(b)). The lag-time between Pleistocene origination and extinction events in Figure 12.1(a) simply reflects the better time resolution for Pleistocene events.

This recognition allows us to look at the Pleistocene origination-extinction lag in a different way. Perhaps the lag is not unique to the Pleistocene, but a trade mark of all widespread extinctions made evident through the enhanced resolving power of the Pleistocene microscope. Stucky (1989) presented an analysis that provides support for this viewpoint. He plotted raw numbers of North American genera originating and disappearing through the Cenozoic at intervals ranging from less than 1 million years in best cases to about 5 million years in worst cases, with most intervals being between 0.75 million and 2 million years. Thereby he recognized four pre-Pleistocene extinction peaks when generic extinctions per interval exceeded 30: late Uintan (late Eocene), Barstovian (middle Miocene), late Hemphillian (late Miocene), and late Blancan (late Pliocene). Peaks of origination preceded peaks of extinction by at least 1 million years for the three Neogene extinctions, but the two peaks appear contemporaneous for the late Eocene event. The Eocene peaks merit more detailed examination because they are based on a time interval of 2 million years; even the Pleistocene peaks appear contemporaneous at this interval.

Body size

The late Pleistocene extinction has been considered notable for the decimation mainly of the large-mammal fauna (Martin, 1984a; 1984b). By Webb's (1984) reckoning, 43 genera disappeared in North America. Thirty-nine of these, or 91%, were large mammals characterized by body-

Table 12.1. Late Neogene extinction episodes. Data are from Webb (1984).

Episode	Time (millions of years BP)	Total genera extinct	Percentage of large-body genera (> 5 kg)
Terminal Pleistocene	0.01 – 0.4	43	91
Late Irvingtonian	0.4 – 1.0	9	56
Early Irvingtonian	1.0 – 1.8	10	50
Late Blancan	1.8 – 3.0	35	57
Early Blancan	3.0 – 4.5	9	22
Late Hemphillian	4.5 – 6.0	62	56
Early Hemphillian	6.0 – 9.0	27	78
Clarendonian	9.0–11.0	39	62

weight exceeding 5 kg. Thirty-three, or 77%, had body weights exceeding 44 kg (Martin, 1984a). Is such a bias towards large animals common in terrestrial extinctions? Webb (1984, p. 192) provided data to test this question for eight mammalian extinction episodes (including the terminal Pleistocene one) in the late Neogene (Table 12.1). Chi-squared comparisons verify that only the late Irvingtonian and early Hemphillian extinctions did not statistically differ from the terminal Pleistocene one in showing a less extreme bias towards taxa with large bodies. However, a plot of number of extinct genera versus percentage of extinct genera with large bodies for each extinction episode reveals an interesting relationship (Fig. 12.2(a)). The more genera that became extinct, the higher the proportion of large-bodied forms that contributed to the extinction count. The terminal Pleistocene event agrees well with this generalization; removal of the Pleistocene event from the plot actually decreases the correlation coefficient (Figure 12.2(b)).

The positive correlation between body size and severity of the cause of extinction (measured by the number of genera that died) probably results from an observation articulated by Guilday (1984, p. 256):

Large mammals are inherently more vulnerable to environmental changes simply because they are large and require a greater expanse of primary habitat to sustain themselves because of greater individual demands for food or space to play out their reproductive and defensive strategies, cover, flight, herding, etc. Greater demands are placed upon the habitat by an elephant than by a small rodent . . .

In addition, large mammals are generally characterized by small populations and small numbers of species within a genus, whereas most small mammals are characterized by large populations and several species per genus. It is statistically easier to destroy the few individuals that compose an elephant population than it is to destroy the many that constitute a

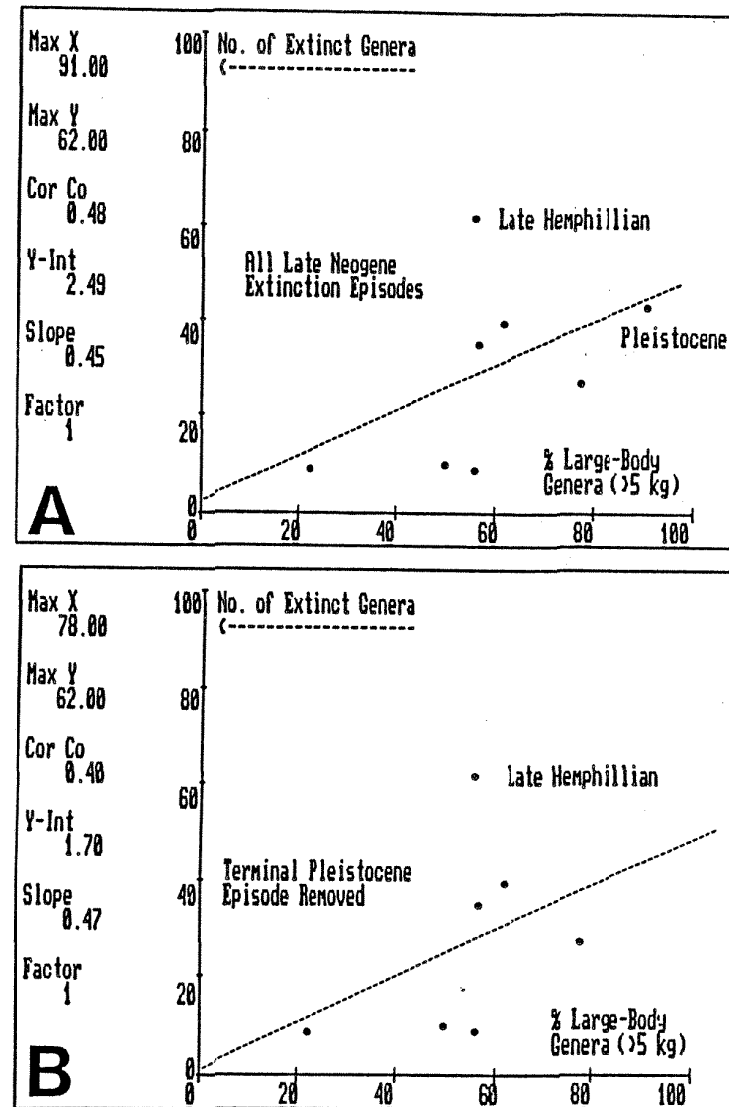


Figure 12.2. Simple linear regression showing the relationship between body size and total number of genera affected by extinction episodes. Data are from Webb (1984) and are presented in Table 12.1. (a) Plot for all late Neogene extinction episodes. (b) Plot for all late Neogene extinction episodes excluding the terminal Pleistocene event. Note that excluding the Pleistocene data has little effect on the correlation coefficient or slope.

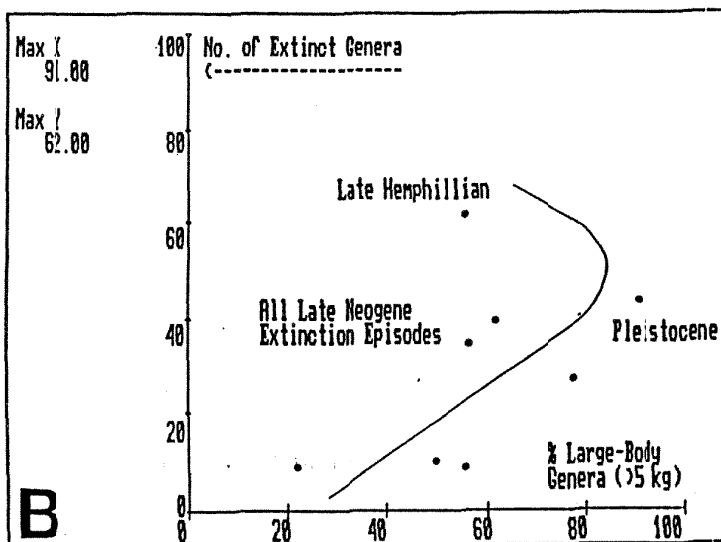
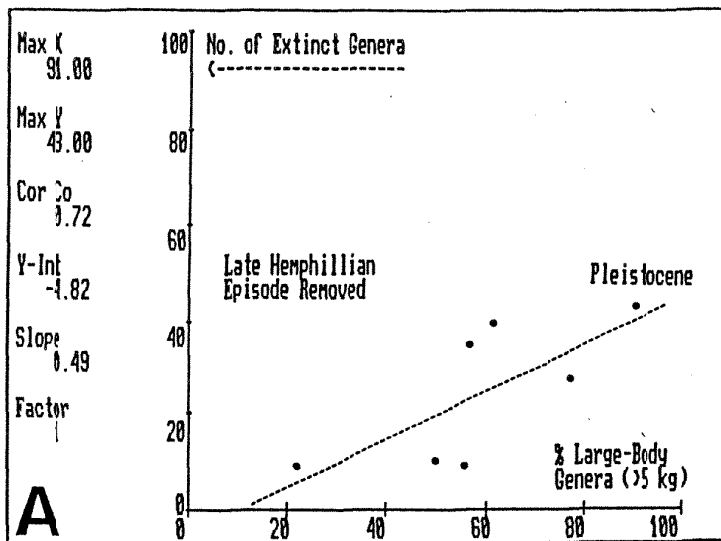


Figure 12.3. (a) as Figure 12.2(a), except the late Hemphillian data point is excluded from the analysis; note that this increases the correlation coefficient considerably, but has little effect on the slope. (b) Hypothesized relationship between body size and total number of genera affected by extinction episodes. The relationship may be linear up to a critical value of about 45% large-body genera, at which point the fauna will be so depleted of large-bodied genera that the proportion of small-bodied genera will begin to rise. Data are from Webb (1984) and are presented in Table 12.1.

mouse population. Similarly, it is easier to wipe out a genus made up of few species than one that includes many species.

If any Neogene extinction needs special explanation in terms of body size, it is the late Hemphillian one. Removal of the late Hemphillian extinction from Figure 12.2(a) increases the correlation coefficient, as illustrated in Figure 12.3(a), which suggests that the late Hemphillian event resulted in 'too many' small mammals becoming extinct in comparison to the other late Neogene events. This probably reflects the fact that large-mammal genera are much less numerous than small-mammal genera, so theoretically there should come a point at which extinction affects so many taxa that most large mammals will be gone from the pool of genera on which extinction can act. When the number of extinct genera reaches this critical value, the proportion of small-bodied forms that become extinct necessarily begins to rise. Thus, the late Hemphillian event may not be simply an 'outlier' on a linear regression; instead, it may give a clue that the critical value at which the relationship becomes non-linear is near 45% extinct genera (Fig. 12.3(b)).

Timing of extinction

That most Pleistocene extinctions, particularly of large mammals, were concentrated towards the end of the epoch is shown by calculating extinction rates for time intervals within the Pleistocene (Gingerich, 1984; Martin, 1984b). This terminal Pleistocene extinction is the best-dated extinction in the geologic record because it falls within the effective range of radiocarbon dating, which resolves time to plus-or-minus hundreds of years rather than the plus-or-minus thousands, hundreds of thousands or more years typical of other dating techniques. The radiocarbon record leaves little doubt that the terminal Pleistocene extinction took at longest 10,000 years. Mead and Meltzer (1984, p. 447) documented the youngest reliable radiocarbon dates for 23 extinct large-mammal taxa. All of the reliable dates fall between 9,000 and 18,000 years BP. Expressed more graphically, 18,000 years ago North America was filled with strange beasts; 9,000 years ago they were gone. The extinction was instantaneous on a geological time-scale (but possibly very slow in ecological time). Does such a geologically rapid pulse of dying typify most widespread mammalian extinctions?

As Webb (1984, p. 190) has noted, our arguments for answering 'yes' or 'no' are built on equally shaky ground. With increasing age of the sedimentary record, the ability to differentiate short intervals of time decreases, both because the sedimentary record becomes less complete and because high-resolution radiometric dating techniques are lacking. Either we assume the extinctions of each taxon were distributed through the whole stratigraphic interval under consideration (for example, through a whole land-mammal age), or we assume that all the extinctions were concentrated in a certain shorter time within the interval, commonly at its

stratigraphic top. The only assumption that has been supported objectively—by the Pleistocene record—is the latter one. Therefore, the most reasonable working hypothesis is 'Most widespread extinctions were rapid, like the terminal Pleistocene event', rather than 'The Pleistocene extinction was unique in being rapid'.

Cause of extinction

A purported cause must fulfil three criteria before we can reasonably infer that it triggered an extinction (Grayson, 1984, p. 816). First, the suspected cause and the extinction must demonstrably coincide in time. Second, the magnitude of the cause should match the magnitude of the extinction. And third, a mechanism must be provided to show how the purported cause would result in the extinction.

For the terminal Pleistocene extinction, all three of these criteria have been more fully attained than for any other extinction event (Martin and Klein, 1984). In North America the timing of extinction coincided with two major perturbations to existing biotic systems: climate change and the arrival of humans. Convincing mechanisms have been advanced to argue that either event by itself could have decimated the Pleistocene fauna (Mossiman and Martin, 1975; Martin, 1984a; 1984b; Graham and Lundelius, 1984; Guthrie, 1984a; Barnosky, 1986; Owen-Smith, 1987). Indeed, current debates focus not on if Pleistocene extinctions resulted from these causes, but on which of the two was most important.

Climate change

On both local (King and Saunders, 1984; Barnosky, 1986) and regional scales, climate change can be shown to correlate with terminal Pleistocene extinctions in numerous parts of the world. Perhaps nowhere is the regional relationship better documented than in the mid-Appalachian Mountain area (Guilday, 1984) and northcentral Great Plains of the United States (Wendlund *et al.*, 1987).

In the mid-Appalachian region, which includes much of Pennsylvania, West Virginia, western Virginia, western Maryland, and parts of Ohio, Kentucky, and Tennessee between latitudes 36° and 45°N, a regional change in climate is indicated by palynological data (Gaudreau and Webb, 1985; Watts, 1979, 1983; Delcourt and Delcourt, 1981; 1985). From about 18 000 years BP to 10 500 years BP, the northernmost vegetation of this area resembled a periglacial tundra, and the remainder a parkland composed of *Picea*, *Pinus banksiana*, *Abies*, *Beula* and an understorey of woody shrubs, grasses, sedges and herbs. Although the vegetational composition was without modern analogues, in general it indicates boreal conditions. By 10 000 years BP regional vegetation began to shift from open coniferous forest to the present closed-canopy deciduous forest, indicating postglacial warming. It was during this same time that the fauna changed drastically:

Eighteen large and one small species of mammal [became] biologically extinct . . . three large and ten small species [were extirpated]. Of those mammal species that still occur in the area, four are rare and local boreal relicts; nine others have become less common or have undergone some measure of ecological readjustment expressed in range reductions. Nine mammals have undergone a Holocene size reduction, while four have increased in size within the area during the last 11,000 years, paralleling, for the most part, modern latitudinal size clines (Guilday, 1984, p. 254).

Similar kinds of faunal changes also took place in the northcentral Great Plains. In Iowa between around 18 000 and 10 500 years BP the fauna was composed of about 70% boreal species and 20% steppe or deciduous species. Near 10 500 years BP these percentages switched to less than 30% boreal species and more than 50% steppe or deciduous species, and remained basically that way until the present (Wendlund *et al.*, 1987, p. 461). In Illinois and Missouri, the change was less drastic, but still evident, from about 15% boreal species between 16 000 and 13 000 years BP to less than 5% boreal species by 11 000 years BP. Extinct taxa are commonly found in the faunas of boreal aspect, but not in the more temperate ones.

Evidence that these biotic responses were linked to climate change is provided by comparing them to climate model simulations. Webb *et al.* (1987) showed how fossil-pollen percentages relate to climate variables by using response surfaces, and noted a general agreement between palaeoclimate inferences derived from fossil-pollen data and climate model simulations. For fossil vertebrates in the northcentral Great Plains, the terminal Pleistocene event corresponded both in time and kind with predictions arising from climate-model experiments (Graham and Mead, 1987; Wright, 1987; Kutzbach and Wright, 1985). Model results suggest that between 18 000 and 12 000 years BP, the westerly jet stream split around the Laurentide ice-sheet, deflecting storm tracks to the south of their present position (Kutzbach, 1987). A glacial anticyclone centred over the ice-sheet and caused surface easterlies to blow south of the ice. As air descended down the ice it was adiabatically warmed. In the northcentral United States, adiabatic warming and the constraints imposed by the Milankovitch cycles would result in less extreme differences between summer and winter during late-glacial time as compared to the present, even though mean annual temperature would have been cooler. In contrast, by about 9000 years BP, further retreat of the ice-sheet and changes in isolation associated with the Milankovitch cycles increased seasonality, so that summers were warmer and winters were cooler than today.

The biological consequences that one might expect of such a change in seasonality parallel closely what is observed in the fossil record. With more seasonal climates, communities should reassemble as animals limited by winter temperatures withdrew to the south, and those limited by hot summer temperatures withdrew to the north. This pattern is evident in the destruction of the late Pleistocene disharmonious mammal assemblages, which were characterized by sympatry of taxa that are allopatric today

(Graham and Lundelius, 1984; Graham and Mead, 1987). Changes in vegetational patterns—from no-analogue assemblages to modern compositions (Webb *et al.*, 1987)—accompanied destruction of the disharmonious faunas. In general, the large herbivores that survived were ruminants, whose digestive systems are adapted to feeding in habitats with low vegetational diversity, and to digesting toxins in their multiple stomachs: bison, deer, moose, sheep and the like. They were able to follow their preferred food plants, even though the plant communities were restructured. In contrast, herbivores whose monogastric digestive systems required them to eat a wide variety of vegetation and did not tolerate toxins became extinct or were extirpated over wide regions: mammoths, mastodons, horses, camels, sloths and peccaries (Guthrie, 1984a). Such taxa required vegetational mosaics, where many different kinds of food plants can be found within the distance they normally forage. Extinction was also the fate of herbivores whose physiology was tightly linked with the 'old' seasonality pattern, for example cervids with extremely large antlers such as *Cervalces* (Guthrie, 1984b). The disappearance of large herbivores led to the extinction of large carnivores and scavengers dependent on them. Disappearance of certain taxa, particularly proboscideans, may have disrupted intricate grazing successions, further altering community compositions and thus contributing to extirpation and extinction (Graham and Lundelius, 1984; Owen-Smith, 1987).

In short, communities that had evolved to suit a particular set of climatic conditions fell apart when the conditions changed. This model of extinction has been dubbed 'coevolutionary disequilibrium' by Graham and Lundelius (1984), who discuss it in detail.

Overkill

In North America, an important element in the restructuring of terminal Pleistocene communities was the addition of a new predator: *Homo sapiens*. Humans with an efficient hunting technology arrived in North America around 12 000 years ago, as indicated by the earliest dates on sites with Clovis-style artefacts (Haynes, 1984). It is probably no coincidence that this date corresponds so closely with the glacial–interglacial transition, as dispersal through Beringia would have required an ice-free corridor between the Cordilleran and Laurentide ice-sheets. Hunting by humans is thought to have contributed to Pleistocene extinction in North America because human arrival correlates closely in time with extinction (Martin, 1984a); predominantly large herbivores—animals most likely to be hunted—succumbed (Martin, 1984a; 1984b); Shasta ground sloths (*Notrotheriops shastensis*) became extinct, even though their supposed habitat remained (Martin, 1984b); artefacts have been found associated with five of the 27 genera of large vertebrates that disappeared (mammoth, mastodons, horses, camels and giant tortoises) (Webb and Barnosky, 1989); and world-wide extinction of the megafauna may be diachronous, with extinction time roughly correlating with the first appearance of humans (Martin,

1984a). The case for diachronous extinction rests mainly on the observations that in Africa and Europe, where megafauna had coevolved with humans, late Pleistocene extinctions were minimal, and that human predation was responsible for the decimation of the New Zealand/Madagascar fauna between around 0.5 and 1 Ka. Despite the reasoning of Martin (1984a, pp. 375, 395), it remains to be demonstrated by radiocarbon dates that extinction in South America and Australia coincided with the arrival of humans (Grayson, 1984, p. 808). Nevertheless, the North American record, coupled with Diamond's (1984) observations of the naivety of large-game species unfamiliar with human predators, supports the view that human activity played a role in terminal Pleistocene extinctions.

The components of extinction

It seems clear that both climate change and humans contributed to late Pleistocene extinctions in North America. Whether 'one set up the punch which the other delivered . . . or vice versa' may be unknowable (Guilday, 1984, p. 257), but the data do suggest that both physical and biological stresses must act together to cause extinction. The physical stress in the case of the late Pleistocene was a rapid change in climate. The biological stress was a spatial reorganization of the biota as species responded individually to changing climate and changing biogeographic ranges of competitors and predators. The addition of human predators was but one facet of this community reorganization, and in this respect can be accommodated within Graham and Lundelius's (1984) model of coevolutionary disequilibrium.

How strong must the physical and biological punches be, and how close together must they hit, to cause extinction? Is one more important than the other? A clue is provided by comparing the timing of immigration events, glacial–interglacial transitions and extinction episodes of the last million years. Three immigration events, one each at approximately 850 000, 400 000 and 150 000 years BP, are recognizable mainly by the record of arvicoline rodents (Repenning, 1987). The first of these three events, at 850 000 years BP, falls near the boundary of oxygen-isotope warm stage 23 and cold stage 22 (Repenning, 1984). The second event, at 400 000 years BP, correlates roughly with a glacial–interglacial transition of oxygen-isotope stage 12 to stage 11 (Repenning, 1984), but may be as much as 40 000 years later (Bradley, 1985, p. 187) or earlier (Repenning, 1984, p. 106) than the actual transition. The third event, at 150 000 years BP, took place in the middle of a glaciation signalled by oxygen-isotope stage 6. None of these events coincides with a rise in extinction rate (Gingerich, 1984, p. 220). The two earlier events thus illustrate that immigration plus a major climate change does not always equal extinction, so it is no surprise that the third event shows that immigration by itself does not cause widespread extinction. Moreover, the absence of widespread extinction at any of the pre-Wisconsinan glacial–interglacial transitions suggests that pronounced climate change alone is an insufficient stimulus.

The extinction equation thus seems to require not only change in the physical environment *plus* appearance of new players on the biological scene, but that at least one of these components be of a certain critical magnitude. Recognizing the critical magnitude depends on identifying how the terminal Pleistocene changes differed from other glacial–interglacial changeovers.

The glacial–interglacial cycles are driven by orbitally induced Milankovitch cycles: the eccentricity of the Earth's orbit around the Sun (periodicity of 100 000 years), the tilt of the earth's axis relative to the ecliptic (periodicity of 41 000 years), and the season of perihelion, which is the Earth's closest approach to the Sun (periodicity of 23 000 years). The three different periodicities are superimposed upon one another such that there is constant change through time in the relative relationships of Earth's distance from the Sun, its tilt, and timing of perihelion. Their relationship affects the latitudinal and seasonal distribution of solar radiation, which in turn modulates atmospheric and oceanic circulation, ice-sheet growth and levels of CO₂. Bartlein and Prentice (1989) speculated that species evolve to withstand the environmental perturbations caused by frequently recurring combinations of the three cycles, for example, combinations that in the late Pleistocene forced alternation between glacial and interglacial conditions about every 75 000–100 000 years (Hays *et al.*, 1976). Hence, climate changes of this magnitude should not result in extinction, which is in agreement with the pre-Wisconsinan Pleistocene record. However, infrequent combinations of the cycles, perhaps superimposed on climate change on different time-scales such as that triggered by epeirogeny (Raymo *et al.*, 1988), might result in widespread extinction. The transition from the end of the Pleistocene into the present interglacial exemplifies an infrequent combination of Milankovitch forcings that caused particularly extreme climate change. Rather than being typical of glacial–interglacial transitions, the climatic differences between the Wisconsinan and Holocene represent nearly the maximum change that would be expected in insolation and ice-volume (Bartlein and Prentice, 1989). The resulting hypothesis is that, in order to contribute to a widespread extinction, the magnitude of climatic change does not have to increase very much over what is normally produced by Milankovitch-based orbital variations on about the 100 000-year time-scale, but that it does have to increase a little. If infrequently occurring combinations of the three Milankovitch cycles are an important trigger of extinction, such combinations should be found to have a periodicity longer than the average life-span of mammalian species, which is a little over 1 million years (Stanley, 1978, p.30).

In North America, we can also implicate arrival of a single species—humans—in contributing to extinction. Numerous Pleistocene immigration events prior to the Wisconsinan are unassociated with extinction. The biological input to extinction therefore depends as much (or more) on the kind of taxa inserted into the fauna as on the sheer numbers of new taxa. Immigrants such as efficient predators, large herbivores and pathogens,

which interact with a large proportion of the native fauna, are more likely to contribute to extinction than are those that simply compete with single or small groups of species, for example, most small herbivores. However, with increasing numbers of immigrants, the chance that one of the immigrants will be a significant taxon increases.

A PARADIGM FOR WIDESPREAD MAMMAL EXTINCTION

If the Pleistocene extinction was typical of widespread mammal extinctions, its enhanced detail and time-resolution may spotlight some rules that glimmer so faintly as to be overlooked in the more distant geologic past. These rules, derived from the Pleistocene, offer a general paradigm for how the process of widespread mammal extinction might work, but a paradigm is useful only in so far as it can be tested. Tests that arise from each of the rules are therefore articulated as well.

Rule 1: *There is a time-lag between a period of high origination rates (immigration plus evolution) and high extinction rates.* The origination event must precede the extinction event in order to inflate faunal diversity nearly to oversaturation, and stimulate production of complexly coevolved communities.

Test: When calculated over refined time-intervals, pre-Pleistocene peaks in origination rates should precede peaks in extinction rates. Generally, intervals of around 1 million years should be fine enough, because that interval makes the Pleistocene lag evident.

Rule 2. If Rule 1 is fulfilled, *widespread extinction will result when climate changes by a critical amount and one or more critical taxa arrive in the fauna.* By itself, neither climate change nor the new taxa will act fast enough to cull the fauna on a continental or world-wide scale. If only climate change or arrival of new taxa takes place, extinctions may occur, but they should be fewer in number than what characterizes widespread extinction (at least 30 genera on one continent). In the case of only climate change, there should be enough time and spatial opportunity for most faunal elements to migrate with suitable habitats. In the face of only new taxa, the biotic system should accommodate the intruders either by niche partitioning or extinction of only direct competitors.

Test: Within a short stratigraphic interval, many mammal taxa should disappear, there should be changes in depositional environment that would be consistent with the purported climate change and critical taxa should first appear (see Rule 4 for more discussion on critical taxa).

Rule 3. *The magnitude of climate change must increase over that typically caused by Milankovitch orbital variations on the 100 000-year time-scale.* However, the increase may be small and result from infrequently occurring combinations of the three cycles, as well as from superimposition of

Milankovitch cycles on longer-term causes of climatic change (Bartlein and Prentice, 1989).

Test: As detailed climate models become available for pre-Pleistocene segments of the geologic time-scale, the predicted timing and results of 'unusual' Milankovitch combinations can be compared with timing of widespread mammal extinction. Likewise, the timing of non-Milankovitch-based climate change can be examined. The model predictions and the extinctions should coincide in time.

Rule 4. *The new taxa that contribute to extinctions must be of a kind or number that interacts with a wide variety of the native fauna.* The greater the magnitude of an immigration event or evolutionary radiation, the greater the probability that this will happen. But even arrival of a single taxon is sufficient if it is the right taxon.

Test: Taxa whose first appearance seems to coincide with an extinction event should include those that would influence a wide spectrum of the palaeocommunity, for example, more efficient predators, or large herbivores that substantially impact vegetational composition and distribution (like proboscideans or large herds of bison).

Rule 5. *The main mechanism of widespread extinction is coevolutionary disequilibrium.* Each species responds to climate change and newly-arrived taxa individually, leading to the dissolution of previously tightly coevolved communities. Some taxa become extinct because they were affected directly by a new climate, predator or competitor; others because they were dependent on linked components within no-longer existing communities.

Test: Some species that survive the extinction should show a substantially altered geographic range. Some that were sympatric before the event should become allopatric after it, or *vice versa*. The species most affected by extinction should be those most dependent on complex communities, such as herbivores that might fit into grazing successions or require a wide variety of plants in a small area.

Rule 6. *Widespread extinction is concentrated in a short time interval, compared to intervals between widespread extinction episodes.* This follows from Rules 2–5, which when summed mean that widespread extinction takes place when the amplitude of environmental oscillations (climatic plus biological) becomes higher than the amplitudes a biotic system has evolved to withstand. At this critical threshold, the rules of survival change fast; species either learn them quickly, or they are out of the game.

Test: Most disappearances of taxa should occur in the upper part of a stratigraphic unit that records an extinction event, rather than being more or less evenly distributed throughout the vertical extent of the unit.

Rule 7. *The proportion of large-bodied genera that become extinct is a function primarily of magnitude of extinction.* The proportion increases linearly in a predictable way when plotted against total number of genera wiped out by an extinction event, up to about 45 extinct genera. Above 45 extinct genera, the proportion of small-bodied genera should begin to increase.

Test: For a given extinction episode, the proportion of extinct large-bodied genera to total extinct genera should not differ significantly from the relationships indicated in Figures 12.2(a) and 12.3(b).

The proof, of course, lies in putting the rules to the tests. Should the rules hold fast against the weight of pre-Pleistocene evidence, we gain confidence that nature has a motor of extinction, just as she has a motor of evolution. Should the tests result in demoting the 'rules' to 'special explanations', we learn that different extinctions need not be bound by a common process; each may be just a chance combination of unlucky events. The road between these extremes will be marked by other insights into extinction, waiting to be discovered. Whatever the outcome of testing the paradigm, we stand to gain in our quest to understand the process of extinction.

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