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Saving a Million Species

EXTINCTION RISK FROM CLIMATE CHANGE

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Chapter 11

Quaternary Extinctions and Their Link to Climate Change

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Millennia before the modern biodiversity crisis—a worldwide event being driven by the multiple impacts of anthropogenic global change—a mass extinction of large-bodied fauna occurred. After a million years of severe climatic fluctuations, during which the earth waxed and waned between frigid ice ages and warm interglacials, with apparently few extinctions, hundreds of species of mammals, flightless birds, and reptiles suddenly went extinct over the course of the last 50,000 years (Barnosky, 2009). Due both to our intrinsic fascination with huge prehistoric beasts and to the possible insights these widespread species losses might lend to the modern extinction problem, the mystery of the "megafaunal" (large animal) extinctions have led to much theorizing, modeling, and digging (for their fossils or environmental proxies) over the last 150 years (Martin, 2005). The topic continues to invoke strong scientific interest (Koch and Barnosky, 2006; Grayson, 2007; Gillespie, 2008; Barnosky and Lindsey, 2010; Nogues-Bravo et al., 2010; Price et al., 2011).

In this chapter, we focus on recent work that explicitly considers the relative role of natural climate change compared to nonclimate human-caused threatening processes (such as habitat loss and hunting) in driving the megafaunal extinctions. We begin with a short review of the global pattern of Quaternary extinctions and summarize some general reasons why large animals might be particularly vulnerable to direct human impacts and climate change. We then explore how the pattern of megafaunal extinction corresponds to both the chronology of human expansion and climate change and their projected impacts. Taken together, this body of information leads us to conclude that climate change alone did not drive the mass extinction of late Quaternary megafauna, but overlain on direct and indirect human actions, it exacerbated overall extinction risk tremendously. The take-home message is that the synergy of fast climate change with more direct human impacts can have particularly fatal consequences for many nonhuman species—and this is particularly true today, when human influences, including climate disruption, are so dramatically greater than they have ever been in the past.

Extinction and Vulnerability of Megafauna

The end-Quaternary (late Pleistocene and Holocene) die-offs comprised a significant global mass extinction event, which led to the elimination of half of all mammal species heavier than 44 kilograms (100 pounds) and other large-bodied fauna across most continents (Australia, Eurasia, North and South America) and large islands (West Indies, Madagascar, and New Zealand), between 50,000 and 600 years before present (Koch and Barnosky, 2006). The losses included large mammals (e.g., mammoth, genus *Mammuthus*), reptiles (e.g., giant lizards such as *Megalania*), and huge flightless birds (e.g., New Zealand moa and Australian *Genyornis*). In Australia, around fifty species, including rhinoceros-size wombats, short-faced kangaroos, and predatory possums disappeared (MacPhee, 1999). In North America, the death toll was some sixty species of large mammals plus the largest birds and tortoises, and South America saw the disappearance of at least sixty-six large-mammal species. Eurasia and Africa were less hard hit, but nevertheless saw major losses in their large-mammal fauna, fifteen and seventeen species, respectively. Region by region, these extinction events followed within a few centuries to a few millennia the first dispersal of *Homo sapiens* to new lands, and were particularly severe when they were also entwined with changes in the regional or global climate system (fig. 11-1).

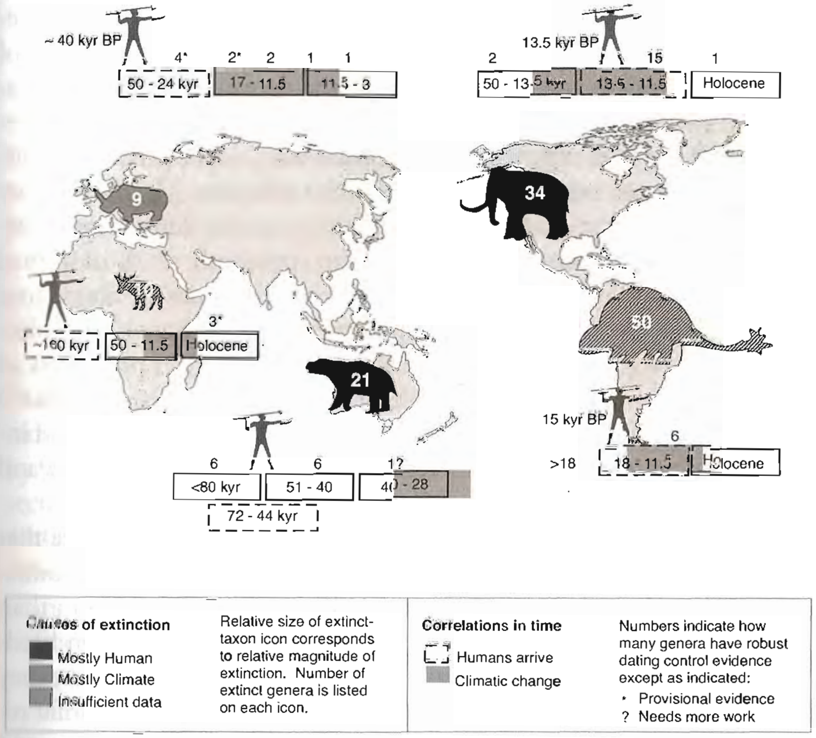

FIGURE 11-1. Late Quaternary megafaunal extinctions, human hunting, and climate change on the continents. The dashed box indicates the credible bounds of the first arrival of modern people, *Homo sapiens sapiens*, with the best estimate adjacent to the human figure (the latest estimate for Australia is about 48,000 years ago [kyr BP]). Substantial climate change events, predominantly the last glacial maximum and Holocene warming, are indicated by gray shading inside boxes. Source: Koch and Barnosky, 2006.

So what was the causal mechanism behind these extinctions—climate, humans, or both? The drivers of biotic extinctions, past and present, are often surprisingly difficult to pin down (McKinney, 1997), but plausibly include: (i) being outcompeted by newly evolved or invasive species; (ii) failing to adapt to long-term environmental change (e.g., climatic shifts); and (iii) reduction in abundance caused by random disturbance events (e.g., epidemics, severe storms) with a subsequent failure to recover to a viable population (Blois and Hadly, 2009). A commonly cited generalization is that larger-bodied vertebrates (with the extreme recent form being the Quaternary megafauna) are more extinction-prone than smaller bodied ones (Bodmer et al., 1997; McKinney, 1997). Because body size is inversely correlated with population size, large-bodied animals tend to be less abundant and so more intrinsically vulnerable to rapid change and demographic disruption. Indeed, when armed with some knowledge of empirically well established biological scaling rules (allometry; Damuth, 1981), such a hypothesis makes a lot of sense. Large-bodied animals such as elephants or whales produce only a few, precocious offspring, but invest substantial resources into their care. This life-history strategy leads to the death of juveniles being a major demographic setback. On a population-wide basis, even an apparently small additional level of chronic mortality can result in rapid declines in abundance and, within a few centuries, a collapse to extinction (Brook and Johnson, 2006; Nogues-Bravo et al., 2008). The extinction proneness of large-bodied animals is further enhanced because of other correlated traits such as their requirement of large foraging area, greater food intake, high habitat specificity, and lower reproductive rates (West and Brown, 2005).

Why then (in evolutionary terms) be big? Three reasons are that large animals are long-lived (so have multiple attempts at reproduction), have relatively better heat regulation and water retention than small animals, and have lower predation rates, especially when herding. Their size protects them from all but the biggest predators, they have a great capacity to ride out hard times by drawing on their fat reserves, they can migrate long distances to find water or forage, and they can opt not to reproduce in times when environmental conditions are unfavorable, such as during a drought (Brook et al., 2007). Thus in the majority of circumstances, being big is good, because it acts as a demographic buffer. Indeed, such ecological specialization tends to evolve repeatedly because, in relatively stable environments, specialist species tend to be better than generalists at particular narrow tasks. However, when an environment is altered abruptly at a rate above normal background change, specialist species with narrow ecological preferences bear the brunt of progressively unfavorable conditions such as habitat loss, degradation, and invasive competitors or predators (Balmford, 1996; Harcourt et al., 2002). An extreme event, such as a bolide strike from space (Haynes, 2008) or an intelligent, weapon-wielding bipedal ape (Martin, 2005), that also widely alters landscapes by practices such as burning and farming, can be the lever that unhinges the optimality of this regularly evolved strategy of large body size.

The environmental context and type of threat also helps dictate an organism's response to change or novel stressors. For instance, when hunted by invading prehistoric people in Pleistocene Australia, arboreal (tree-dwelling) species occupying closed forests suffered far fewer extinctions than savanna (grassland) species, and of the latter group, those with high per capita population replacement rates (e.g., grey kangaroos; *Macropus giganteus*) or the ability to escape to refuges such as burrows (e.g., wombats; *Vombatus ursinus*) were best able to persist (Johnson, 2005).

The Role of Human Arrivals

During the last 100,000 years, modern humans have spread across the world from their center of origin in Africa, reaching the Middle East by 90,000 years ago, Australia by 48,000 years ago (based on the most secure evidence presently known, Gillespie et al., 2006), Europe by 40,000–50,000 years ago, South America by 14,600 years ago, North America by 13,000 years ago, most of the Pacific Islands by 2,000 years ago, and New Zealand by 800 years ago. (For dates estimated by radiocarbon dating, the radiocarbon age is calibrated to calendar years.) This wave of human dispersal was likely to have been mediated by climate change: a wet penultimate interglacial probably encouraged the spread of early *Homo sapiens* out of Africa, and in the Northern Hemisphere, end-Pleistocene immigration into the Americas was facilitated by glacial ice sequestering water and lowering sea levels, which in turn exposed a land bridge between Eurasia and North America and opened coastal migration routes. At the very end of the Pleistocene, it was global warming that melted ice and opened an ice-free corridor through central Canada for a wave of Clovis hunters.

A striking feature of the megafaunal extinctions is that, in every major instance where adequate data exist, the extinction follows the first arrival of people on a "virgin" continent or large island within a few hundred to a few thousand years (fig. 11-1). This point is further underscored in figure 11-2, which shows the short overlap period for well dated megafaunal remains and archeological artifacts, in New Zealand, North America, and Australia, based on the latest dating and sample selection protocols (Gillespie, 2008). (Note the different time scales on panels A, B, and C—these three events were not synchronous in time.) Coincidence alone is not sufficient evidence for causation, but this consistency at the very least provides strong circumstantial support for the idea that a human presence was a necessary precondition for accelerated

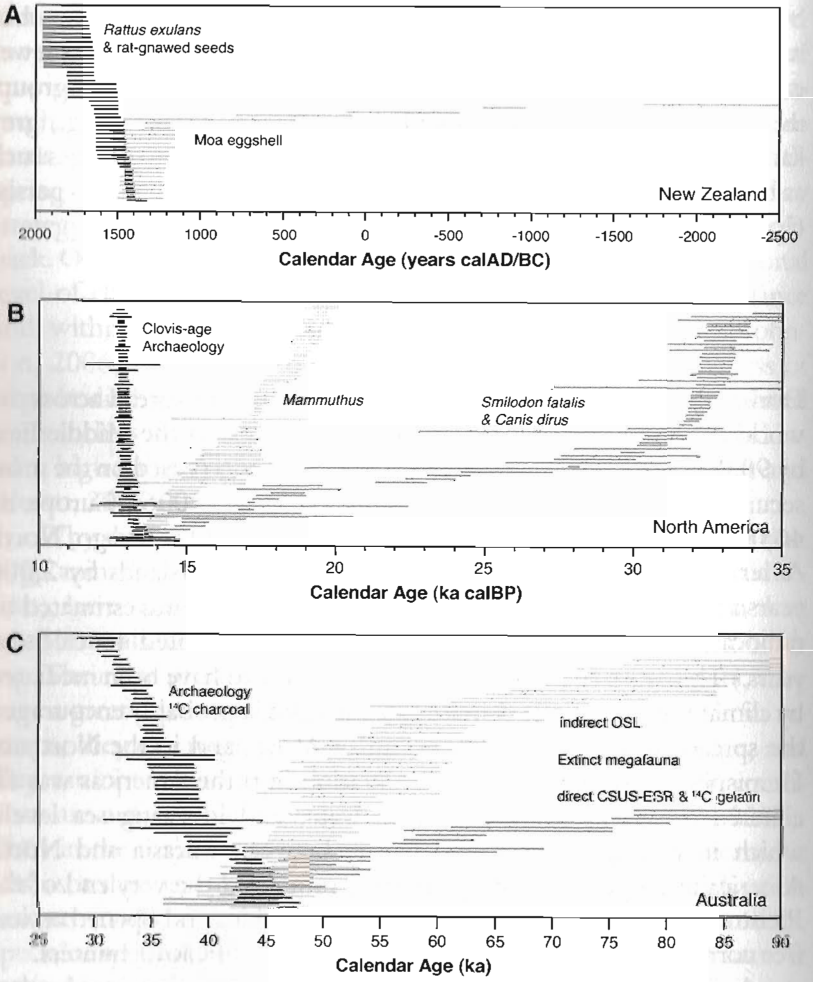

FIGURE 11-2. Dating data on human-megafauna overlap in New Zealand (A), North America (B), and Australia (C). The dates are stacked from youngest (top) to oldest (bottom) for the archeology (dark shading) and oldest (top) to youngest (bottom) for the animal remains or proxies (light gray shading). Bars represent dating uncertainties. Source: Gillespie, 2008 (includes detailed legend).

megafaunal extinction, especially given the evidence that most of the extinct taxa survived through previous, equally pronounced environmental perturbations before humans arrived.

A further line of indirect evidence comes from assessing jointly the global rise in human abundance and the precipitous loss of megafauna. We are a species that broke a fundamental ecological rule: large predators and omnivores are typically rare (Tudge, 1989). A recent analysis by one of us (Barnosky, 2008) has shown that in achieving ecological dominance, a rising biomass of people ultimately and permanently displaced the once-abundant biomass of megafauna. The point, well illustrated in figure 11-3, is that when the species richness of megafauna crashed to today's low levels, their equivalent total biomass was replaced by one species (*Homo sapiens*). Indeed, we surpassed the normal prehistoric levels of megafaunal biomass when the Industrial Revolution commenced, and now, when combined with our livestock, vastly outweigh the biomass of mammal faunas of the deep past—an explosion of living tissue supported primarily by the use of fossil energy (which, for example, makes it possible to produce and distribute inorganic fertilizers). The energetic trade-off between a large human biomass (lots of people) and a large nonhuman biomass (lots of other species) demonstrated by this Pleistocene history has a clear conservation implication: to avoid losing many more species as the human population grows in the very near future, it will be necessary to formulate policies that recognize and guard against an inevitable energetic trade-off at the global scale. The pressing need is to consciously channel some measure of natural resources toward supporting other species, rather than

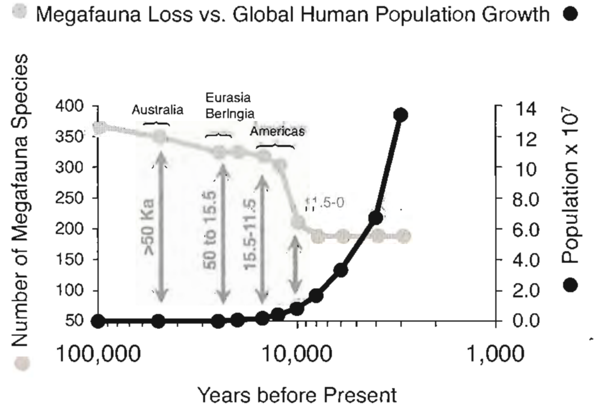

FIGURE 11-3. Decline in global megafauna biodiversity (number of species; light gray) over the last glacial-interglacial cycle, plotted against the increase in world population size of *Homo sapiens*. Major extinction events by continent are indicated by dark gray arrows. Ka = thousands of years before present) Source: Barnosky, 2008.

solely toward humans, for example, in the form of enhanced sustainable farming practices and stepped-up efforts to protect and expand existing nature reserves. Also critical will be developing alternatives to fossil fuels for the energy that currently sustains the global ecosystem, especially humans, so far above its pre-anthropogenic level of megafauna biomass.

Human impacts on late Quaternary environments were many and varied (Barnosky et al., 2004; Lyons et al., 2004a). The role of prehistoric people as hunters of big and small game has been reviewed extensively (Martin, 2005; Surovell et al., 2005; Grayson, 2007); meat was clearly a component of the hunter-gatherer lifestyle (Bulte et al., 2006), but killing may have also occurred for reasons beyond subsistence (e.g., hunter prestige). Beyond direct predation, however, humans seem to have stressed megafauna by burning vegetation on a landscape scale (and in doing so, perhaps radically altering local climate: Miller et al., 2005) and by introducing commensal species such as dogs (Fiedel, 2005), rats (Duncan et al., 2002), and disease (Lyons et al., 2004b). Overkill, the hunting of a species at a level sufficient to drive it to extinction, with or without an additional pressure from factors such as habitat modification and climate change, has been shown to be a viable killing mechanism for megafaunal species (fig. 11-4) if the hunters also could use other species when they deplete the original target species below viable abundances (Bodmer et al., 1997; Alroy, 2001, Brook and Johnson, 2006).

Role of Climate Change

Niche modeling indicates strong correlation between specific climate variables and species distributions (Hijmans and Graham, 2006; Nogues-Bravo et al., 2008), and it now seems clear that climate is a key determinant of whether or not a species can exist in a given locale. Just like human impacts, climatic impacts on species are direct and indirect. Direct impacts include exceeding physiologically imposed temperature and precipitation limits on a species, such as critical temperature thresholds for musk oxen or pikas, which have limited heat-loss abilities. Indirect impacts include mismatch of life history strategy with timing of seasons or other climatic parameters (phenology), for example, emerging from hibernation too early in the spring, before snowmelt has exposed critical food resources (Parmesan, 2006; Barnosky, 2009).

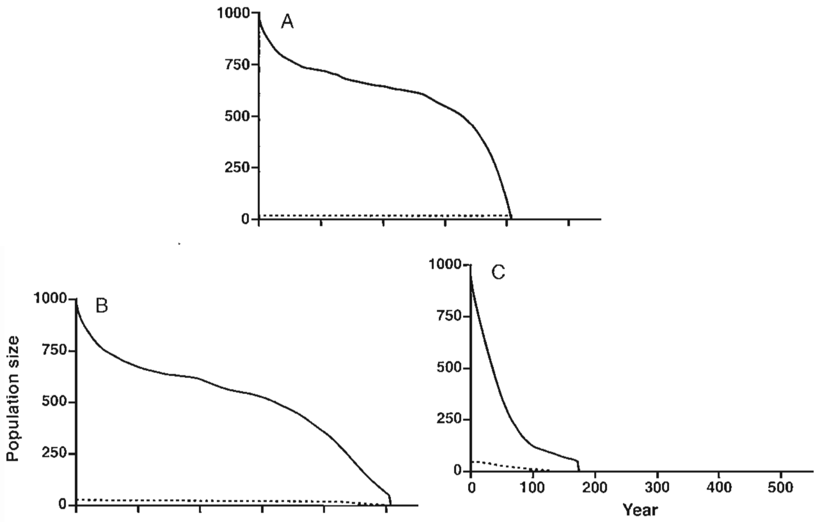

FIGURE 11-4. Overkill by the selective harvest of juveniles (less than 6 years old) of a simulated population of the extinct giant marsupial *Diprotodon optatum*. Solid line is the total regional population (carrying capacity = 1,000) and the (barely visible toward the bottom of each graph) dotted line is the annual number of juveniles killed by hunting (human population size = 150). (A) Constant hunting offtake. (B) Type II functional response (assumes prey are naïve). (C) Type III functional response (assumes adaptive prey and higher hunting pressure). Source: Brook and Johnson, 2006.

Although numerous examples of climatic change stimulating changes in local abundance or geographic range changes exist, there are few examples of climate change causing worldwide extinction in the absence of any other biotic stressor. Examples such as the golden toad (*Bufo periglenes*) and harlequin frogs (genus *Atelopus*) may qualify (Parmesan, 2006) for recent times, and in deeper time, the demise of Irish elk (*Megaloceras*) in Ireland, and horses (*Equus*) and short-faced bears (*Arctodus*) in Beringia seems attributable mainly to late Pleistocene climate changes (Barnosky, 1986; Guthrie, 2003; Barnosky et al., 2004; Koch and Barnosky, 2006). Although available models fail to adequately simulate megafaunal extinctions based on climate change alone (Brook and Bowman, 2004; Lyons et al., 2004a), modeling and empirical evidence has shown climate change alone to cause extinctions *if* species ranges are restricted by barriers that prevent them from moving to track their needed climate space (Barnosky, 1986, 2009; Thomas et al., 2004). It is precisely this latter situation in which the world's fauna (and flora) today find themselves.

The late Quaternary was a period of major natural climate change (fig. 11-5). The most prominent events were the glacial-interglacial cycles, which have repeated thirty-nine times over the last 1.8 million years; the last nine cycles show about a 100,000-year periodicity. During these shifts in climate, the globally averaged temperature changed by 4–6 degrees Celsius—comparable in magnitude to but at a much slower rate than that predicted for the coming century due to anthropogenic global warming under the fossil fuel–intensive, business-as-usual scenario (A1FI; http://www.ipcc.ch: IPCC, 2007). Triggered by orbital forcing and reinforced by albedo changes (ice-sheet retreat or growth) as well as the feedback of terrestrial and oceanic greenhouse gas release, the longer-term glacial cycles also were punctuated by numerous short-lived (and likely regional-scale) abrupt climatic changes, such as the Younger Dryas, Dansgaard-Oeschger, and Heinrich climate events (Overpeck et al., 2003). These short-term, high-magnitude climatic changes probably exacerbated any stresses that the larger-scale glacial-interglacial shifts were placing on species, although all of these kinds of cyclical changes seem within bounds of what species have evolved to withstand in the absence of impermeable geographic barriers (Barnosky, 2001; Barnosky et al., 2003; Benton, 2009).

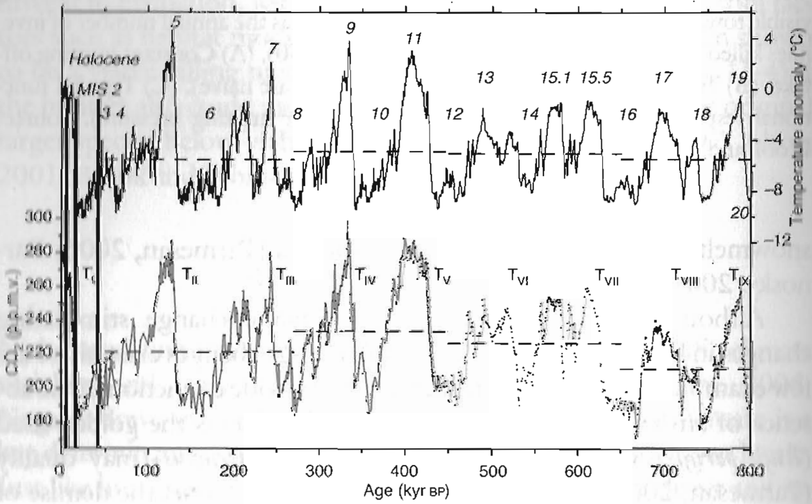

FIGURE 11-5. Antarctic ice core record of polar temperature (top; deuterium data) and carbon dioxide concentration (bottom) for the past 800,000 years. Horizontal lines show mean temperature and carbon dioxide values over different intervals. Marine isotope stages are in italics and glacial terminations by Tx (e.g., T_I). The vertical black lines show the timing of megafaunal extinctions in New Zealand, North America, and Australia (left to right). Source: Modified from Luthi et al., 2008.

Mechanistically, climate change over the last 100,000 years changed vegetation substantially in many parts of the world, although the nature and magnitude of the changes were different in different places (Barnosky et al., 2004). In central North America, for example, the end-Pleistocene witnessed a relatively rapid transition of vegetational structure and composition from a heterogeneous mosaic to a more zonal pattern that was relatively less suitable to large herbivores (Graham and Lundelius, 1984; Guthrie, 1984). Abrupt events such as the Younger Dryas probably superimposed even more rapid vegetation shifts (Stuart et al., 2004). In Australia, the climate became more arid as the depth of an ice age was approached, and the surface water available to large animals would have become scarcer and more patchily distributed (Wroe and Field, 2006). Yet, most megafauna species appear to have persisted across multiple glacial-interglacial transitions, only to become extinct within a few thousand years of, and in some cases, coincident with, the most recent one (fig. 11-5; extinctions marked with black vertical bars).

The resilience of species can be inferred from the fossil record and molecular markers (Lovejoy and Hannah, 2005). In the Northern Hemisphere, populations shifted ranges southward as the Fennoscandian and Laurentide ice sheets advanced (or persisted in locally equable refugia; Hewitt, 1999), and then reinvaded northern realms during interglacials. Some species may have also persisted in locally favorable refugia that were otherwise isolated within the tundra and ice-strewn landscapes (Hewitt, 1999). In Australia, large-bodied mammals were able to persist throughout the Quaternary (Prideaux et al., 2007b), even in remarkably arid landscapes such as the Nullarbor Plain (Prideaux et al., 2007a).

There were many times during the last 100,000 years when the climate apparently shifted from cool-dry to warm-wet conditions, and back again (fig. 11-6, based on the Greenland ice core data), a point

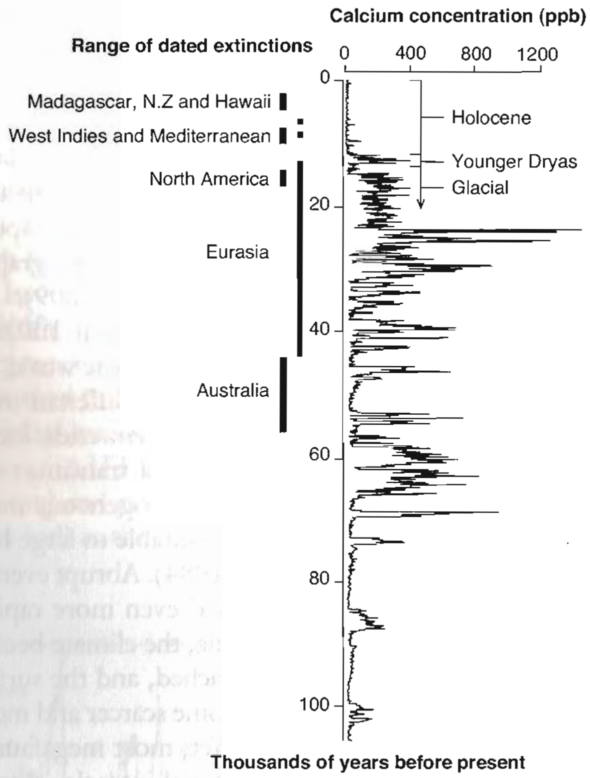

FIGURE 11-6. Greenland ice core calcium concentrations (parts per billion) over the last 100,000 years. Low values indicate wet-warm conditions with relatively denser vegetative cover, and high values point to a cool-dry climate with sparser global vegetation. Also marked are the last glacial maximum, Younger Dryas abrupt cooling event, and the Holocene warm period. The timing of extinctions on islands and continents is indicated; also shown are the earliest and latest extinctions in Beringia with Eurasia. Source: Burney and Flannery, 2005.

reinforced by new stable isotope data from Australia, as described in Brook et al. (2007) and summaries presented in recent reviews (Barnosky et al., 2004; Koch and Barnosky, 2006). Although such changes undoubtedly led to the disappearance of various species in local areas and altered their abundance where they remained on the landscape, nevertheless they persisted regionally or globally until the die-offs clustered in the last few tens of millennia of the Pleistocene and into the Holocene. If climate change were a driver of those extinctions, what was so different as to make the seemingly normal global warming (in comparison to previous glacial-interglacial transitions) at that time negatively affect such a wide range of species and habitats (Burney and Flannery, 2005; Johnson, 2005) to the extent that once-abundant, ecologically dominant animals simply disappeared? The answer to this question probably lies in threat synergies.

Threat Synergies, Past and Present

The Pleistocene megafaunal die-offs provide a salutary lesson about the future of biodiversity under projected global warming scenarios. Over most of the last 2 million years, there was a lack of widespread extinctions, particularly of plants (Willis et al., 2004), despite regular bouts of extreme climatic fluctuations (fig. 11-5). So what made the last glacial cycle different? We believe it was the synergy of mutually reinforcing events brought by the double blow of anthropogenic threats and natural climate change. Together, these produced a demographic-ecological pressure of sufficient force and persistence to eliminate a sizeable proportion of the world's megafauna species (Barnosky et al., 2004; Brook, 2008; Barnosky, 2009; Blois and Hadly, 2009)—a group whose evolved life-history strategy left them particularly vulnerable to chronic mortality stress from a novel predator and modifier of habitats (Brook and Bowman, 2005). Without humans on the scene, climate change would not have been enough.

A good example of this interaction, using a method of coupling bioclimate envelopes and demographic modeling in woolly mammoth (Nogues-Bravo et al., 2008), shows how the human-climate synergy probably operated in the High Arctic. The model indicates that mammoths survived multiple Pleistocene climatic shifts by condensing their geographic range to suitable climate space during climatically unfavorable times. Finally, however, the new presence of modern humans during the late-Pleistocene and Holocene, at the same time as a climatically triggered retraction of steppe-tundra reduced maximally suitable habitat by some 90 percent (fig. 11-7), resulted in extinction. The important message is that mammoth populations' resilience was weakened by habitat loss and fragmentation, as it may well have been in previous interglacials, but during that last range reduction the mammoths were unable to cope because of the addition of predatory pressure (and possibly other landscape modifications) by human hunters.

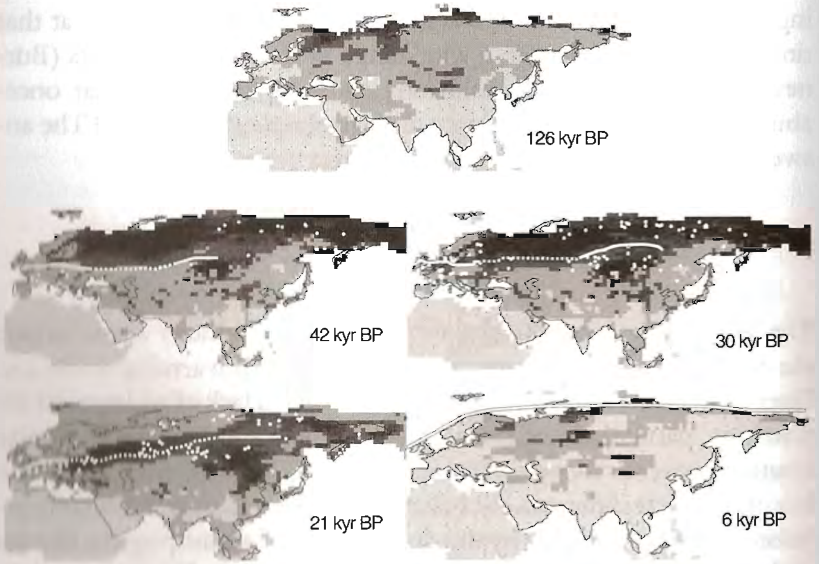

FIGURE 11-7. Climate envelope model of habitat suitability in Eurasia for woolly mammoth (*Mammuthus primigenius*) at five times over the last interglacial-glacial-interglacial cycle. Darker shading indicates higher suitability. Full glacial conditions occurred at 21,000 years before present (kyr BP), warm conditions (as warm or warmer than today) at 126 and 6 kyr BP. The white lines indicate likely northern limit of people. Line is dotted where there is uncertainty about the limit of modern humans. Source: Nogues-Bravo et al., 2008.

In principle, the same sort of fatal synergy is now attacking many species, but in a much magnified way. Modern climate change is occurring at a much faster rate than past events (Barnosky et al., 2003) and began in a world that was already relatively hot because warming started in an interglacial rather than in a glacial. By 2050, the planet is projected to be hotter than it has been at any time since humans evolved as a species. And the backdrop of human pressures on which this extreme climate change is taking place is more pronounced than ever before; in the twenty-first century the human enterprise reaches into all corners of the planet (Brook et al., 2008). Not only are we causing the climate itself to change (Miller et al., 2005), but thanks to our already high population density and ongoing population growth (fig. 11-3), extensive appropriation of natural capital, and technological expansion (Steffen et al., 2007), we are limiting more than ever before other species' ability to track their needed habitats as climate zones rapidly shift across the earth's surface. In short, we are witnessing a similar collision of human impacts and climatic changes that caused so many large animal extinctions toward the end of the Pleistocene. But today, given the greater magnitude of both climate change and other human pressures, the show promises to be a wide-screen, technicolor version of the (by comparison) black-and-white letterbox drama that played out the first time around.

Conclusions

The important message from the late Quaternary megafaunal extinctions is not so much that humans caused extinctions in many (maybe most) places and climate caused them in others. Rather, the key point is that where direct human impacts and rapid climate change coincide, fatalities are higher and faster than where either factor operates alone. It is the synergy that presents the biggest problem, and that synergy is exactly what we find ourselves in the middle of today. Indeed, synergies between seemingly different causal mechanisms seem to characterize mass extinctions in general (Barnosky et al., 2011).

Today, that intelligent predatory ape, the human species, is driving a planetwide loss and fragmentation of habitats, overexploitation of populations, deliberate and accidental introduction of alien species beyond their native ranges, release of chemical pollution, and the global disruption of the climate system. Most damaging of all is the interactions among these different threats, which mutually reinforce each individual impact. Are the modern extinctions resulting from these processes a much magnified version of what already happened once to cause the late Quaternary megafauna extinctions, and can this perspective illuminate how to chart the future to avoid an even more severe biotic collapse? The emerging consensus quite clearly says yes, and that conclusion, in turn, implies that only a systems-based approach to threat abatement will be effective in staving off future extinctions.

Conversely, coming at the problem from trying to figure out what caused Quaternary extinctions, the question "Was it humans or natural climate change that forever ended the evolutionary journey of hundreds of megafaunal species?" is the wrong one to ask. That question anticipates a unicausal mechanism, which might be appealing on parsimonious grounds, but cannot be supported by fossil, archeological, climatological, and modeling evidence. Just as for our modern global biodiversity crisis, one factor (e.g., overhunting) may dominate in one place, and a second factor somewhere else (e.g., a species disappearing off a mountaintop that heats up too much). But at the global scale, synergy among the distinct proximate causes adds up to more than the sum of each individual cause. If one insists on a minimalistic answer for what caused the late Quaternary extinctions, it seems to be this: the actions of colonizing and expanding prehistoric humans (primarily hunting and habitat modification) seems omnipresent in the past global extinction (Brook et al., 2007; Gillespie, 2008), but in many cases, species were left much more vulnerable because of climate-induced range contractions and changes in habitat quality (Guthrie, 2006; Nogues-Bravo et al., 2008).

The degree to which climate change was the "straw that broke the camel's back" probably differed to some extent for each species of extinct Quaternary megafauna, and will only be really understood after detailed study of each extinct species (Koch and Barnosky, 2006). But the fact that even "natural" climate change synergistically exacerbated extinctions when human pressures first increased is worrisome in the modern context. The climate change is now far outside the bounds of what is normal for ecosystems (Barnosky, 2009), and the other kinds of human pressures on species are so much greater than Earth has ever seen. In the end, it will not only be the extent to which we can minimize each individual cause of extinction—increasing human population and attendant resource use, habitat fragmentation, invasive species, and now, global warming—but also the degree to which we can minimize the synergy *between* each separate cause that will determine just how many species we lose.

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Chapter 12

Quaternary Tropical Plant Extinction: A Paleoecological Perspective from the Neotropics

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We have found no examples of global plant extinctions from the tropics within the Quaternary. Examples of extinctions over longer periods of time are readily documented within the fossil record, with the loss of whole families evident between Eocene and modern times (Morley, 2000, 2007). Herein lies a clue to the problem of detecting extinction of tropical plants—the taxonomic resolution of the fossil record.

Most of the paleobotanical records that we have from the tropics are based on fossil pollen, plus a few on wood, and even less on seeds and other macrofossils. With a few exceptions, fossil pollen identifications are at the genus or family level, and so an extinction sufficient to remove an entire genus would be the minimum detectable level of loss. Because many tropical genera contain congeners that occupy very different habitats, losing all of them requires a huge change in the ecosystem, or a lot of bad luck. Over long enough periods of time, evolution, luck, and continental-scale modifications of climate are possible, and extinction does become evident. Because of this taxonomic bias, we actually have a clearer vision of extinction that took place between the Eocene and the Miocene than we do across the much shorter timescale of the Quaternary. We can see at that scale that major climatic events and spread of fire initiated cycles of species loss and speciation. It is not unreasonable to suppose that the spread of fire