

Assessing the Causes of Late Pleistocene Extinctions on the Continents

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One of the great debates about extinction is whether humans or climatic change caused the demise of the Pleistocene megafauna. Evidence from paleontology, climatology, archaeology, and ecology now supports the idea that humans contributed to extinction on some continents, but human hunting was not solely responsible for the pattern of extinction everywhere. Instead, evidence suggests that the intersection of human impacts with pronounced climatic change drove the precise timing and geography of extinction in the Northern Hemisphere. The story from the Southern Hemisphere is still unfolding. New evidence from Australia supports the view that humans helped cause extinctions there, but the correlation with climate is weak or contested. Firmer chronologies, more realistic ecological models, and regional paleoecological insights still are needed to understand details of the worldwide extinction pattern and the population dynamics of the species involved.

Fifty thousand years ago, continents were populated with more than 150 genera of megafauna (animals >44 kg) (1–4). By 10,000 years ago, at least 97 of those genera were gone (Fig. 1, Table 1, and table S1) (5). Prevailing explanations include human impacts (1, 2, 6–8), environmental changes (1, 2, 9–11), and a combination of both (1, 3, 4, 12–14). If humans caused the extinctions, it will profoundly influence our thinking about what is “natural” (15), how ecosystems respond to different scales and kinds of environmental change (16), how long extinctions take (17), and conservation of species and ecosystems (2, 18, 19).

Anthropogenic extinction models, including overkill (20), blitzkrieg (rapid overkill) (21), and sitzkrieg (fire, habitat fragmentation, and the introduction of exotic species and diseases) (6), have been considered plausible because large animals were preferentially affected (1, 2, 5, 22, 23). Species with low reproductive rates, with which large body size correlates, were hit hardest (24, 25). Almost all of the slow-breeding survivors in Australia, Eurasia, the Americas, and Madagascar are nocturnal, arboreal, alpine, and/or deep-forest dwellers, which is consistent with overkill models of extinction but hard to explain by environmental change

alone (24). Survival of large, open-country, slow-breeding animals in Africa is an exception to this pattern that must factor into extinction explanations.

On islands, humans cause extinctions through multiple, synergistic effects, including predation and sitzkrieg (1, 2, 6, 26). Only rarely have island megafauna been demonstrated to go extinct because of environmental change without human involvement (27–29). Incontrovertible impacts of humans on islands have been cited as a potent argument that prehistoric humans also caused extinctions on continents (1, 2, 6), but extrapolation of extinction mechanisms from islands to continents is often disputed (4, 26). Here, we focus on the continents, where causes of extinction remain controversial (8, 19, 30–32).

The perspective from Eurasia and Africa has been that humans exerted at most a minor influence on Pleistocene extinctions, whereas in Australia, North America, and South America, a primary role for humans has been strongly argued (1–3). How consistent with that perspective is recent evidence from simulations, chronology, archaeology, paleontology, climatology, and ecology?

Simulations

Most simulations (table S2) (5) treat prey as a single species with life history parameters [initial biomass, population growth rate (r), and carrying capacity (K)] that are varied, either to simulate effects on particular species [such as mammoth (33) or moa (34, 35)] or to understand values that render prey vulnerable to extinction (20, 21, 36, 37). Either human population dynamics are modeled

with parameters that respond to prey population size (20, 21), or human population densities are varied independently in sensitivity tests (34–37). Hunting efficiency is varied too.

Results differ depending on the input parameters (5). Overkill occurs consistently in single-prey simulations with coupled human-prey population dynamics, but stability analyses suggest this may be a mathematically inevitable outcome (38). Simulations with uncoupled human and prey population dynamics produced blitzkrieg for New Zealand moas (34, 35), but other simulations counterintuitively found that overkill was less likely for large, slow-breeding prey (36, 37), perhaps because the models feature low human population densities and assume hunting efficiency drops as prey become rare.

Simulations of humans foraging on multiple prey (as opposed to one prey species) yield the crucial idea that overkill of slow-breeding prey is more likely when hunter populations become large, because hunters are subsidized by eating rapidly breeding prey or gathered foods when preferred slow-breeding prey becomes scarce (38, 39). The most comprehensive simulation (8) involves predation by North American immigrants on 41 species of large animals and a single, undifferentiated secondary resource (plants and small game). Assuming that hunters nonselectively took prey as it was encountered, overkill resulted for a range of hunting efficiencies, geography of invasion, and competitive interactions (5). The best model correctly predicted the fate of 34 of 41 species, with final human population densities of ~28 people per 100 km² receiving ~30% of their calories from large animals. The median time to extinction was 895 years (40). The rules of this simulation did not allow prey species to disperse outside geographic ranges estimated from fossil data (41), whereas humans were allowed to disperse anywhere. Such assumptions are consistent with climatic or other environmental limits to the ranges of large mammals and show how climate could modulate an extinction driven primarily by human hunting.

Logical next steps would be to apply sensitivity tests to assumptions about geographic ranges, carrying capacity, and rules of

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dispersal and to allow realistic, selective foraging by humans. Assumptions about prey naïveté influence outcomes of single-prey simulations (4, 37) and need to be explored for multiple-prey simulations [e.g., (8, 39)]. It will be important to learn if realistic models can simulate the survival of megafauna in Africa or the magnitude of extinction in Australia, a continent where some question whether human populations were ever large or technologically sophisticated enough to drive overkill (4).

Chronology

Recent work has confirmed two salient points for northern high- and mid-latitudes:

1) In northern Europe, Siberia, and Alaska, extinction occurred in two pulses coincident with climatic change (Fig. 2C), with the loss of warm-adapted animals from 45 to 20 thousand radiocarbon years before present (ky RCBP) and cold-adapted animals from 12 to 9 ky RCBP (5). The pulsed demise of the megafauna in Eurasia also coincides with first the spread and then increases in population sizes of *Homo sapiens sapiens* (42), who had a more diverse suite of tools and broader diets (14, 43) than the pre-*sapiens* hominins. Pre-*sapiens* hominins hunted megafauna in Europe for at least 400,000 years (44) without inducing extinctions, but may have lived at densities too low to have a pronounced impact on prey populations (43). Some species survived in northern Eurasia into the mid-Holocene (5); these late survivors were in areas where human populations were never large.

2) In central North America, the arrival of Clovis-style hunters, extinction of megafauna, and marked climatic change all cluster between 11.5 and 10 ky RCBP (31, 45). Published accounts suggest that at least 15 species became extinct near the start of or during the Younger Dryas climate event,

perhaps within the short “Clovis window” between 11.4 and 10.8 ky RCBP (19, 31, 46). A close correspondence of extinction with both human arrival and climatic change is well supported.

Thus, in mid-latitudes of the Northern Hemisphere, extinction was most pronounced where climatic change and new (North America) or potentially increased (Eurasia) human impacts hit simultaneously. In the far north, the geographically complex chronology of extinction suggests that an interplay between human impacts and climatic change governed extinction dynamics. For some species [such as mammoths (29, 47–49) and giant Irish deer (50)], Siberia and certain islands apparently offered refugia in regions that lacked large human populations. In other areas and for other species [such as horses and mammoths in mainland Alaska (11)], extinction occurred with climatic change even in the absence of significant human populations.

In the Southern Hemisphere, the story is still unfolding, with new information from

and whether ocean-based climatic records are reliable proxies for environmental change on the Australian continent (4, 5).

In South America, generally accepted dates place humans in coastal Chile and Patagonia at 12.9 to 12.5 ky RCBP (53–55), and sites younger than 10 ky RCBP are common (56). The megafauna went extinct in the late Pleistocene, probably after humans arrived and as climate changed, but until more comprehensive analyses are undertaken, little else can be said with certainty.

Supporters of overkill have long argued that extinctions in Africa (5) and central Eurasia were milder (Fig. 1, Table 1, and table S1) because humans coevolved with megafauna there for hundreds of thousands of years, whereas they were an invasive species in the Americas and Australia. That would explain the magnitude of extinction in the Americas and Australia, but it offers no insights as to why any extinctions took place in Africa, or why Eurasia experienced a 36% loss of its megafauna.

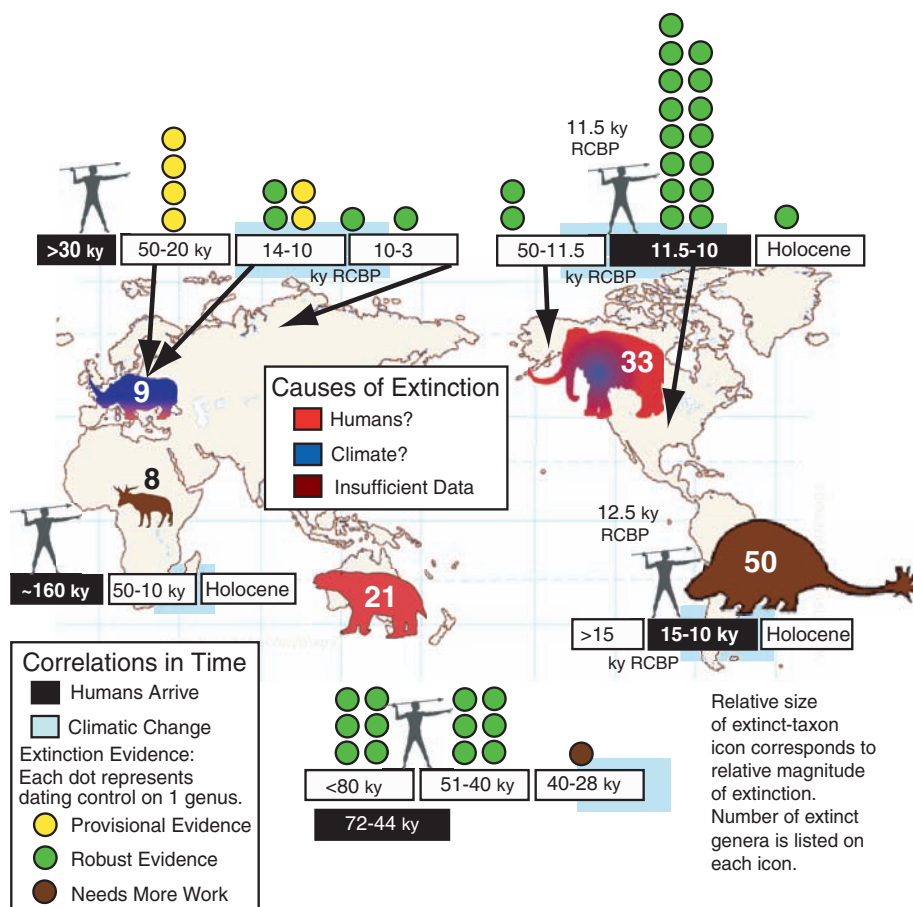


Fig. 1. Summary of the numbers of megafaunal genera that went extinct on each continent (Table 1), the strength of the extinction chronology, and a comparison of the timing of extinction with the timing of human arrival and late Pleistocene climatic change. Extinction timing for individual genera was judged as robust or provisional based on previous publications that evaluated quality of dates. Sources are as follows: Europe (3, 14, 47), Siberia (48), North America (11, 29, 46, 57), and Australia (4, 7). For humans, the date is the earliest generally accepted arrival of *Homo sapiens sapiens*; pre-*sapiens* hominins were present in Eurasia and Africa much earlier.

Solving those problems will require a better understanding of the extinction chronology, background extinction rates, timing and details of climatic change, and patterns of human population growth and resource use.

Archaeology and Paleontology

On all of the involved continents, archaeological remains and extinct megafauna have been found in association (5). Debate continues on two unresolved questions:

1) What constitutes evidence that humans hunted megafauna? In Africa and Eurasia, acceptable evidence includes cut marks and breakage of fossil bones. In contrast, cut marks and breakage alone are seldom regarded as strong evidence in North America (57, 58). New insights are possible by applying uniform criteria across continents to recognize kill sites, but such comparisons have not yet been done.

2) Are there too few kill sites to support overkill models? Until recently, it was not possible to determine if the number of kill sites (however one defines them) was consistent with a given overkill model, because we could not quantify the proportion of kill sites relative to all fossil occurrences of extinct taxa. With electronic databases (41, 57), estimating these proportions is now feasible for North America. Under certain assumptions (5), the data suggest that on that continent (i) kill sites are very frequent for mammoths; (ii) at least one taxon (*Platygonus*, the peccary) is found at fewer kill sites than expected; and (iii) most taxa are too rare in the fossil record

to reliably judge their kill-site frequency (table S3).

Climatic Change and Ecological Effects

Climatic change is known to affect animals, often by triggering vegetation changes (5). The question is whether late Pleistocene climatic changes were unusual enough to trigger unusual ecological response. Three ecological models with general explanatory power have been applied to the Pleistocene extinctions debate: the proboscideans-as-keystone species model (2, 5, 59), co-evolutionary disequilibrium (5, 10), and the mosaic-nutrient model (5, 60). One prediction of the keystone-species model is that proboscideans should be the first to disappear in the fossil record, but in Eurasia (47, 48, 61), Alaska (11), and probably central North America (31, 62, 63), they were among the last to go. The co-evolutionary disequilibrium and mosaic-nutrient models require that the changes in climate and ecosystem structure at the time of extinction were unusual relative to earlier conditions in the Pleistocene. This is underscored

by recent work demonstrating that megafaunal extinction did not characterize earlier glacial-interglacial transitions in Europe (3, 14), Australia (5, 64), or North America (5, 65, 66).

Paleoclimate records do not support a unique late Pleistocene transition. Global-scale oxygen-isotope records indicate that the most recent deglaciation was neither more rapid nor of greater magnitude than other shifts in the past 700,000 years (Fig. 2A). At a regional scale, climatic shifts around North and South America, Eurasia, and Africa at the time of extinction, although large, were not unusual (Fig. 2, B and C). If the extinction in Australia occurred before 40 ky BP, it would have occurred when ocean records were relatively placid (Fig. 2B).

Long pollen records from areas with megafaunal remains are few, but they allow a first approximation of how the magnitude of floral change compares to the timing of extinction in various regions. The comparison requires converting published pollen records to a standardized scale (Fig. 3). In

Table 1. Numbers of mammalian megafaunal genera affected by Pleistocene extinction. Numbers are based on our vetting of the primary literature (5), including but not restricted to (1–4) and (7). Column A gives the number of genera on a given continent that went extinct globally; column B, the number of extinct genera that survived on another continent; column C, the number of Pleistocene genera on the continent that were still alive historically; and column D, the percent of megafaunal genera that went extinct on each continent (columns A + B divided by columns A + B + C).

Continent	A	B	C	D
Africa	5	3	36	18
Australia*	14	–	2	88
Eurasia†	5	4	16	36
North America	28	5	13	72
South America	49	1	10	83

*Australia also has seven extinct (and no surviving) genera of megafaunal reptiles and birds. †Our use of "Eurasia" encompasses only northern Asia (part of the Palearctic Region), because insufficient data exist to include southern Asia (the Oriental Region).

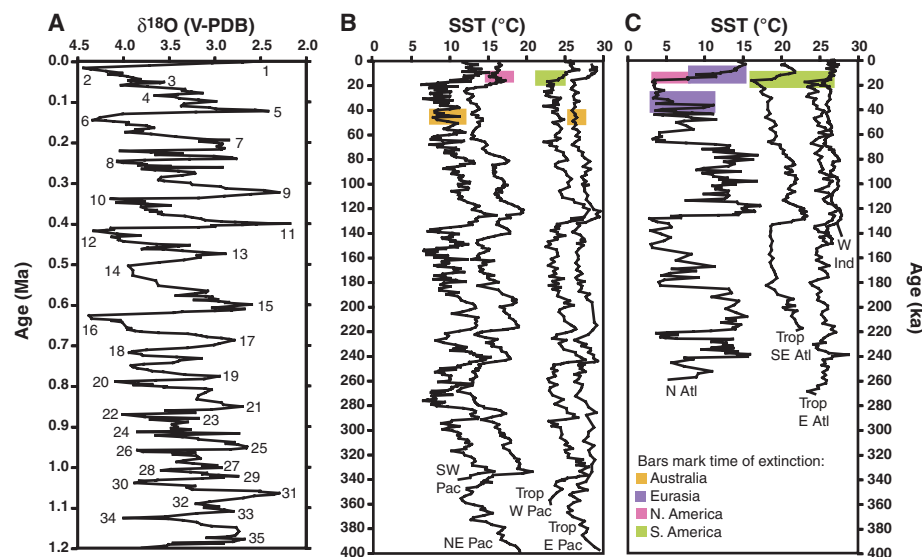


Fig. 2. (A) Oxygen isotope data from benthic foraminifera at North Atlantic Deep-Sea Drilling Program site 607 (81, 82). The isotopic signal ($\delta^{18}O$) in benthic foraminifera largely reflects variations in continental ice volume, with a smaller effect due to changes in ocean bottom temperatures. Numbers refer to marine isotope stages (81, 82). Most well-constrained extinctions and drops in abundance occurred in stages 2 and 3. V-PDB, Vienna–Pee Dee Belemnite. (B and C) Sea-surface temperature (SST) records from the (B) Pacific and (C) Atlantic and Indian oceans, respectively. Colored bars indicate the time of extinction on nearby continents. The core label, latitude, longitude, type of SST estimate, and source are as follows: northeast Pacific (NE Pac), Ocean Drilling Program (ODP) 1020, 41.00°N, 126.43°W, alkenone (83); tropical east Pacific (Trop E Pac), TR 163-9, 2.26°N, 90.95°W, Mg/Ca (84); tropical west Pacific (Trop W Pac), ODP 806B, 1.32°N, 159.36°E, Mg/Ca (84); southwest Pacific (SW Pac), MD 97-2120, 45.53°S, 174.93°E, Mg/Ca (85); west Indian (W Ind), MD 85674, 3.18°N, 50.43°E, alkenone (86); north Atlantic (N Atl), K 708-1, 50.00°N, 23.73°W, foraminiferal transfer function (average of data reported for August and February) (87); tropical east Atlantic (Trop E Atl), GeoB 1112, 5.77°S, 10.75°W, Mg/Ca (88); and tropical southeast Atlantic (Trop SE Atl), GeoB 10285, 20.10°S, 9.19°E, alkenone (89). All ages in this figure are in calendar years (ky BP), not ^{14}C years (ky RCBP), using age models in primary publications, except for core K 708-1, where ^{14}C ages reported in (87) were converted to calendar years with CALIB 98 (90) from 0 to 22,000 ^{14}C years and with data from (91) for 22,000 to 45,000 ^{14}C years.

some areas, vegetation change coincides with extinction (Fig. 3, E, G, and L), but in others it does not (Fig. 3, D, F, H, and M). Elsewhere, the last phases of extinction correlate with vegetation change but the initial extinctions may not (Fig. 3, I and J). In still other regions, extinctions are not well enough dated to compare with vegetation change (Fig. 3, A to C, K, and N). Particularly interesting is northeastern Australia (Fig. 3O), where the extinction may coincide with a rapid transition to full glacial biomes unlike any seen in 150,000

years, including the prior full glacial period around 130 ky BP; this might support an environmental component to extinction at that location.

A generalized ecological model that has just begun to receive attention is that of state-changes in ecosystems, either when certain thresholds are crossed (67) or because of intrinsic nonlinear dynamics (68). Future work could gainfully explore whether the nature of climatic change in certain areas is consistent with threshold effects, as well as whether ecological sys-

tems exhibit dynamical properties that indicate a susceptibility to collapse.

Current State of the Evidence

How far has the debate about Pleistocene extinction on continents progressed in the last 40 years? The case for humans contributing to extinction is now much stronger than it was in the early days, with support from recent work on chronology, simulations, paleoclimatology, paleontology, and archaeology. Yet it is an oversimplification to say that an abrupt wave of hunting-

South & North American Floral Records

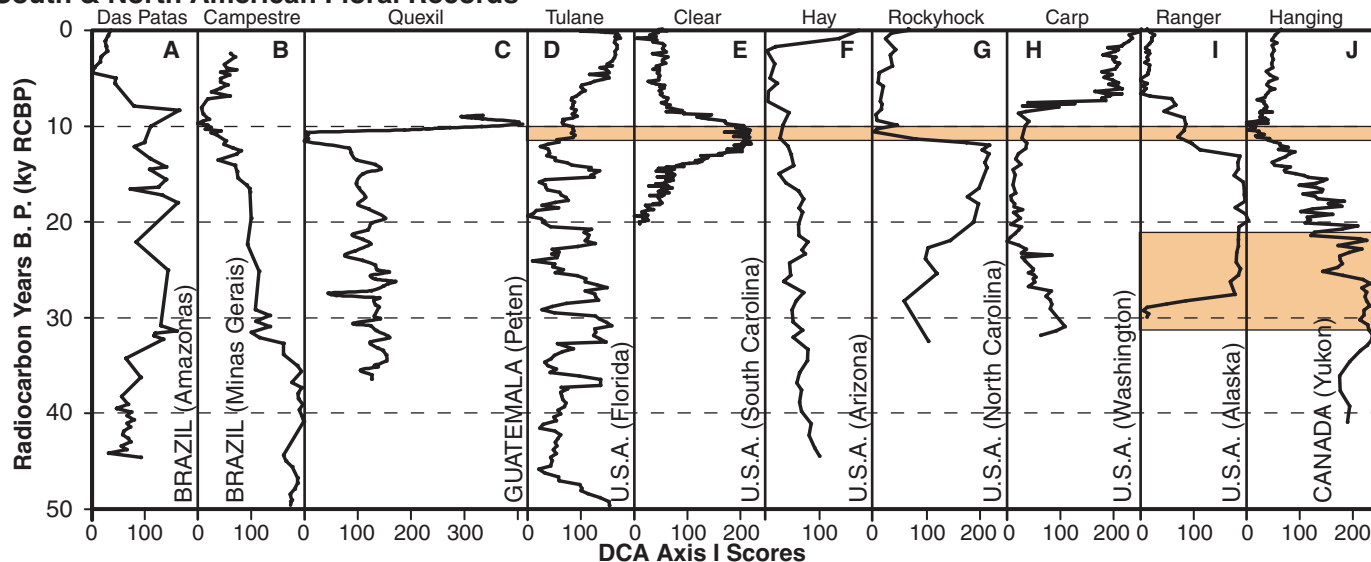
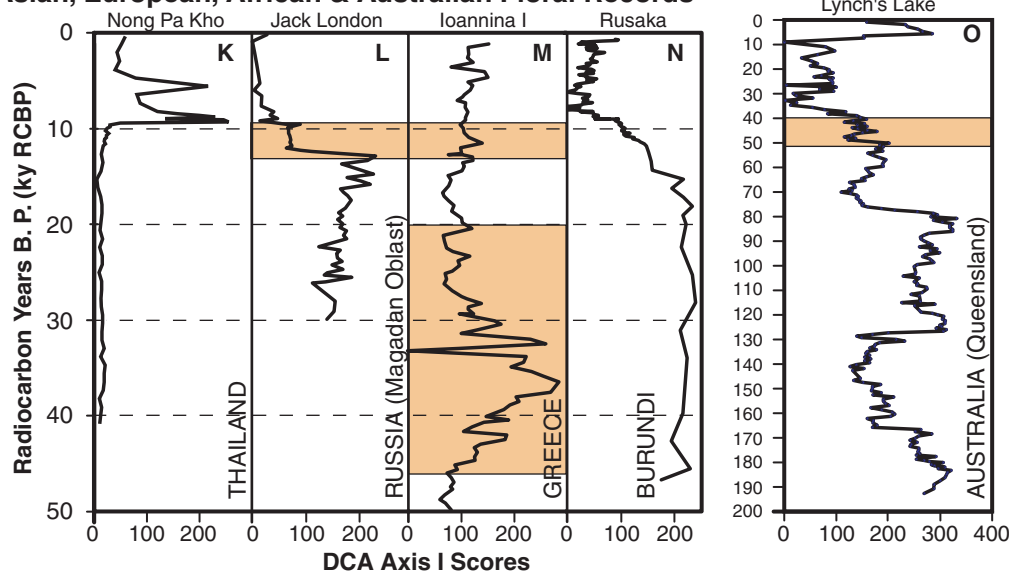


Fig. 3. Timing of vegetational changes in relation to timing of extinction (shaded intervals) in different parts of the world. Vegetation is inferred from published palynological records (78). The following list gives the site name with latitude, longitude, and elevation (m) in parenthesis: (A) Lagoa das Patas (0.3°N, 66.7°W, 300); (B) Lagoa Campestre (19.0°S, 46.8°W, 980); (C) Lake Quexil (coordinates not available); (D) Lake Tulane (28.0°N, 82.0°W, 34); (E) Clear Pond (33.8°N, 79.0°W, 10); (F) Hay Lake (37.0°N, 109.0°W, 2780); (G) Rockyhock Bay (36.0°N, 77.0°W, 6); (H) Carp Lake (45.0°N, 121.0°W, 714); (I) Ranger Lake (67.1°N, 153.7°W, 820); (J) Hanging Lake (68.0°N, 138.0°W, 500); (K) Nong Pa Kho (17.0°N, 103.0°E, 180); (L) Jack London Lake (62.2°N, 149.5°E, 820); (M) Ioannina I (39.8°N, 20.7°E, 470); (N) Rusaka Swamp (3.4°S, 29.6°E, 2070); and (O) Lynch's Lake (17.4°S, 145.7°E, 760). The different pollen records were standardized for comparison by Detrended Correspondence Analysis (DCA); the DCA Axis I score is used to depict when pollen abundances shift, which in turn reflects changes in surrounding vegetation. The standardization proceeded by downloading the taxon abundance matrix for each core from (78), removing the aquatic taxa (e.g., floating and emergent aquatics and algae), and calculating the percent abundance for each terrestrial sporomorph type in each sample. Each matrix was

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independently subjected to DCA with the software package MVSP 3.12a (92). Taxon abundances were unweighted and 26 segments were used in four detrending cycles. The score of each sample on the first axis of the DCA (which for these analyses expresses 20 to 40% of the total variation in the data set) is used to quantify its floral composition in relation to the other samples from the same core. The age of each sample is from the published age model (78) for each site.

induced extinctions swept continents right after first human contact. Instead, the evidence shows that blitzkrieg *sensu stricto* can be firmly rejected in western Europe, Siberia, Alaska, and probably Australia and central North America. Without late Pleistocene climatic change, it is likely that species such as horses in Alaska and mammoths and giant Irish deer in central Eurasia would have survived longer, despite the presence of humans. The recent information now points toward humans precipitating the extinction, but also to an instrumental role for late Pleistocene climatic change in controlling its timing, geographic details, and perhaps magnitude. The mechanism for climatic effects is likely to be found in detailed species-by-species analyses (19), rather than in one of the three existing global ecological models (10, 59, 60), none of which is fully consistent with observations.

Data density and quality are still uneven. The Eurasian record is increasingly good and reveals that late Pleistocene climatic change contributed to extinction by driving range adjustments in large mammals. An idea that needs further testing is that the arrival and population expansion of *Homo sapiens sapiens* began to fragment megafaunal ranges by 30,000 years ago, ultimately restricting megafauna to inviable populations in far northern refugia by the end of the Pleistocene. Australian evidence suggests that megafaunal extinction followed human arrival, and that both probably preceded significant global or regional South Pacific climatic change, which is consistent with a role for humans. However, the timing of key events still cannot be bracketed within error bars less than ~10,000 years, the youngest records of extinct megafauna are controversial, and local environmental changes may differ from the global or regional pattern (4, 5). In South America, published data on extinction chronology is accumulating but awaits critical analysis. In Africa, better temporal resolution is needed to assess how the timing of the few extinctions matches local environmental changes and human impacts.

In contrast, robust dating verifies simultaneous climatic change and first human contact in the conterminous United States, where extinctions were particularly rapid and pronounced. Support for human impacts includes (i) indisputable hunting of two extinct species, (ii) clustering of extinctions within 1,500 years (and perhaps less) of first contact with Clovis hunters, (iii) widespread distribution of Clovis hunters, (iv) simulations, and (v) more pronounced extinction than in mid-Pleistocene glacial-interglacial transitions. On a broader North American scale, the demise of megafaunal species without significant human presence in Alas-

ka is consistent with some role for climate (11).

General Implications

The data show that the late Pleistocene extinction event was spread over more than 50,000 years globally; was the accumulation of diachronous, shorter-term pulses that took place on a regional basis; and was amplified by the interaction of both biotic (humans as invasive species) and abiotic (climatic) drivers.

A significant implication for conservation biology is that the coupling of marked climatic change with direct human impacts on fauna is especially pernicious. Both effects are under way today at unprecedented rates. Data generated in the Pleistocene extinctions debate are now robust enough to support earlier contentions (15) that the modern global ecosystem is unique in having vast populations of one species (humans) and a depauperate array of megafauna. The net effect, through loss of many herbivores, carnivores, and scavengers, has been simplification and loss of redundancy in food webs (69). This has implications for the stability of global ecosystems.

Productive Future Directions

The accumulated evidence suggests it is time to move beyond casting the Pleistocene extinction debate as a dichotomy of humans versus climate and instead to untangle the complex impacts that both had on megafauna. From the archaeological perspective, we need to know when human population sizes on each continent became large enough to affect vulnerable fauna. Kill-site and dating criteria must be standardized between continents. To understand the effects of environmental changes, much remains to be done in determining how changes in particular climatic parameters would have impacted population sizes of affected species. Particularly promising in this regard are advances in the study of fungal spores from megafaunal dung in lake sediments (70) and the use of ancient DNA to model population-level change (71–74). Improvements in the chronology of extinction and paleoclimatic reconstructions for South America and Africa are especially needed, as is a more detailed understanding of whether the last glacial-interglacial transition was different from earlier ones in pertinent ways. Rigorous, ecologically based models of range contraction and extinction must be formulated through linkage of work that has proceeded largely independently in paleoecology and ecology, especially in such areas as food-web dynamics, keystone species, and ecosystem state-change. Some problems were intractable when the Pleistocene extinctions

debate began but can now be addressed through new dating techniques (7, 75, 76); through the assembly and analysis of paleoecological, paleoclimatic, and archaeological databases (41, 77, 78); and through isotopic studies to reconstruct details of both the paleoclimate and paleoecology (79, 80).

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