Late Quaternary Extinctions: State of the Debate

Paul L. Koch[1] and Anthony D. Barnosky[2]

[1]Department of Earth and Planetary Sciences, University of California, Santa Cruz, California 95064; email: pkoch@pmc.ucsc.edu

[2]Department of Integrative Biology and Museums of Paleontology and Vertebrate Zoology, University of California, Berkeley, California 74720;
email: barnosky@berkeley.edu

Annu. Rev. Ecol. Evol. Syst. 2006. 37:215–50

The *Annual Review of Ecology, Evolution, and Systematics* is online at http://ecolsys.annualreviews.org

This article's doi:
10.1146/annurev.ecolsys.34.011802.132415

1543-592X/06/1201-0215$20.00

Key Words

mammal, overkill, paleoclimate, paleoecology, Pleistocene

Abstract

Between fifty and ten thousand years ago, most large mammals became extinct everywhere except Africa. Slow-breeding animals also were hard hit, regardless of size. This unusual extinction of large and slow-breeding animals provides some of the strongest support for a human contribution to their extinction and is consistent with various human hunting models, but it is difficult to explain by models relying solely on environmental change. It is an oversimplification, however, to say that a wave of hunting-induced extinctions swept continents immediately after first human contact. Results from recent studies suggest that humans precipitated extinction in many parts of the globe through combined direct (hunting) and perhaps indirect (competition, habitat alteration) impacts, but that the timing and geography of extinction might have been different and the worldwide magnitude less, had not climatic change coincided with human impacts in many places.

INTRODUCTION

LQE: late Quaternary extinction

Overkill hypothesis: hypothesis that extinction results because human hunting causes death rates to exceed birth rates in prey species

Megafauna: animals with a body mass greater than 44 kg

kyr BP: 1000 years before present

Fifty thousand years ago, ecosystems around the globe were populated with large animals that are now extinct. On continents worldwide, about 90 genera of mammals weighing ≥44 kg disappeared (see **Supplemental Table 1**; follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org/**). North America had proboscideans, giant ground sloths, camels, saber-tooth cats, and a giant beaver, among others. In Eurasia, woolly mammoth and rhinoceros, and giant deer with antlers spanning 3 m were common. South America hosted the car-sized glyptodont and the three-toed litoptern, which resembled a horse with a camel's neck and a short elephantine trunk. In Australia, the rhinoceros-like *Diprotodon*, the largest marsupial that ever lived, coexisted with hog-sized wombats. Timing varied across the globe, but by 10,000 years ago, these animals had vanished except at very high latitudes, on islands (where the extinction of large and small animals was more recent), and in Africa (where many large animals survive today) (Martin & Steadman 1999).

This late Quaternary extinction (LQE) was recognized by the nineteenth century, when explanations included climatic catastrophes, gradual climate change, and overkill by human hunters (Grayson 1984). The debate took on new life after the revolution in ^{14}C dating, as Martin and colleagues began to articulate and test more explicit overkill hypotheses (Martin 1966, 2005; Mosimann & Martin 1975). Growing knowledge of shifts in Quaternary climate, vegetation, and animal communities, as well as doubts about the capabilities and impacts of human hunters, led others to offer more focused environmental extinction hypotheses (Guilday 1967, Slaughter 1967). Some argued for a "one-two punch" combining human impacts and climatic changes (Barnosky 1989, Haynes 2002a). The debate has produced a vast literature spanning archaeology, (paleo)ecology, and climatology. **Table 1** summarizes the main hypotheses advanced and explored over the past 25 years to explain the LQE.

Here, we offer a continent-by-continent summary of the LQE, focusing mostly on mammals. We do not discuss Holocene island extinctions in any detail because most researchers accept that anthropogenic factors were pivotal. We evaluate the main hypotheses proposed to explain the LQE and focus on the impacts on herbivores, as their extinction by any means would precipitate extinctions among carnivores and scavengers. We define megafauna as animals weighing ≥44 kg, "large" as animals between 44 kg and 10 kg, and "small" as animals <10 kg. Counts of extinct versus extant genera are based on our vetting of the literature (Barnosky et al. 2004b). Species counts and body-size data follow Smith et al. (2003), with minor additions from Brook & Bowman (2004) and Johnson (2002). Ages of events are reported in units of 1000 calendar years before present (kyr BP). Ages reported in ^{14}C years were converted to calendar years using CALIB 4.4 for ages between 0 and 20,050 years BP (Stuiver et al. 1998) and the GISP2-tuned equation from Bard et al. (2004) for ages between 20,050 and 45,000 years BP.

Table 1 Hypotheses to explain the late Quaternary extinctions

Type or name	Description
Environmental hypotheses	
Catastrophes	Megadrought, rapid cooling, bolide impact?
Habitat loss	Preferred habitat types lost or too fragmented
Mosaic-nutrient hypothesis	Loss of floras with high local diversity
Co-evolutionary disequilibrium	Disruption of coevolved plant-animal interactions due to flora rearrangement
Self-organized instability	Collapse of system due to intrinsic dynamics
Human impacts other than hunting	
Habitat alteration	Loss or fragmentation of viable habitat due to human impacts, including fires
Introduced predators	Direct predation by dogs, rats, cats, pigs, etc.
Hyper-disease	Introduction of virulent diseases
Overkill hypotheses	
Blitzkrieg	Rapid loss of prey due to overhunting
Protracted overkill	Loss of prey after prolonged interaction with predator
Combined hypotheses	
Keystone megaherbivores	Ecosystem collapse due to loss of landscape altering megaherbivores, perhaps with increase in fire
Prey-switching	Nonhuman carnivores switch prey as humans usurp preferred prey
Predator avoidance	Herbivores restricted to inviable refugia

Modified from Burney & Flannery (2005).

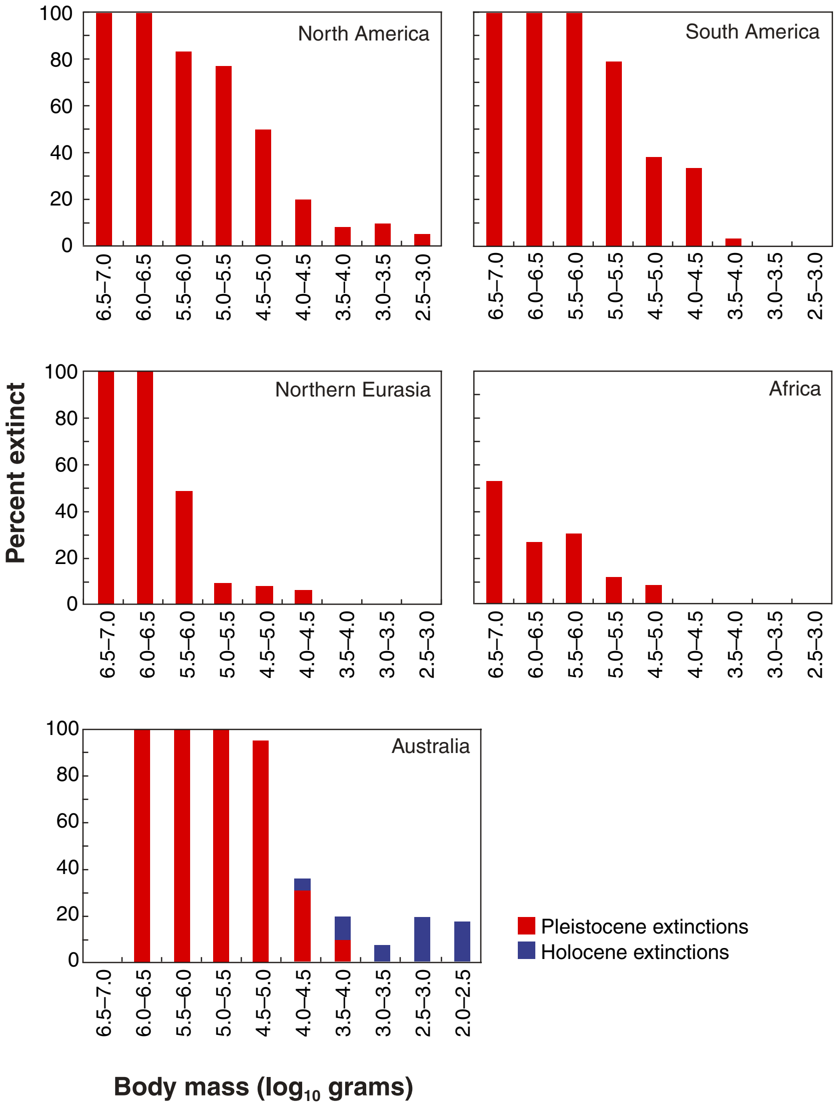
WHAT HAPPENED?

In North America south of Alaska, 34 Pleistocene genera of megafaunal mammals did not survive into the Holocene; two mammalian orders (Perissodactyla, Proboscidea) were eliminated completely (**Table 2**, **Supplemental Table 1**). Six of the extinct genera survived elsewhere, and within genera that survived, species were lost. Besides the megafauna, large and small mammal genera became extinct, including an antilocaprid (*Capromeryx*), a canid (*Cuon*, an Asian survivor), a skunk (*Brachyprotoma*), and a rabbit (*Aztlanolagus*). At the species level, the extinction was total for mammals larger than 1000 kg, greater than 50% for size classes between 1000 and 32 kg, and 20% for those between 32 and 10 kg (**Figure 1**, **Supplemental Table 2**). There were also cases of pseudoextinction at the species level. For example, genetic analyses suggest that Holocene bison from south of the Laurentide ice sheet (*Bison bison*) are descendents of larger, morphologically distinct Pleistocene bison from the region (*Bison antiquus*) (Shapiro et al. 2004). Robust temporal brackets place the last occurrences for 15 genera between 15.6 and 11.5 kyr BP (**Figure 2**, discussion of dates is based on review by Barnosky et al. 2004b unless noted).

The South American LQE was even more profound, with the loss of 50 megafaunal genera (~83%, **Table 2**). Three orders of mammals disappeared (Notoungulata,

Figure 1

Percent extinction by body size class for five continents. Data are the percent of Pleistocene species that became extinct in the late Quaternary. Data for the histogram and a description of data sources are provided in **Supplemental Table 2**.



Proboscidea, Litopterna), as did all megafaunal xenarthrans. At the species level, the extinction was total for mammals larger than 320 kg, was high for the size class between 320 and 100 kg, and was moderate for size classes between 100 and 10 kg (**Figure 1**, **Supplemental Table 2**). The timing of extinction is poorly constrained. Most taxa are only dated biostratigraphically as members of the Lujanian South American Land Mammal Age (100 to 11.5 kyr BP) (**Supplemental Table 1**). Many reported ^{14}C dates do not pass rigorous criteria for accepting dates (Grayson 1991), including reports that suggest survival of South American megafauna into the Holocene, which

Table 2 Continental extinctions of mammalian megafauna at the generic level

	Number globally extinct genera	Number extinct genera surviving on other continents	Number Holocene survivors	% extinct
Africa	7	3	38	21
Australia[a]	14	—	2	88
Eurasia[b]	4	5	17	35
North America[c]	28	6	13	72
South America	48	2	10	83

[a] Australia also has seven extinct (and no surviving) genera of megafaunal reptiles and birds.

[b] Eurasia encompasses only northern Asia, because insufficient data exist to include southern Asia.

[c] Table does not account for the late survival of mammoths on Bering Sea islands.

we therefore consider equivocal. Robust dates indicate the survival of equids (*Hippidion*, *Equus*), ground sloths (*Eremotherium*, *Mylodon*, *Nothrotherium*) (Steadman et al. 2005), and *Cuvieronius* (a proboscidean) into the latest Pleistocene (15.6–11.5 kyr BP). It is likely that many other taxa were also lost near the Pleistocene-Holocene boundary, but we emphasize that this remains to be demonstrated.

Northern Eurasia (Europe and northern Asia) lost 9 genera (35%) (**Table 2**, **Supplemental Table 1**). It is unclear if Pleistocene forms of bison and camel became extinct or survived by evolution into Holocene species (Stuart 1991). Comprehensive dating campaigns in Eurasia and the extension of Eurasian steppe biomes in Alaska and the Yukon reveal that the extinction occurred in two pulses (Guthrie 2003, 2004; MacPhee et al. 2002; Stuart et al. 2002, 2004). In Eurasia, warm-adapted megafauna that were abundant during prior interglacials (straight-tusked elephants, hippos) became extinct between 48.5 and 23.5 kyr BP. In Alaska and the Yukon, hemionid horses and short-faced bears disappeared at 35.4 and 24.8 kyr BP, respectively. A coalescence analysis of DNA sequences suggests that bison populations began to decline in size in Beringia at roughly this time (e.g., 35–40 kyr BP) and attributed bison demise to climate change rather than human impacts (Shapiro et al. 2004). However, different treatment of the same data by some of the same researchers contradicts this conclusion (Drummond et al. 2005), estimating instead a severe bottleneck coincident with earliest evidence for abundant humans in Beringia around 10 kyr BP. The second pulse of extinctions began in the latest Pleistocene and hit cold-adapted animals. Mammoths dropped in abundance across Eurasia and Alaska after 14 kyr BP, but survived into the Holocene on the Taimyr Penisula and the Wrangell and Pribilof Islands. Giant Irish deer dropped in abundance and began to dwarf about 13 kyr BP before disappearing from Europe and Siberia in the Holocene. Muskox appear to have reduced genetic diversity sometime between 18 and 10 kyr BP, and became extinct in Eurasia in the Holocene (MacPhee et al. 2005). In Alaska, caballoid horses began to dwarf at 29.2 kyr BP and became extinct 15 kyr BP. While the largest megafaunal size classes were eliminated by the LQE, the impact on mammals in the size range from 1000 to 100 kg was less than in the Americas (**Figure 1**, **Supplemental Table 2**).

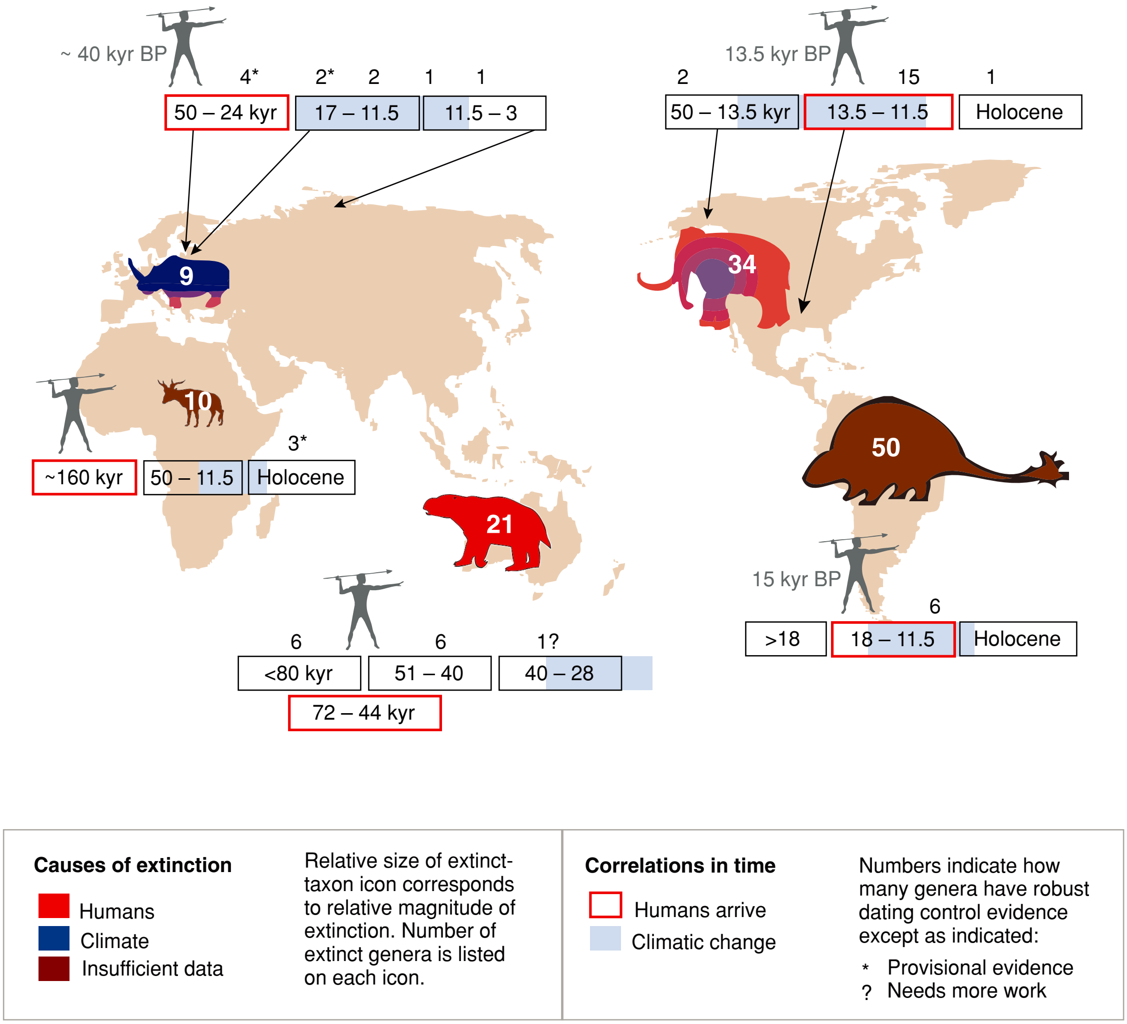


Figure 2

Chronology of the late Quaternary extinction, climate change, and human arrival on each continent. The timing of extinction for each genus was judged as robust or provisional based on previous publications that evaluated quality of dates (see Barnosky et al. 2004b). For humans, the earliest generally accepted arrival of *Homo sapiens sapiens* is indicated. Pre-*sapiens* hominins were present in Eurasia and Africa much earlier.

Australia lost 14 of its 16 genera of Pleistocene mammalian megafauna along with all megafaunal reptiles (6 genera) and *Genyornis*, a giant flightless bird (Flannery & Roberts 1999) (**Table 1**, **Supplemental Table 1**). Three marsupial families became extinct (diprotodontids, palorchestids, thylacoleonids), and the extinction removed entire guilds, such as megafaunal browsers and carnivores. The LQE was catastrophic for large body sizes, with the complete loss of all animals larger than 100 kg, almost total extinction for animals between 100 and 32 kg, and lesser impacts on smaller size classes. A recent analysis of dates of last occurrence included only articulated skeletons, assuming that such carcasses are unlikely to be mixed from other deposits (Roberts et al. 2001). Of the 21 extinct megafaunal genera, 12 lasted to 80 kyr BP, and at least 6 persisted to between 51 kyr BP and 40 kyr BP (**Figure 2**). Yet disarticulated skeletons of megafauna occur at many sites younger than 40 kyr BP, especially those with signs of human occupation (Johnson 2005). An especially contested site is Cuddie Springs, where lithic artifacts and extinct megafauna are in firm association in sediments dated between 40 kyr BP and 32 kyr BP (Trueman et al. 2005, Wroe et al. 2004). The scarcity of articulated carcasses in younger nonanthropogenic contexts may be evidence that megafaunal abundance declined at ~40 kyr BP, with ultimate extinction occurring at a more recent date (Johnson 2005).

Africa is a fortunate anomaly in this story. Although 10 genera of Pleistocene megafauna (21%) disappeared, extinction of 7 of these cannot be bracketed tighter than in the last 100 kyr BP, and three went extinct in the Holocene (**Table 1**, **Supplemental Table 1**, **Figure 2**). Yet even in Africa, the species-level extinction was most intense for larger megafauna (40% to 50% for mammals between 10,000 and 1000 kg and moderate for those between 1000 and 320 kg) (**Figure 1**).

WAS THE LATE QUATERNARY EXTINCTION UNUSUAL?

To evaluate hypotheses for the LQE, the event must be viewed in context. Early work on extinction dynamics in North America, which has the best synthesized Cenozoic mammal record, offered little support for the idea that the LQE was exceptionally intense, though most studies noted that larger mammals were severely affected (Barnosky 1989, Gingerich 1984). However, recent analyses that account for temporal and sampling biases in the fossil record recognize a LQE spike that exceeds all but one other extinction in the past 55 million years (Alroy 1999). Even taking into account that larger animals are preferentially impacted by extinction events, and that smaller species are increasingly affected as extinction intensity rises, by Alroy's metrics the LQE appears more selective than any extinction event in the preceding 65 million years of mammalian history in North America.

Studies of Cenozoic extinction dynamics are not available for other continents, but the size selectivity of the LQE has been examined. Before the extinction, body size distributions were bimodal and similar in North America, South America, and Africa, whereas Australia had a right-skewed distribution (Lyons et al. 2004a). On all four continents, however, extinct species were significantly larger than surviving species, and for the Americas and Australia, almost the entire large mode or tail of the distribution was removed. The probability of extinction increases with body mass, without a strong threshold in mass separating extinct and extant mammals (**Figure 1**, **Supplemental Table 2**) (see also Brook & Bowman 2004).

ENVIRONMENTAL HYPOTHESES

Description of Environmental Hypotheses

The LQE roughly coincided with the most recent glacial-interglacial transition, leading some to conclude that extinction was due to environmental change. Early hypotheses calling for a sudden climatic catastrophe (deep freeze, drought) have been discredited (Grayson 1984). The more lasting hypotheses focus on the ecological effects of climate change that would lead to extinction: habitat loss hypotheses, the mosaic-nutrient hypothesis, coevolutionary disequilibrium, and self-organized instability. Habitat loss hypotheses (HLH) argue that as climate changed, areas with adequate conditions to maintain megafauna either disappeared entirely or became too small and/or fragmented to support viable populations (e.g., Barnosky 1986, Ficcarelli et al. 2003, King & Saunders 1984). The mosaic-nutrient hypothesis (MNH) is a special case of habitat loss. It argues that climate change reduced the growing season and local plant diversity, and also increased plant antiherbivore defenses, all of which reduced the carrying capacity for herbivores (Guthrie 1984). HLHs, including the MNH, tend to offer regionally and taxonomically specific explanations for extinction; they are difficult to generalize to explain the broad pattern of extinction across diverse habitats and many clades. Co-evolutionary disequilibrium (CED) is a more general hypothesis. It posits that the high herbivore diversity of Pleistocene ecosystems was maintained by extensive resource partitioning, analogous to the grazing succession of modern African savannas, and that an extremely rapid glacial-interglacial transition reorganized floras, disrupting this tightly coevolved system (Graham & Lundelius 1984). Self-organized instability (SOI) argues that extinction results from a slight perturbation that is amplified into a catastrophe by dynamics intrinsic to complex, multicomponent ecosystems with interacting subunits (Forster 2004). The key to extinction under HLH, MNH, CED, and to some extent SOI, is the claim that the last glacial-interglacial transition was unusually large and unusually rapid relative to earlier glacial-interglacial transitions, too fast for animal adaptation and/or redistribution in climate space.

Habitat loss hypotheses (HLH): as climate changed, areas with adequate conditions to maintain megafauna either disappeared or became too small/fragmented to support populations

Mosaic-nutrient hypothesis (MNH): climate change reduced growing season and plant diversity, and increased plant defenses, reducing herbivore carrying capacity and leading to extinction

Co-evolutionary disequilibrium (CED): disruption of extensive Pleistocene networks of resource partitioning by rapid glacial-interglacial transition led to extinction

Self-organized instability (SOI): extinction results from a slight perturbation amplified into a catastrophe by dynamics intrinsic to complex, multicomponent ecosystems with interacting subunits

Plausibility of Environmental Hypotheses

The response of the modern biota to anthropogenic perturbations offers insights into the plausibility of environmental hypotheses. Anthropogenic warming has led to changes in seasonal activities, geographic range, local abundance, species composition, phenotype, and genotype (Root et al. 2003, Walther et al. 2002). Most cases involve impacts on taxa of lower trophic level and smaller body sizes. However, climate change has precipitated geographic range and relative abundance shifts in large mammals (e.g., Post & Forchhammer 2002). Global extinctions of some smaller animals are attributed to current warming (Pounds et al. 2006), and the experiment is still in progress, with simulations suggesting that substantial extinction may result (Thomas et al. 2004).

The effects of habitat fragmentation and loss have been studied to understand controls on the diversity and viability of species and populations. A loss of species diversity with habitat fragmentation is often observed in natural and simulated systems (Crooks 2002, Lindenmayer et al. 2000, Wahlberg et al. 1996). As diversity drops, some species irrupt following release from predation or competition, which can itself lead to ecological reorganization (Terborgh et al. 2001). Organisms at high trophic levels, or which occur at low abundance, and those with low rates of dispersal, are susceptible to local extinction with habitat fragmentation. Herbivorous megafauna possess one trait predisposing them to extinction by habitat fragmentation (low abundance), but often exhibit pronounced dispersal and migration.

The response of faunas to climate change on islands that lack humans offers a means to assess the plausibility of environmental hypotheses. New Zealand has a rich Pleistocene paleontological record, and there is ample evidence for strong climatic and environmental changes across the Pleistocene-Holocene boundary. Yet the diverse avifauna of New Zealand, which included megafauna such as moas and more abundant smaller birds, persisted through these climate shifts only to collapse in the late Holocene following first contact with humans and rats (Holdaway 1999). A similar pattern is emerging for extinct sloths in the West Indies (Steadman et al. 2005). On the other hand, in at least two cases, islands without humans record the demise of megafaunal populations. Giant deer on Ireland became extinct coincident with a major shift in vegetation, pointing to habitat loss as the cause of local extinction (Barnosky 1986). Guthrie (2004) argued that postglacial sea-level rise made Bering Sea islands too small to sustain mammoth populations.

In summary, climate and habitat change affect geographic ranges and population density, and so plausibly may affect the extinction vulnerability of animals. On some islands, environmental change probably caused extinction. It is not clear, however, which megafaunal species would be most susceptible to specific environmental changes, or how population dynamics in susceptible species would translate into extinction in the late Quaternary. Contradicting the plausibility of environmental causes for extinction are island cases in which megafaunal extinction clearly followed first human contact, but did not result from earlier environmental change (Burney et al. 2004, Holdaway 1999).

Are the Assumptions of Environmental Hypotheses Correct?

Dietary assumptions about Pleistocene herbivores under environmental hypotheses can be tested with stable isotope data (Koch et al. 1994). Carbon isotope data can discriminate between diets rich in C_3 plants (trees, shrubs, cool-climate grasses) and those rich in C_4 plants (warm-climate grasses). In addition, animals feeding deep under closed canopy forests may have especially low carbon isotope values. The strong resource partitioning among herbivores assumed under CED is supported by isotopic studies from the United States. (**Supplemental Table 3**). For example, the three North American proboscidean genera all had very different diets, as did the three camelids. In contrast, proboscideans in South America seem to have had less specialized diets containing a broad mix of both C_3 and C_4 plants (Prado et al. 2005), which is in line with the dietary assumptions of the MNH, but does not support the assumptions of CED.

LGM: last glacial maximum

Other key assumptions of the CED, MNH, and HLH are unverified. These hypotheses assume that local plant diversity was higher in Pleistocene biomes, and that Holocene biomes were more homogeneous with vast tracts of forest or grassland or tundra rather than more integrated biomes with a mix of vegetation types. Compelling pollen or macrofloral evidence that Pleistocene biomes had higher alpha diversity than Holocene biomes is lacking. In some regions, such as the eastern United States, Alaska, and northern Eurasia, there is evidence that Holocene forests replaced the more open vegetation that dominated under full and late glacial climates. However, robust paleoecological reconstructions of the structure of Pleistocene biomes are in their infancy (e.g., Williams et al. 2000). As this work proceeds, vertebrate paleoecologists should push for inferences about changes in plant alpha diversity, functional type, growing season, antiherbivore defenses, and net primary production.

Chronologic Tests of Environmental Hypotheses

Given the unusual nature of the LQE, most environmental hypotheses require that climate or ecosystem structure at the time of extinction was unusual relative to conditions earlier in the Pleistocene. Therefore it is important to look beyond the Last Glacial Maximum (LGM), recognizing that Pleistocene faunas survived many earlier events only to succumb during the most recent glacial-interglacial transition. Barnosky et al. (2004b) offered a more complete discussion of climatic and vegetation changes associated with the LQE; we summarize their conclusions here.

Benthic marine oxygen isotope records, which chiefly record the waxing and waning of continental ice sheets (Raymo 1994), show that the most recent deglaciation was neither more rapid nor of greater magnitude than other shifts in the past million years (**Figure 3**). The Holocene is not (yet) the most extreme deglaciation; the LGM, while extreme, was similar to several prior glacial advances. Climate shifts around the Americas and Eurasia at the time of extinction, as measured by continuous records of ocean surface temperature, were large but not unusual (**Figure 3**). Even if one accepts the younger dates for the LQE in Australia, it preceded the LGM, at a time when ocean records are almost invariant. There is evidence from Australian lake records that the LQE occurred during a prolonged arid interval (Magee et al. 2004), but it is not yet clear if this aridity was unusual relative to earlier time intervals. Finally, Johnson (2005) has noted that late, contested megafaunal sites occur in a range of habitats; they are not restricted to more mesic, coastal sites as expected if aridity in the Austrialian interior was the dominant factor driving extinction.

Multivariate analysis of pollen records from around the globe show that in Europe, northern Asia and the Americas, the LQE occurred at a time when vegetation was changing rapidly, but that the situation is less clear for Australia (Barnosky et al. 2004b). Tests of the uniqueness of floras at the LQE are possible with long, high-resolution pollen records spanning more than one glacial cycle. Few such records are publicly available on pollen databases for quantitative analysis, but from inspection of published records it appears that floras of prior interglacials were similar to those of

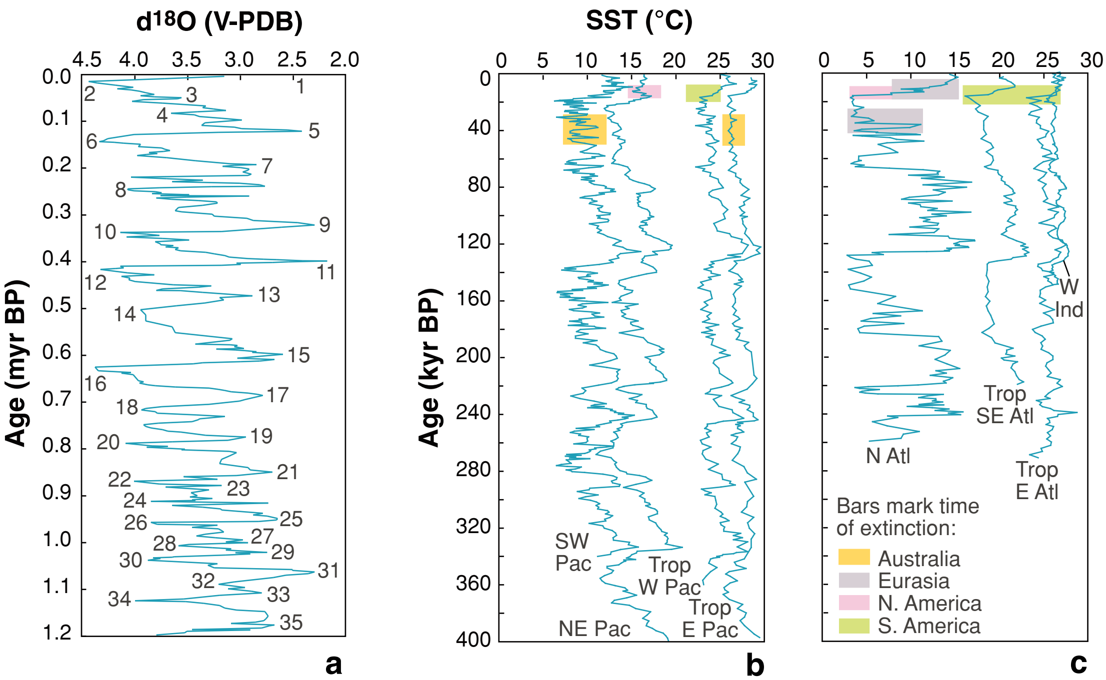


Figure 3

(*a*) Oxygen isotope data from benthic foraminifera at North Atlantic DSDP site 607. Numbers refer to marine isotope stages (MIS). The majority of well-constrained extinctions and drops in abundance occurred in MIS 2 and 3. (*b*) and (*c*) Sea surface temperature (SST) records from the Pacific and Atlantic/Indian Oceans, respectively. Colored bars indicate the time of extinction on nearby continents. Core location, core label, and type of SST estimate: northeast Pacific, ODP 1020, alkenone; tropical east Pacific, TR 163–9, Mg/Ca; tropical west Pacific, ODP 806B, Mg/Ca; southwest Pacific, MD 97–2120, Mg/Ca; west Indian, MD 85674, alkenone; north Atlantic, K 708–1, foraminiferal transfer function (average of August and February); tropical east Atlantic, GeoB 1112, Mg/Ca; tropical southeast Atlantic, GeoB 10,285, alkenone. For core K 708–1, ^{14}C ages were converted to calendar years. All other age models are as reported in primary publications. Modified from figure 2 in Barnosky et al. (2004), where primary citations for data are reported.

the Holocene, and that rapid transitions in floral composition are typical of glacial-interglacial transitions. So far, no evidence has shown that the states or rates of change in vegetation or climate at the time of the LQE were unprecedented relative to earlier in the Pleistocene. Finally, records of floral change in regions that did not experience strong extinction in the late Pleistocene (e.g., Thailand, New Zealand) vary as much as records from places that did (e.g., eastern North America).

HLHs assume that preferred habitats for extinct species shrank just before the extinction. Two recent studies cast doubt on this assumption for extinct North American megafauna. To explore the relationship between ecosystem change and herbivore abundance, Robinson et al. (2005) studied the concentration of pollen and spores of the dung fungus *Sporormiella* (a proxy for megafaunal biomass) at mastodon and stag-moose fossil sites in southeastern New York. Drops in *Sporormiella* (and presumably megafaunal) abundance spanned a millennium. At most sites, megafaunal abundance dropped as spruce was rising in abundance or dominant, falsifying the hypothesis of King & Saunders (1984) that linked the disappearance of mastodons to the loss of spruce forest habitats. The abundance-drop also preceded the homogenization of floras at the beginning of the Holocene, falsifying the MNH of Guthrie (1984) for this region. Martínez-Meyer et al. (2004) took a more theoretical approach. They modeled where the climate-space occupied by eight Pleistocene mammal species would occur on the present landscape and concluded that niche-space for six of the extinct species actually increased in the Holocene. For the other two, it did not decrease enough to explain their extinction by habitat loss alone.

Do Environmental Hypotheses Explain the Selectivity of the Late Quaternary Extinction?

The determinants underpinning extinction selectivity are coming into focus. In a study of mammalian victims and survivors in Australia, Eurasia, the Americas and Madagascar, Johnson (2002) used clade-specific allometric relationships to estimate reproductive rates. In the nine groups he studied, the species with low reproductive rates had high probabilities of extinction, regardless of their body size. The probability of extinction exceeds 0.5 when the reproductive rate is $\leq$1 offspring per female per year. For all surviving mammals in these regions that reproduce this slowly, most live in arctic, alpine, or deep forest habitats or are arboreal or nocturnal; only three surviving slow breeders lack all these traits. Because large body size is correlated with slow breeding, large animals would be more susceptible to extinction under any environmental or anthropogenic impact that targeted slow breeders. Environmental causes could explain the survival of alpine or deep-forest animals if those habitats increased at the last glacial-interglacial transition. However, it is difficult to explain why extinction susceptibility would be lower for nocturnal or arboreal animals under a model that invokes environmental change as a sole cause of the LQE.

Among herbivores, extinction is not related to diet in any simple way. In North America, where the most isotopic data on diet are available, victims include grazers (mammoths) and a wide range of browsers (antilocaprids, a musk-ox-like bovid, camelids, tapirs, peccaries, stagmoose, mastodons) (**Supplemental Table 3**). CED predicts that herbivores with very broad dietary tolerances would fare better than those with highly specialized diets, yet animals with little dietary specificity (e.g., *Camelops*, *Hemiauchenia*, *Equus*) were victims. The MNH gains support from the observation that the animals with the most extreme diets survived (e.g., *Bison*, the end-member for grazing, and *Odocoileus*, an end-member for browsing). If floras did become more homogeneous locally, with uninterrupted stretches of forest, grassland or tundra, we might expect these "hyper"-grazers and "hyper"-browsers to be favored. Some researchers have argued that environmental change (either natural or anthropogenic) led to a loss of woodland and shrubland in Australia, preferentially impacting browsers. Yet a recent study revealed that large browsers and grazers were victims of the LQE in proportion to their species abundance prior to the extinction (Johnson & Prideaux 2004); the extinction did not preferentially target browsers.

Body size decreased near and across the Pleistocene-Holocene boundary in victims and survivors of the LQE (Guthrie 1984, 2003; King & Saunders 1984). Size reduction has been viewed as evidence for nutritional limitation under "decaying" environmental conditions. For example, in the relatively small giant deer from Ireland, nutritional stress prior to extinction is indicated by the small antlers relative to body size (Barnosky 1985, 1986). However, populations that lingered into the early Holocene on the Isle of Man seem not to have been nutritionally stressed, judging by their antler proportions (Gonzalez et al. 2000). Body size decreased in many taxa in prior warm intervals (Kurtén 1968) and it is unclear if the magnitude of size reduction in the Holocene is unusual. Finally, size reduction is also a possible outcome of selection by human predators if they preferentially targeted large animals either because of added food payoff or as trophies (e.g., Olsen et al. 2004). The overall lesson is that body-size arguments are complex. Depending on the situation, they can support environmental hypotheses or anthropogenic impacts or simply indicate ecophenotypic variation of little consequence to extinction per se.

When the LQE debate heated up in the 1960s, little information existed on mammal communities of earlier Pleistocene times outside Europe. In Europe, cold-stage faunas, which include reindeer, arctic lemming, mammoth, and woolly rhinoceros, alternated with warm-stage faunas, which include wild boar, giant Irish deer, red and fallow deer, straight-tusked elephants, and different rhinoceroses (Stuart 1991, 1999). Holocene faunas differ from earlier warm interval faunas only in their lack of typical large community members. Records of mammalian community response to prior glacial-interglacial transitions outside of Europe reveal that diversity and the size, trophic, and taxonomic structure of communities changed more from the late Pleistocene to the late Holocene than they had in the previous million years (Moriarty et al. 2000, Barnosky et al. 2004a). The climatic shifts that precipitated faunal change at earlier glacial-interglacial transitions more strongly affected lower size and trophic categories. In contrast, at the time of the LQE, the range shifts and abundance changes at lower size and trophic levels, which were similar to those at earlier transitions, were accompanied by megafaunal extinctions.

On balance, it is not possible to explain many aspects of the LQE solely by existing environmental hypotheses. Some selectivity with respect to diet matches expectations of the mosaic-nutrient and habitat loss hypotheses, but key assumptions about floral change underpinning these models are unverified. At a continental or global scale, there is little evidence for the complete elimination of favored habitats. Indeed, existing models suggest expansion of favored climate-space. No environmental hypothesis has explained why the last glacial-interglacial transition should have spared slow-breeding arboreal or nocturnal mammals. Finally, there is no compelling evidence that the last glacial-interglacial transition was so different from previous ones that wholesale extinction of megafaunal species would result, in view of the fact that those species had survived many previous glacial-interglacial transitions.

The conclusion that existing environmental hypotheses are unable to explain many aspects of the LQE does not mean that environmental change did not contribute to the extinction. Climate has shifted dramatically over the past 50,000 years, and the geographic ranges, abundance, and morphology of both large and small mammals have changed in response. Some regions did become inhospitable to prior inhabitants. For example, the replacement of steppe grasslands with tundra and forest in parts of Beringia must have been detrimental to grazers. While environmental drivers seem inadequate as a total explanation for the LQE, they in fact seem necessary to explain some details of the event, particularly the timing and magnitude at a regional level.

Future Work on Environmental Impacts on Extinction

Progress on environmental contributions to the LQE will require a more quantitative approach. As biome reconstructions yield more detailed information on factors of import to herbivores, quantitative models of animal energetics and foraging must be used to test whether Pleistocene biomes were more capable of sustaining large mammals than early Holocene biomes (Matheus 1997, Moen et al. 1999). Methods to study population viability in parks and preserves can be applied as well. O'Regan et al. (2002) applied the VORTEX model, which inputs life history data and tracks the fate of animal populations, to assess the minimum range needed to sustain a large carnivore (*Panthera gombaszoegensis*) in southern Europe during glacial intervals. They concluded that Mediterranean islands were too small; persistence for >1 kyr required an area equivalent to the Italian peninsula. A similar approach could be used to ask whether range restriction to northern Siberia in the Holocene would be fatal for cold-stage mammals. Studies such as that by Martínez-Meyer et al. (2004) should illuminate the extent to which niches may or may not have been reduced for many species.

The extraction of mitochondrial DNA (mtDNA) from Quaternary fossils is becoming a reliable source of information on extinct populations and species (Hadly et al. 1998, Wayne et al. 1999). Phylogeographic studies of Pleistocene brown bears (*Ursus arctos*) from Alaska and Canada point to geographic shifts that precede the arrival of humans, suggesting a role for environmental change and/or interactions with competitors or diseases arriving from Asia (Barnes et al. 2002, Leonard et al. 2000). Paleogenetic data potentially can clarify if the typical response of Pleistocene populations to environmental change or human occupation is a regional demographic crash (Shapiro et al. 2004, Drummond et al. 2005), especially when treated in the context of newly developing phylochronologic techniques (Hadly et al. 2004). An understanding of the demographic consequences of climate change is central to any explanation for large mammal extinction.

An idea meriting further exploration is that ecological threshold events can cause dramatic restructuring of ecosystems (Scheffer et al. 2001). In concept, coevolutionary disequilibrium is such a model, but it has been presented in only qualitative terms. Forster (2004) has taken the threshold concept further by exploring the idea that the Australian extinction reflects the collapse of a system poised at a critical state and "pushed over the edge" by the arrival of humans with their catholic diets. To paraphrase Solé et al. (2002), highly diverse ecosystems may be poised at the cusp between stable and unstable states because of the tension between a tendency toward higher diversity (due to immigration and speciation) and the constraints on diversity imposed by the increasing numbers of ecological links, a process he called SOI. SOI makes predictions about the time series behavior of communities that could be tested. Furthermore, simulations suggest that SOI will be a property of highly diverse ecosystems (tropical forests, coral reefs); it is unclear if such dynamics would characterize more species-poor temperate and boreal systems, or if they can explain the size-selectivity of the LQE.

HUMAN IMPACTS OTHER THAN HUNTING

Three indirect anthropogenic impacts have received attention as potential agents of extinction: habitat alteration, introduced predators, and "hyperdisease." By indirect impacts we mean anthropogenic influences other than intentional killing of prey. We also note that habitat alteration might involve habitat loss, in which niches disappear, or habitat fragmentation, in which critical niches remain but are reduced in extent and connectedness.

Human habitat alteration by clearing land and the use of fire is a factor in Holocene extinctions on islands (Burney et al. 2004, Diamond 1984, Steadman & Martin 2003). Flannery (1994) and Miller et al. (1999, 2005) extended this idea to Australia, arguing for more frequent intense fires after the LQE as fuel loads rose with the loss of herbivores and as Aboriginal people began to use fire. The primary evidence for habitat alteration comes from abundance shifts in pollen records and dramatic increases in charcoal abundance (Edwards & Macdonald 1991). The coincidence of such shifts with faunal loss supports the role of habitat alteration in many island studies. The Australian case is more difficult because of chronologic problems, inconsistencies among charcoal records, and debate as to whether charcoal spikes are natural or anthropogenic (Bowman 1998). Robinson et al. (2005) extended these ideas to eastern North America, noting that the concentration of charcoal (indicating human-set fires) increased after the megafaunal dung spore *Sporormiella* dropped in abundance. It is not clear, however, that this increase in fire use led to major habitat alteration; to our knowledge, there is no evidence for extensive, anthropogenically driven habitat alteration in the Americas coincident with the LQE.

When humans arrived on the Pacific islands, they brought along pigs and dogs, and inadvertently introduced rats, all of which functioned as new predators. The impacts on island faunas were immense. Many islands lacked terrestrial predators and thus had faunas that were both behaviorally and evolutionarily naïve to being preyed upon (Wroe et al. 2004). The main islands of New Zealand lost 60% of their avifauna in the last 2000 years. Holdaway (1999) conducted an elegant analysis of this extinction, considering both the ecology of the prey and the time of arrival and ecology of potential predators. He argued that the avifauna was sequentially stripped of species that were most susceptible to newly arrived predators (e.g., rats, humans, dogs, etc.).

The role of introduced nonhuman predators in Australia and the Americas is less clear, but seems too small to explain the LQE. Those regions had native terrestrial carnivores, so prey would not have been highly naïve. Dingoes did not reach Australia until 3.5 kyr BP, long after the LQE (Johnson & Wroe 2003). Domestic dogs must have come to the New World with humans, but the time of their arrival is a question. The oldest archaeological evidence for domestic dogs in the New World dates from 9–10 kyr BP, after the first appearance of abundant humans (12–14 kyr BP) and after the LQE, though Fiedel (2005) makes cogent arguments that dogs were present earlier. In any case, coyotes and wolves preyed on North American megafauna for at least one million years prior to the LQE (Anderson 2004), so the introduction of domestic, pack-hunting canids is unlikely to have significantly affected the predator-prey balance, absent their use in hunts coordinated by humans.

Hyper-disease hypothesis: extinction results from introduction of hypervirulent, hyperlethal diseases to immunologically naïve species on first contact with humans and associated fauna

MacPhee & Marx (1997) explored a third indirect-effect hypothesis, that extinction might result from the introduction of hypervirulent, hyperlethal diseases (hyperdiseases) to immunologically naïve species in the Americas and Australia on first contact with humans and their associated fauna (hyper-disease hypothesis; HDH). To cause the sudden collapse of so many species, such diseases would have to have reservoir species in which they are not fatal, be an entirely new pathogen on the affected landmasses, kill infected species rapidly, spread by vectors other than reproductive behavior, and "jump" species easily.

We do not favor the hyperdisease idea for several reasons. First, such extremely lethal, cross-species pathogens are not known today. Perhaps the closest analog is West Nile virus, which recently invaded North America and infects many bird species and humans. West Nile virus has not yet led to extinctions, and if they do occur, they are highly unlikely to show the phylogenetic diversity and strong size-bias of the LQE (Lyons et al. 2004b).

Second, at the time of the LQE, North and South America were not isolated continents. Faunal exchange among North America, Eurasia, and Africa occurred throughout the late Cenozoic (Woodburne & Swisher 1995), and the Americas have exchanged taxa for the past 4 million years. MacPhee & Marx (1997) recognized that regular exchange rules out typical animal-borne diseases. For hyperdisease to be a viable mechanism, they argued it would have to be hosted or transmitted by humans or their associates, have emerged just before human dispersal to Australia, and have then disappeared or lost virulence.

Third, rapid extinction immediately postcontact (within a few generations) is required under the hyperdisease model. Evidence for human arrival in the Americas thousands of years prior to the LQE (discussed below) would falsify this model in the Americas.

In summary, none of the indirect-effect models makes strong predictions regarding the size-selectivity of extinction. While anthropogenic habitat alteration and/or human-introduced predators were factors in many island extinctions, and may have contributed to Holocene extinctions in Australia, it is unlikely they were dominant causes of the LQE in the Americas and Australia. Finally, while diseases transmitted from humans and associated fauna might have contributed to population declines in some species, the hyperdisease model seems implausible as a general explanation for the LQE.

OVERKILL HYPOTHESES

Under overkill hypotheses, extinction occurs because hunting causes death rates to exceed birth rates in prey species. Period. Hunters need not be large game specialists, or gain most of their calories from hunting. Most deaths in the victims need not be due to hunting; hunting merely adds to the cumulative number of deaths by some critical amount. The extinction could be sudden or gradual. It could happen at first contact with humans or after millennia of interaction. This wide range of possibilities does not make overkill untestable. Rather, it requires the framing of specific overkill models with quantitative parameters and predictions about people and their prey that can be compared with data.

Blitzkrieg hypothesis: human geographic expansion and population growth fueled by large game hunting leads to rapid extinction

Prey naïveté: failure of prey species to recognize the threat presented by new predator species or to respond by fight or flight

The blitzkrieg hypothesis has been the focus of much debate and testing (Martin 1973, Mosimann & Martin 1975). Under blitzkrieg, extinction at a continental scale occurs rapidly, within 500 to 1000 years, due to human geographic expansion and population growth fueled by intense predation on large game. Early versions called for extinctions to travel in a wave across the landscape from the point of first human arrival, with extinction at a local scale occurring in decades rather than centuries, but later models relaxed this constraint (Whittington & Dyke 1984). Blitzkrieg assumes high kill rates are possible because naïve prey lack behavioral and evolutionary adaptations to escape human predation. Martin (1973) viewed blitzkrieg as a solution to two perceived problems with the overkill hypothesis. First, prey naïveté was invoked to explain why the magnitude of extinction was high in the Americas and Australia, but low in the region of human origins, Africa and Eurasia. Second, Martin speculated that because the interaction between humans and extinct prey would have been brief, blitzkrieg explained why so few archaeological sites in the Americas and Australia contain extinct fauna.

Plausibility of Overkill Hypotheses

Hunting by nonindustrial humans has been a factor in the extinction of island endemics and populations of marine birds and mammals (Diamond 1984). These societies may maximize their short-term harvesting rates without regard for the long-term sustainability of prey, and take highly ranked prey if they are encountered, even after they have become rare (Alvard 1993, Winterhalder 2001). Extrapolating the behaviors of extant hunter-gatherers to prehistoric humans is problematic, however, given that prehistoric environments differed from anything today, that modern hunter-gatherers have been limited to relatively unproductive landscapes that are not suitable for agriculture, and that human behavior and material culture have evolved.

Some researchers are skeptical that humans armed solely with stone and wood tools could hunt large animals to extinction. All acknowledge, however, that the weapons carried by late Pleistocene humans in Eurasia and the Americas could be used to hunt megafauna because stone points have been found in the body cavities of extinct species (Grayson & Meltzer 2002). The efficacy of the tool kit carried by early Australians is a greater question (Wroe et al. 2004). Stone spear points and dogs, which are used by modern hunter-gatherers that take large megafauna (>300 kg), were not present in Australia until the mid-Holocene. Proponents of overkill suggest the early Australians may have used wooden weapons, but these are less lethal than stone tipped spears. Finally, unlike the situation in Eurasia and the Americas, there are no sites with extinct megafauna that were clearly killed by humans, and only one site where extinct mammalian megafauna are associated with stone artifacts. These observations cast doubt on the plausibility of overkill in Australia, but are insufficient to falsify the hypothesis.

Simulations of Overkill: Single-Species and Related Models

Simple predator-prey models offer insights into the plausibility of overkill. Many simulations treat prey as a single species, with population parameters (initial biomass, replacement rate [r], and carrying capacity [K]) that are varied in sensitivity analyses (**Supplemental Table 4**). Human population dynamics are either modeled using parameters (initial biomass, r, K, migration rate) that respond to prey population size, or else population densities are set at fixed values that are varied in sensitivity tests. In some models, hunting efficiency is varied as well, and prey can lose naïveté.

Many early simulations with coupled human and prey population dynamics yielded overkill; however, stability analyses suggested that extinction was a mathematically inevitable outcome of these models (Belovsky 1988). Several simulations with uncoupled human and prey population dynamics counter-intuitively found that overkill was less likely for large, slow-breeding prey, perhaps because they fixed human population densities at a very low value or assumed that hunting efficiency dropped as this single prey became rare (Brook & Bowman 2002, Choquenot & Bowman 1998).

Single-prey simulations implicitly assume that humans are switching to alternate resources as prey become scarce, but they do not consider the properties of these resources that might make overkill more or less likely. Winterhalder & Lu (1997) developed multiprey simulations based on optimal foraging theory with coupled human and prey population dynamics. In these simulations, if large prey are present, they are always part of the diet; if they breed slowly, they go extinct when other, rapidly reproducing prey are available. Humans in these simulations take large prey when encountered, but are sustained by fast-breeding, “fall-back” prey such as tubers or small animals. Belovsky (1988) constructed an optimal foraging model to examine the demographic consequences of differences in nutrition when humans consumed hunted versus gathered resources. He found that prey extinction increased as primary production rose (i.e., when gathered foods become more abundant). Prior to prey extinction, people in high productivity environments had a smaller percentage of meat in their diets than people in low productivity environments, but humans were so abundant that prey extinction was likely.

These simple models offer a key insight that has not received enough consideration in the overkill debate. Extinction of prey due solely to overkill is highly unlikely if human diets are composed of a just few types of hunted megafauna. Such human populations will exhibit boom-bust dynamics that follow those of their prey. The most likely outcome in such situations is that human populations will go extinct, not prey populations. For large, slow-breeding animals, the most dangerous predators are omnivores who are sustained by small game and gathered food. A conclusion from these foraging models is that the traditional view of overkill, which attributes extinction to voracious predation by Pleistocene humans who specialized in hunting large game, is flawed, as are attempts to falsify overkill by noting that late Pleistocene humans had broad diets. Indeed, a recent study of the potential for megafaunal specialization by North American Paleoindians in a quantitative, optimal foraging framework suggested that foragers should have taken a wide array of taxa including not only proboscideans, but also ungulates and smaller game (Byers & Ugan 2005).

Models and Prey Naïveté

Wroe et al. (2004) critiqued the idea that prey naïveté in the Americas and Australia would have been great enough to permit blitzkrieg. Completely naïve prey that fail to protect themselves or flee from a predator are restricted to remote islands that lack all large terrestrial carnivores. Such island species can have deeply rooted behaviors (e.g., ground nesting) that place them in peril when terrestrial predators arrive. They may also have morphological adaptations (e.g., flightlessness) that leave them vulnerable. On continents with carnivores, such morphological and behavioral adaptations are rare, and potential prey soon learn to flee from new predators (Berger et al. 2001). Given the long history of predator-prey interactions in the Americas and Australia, we agree that it is unlikely that megafauna would have remained naïve very long to newly introduced predators, even ones as clever as humans. Prey naïveté might have had some impact if the response to predators did not involve flight or hiding, but rather grouping or fighting [as Martin (2005) suggests for ground sloths]; these tactics would not be effective when facing armed humans.

Brook & Bowman (2002) critiqued models that do not allow predators to develop antipredation strategies. This criticism is valid for single-prey simulations (as predator avoidance would make the single prey increasingly difficult to locate), but is of less concern for multiprey simulations, in which predators take rare, predator-shy prey encountered incidentally while hunting more abundant prey.

Tests of Overkill with Realistic Predator-Prey Models

Models show what is possible, not what actually happened. Ideally, they establish quantitative predictions constrained by input parameters that portray reasonable assumptions about starting points and “rules” that govern the process under examination. The most useful models are those that clearly specify the input parameters, how robust the predictions are in terms of statistical probabilities, and how predictions can be tested against archaeological or paleontological data. It is the iterative feedback between what models predict and what the data actually say that gives both models and data meaning. For example, arguments about the number of kill sites in the fossil record have been used to support (Mosimann & Martin 1975) or refute (Grayson & Meltzer 2003) blitzkrieg. None of these arguments is robust in the absence of a clear statement of how many kill sites would be expected given the total number of appropriately aged sites, probabilities of fossil preservation derived from firm taphonomic studies, and realistic quantitative models of human-faunal interactions that include multiple species.

Quantitative predator-prey models have proven useful in studying the extinction of particular species, such as Eurasian mammoths, moas in New Zealand, or megafauna in northern Australia (**Supplemental Table 4**). The most comprehensive model coupled human and prey population dynamics to simulate predation on 41 large species and an undifferentiated secondary resource (plants, small game) in North America (Alroy 2001b). Hunting efficiency, the geography of invasion, and competitive interactions were varied, and all simulations assumed that hunters nonselectively took prey as encountered. Overkill occurred for a range of parameter values, although an error in the parameterization of prey r values makes it difficult to assess these results (Slaughter & Skulan 2001). In a recalculation of the best-fit trial with appropriate r values, the model correctly predicted the fate of 34 out of 41 species, with a median time to extinction of 895 years (Alroy 2001a). In that trial hunters obtained 30% of their calories from large mammals and occurred at densities of 28 people per 100 km^2, both within the range of values for modern hunter-gatherers. As in more generalized optimal-foraging models, the key to overkill was a relatively high human population density subsidized by smaller, faster-breeding prey. Hunting ability matters too, with greater hunting success leading to greater extinction rates, but overkill occurred even when success rates were fairly low.

This realistic simulation is an elegant first step, but interpretation of its results is complicated by assumptions about prey dispersal, geographic range, and carrying capacity that should be subject to sensitivity tests. More realistic models would allow for variation in primary production across the modelled landscape and through time and for feedbacks between primary production and prey population dynamics and would explore selective hunting strategies. New models could make explicit predictions for the archaeological record by calculating the fractions of individuals that die at human hands and, given plausible estimates of preservation potential, how many of these bodies are likely to be found and recognized as cases of human predation.

Chronologic Tests of Overkill

A linchpin of the overkill argument is the purported synchrony of the first appearance of substantial numbers of technologically sophisticated humans with the last records of megafauna (Martin & Steadman 1999). For Holocene extinctions on islands, the pattern is crystal clear; island ecosystems collapse following contact with humans, though the timescale may vary from centuries to millennia, depending on differences in abiotic, biotic, and cultural factors (Rolett & Diamond 2004, Steadman & Martin 2003). Many continental extinctions are now dated with enough security to know that they too occurred postcontact.

In North America south of the Laurentide ice sheet, at least 15 species became extinct coincident with the appearance of Clovis-style tools (13.5 kyr BP to 11.5 kyr BP) near or in the Younger Dryas climate event (Grayson 2006, Grayson & Meltzer

2003) (**Figure 2**). Debate continues about pre-Clovis humans in the Americas, but there is no evidence for large numbers of people before Clovis times (Fiedel & Haynes 2004). In South America, humans were present in coastal Chile and Patagonia at 15.5 kyr BP to 14.8 kyr BP (Alberdi et al. 2001, Meltzer et al. 1997), and sites younger than 11.5 kyr BP are common across the continent (Dillehay 2000). It seems clear that the megafauna went extinct in the late Pleistocene, probably after humans arrived, but comprehensive analyses are needed.

Humans or their predecessors have been in Eurasia for 2 million years, with good evidence for predation on large game back to 400 kyr BP (Thieme 1997). This chronology falsifies blitzkrieg, but other human impacts cannot be rejected. The pre*sapiens* hominins who lived and hunted in Europe from 400 kyr BP to 50 kyr BP without inducing extinctions had simple tools, and isotopic data suggest they were highly carnivorous with diets focusing on large open country herbivores, such as mammoths and woolly rhinoceros (Bocherens et al. 2005); they may have waxed and waned in response to changes in their prey (Kuhn & Stiner 2001). In contrast, the first megafaunal extinctions beginning 45 kyr BP roughly coincide with the arrival and spread across Europe of anatomically modern humans (*Homo sapiens sapiens*), with their diverse suites of tools and broad diets (Mellars 2004). The extinctions and population crashes that began 14 kyr BP may be associated with a rise in population densities at the end of the glacial interval (Bar-Yosef 2002).

As discussed above, the timing of megafaunal extinction in Australia remains contentious. Humans arrived sometime between 72 and 44 kyr BP (Brook & Bowman 2002). If we accept the earlier dates for extinction (50–40 kyr BP), then human arrival and megafaunal extinction roughly coincide. If the younger dates for extinction are correct, then extinction is temporally decoupled from the first appearance of humans. Either way, the seemingly long period of overlap between megafauna and humans casts doubt on blitzkrieg.

Africa is the continent of origin of *Homo sapiens*, and many human ancestors. *Homo sapiens* appeared in Africa 195 kyr BP (McDougall et al. 2005), long before the few poorly dated Pleistocene or better-dated Holocene extinctions.

Archaeological Tests of Overkill

The harshest critiques of overkill have come from archaeologists, who argue there is no "empirical" evidence of overkill in the Americas and Australia. Thousands of diagnostic fluted points are known from the late Pleistocene of North America, but our understanding of human-megafaunal interaction and human diets are based on a few dozen sites (Haynes 2002b). There are large regions of the United States that had people for which we have no archaeofaunal evidence at all (Waguespack & Surovell 2003). This sparse record reflects a bias against bone preservation (e.g., southeastern United States) and a lack of study.

A recent rigorous vetting of putative human-megafaunal interaction required either unambiguous association of megafauna with Clovis artifacts or clear evidence of bone modification by humans (Grayson & Meltzer 2002). Using these criteria, four extinct genera were recognized as being hunted by humans in North America

(*Mammuthus*, *Mammut*, *Equus*, and *Camelops*) at 14 sites. The culling excluded ~50 other putative associations of humans with *Mammuthus* or *Mammut*. Also excluded were sites where megafaunal bones or ivory were fashioned into tools (Haynes 2002b), because this material could have been scavenged. More lax definitions of association suggest that late Pleistocene humans in North America regularly hunted large game (Haynes 2002b, Waguespack & Surovell 2003).

Even with its holes, the North American record is much better known than those of South America, Australia, Africa, and much of northern Asia. Haynes (2002b) notes there are fewer than a dozen well-documented proboscidean kill sites in Africa older than mid-Holocene. In South America, evidence for use of extinct megafauna by humans exists at a few sites (Fiedel & Haynes 2004, Meltzer et al. 1997), and associations of artifacts and extinct megafauna are generally accepted, although the criteria for accepting associations is not consistently specified (Dillehay 2000, Scheinsohn 2003). In Australia, there is no evidence for human butchery of extinct megafauna (Mulvaney & Kamminga 1999) and only one site (Cuddie Springs) has lithic artifacts associated with extinct megafaunal mammals (Field & Dodson 1999).

Is it possible to assess the claim that the paucity of kill sites falsifies overkill? Even with a quantitative model of overkill, we do not know the probability of a kill site being preserved. Barnosky et al. (2004b) used the FAUNMAP database to explore this issue for North America. Humans became abundant there in the late glacial period. Roughly 25% of the mammoth sites from this interval have firm archaeological associations (as vetted by Grayson & Meltzer 2002**)**. Barnosky et al. (2004b) tested whether other late Pleistocene mammals have rates of archaeological association significantly different from that of mammoths (**Table 3**). A chi-square analysis showed that for many taxa, even complete absence from archaeological sites does not refute the hypothesis of human association at the same frequency as accepted *Mammuthus*-human associations. Put another way, the apparent paucity of archeological associations with most taxa is not strong evidence that humans did not hunt them. Rather, it reflects that there are few well-dated late glacial sites—either with or without archaeological associations—that preserve extinct mammals other than mammoths. There were two exceptions. *Mammut* and *Platygonus* were significantly less frequently associated with humans than were mammoths, suggesting that humans probably hunted them less. For *Mammut*, this situation would be reversed if some of the many putative *Mammut* butcher sites were better documented. For *Platygonus*, there are few sites with even potential archaeological associations, so the result seems solid.

The frequency of late glacial North American mammoth sites accepted to be in archaeological association is quite high (25%). If these sites do represent kills, and if killing was a new mode of death, it would indicate a 30% rise in mortality. Megafauna can increase their intrinsic rate of increase or survival (which allows more offspring) when food is abundant, as might occur when hunters thin the herd (Fisher 1996). It is unlikely, however, that they could tolerate such a high level of new mortality unless it was strongly skewed toward males. That said, we emphasize that biases in site preservation, discovery, and description make it very unwise to assume anything about the fraction of animals taken by hunting from site or carcass counts at this point.

Table 3 Clovis-age kill-sites and total number of late-glacial occurrences of some extinct mammals documented in the FAUNMAP database

Taxon	# of kill sites[a]	Total # of late-glacial sites[b]	Ratio of kill sites to all sites	X^{2c}
Arctodus	0	8	0	0.15
Camelops	1	15	0.06	0.17
Capromeryx	0	1	0	0.61
Equus	2	17	0.11	0.30
Glossotherium	0	8	0	0.15
Hemiauchenia	0	5	0	0.25
Holmensina	0	3	0	0.37
Mammut	2	68	0.03	**0.001**
Mammuthus	12	45	0.25	
Megalonyx	0	4	0	0.31
Platygonus	0	16	0	**0.05**
Smilodon	0	3	0	0.37
Tapirus	0	6	0	0.21

[a] Sites with robust evidence for human predation (Grayson & Meltzer 2002).

[b] All late-glacial age (18.5–10.5 kyr BP) sites with the genus contained in the online FAUNMAP database (**http://museum.state.il.us/research/faunmap**), except *Tapirus*, which is from published literature (FAUNMAP Working Group 1994).

[c] Chi-square probability that the ratio for the genus is the same as the ratio for *Mammuthus*. Bold text indicates significantly fewer archaeological associations than expected relative to *Mammuthus*.

Archaeological data can sometimes reveal causes of extinction. For example, on some islands, large accumulations of bones from vulnerable prey occur in archaeological middens immediately after first contact (Holdaway & Jacomb 2000, Steadman & Martin 2003). This is compelling evidence of overkill. Such examples usually are found where faunas lacked bone-crushing scavengers and the extinction was mid- to late Holocene. The LQE in Australia and the Americas occurred much earlier, and in the Americas, bone crushers were present. It is unreasonable to expect catastrophic assemblages representing the last generations of extinct fauna in these regions.

The archaeological record has also revealed cases where prey species were depleted over an interval of time. Signs of prey depletion include a drop in ratio of high-yield prey relative to low-yield prey, increased human diet breadth, and a size decrease in prey species with indeterminate growth (Grayson 2001). Demonstration of prey depletion requires large samples spanning multiple time intervals, typically generated at stable residential or food processing sites. People in the Americas at the time of the LQE were highly mobile. Most late glacial archaeological sites are interpreted as briefly occupied hunting camps with relatively sparse faunal data (Kelly & Todd 1988), and thus are not amenable to study of resource depletion.

Testing Overkill with Data on Faunal Population Dynamics

Fisher (1987, 1996) has suggested an approach to test for the contributions of overkill and environmental change to proboscidean extinctions. Measurements of the thickness of annual growth increments in tusks may reveal key life history parameters, such as onset and shut down of reproduction and calving interval. When under nutritional stress, modern elephants mature later, cease reproduction earlier, and nurse longer (and thus increase the calving interval), all of which lead to reduced or negative population growth. In contrast, when resources are replete (often due to over hunting) elephants mature earlier, cease reproduction later, and wean faster (decreasing the calving interval). Thus overkill and environmental deterioration lead to mutually exclusive predictions regarding life history change. This approach requires further development and is labor intensive, but it may yield the "cleanest" answer about the fates of several key victims of the extinction.

Future Work on Overkill Hypotheses

More work is needed to refine the dates of first human contact and last records of megafauna, especially in South America and Australia. Consistent criteria for determining whether megafaunal remains were produced by human hunting need to be applied worldwide. Taphonomic work must focus on evaluating how fossil abundance relates to the relative abundances of animals, and on the probabilities of preservation of anthropogenically versus naturally generated carcasses. These are all daunting, long-term tasks.

Simulations may offer further breakthroughs if they are designed to address specific questions and yield predictions that can be tested with archaeological and paleontological data. Among questions that would be fruitful to explore are the following. Is it plausible that late Pleistocene North Americans, living at a density of 28 people per 100 km^2 and obtaining 30% of their calories from hunting large prey over 500 to 1500 years (Alroy 2001a,b), would leave such a sparse archaeological record for relatively abundant prey species other than proboscideans? Or is it possible that many prey species were not as abundant as overkill models assume, perhaps due to a climatically driven drop in carrying capacity? Can realistic models simulate the extinction of megafauna in Australia, where some researchers question whether human populations were ever large enough to drive overkill (Wroe et al. 2004), or the coexistence of humans and megafauna in Africa?

COMBINED HYPOTHESES

Various models have been proposed that require the confluence of anthropogenic, ecologic, and climatic phenomena.

Owen-Smith (1987, 1999) recognized the profound ability of megaherbivores to tranform landscapes, creating mosaic habitats that promote the diversity of other herbivores and carnivores. His Keystone Herbivore hypothesis posits that the loss of critical megaherbivores, either from overkill or climate change, would lead to shifts in vegetation and cascading negative impacts on other species. Zimov et al. (1995) offered a provocative version of this hypothesis, arguing that the Beringian climate permits two vegetational states, the soggy, moss-dominated, nutrient-poor tundra present today, and a drier, grassy, nutrient-rich steppe that characterized the

Pleistocene. They suggested that steppe vegetation was promoted by megaherbivore disturbance, and that the spread of tundra coincident with the Pleistocene-Holocene boundary was an effect of megafaunal extinction. Whatever its cause, widespread tundra was detrimental to grassland species such as bison and horses. One prediction of these models is that proboscideans, the most abundant megaherbivores, should disappear before major floral change and before the disappearance of other taxa. At present, data from Eurasia, Alaska, and probably central North America suggest proboscideans were among the last to go. However, drops in proboscidean abundance, not presence/absence, drive landscape change. Microstratigraphic analysis to estimate megafaunal herbivore abundance from dung spore abundance may offer a key test. In eastern North America, at least, it appears that megaherbivore abundance does drop well before final extinction and major floral reorganization (Robinson et al. 2005).

Late Pleistocene faunas had a diverse suite of extinct carnivores, many of which were larger than surviving carnivores. If humans began to reduce populations of preferred prey (e.g., proboscideans, sloths, etc.), or even scavenged the carcasses of megafauna, other carnivores might have intensified their predation on other herbivores (horses, peccaries, etc.). Terrestrial carnivores are certainly capable of prey switching on rapid timescales, though predator densities might drop if new prey were more difficult to hunt. It will be difficult to test this idea. Careful taphonomic analysis of predators from before and during the extinction event has revealed evidence for an increase in the intensity of carcass utilization (Van Valkenburgh 1993). This observation is consistent with the expectation of competitive interference with humans, but also with an environmentally driven drop in the abundance of prey.

A third possibility is that predator avoidance strategies limited Pleistocene mammals to unsustainably small geographic refuges that lacked humans. An observation that would support this idea would be the development of cryptic behaviors postcontact. The observation that most surviving, slow-breeding animals outside of Africa occur in habitats that humans have difficulty occupying at high density is consistent with this idea (Johnson 2002). An issue that has not been examined is whether late surviving populations of extinct species were restricted to small subsets of viable habitat (as demonstrated by their distribution in prior interglacials), or if the viable habitat from which they were absent had high human population densities in the late Pleistocene.

These combined models highlight that the extinction of any species is likely to involve a complex interaction of factors that vary in space and time. If we want to understand the proximate mechanisms of extinction, the most profitable approach will be a series of wholistic, species-by-species analyses that consider animal behavior and life history, environmental pressures, the impact of human predation—as well as indirect human impacts—and a realistic evaluation of taphonomic processes (Fisher 1987, Grayson et al. 2001).

SUMMARY

The Pleistocene extinction debate has progressed greatly in the past decade. It is now clear that species with low reproductive rates were hard hit, regardless of body size. Even so, North American evidence indicates that, in comparison to earlier extinctions, the LQE was exceptional in its impact on large-bodied animals and that it was one of the two biggest of the past 55 million years. In North America, then, the tenet that the LQE was unusual both in intensity and in affecting large mammals preferentially has withstood the test of time. We suspect that data from other continents will mimic the North American situation.

These unusual characteristics are consistent with variants of anthropogenic models, but are difficult to explain with models that rely solely on environmental causes. Thus they provide the strongest support for a human contribution to the LQE. However, it is an oversimplification to say that an abrupt wave of hunting-induced extinctions swept continents right after first human contact. It is this extreme view of overkill, which irks many critics, that has been subjected to most archaeological and chronologic tests. Blitzkrieg can now be firmly rejected in western Europe, Siberia, Alaska, and probably Australia and central and eastern North America. A more complicated portrait of the LQE is emerging from recent studies. Taken as a whole, recent studies suggest that humans precipitated the extinction in many parts of the globe through combined direct (hunting) and perhaps indirect (competition, habitat alteration and fragmentation) impacts, but that late Quaternary environmental change influenced the timing, geography, and perhaps magnitude of extinction. Put another way, absent the various impacts of *Homo sapiens sapiens*, it is highly unlikely global ecosystems would have experienced a mass extinction of large, slow-breeding animals in the late Quaternary. But, absent concurrent rapid climatic change evident in many parts of the globe, some species may have persisted longer.

Overall, evidence from Eurasia points to a role for climate change in pacing the decline of late Pleistocene megafaunal populations, but whether or not these declines would have led to extinction absent coincident human impacts is not yet clear. An idea that merits further testing is that the arrival and population expansion of modern humans began to fragment megafaunal ranges, restricting populations to inviable Arctic refugia. Further work on Neanderthal paleoecology should illuminate why these early humans did not precipitate megafaunal extinctions earlier in the Pleistocene. Megafaunal scavenging (rather than hunting) or extreme reliance on megafaunal prey are two plausible explanations.

Australian evidence suggests that megafaunal extinction followed human arrival. Unfortunately, neither the arrival of humans nor the timing of megafaunal extinction can be bracketed within less than 10 kyr, though the extinction probably lags behind human arrival by enough time to preclude blitzkrieg. There is no simple association between extinction and environmental change, and climates and floras at the LQE were not unusual relative to states earlier in the Pleistocene, when climatic transitions did not induce extinction. To complicate matters further, early Australians lacked efficient stone weapons, there are no uncontested butcher sites, and some doubt that human populations were large enough to have a substantial impact on prey. Thus while the timing and the uniqueness of the event point to an anthropogenic impact of some sort, it is not clear if it was through hunting or habitat alteration, or that environmental change did not contribute as well.

In South America, data on extinction chronology are accumulating but await critical analysis. It is likely that humans hunted megafauna, and that the LQE postdates human arrival, but not much more can be said at present. In contrast, robust dating verifies simultaneous climate change and the first contact with substantial human populations in the conterminous United States, where extinctions were rapid and pronounced. Support for human impacts includes (*a*) indisputable hunting of two extinct species, (*b*) clustering of extinctions within 1500 years (perhaps less) of first contact with Clovis hunters, (*c*) widespread distribution of Clovis hunters, (*d*) simulations, and (*e*) more pronounced extinction than in earlier glacial-interglacial transitions. On a broader North American scale, the demise of megafaunal species without significant human presence in Alaska is consistent with a stronger role for climate at the edges of species' geographic ranges.

Africa remains an anomaly. Perhaps coevolution between humans and their prey did give megafauna an advantage (Martin 1984). Yet many African animals do not use cryptic habitats, and many lack defensive behaviors that would deter armed, group-hunting humans. If we accept that similarly armed and technologically sophisticated humans precipitated an extinction of most large mammals elsewhere around the globe, the lack of extinction in Africa is troubling. We offer three speculations on this issue.

First, perhaps small game and gathered food were so abundant that they were more remunerative than larger prey (Wroe et al. 2004). Yet with abundant resources, human populations should have grown until larger game was added to human diets, though perhaps not enough to impact prey populations. Second, perhaps human population density across Africa was lower than in Europe or the Americas. One intriguing possibility is that as the site of human origins, Africa harbors the greatest density of coevolved pathogens and parasites (Martin 1984). Humans would have been released from some of these warm-adapted pathogens as they moved to and through cooler regions. Finally, perhaps between human disease hot-zones and the patchiness of its ecosystems, Africa offered more refugia from human predation than other continents.

We believe it is time to move beyond casting the Pleistocene extinction debate as a simple dichotomy of climate versus humans. Human impacts were essential to precipitate the event, just as climate shifts were critical in shaping the expression and impact of the extinction in space and time. The unanswered questions now revolve around why some species succumbed to this combination of expanding human populations and climate change as it played out globally over thousands of years, whereas other species emerged essentially unscathed. Such understanding is essential for informed predictions about the future of surviving biota.

BROADER ECOLOGICAL IMPLICATIONS

From the perspective of conservation biology, a significant implication is that the intersection of dramatic climate change with human impacts on fauna is especially pernicious. The late Quaternary event provides a sobering example of what to expect as contemporary exploding human population densities collide with higher-than-normal rates of climate change under a "business as usual" model (Houghton et al. 2001): accelerated extinction rates and continued wholesale restructuring of Earth's ecosystems.

In addition, the extinction affects our understanding of the adaptations and ecology of surviving species. Some species are relicts of disrupted coevolutionary partnerships (Barlow 2001, Janzen & Martin 1982). Examples include plants that have lost their primary agents of seed dispersal or that are replete with defenses for herbivores that no longer exist, herbivores that are "overdesigned" for all existing predators, and scavengers such as condors that have no naturally occurring carcasses to eat in continental settings.

The recent data continue to support Martin's (1970) contention that modern ecosystems are unique in having vast populations of one species (humans) while lacking the array of megafauna that had populated terrestrial ecosystems for at least the past 20 million years. The net effect has been simplification of and loss of redundancy in food webs, which may not portend well for the stability of communities (Bengtsson et al. 2003).

Finally, such observations raise vexing value judgments for restoration ecology. Should we attempt to "resurrect" ecosystem processes that were in place before the LQE by introducing phylogenetically related species with ecological preferences similar to those of extinct megafauna (Donlan et al. 2005, Martin 2005)? Or should the goal be restoration of species and processes that were in place a few hundred years ago in ecosystems that were "wild," but clearly highly modified relative to their condition prior to prehistoric human occupation? While the feasibility of resurrecting Pleistocene ecosystems in the Americas and Eurasia is open to debate, a clear benefit of such efforts would be increasing the geographic range of various existing megafauna such as elephants and rhinoceros, which today are under threat of extinction from a variety of human-induced pressures.

The last frontier for megafaunal extinctions is the oceans. Marine communities are in the throes of a modern megafaunal extinction event (Hughes et al. 2003, Jackson et al. 2001, Steneck et al. 2002). Populations have crashed, but with a few notable exceptions (Caribbean monk seal, Steller's sea cow), species have not yet been driven to extinction, so marine communities are not yet beyond saving. The Quaternary extinction has taught us that the unfortunate intersection of human activities and climate change wiped out whole sectors of Earth's terrestrial ecosystems. Knowing that, are we willing to let overexploitation, habitat alteration, and climate change (this time anthropogenically induced) exterminate the marine megafauna and forever change those communities as well?

SUMMARY POINTS

1. Between fifty and ten thousand years ago, most large mammals became extinct everywhere except Africa.
2. This extinction, with its extreme focus on large and slow-breeding animals, was unusual relative to extinctions earlier in the Cenozoic.

3. The unusual body-size selectivity of the extinction, and its rough synchrony with the global geographic expansion of modern humans are compelling evidence that the extinction was precipitated by human activities, especially hunting.
4. Climate change likely affected the timing, geography, and perhaps magnitude of this anthropogenically triggered extinction.
5. The intersection of rapid climate change with initial human contact seemed especially deadly for megafauna.
6. The extinction of so many species in near-time raises vexing questions for ecologists and conservation biologists.

ACKNOWLEDGMENTS

We thank R.S. Feranec and A.B. Shabel for helping to compile information and S.L. Wing for his careful review of the manuscript. Members of the extinctions discussion groups and our labs at UC Santa Cruz and UC Berkeley helped in crystallizing these ideas. Research on climate's role in ecosystem change was in part funded by National Science Foundation grants.

LITERATURE CITED

Alberdi MT, Miotti L, Prado JL. 2001. *Hippidion saldiasi* Roth, 1899. (Equidae, Perissodactyla), at the Piedra Museo Site (Santa Cruz, Argentina): its implications for the regional economy and environmental reconstruction. *J. Archaeol. Sci.* 28:411–19

Alroy J. 1999. Putting North America's end-Pleistocene megafaunal extinction in context: large-scale analyses of spatial patterns, extinction rates, and size distributions. See MacPhee 1999, pp. 105–43

Alroy J. 2001a. Did human hunting cause extinction? *Science* 294:1459–62

Alroy J. 2001b. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292:1893–96

Alvard MS. 1993. Testing the "ecologically noble savage" hypothesis: interspecific prey choice in Piro hunters of Amazonian Peru. *Hum. Ecol.* 21:355–87

Anderson E. 2004. The carnivora from Porcupine Cave. In *Biodiversity Response to Climate Change in the Middle Pleistocene*, *The Porcupine Cave Fauna from Colorado*, ed. AD Barnosky, pp. 141–54. Berkeley: Univ. Calif. Press

Bard E, Rostek F, Menot-Combes G. 2004. Radiocarbon calibration beyond 20,000 ^{14}C yr BP by means of planktonic foraminifera of the Iberian Margin. *Quat. Res.* 61:204–14

Barlow C. 2001. *The Ghosts of Evolution*. New York: Basic Books. 254 pp.

Barnes I, Matheus P, Shapiro B, Jensen D, Cooper A. 2002. Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* 295:2267–70

Barnosky AD. 1985. Taphonomy and herd structure of the extinct Irish elk, *Megaloceros giganteus*. *Science* 228:340–44

Barnosky AD. 1986. "Big Game" extinction caused by late Pleistocene climatic change: Irish Elk (*Megaloceros giganteus*) in Ireland. *Quat. Res.* 25:128–35

Barnosky AD. 1989. The late Pleistocene event as a paradigm for widespread mammal extinction. In *Mass Extinctions: Processes and Evidence*, ed. SK Donovan, pp. 235–54. London: Belhaven

Barnosky AD, Bell CJ, Emslie SD, Goodwin HT, Mead JI, et al. 2004a. Exceptional record of mid-Pleistocene vertebrates differentiates climatic from anthropogenic ecosystem perturbations. *Proc. Natl. Acad. Sci. USA* 101:9297–302

Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB. 2004b. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306:70–75

Bar-Yosef O. 2002. The Upper Paleolithic revolution. *Annu. Rev. Anthropol.* 31:363–93

Belovsky GE. 1988. An optimal foraging-based model of hunter-gatherer population dynamics. *J. Anthropol. Archaeol.* 7:329–72

Bengtsson J, Angelstam P, Elmqvist T, Emanuelsson U, Folke C, et al. 2003. Reserves, resilience and dynamic landscapes. *Ambio* 32:389–96

Berger J, Swenson JE, Persson IL. 2001. Recolonizing carnivores and naive prey: Conservation lessons from Pleistocene extinctions. *Science* 291:1036–39

Bocherens H, Drucker DG, Billiou D, Patou-Mathis M, Vandermeersch B. 2005. Isotopic evidence for diet and subsistence pattern of the Saint-Cesaire I Neanderthal: review and use of a multi-source mixing model. *J. Hum. Evol.* 49:71–87

Bowman DMJS. 1998. Tansley Review No. 101: The impact of Aboriginal landscape burning on the Australian biota. *New Phytol.* 140:385–410

Brook BW, Bowman DMJS. 2002. Explaining the Pleistocene megafaunal extinctions: Models, chronologies, and assumptions. *Proc. Natl. Acad. Sci. USA* 99:14624–27

Brook BW, Bowman DMJS. 2004. The uncertain blitzkrieg of Pleistocene megafauna. *J. Biogeogr.* 31:517–23

Burney DA, Burney LP, Godfrey LR, Jungers WL, Goodman SM, et al. 2004. A chronology for late prehistoric Madagascar. *J. Hum. Evol.* 47:25–63

Burney DA, Flannery TF. 2005. Fifty millennia of catastrophic extinctions after human contact. *TREE* 20:395–401

Byers DA, Ugan A. 2005. Should we expect large game specialization in the late Pleistocene? An optimal foraging perspective on early Paleoindian prey choice. *J. Archaeol. Sci.* 32:1624–40

Choquenot DM, Bowman JS. 1998. Marsupial megafauna, Aborigines and the overkill hypothesis: Application of predator-prey models to the question of Pleistocene extinction in Australia. *Glob. Ecol. Biogeogr. Lett.* 7:167–80

Crooks KR. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv. Biol.* 16:488–502

Diamond JM. 1984. Historic extinctions: A Rosetta Stone for understanding prehistoric extinctions. In *Quaternary Extinctions: A Prehistoric Revolution*, ed. PS Martin, RG Klein, pp. 824–62. Tucson: Univ. Ariz. Press

Dillehay TD. 2000. *The Settlement of the Americas: A New Prehistory*. New York: Basic Books. 371 pp.

Donlan CJ, Greene HW, Berger J, Bock CE, Bock JH, et al. 2005. Re-wilding North America. *Nature* 436:913–14

Drummond AJ, Rambaut A, Shapiro B, Pybus OG. 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. *Mol. Biol. Evol.* 22:1185–92

Edwards KJ, MacDonald GM. 1991. Holocene palynology. II. Human influence and vegetation change. *Prog. Phys. Geogr.* 15:364–91

FAUNMAP Work. Group. 1994. FAUNMAP: A database documenting Late Quaternary distributions of mammal species in the United States. *Ill. State Mus. Sci. Pap.* 25:1–690

Ficcarelli G, Coltorti M, Moreno-Espinosa M, Pieruccini PL, Rook L, Torre D. 2003. A model for the Holocene extinction of the mammal megafauna in Ecuador. *J. South Am. Earth Sci.* 15:835–45

Fiedel SJ. 2005. Man's best friend—mammoth's worst enemy? A speculative essay on the role of dogs in Paleoindian colonization and megafaunal extinction. *World Archaeol.* 37:11–25

Fiedel SJ, Haynes G. 2004. A premature burial: comments on Grayson and Meltzer's "Requiem for overkill". *J. Archaeol. Sci.* 31:121–31

Field J, Dodson JR. 1999. Late Pleistocene megafauna and archaeology from Cuddie Springs, south-eastern Australia. *Proc. Prehist. Soc.* 65:275–301

Fisher DC. 1987. Mastodont procurement by Paleoindians of the Great Lakes Region: Hunting or scavenging? In *The Evolution of Human Hunting*, ed. MH Nitecki, DV Nitecki, pp. 309–421. Chicago, IL: Plenum

Fisher DC. 1996. Extinction of proboscideans in North America. In *The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives*, ed. J Shoshani, P Tassy, pp. 296–315. New York: Oxford Univ. Press

Flannery TF. 1994. *The Future Eaters: An Ecological History of the Australasian Lands and People*. Chatswood: Reed Books. 432 pp.

Flannery TF, Roberts RG. 1999. Late Quaternary extinctions in Australasia: an overview. See MacPhee 1999, pp. A239–55

Forster MA. 2004. Self-organised instability and megafaunal extinctions in Australia. *Oikos* 103:235–39

Gingerich PD. 1984. Pleistocene extinctions in the context of origination-extinction equilibria in Cenozoic mammals. See Martin & Klein 1984, pp. 211–22

Gonzalez S, Kitchener AC, Lister AM. 2000. Survival of the Irish elk into the Holocene. *Nature* 405:753–54

Graham RW, Lundelius ELJ. 1984. Coevolutionary disequilibrium and Pleistocene extinction. See Martin & Klein 1984, pp. 223–49

Grayson DK. 1984. Nineteenth-century explanations of Pleistocene extinctions: a review and analysis. See Martin & Klein 1984, pp. 5–39

Grayson DK. 1991. Late Pleistocene mammalian extinctions in North America: taxonomy, chronology, and explanations. *J. World Prehist.* 5:193–231

Grayson DK. 2001. The archaeological record of human impacts on animal populations. *J. World Prehist.* 15:1–68

Grayson DK. 2006. Early Americans and Pleistocene Mammals in North America. In *Handbook of North American Indians: Environment, Origins, and Population*, Vol. 3, In press. Washington, DC: Smithson. Inst. Press

Grayson DK, Delpech F, Rigaud JP, Simek JF. 2001. Explaining the development of dietary dominance by a single ungulate taxon at Grotte XVI, Dordogne, France. *J. Archaeol. Sci.* 28:115–25

Grayson DK, Meltzer DJ. 2002. Clovis hunting and large mammal extinction: A critical review of the evidence. *J. World Prehist.* 16:313–59

Grayson DK, Meltzer DJ. 2003. A requiem for North American overkill. *J. Archaeol. Sci.* 30:585–93

Guilday JE. 1967. Differential extinction during late-Pleistocene and recent times. See Martin & Wright 1967, pp. 121–40

Guthrie RD. 1984. Mosaics, allelochemics, and nutrients: an ecological theory of Late Pleistocene megafaunal extinctions. See Martin & Klein 1984, pp. 259–98

Guthrie RD. 2003. Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature* 426:169–71

Guthrie RD. 2004. Radiocarbon evidence of mid-Holocene mammoths stranded on an Alaskan Bering Sea island. *Nature* 429:746–49

Hadly EA, Kohn MH, Leonard JA, Wayne RK. 1998. A genetic record of population isolation in pocket gophers (*Thomomys talpoides*) during Holocene climatic change. *Proc. Natl. Acad. Sci. USA* 95:6893–96

Hadly EA, Ramakrishnan U, Chan YL, van Tuinen M, O'Keefe K, et al. 2004. Genetic response to climatic change: Insights from ancient DNA and phylochronology. *PLos Biol.* 2:1600–9

Haynes G. 2002a. The catastrophic extinction of North American mammoths and mastodonts. *World Archaeol.* 33:391–416

Haynes G. 2002b. *The Early Settlement of North America: The Clovis Era*. Cambridge, UK: Cambridge Univ. Press. 345 pp.

Holdaway RN. 1999. Introduced predators and avifaunal extinction in New Zealand. See MacPhee 1999, pp. 189–238

Holdaway RN, Jacomb C. 2000. Rapid extinction of the moas (Aves: Dinorninthiformes): model, test, and implications. *Science* 287:2250–54

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosu D, eds. 2001. *Climate Change 2001: The Scientific Basis*. New York: Cambridge Univ. Press

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, et al. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–33

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–38

Janzen DH, Martin PS. 1982. Neotropical anachronisms—the fruits the gomphotheres ate. *Science* 215:19–27

Johnson CN. 2002. Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proc. R. Soc. London Ser. B* 269:2221–27

Johnson CN. 2005. What can data on the late survival of Australian megafauna tell us about the cause of their extinction? *Quat. Sci. Rev.* 24:2167–72

Johnson CN, Prideaux GJ. 2004. Extinctions of herbivorous mammals in the late Pleistocene of Australia in relation to their feeding ecology: No evidence for environmental change as cause of extinction. *Aust. Ecol.* 29:553–57

Johnson CN, Wroe S. 2003. Causes of extinction of vertebrates during the Holocene of mainland Australia: arrival of the dingo, or human impact? *Holocene* 13:941–48

Kelly RL, Todd LC. 1988. Coming into the country: Early Paleoindian hunting and mobility. *Am. Antiq.* 53:231–44

King JE, Saunders JJ. 1984. Environmental insularity and the extinction of the American mastodont. See Martin & Klein 1984, pp. 315–39

Koch PL, Fogel ML, Tuross N. 1994. Tracing the diets of fossil animals using stable isotopes. In *Stable Isotopes in Ecology and Environmental Science*, ed. K Lajtha, RH Michener, pp. 63–92. Oxford: Blackwell Sci.

Kuhn SL, Stiner MC. 2001. The antiquity of hunter-gatherers. See Panter-Brick et al. 2001, pp. 99–142

Kurtén B. 1968. *Pleistocene Mammals of Europe*. Chicago: Aldine. 317 pp.

Leonard JA, Wayne RK, Cooper A. 2000. Population genetics of ice age brown bears. *Proc. Natl. Acad. Sci. USA* 97:1651–54

Lindenmayer DB, McCarthy MA, Parris KM, Pope ML. 2000. Habitat fragmentation, landscape context, and mammalian assemblages in southeastern Australia. *J. Mamm.* 81:787–97

Lyons SK, Smith FA, Brown JH. 2004a. Of mice, mastodons, and men: human mediated extinctions on four continents. *Evol. Ecol. Res.* 6:339–58

Lyons SK, Smith FA, Wagner PJ, White EP, Brown JH. 2004b. Was a 'hyperdisease' responsible for the late Pleistocene megafaunal extinction? *Ecol. Lett.* 7:859–68

MacPhee RDE, ed. 1999. *Extinctions in Near Time: Causes, Contexts, and Consequences*. New York: Kluwer Acad./Plenum. 394 pp.

MacPhee RDE, Marx PA. 1997. The 40,000 year plague: humans, hyperdiseases, and first-contact extinctions. In *Natural Change and Human Impact in Madagascar*, ed. SM Goodman, BR Patterson, pp. 169–217. Washington, DC: Smithson. Inst. Press

MacPhee RDE, Tikhonov AN, Mol D, de Marliave C, Van der Plicht H, et al. 2002. Radiocarbon chronologies and extinction dynamics of the late Quaternary mammalian megafauna of the Taimyr Peninsula, Russian Federation. *J. Archaeol. Sci.* 29:1017–42

MacPhee RDE, Tikhonov AN, Mol D, Greenwood AD. 2005. Late Quaternary loss of genetic diversity in muskox (*Ovibos*). *BMC Evol. Biol.* 5:49

Magee JW, Miller GH, Spooner NA, Questiaux D. 2004. Continuous 150 k.y. monsoon record from Lake Eyre, Australia: Insolation-forcing implications and unexpected Holocene failure. *Geology* 32:885–88

Martin PS. 1966. African and Pleistocene overkill. *Nature* 212:339–42

Martin PS. 1970. Pleistocene niches for alien animals. *BioScience* 20:218–21

Martin PS. 1973. The discovery of America. *Science* 179:969–74

Martin PS. 1984. Prehistoric overkill: the global model. See Martin & Klein 1984, pp. 354–403

Martin PS. 2005. *Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of America*. Berkeley: Univ. Calif. Press. 240 pp.

Martin PS, Klein RD, eds. 1984. *Quaternary Extinctions: A Prehistoric Revolution*. Tucson: Univ. Ariz. Press. 892 pp.

Martin PS, Steadman DW. 1999. Prehistoric extinctions on islands and continents. See MacPhee 1999, pp. 17–55

Martin PS, Wright HEJ, eds. 1967. *Pleistocene Extinctions: The Search for a Cause*. New Haven: Yale Univ. Press. 453 pp.

Martínez-Meyer E, Peterson AT, Hargrove WW. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Glob. Ecol. Biogeogr.* 13:305–14

Matheus PE. 1997. *Paleoecology and ecomorphology of the giant short-faced bear in eastern Beringia*. PhD thesis. Univ. Alaska, Fairbanks. 282 pp.

McDougall I, Brown FH, Fleagle JG. 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature* 433:733–36

Mellars P. 2004. Neanderthals and the modern human colonization of Europe. *Nature* 432:461–65

Meltzer DJ, Grayson DK, Ardila G, Barker AW, Dincauze DF, et al. 1997. On the Pleistocene antiquity of Monte Verde, southern Chile. *Am. Antiq.* 62:659–63

Miller GH, Fogel ML, Magee JW, Gagan MK, Clarke SJ, Johnson BJ. 2005. Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* 309:287–90

Miller GH, Magee JW, Johnson BJ, Fogel ML, Spooner NA, et al. 1999. Pleistocene extinction of *Genyornis newtoni*: Human impact on Australian megafauna. *Science* 283:205–8

Moen RA, Pastor J, Cohen Y. 1999. Antler growth and extinction of Irish Elk. *Evol. Ecol. Res.* 1:235–49

Moriarty KC, McCulloch MT, Wells RT, McDowell MC. 2000. Mid-Pleistocene cave fills, megafaunal remains and climate change at Naracoorte, South Australia: towards a predictive model using U-Th dating of speleothems. *Palaeogeogr. Palaeoclim. Palaeoecol.* 159:113–43

Mosimann JE, Martin PS. 1975. Simulating overkill by paleoindians. *Am. Sci.* 63:304–13

Mulvaney DJ, Kamminga J. 1999. *Prehistory of Australia*. Washington, DC: Smithson. Inst. Press. 480 pp.

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, et al. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–35

O'Regan HJ, Turner A, Wilkinson DM. 2002. European Quaternary refugia: a factor in large carnivore extinction? *J. Quat. Sci.* 17:789–95

Owen-Smith N. 1987. Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* 13:351–62

Owen-Smith N. 1999. The interaction of humans, megaherbivores, and habitats in the late Pleistocene extinction event. See MacPhee 1999, pp. 57–70

Panter-Brick C, Layton RH, Rowley-Conwy P, eds. 2001. *Hunter-Gatherers: An Interdisciplinary Perspective*. Cambridge, UK: Cambridge Univ. Press. 341 pp.

Post E, Forchhammer MC. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature* 420:168–71

Pounds JA, Bustamante MR, Coloma LA, Consuegra JA, Fogden MPL. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161–67

Prado JL, Alberdi MT, Azanza B, Sanchez B, Frassinetti D. 2005. The Pleistocene Gomphotheriidae (Proboscidea) from South America. *Quat. Int.* 126/128:21–30

Raymo ME. 1994. The initiation of northern hemisphere glaciation. *Annu. Rev. Earth Planet. Sci.* 22:353–83

Roberts RG, Flannery TF, Ayliffe LK, Yoshida H, Olley JM, et al. 2001. New ages for the last Australian megafauna: Continent-wide extinction about 46,000 years ago. *Science* 292:1888–92

Robinson GS, Burney LP, Burney DA. 2005. Landscape paleoecology and megafaunal extinction in southeastern New York state. *Ecol. Monogr.* 75:295–315

Rolett B, Diamond J. 2004. Environmental predictors of pre-European deforestation on Pacific islands. *Nature* 431:443–36

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, et al. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–96

Scheinsohn V. 2003. Hunter-gatherer archaeology in South America. *Annu. Rev. Anthropol.* 32:339–61

Shapiro B, Drummond AJ, Rambaut A, Wilson MC, Matheus PE, et al. 2004. Rise and fall of the Beringian steppe bison. *Science* 306:1561–65

Slaughter BH. 1967. Animal ranges as a clue to late-Pleistocene extinction. See Martin & Wright 1967, pp. 155–67

Slaughter R, Skulan J. 2001. Did human hunting cause extinction? *Science* 294:1459–62

Smith FA, Lyons SK, Ernest SKM, Jones KE, Kaufman DM, et al. 2003. Body mass of late Quaternary mammals. *Ecology* 84:3403

Solé RV, Alonso D, McKane A. 2002. Self-organized instability in complex ecosystems. *Philos. Trans. R. Soc. London Ser. B* 357:667–81

Steadman DW, Martin PS. 2003. The late Quaternary extinction and future resurrection of birds on Pacific islands. *Earth Sci. Rev.* 61:133–47

Steadman DW, Martin PS, MacPhee RDE, Jull AJT, McDonald HG, et al. 2005. Asynchronous extinction of late Quaternary sloths on continents and islands. *Proc. Natl. Acad. Sci. USA* 102:11763–68

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, et al. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* 29:436–59

Stuart AJ. 1991. Mammalian extinctions in the Late Pleistocene of northern Eurasia and North America. *Biol. Rev.* 66:453–562

Stuart AJ. 1999. Late Pleistocene megafaunal extinctions: a European perspective. See MacPhee 1999, pp. 257–70

Stuart AJ, Kosintsev PA, Higham TFG, Lister AM. 2004. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. *Nature* 431:684–89

Stuart AJ, Sulerzhitsky LD, Orlova LA, Kuzmin YV, Lister AM. 2002. The latest woolly mammoths (*Mammuthus primigenius* Blumenbach) in Europe and Asia: a review of the current evidence. *Quat. Sci. Rev.* 21:1559–69

Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, et al. 1998. INTCAL98 radiocarbon age calibration, 24,000–0 cal BP. *Radiocarbon* 40:1041–83

Terborgh J, Lopez L, Nuñez VP, Rao M, Shahabuddin G, et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–26

Thieme H. 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385:807–10

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, et al. 2004. Extinction risk from climate change. *Nature* 427:145–48

Trueman CNG, Field JH, Dortch J, Charles B, Wroe S. 2005. Prolonged coexistence of humans and megafauna in Pleistocene Australia. *Proc. Natl. Acad. Sci. USA* 102:8381–85

Van Valkenburgh B. 1993. Tough times at La Brea: tooth breakage in large carnivores of the late Pleistocene. *Science* 261:456–59

Waguespack NM, Surovell TA. 2003. Clovis hunting strategies, or how to make out on plentiful resources. *Am. Antiq.* 68:333–52

Wahlberg N, Moilanen A, Hanski I. 1996. Predicting the occurrence of endangered species in fragmented landscapes. *Science* 273:1536–38

Walther GR, Post E, Convey P, Menzel A, Parmesan C, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–95

Wayne RK, Leonard JA, Cooper A. 1999. Full of sound and fury: The recent history of ancient DNA. *Annu. Rev. Ecol. Syst.* 30:457–77

Whittington SL, Dyke B. 1984. Simulating overkill—experiments with the Mosimann and Martin model. See Martin & Klein 1984, pp. 451–65

Williams JW, Webb T III, Richard PJH, Newby P. 2000. Late Quaternary biomes of Canada and the eastern United States. *J. Biogeogr.* 27:585–607

Winterhalder B. 2001. The behavioural ecology of hunter-gatherers. See Panter-Brick et al. 2001, pp. 12–38

Winterhalder B, Lu F. 1997. A forager-resource population ecology model and implications for indigenous conservation. *Conserv. Biol.* 11:1354–64

Woodburne MO, Swisher CC III. 1995. Land mammal high resolution geochronology, intercontinental overland dispersals, sea-level, climate, and vicariance. In *Geochronology, Time Scales and Global Stratigraphic Correlation*, ed. WA Berggren, DV Kent, M-P Aubry, J Hardenbol. SEPM Spec. Publ. 54, pp. 336–64

Wroe S, Field J, Fullagar R, Jermin LS. 2004. Megafaunal extinction in the Late Quaternary and the global overkill hypothesis. *Alcheringa* 28:291–31

Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS III, Reynolds JF, et al. 1995. Steppe-tundra transition: A herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.* 146:765–94

Annual Review of
Ecology, Evolution,
and Systematics

Volume 37, 2006

Contents

Indexes