Review TRENDS in Ecology and Evolution Vol.20 No.7 July 2005

Paleontology series

Fifty millennia of catastrophic extinctions after human contact

David A. Burney[1] and Timothy F. Flannery[2]

[1]National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, HI 96741, USA
[2]South Australian Museum, Adelaide, South Australia 5000, Australia

Debate continues to rage between enthusiasts for climate change versus humans as a cause of the catastrophic faunal extinctions that have occurred in the wake of human arrival in previously uninhabited regions of the world. A global pattern of human arrival to such landmasses, followed by faunal collapse and other ecological changes, appears without known exception. This strongly suggests to some investigators that a more interesting extinction debate lies within the realm of potential human-caused explanations and how climate might exacerbate human impacts. New observations emerging from refined dating techniques, paleoecology and modeling suggest that the megafaunal collapses of the Americas and Australia, as well as most prehistoric island biotic losses, trace to a variety of human impacts, including rapid overharvesting, biological invasions, habitat transformation and disease.

An abundance of proxy paleoclimatic records from deep-sea drilling, ice cores and other sources has shown that the late Quaternary has been a time of many sudden climate changes. It could be argued, however, that the most important event in the late prehistoric chronology of any previously uninhabited landmass (i.e. any place except Africa and Eurasia) was the arrival of the first humans and their effects. Unlike climatic cycles, a successful initial colonization happens only once.

The last half of the present glacial–interglacial cycle has shown an apparently unprecedented global pattern of temporally stepwise megafaunal collapse, beginning with the Australian continent ~50 000 years ago, spreading to the New World at the end of the Pleistocene ~12 000 years ago, then on to the thousands of oceanic islands. The extinctions begin in the places reached first by colonizing humans, ending with those remote islands that were apparently not colonized until recent centuries, such as Mauritius and the Galapagos Islands [1]. This pattern is without major exception for biotas that included larger animals. Smaller and more remote islands lacking megafauna show losses of many smaller vertebrates, and even invertebrates and plants, within a few centuries of first human contact. The Hawaiian Islands are perhaps the most familiar example, with major losses of waterfowl, finches, land snails and plants. On the larger landmasses, however, there is selective extinction of elephants, camels and other very large animals with a slow reproductive rate. This strong pattern is supported in North America and other well-studied cases [2]. Extinction events before the late Quaternary, including the great turnovers in mammalian faunas on the continents that occurred periodically throughout the Cenozoic, lack such a strong pattern of differential extinction of larger creatures [3].

Although key events surrounding human arrival and megafaunal extinction have received considerable scientific scrutiny in recent years in Australia, New Zealand and Madagascar, much of the heated discussion regarding the causal explanation for these faunal collapses has centered on North America. The original debates of climate versus human agency have given way more recently to an increasing emphasis on combinations of the two. Whatever else can be said for this interchange, it is clear that the original formulation of Martin's version of extremely rapid overkill (the 'Blitzkrieg Hypothesis' [4]) has galvanized a huge body of literature covering research and scientific discussion on the extinction issue, resulting in a host of hypotheses and tests. Many of the more recent theoretical contributions have borrowed ideas from the climate and the overkill camps, invoking interactions of potential factors, or some other mechanism generally involving humans but less directly than with overhunting, such as disease, biological invasion, or habitat alteration (Table 1).

Increasingly sophisticated models have either followed Martin's unicausal orientation but with parameters adjusted for empirical observations and ecological concepts (e.g. [5]), or attempted to integrate other factors, generally human derived, into the quantitative mix [6]. Rather surprisingly, explicit quantitative models for a purely climatic cause that integrate the recent vastly improved baseline information about climate change have not been developed [7]. Perhaps one reason is that global surveys reveal one incontrovertible fact: human arrival predates catastrophic late Quaternary extinction events worldwide. This pattern, from which only Africa and Eurasia are exempt as the original human homelands, suggests that the most interesting question might be how humans could have accomplished this, rather than whether.

Box 1 summarizes the present state of the climate versus human-agency debate. Although there are compelling arguments for and against, one key difficulty for the

---

Corresponding author: Burney, D.A. (dburney@ntbg.org).

www.sciencedirect.com 0169-5347/$ - see front matter © 2005 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2005.04.022

Table 1. Hypotheses proposed to explain late prehistoric extinctions

Type and/or Name	Description	Refs
Climatic hypotheses		
Climate change	Climatic changes, in the form of a slow transition from mosaic vegetation to a more zonal pattern, led to less hospitable environments for megaherbivores	[52,53]
Rapid climate cooling	As above, but change develops rapidly at the Younger Dryas *ca.* 11 000 radiocarbon years ago	[54]
Environmental insularity	Applied only to the extinction of the American mastodon; extinction occurs because boreal forest retreats northwards after glaciation, resulting in expansion of deciduous forest, which is less hospitable to the species	[55]
Overkill hypotheses		
Blitzkrieg, or rapid overkill	Megafauna lacking fear of humans rapidly hunted to extinction; depletion moving as a wave over landscape	[4]
Protracted overkill	Overexploitation of initially naïve fauna gradually leads to population collapse	[29,56]
Predator pit	Native predators contribute to a rapid collapse that is initiated by humans	[57]
Second-order predation	A pulsed extinction event occurs as a result of interactions among humans, carnivores, herbivores and vegetation	[58]
Three-stage overkill	Rapid, pulsed extinction in which overkill alone is sufficient explanation	[5]
Other hypotheses		
Clovis age drought	Rapid onset of arid conditions leads to severe but temporary vegetation change following human arrival, which amplifies the effect of human predation	[59]
Hypervirulent disease	Infectious disease spreads rapidly through wide range of taxa, killing megafauna differentially	[25]
Keystone mega-herbivores	Loss of megaherbivores that maintain open forest causes vegetation changes. For example, fire regime changes as forests close and fuel loads rise	[6,60,61]
Great fire	Landscape transformation by anthropogenic fire; extinction follows rapid loss of forage	[62,63]
Synergy	Human and natural causes interact; megaherbivore decline leads to increased fire occurrence and landscape transformation	[39]

climatic-change proponents is that the biotic transformations around the world have occurred at different times during the past 50 000 years, so that no single climatic shift can be invoked to explain all the transformations (Figure 1). Thus, Australian marsupials, birds and reptiles that were larger than their surviving relatives disappeared tens of thousands of years before the Last Glacial Maximum, whereas at the other temporal extreme, written histories record that the dodo *Raphus cucullatus* died out on Mauritius about three centuries ago. North America is the place where the end of the last ice age, and some climatic flip-flops such as the Younger Dryas event, approximately coincided with the first evidence of humans on the continent and the last evidence of mammoths, mastodons and a host of other large and mid-sized animals [1]. It is no wonder, then, that the climatic explanation has held more sway there, given that the evidence is confounded by the crowding together of events that are separated elsewhere.

Climate explanations are unlikely to go away (see [8,9] for recent examples). The increasing scientific scrutiny of Pleistocene and Holocene climates, and studies of extreme events in modern times, (such as volcanic outbursts with almost immediate short-term teleconnections to global climate trends, and marine-terrestrial interactions including El Niño-Southern Oscillation phenomena) make it clear that climatic uncertainty and rapid changes are a constant background factor in all ecosystems. Climate undoubtedly shapes evolution and occasionally throughout geological time has caused simultaneous extinctions [3].

Fundamental questions being addressed by current research are: (i) Which of these is the key factor in any given case?; (ii) How, and to what extent, do ecological factors interact among themselves as well as with abiotic

Box 1. Climate-driven extinction: arguments for, against, and including

Climate change is believed by most scientists to have had a major role in some of the extinction events in the geological record. It is the last great extinction event, spanning the past 50 millennia, however, where disagreement abounds concerning the importance of climate versus an array of human impacts. Hypotheses that discount the primary importance of humans in these extinctions usually favor some form of climate change (Table 1, main text). Gradual climate change [53] and sudden change [54] have each been invoked as late prehistoric extinction agencies.

The single biggest problem with climate as an explanation for the extinctions is the lack of synchroneity of extinction horizons across landmasses (Figure 1, main text), missing the key climatic events in some areas (Australia, Madagascar, New Zealand, etc.) and roughly coinciding in others (the Americas and Eurasia) [64]. South America appears to lead North America in the onset of postglacial climate changes, but extinctions occur later than in North America [7]. One of the greatest problems in unraveling the threads of cause and effect in the Americas has been that, owing to rapid changes in ^{14}C flux to the atmosphere at this time, radiocarbon dating calibrations to the tree-ring record and other high-resolution proxies are particularly unreliable around the time of the events of interest [65]. In Eurasia, where human ancestors and the megafauna have coevolved for over two million years, the extinctions are generally more spread out than in the Americas, ranging over many thousands of years rather than perhaps a few centuries in the case of North America [18].

Stratigraphic techniques that can recognize and resolve the changes well enough to see the order of events are essential for improved insights regarding causes of prehistoric extinctions. More studies that compare high-resolution paleoclimatic records to well dated faunal disappearances are needed, as is modeling of the interactions of climate, landscape and biota. One great deficiency has been that few studies address how a particular climatic change would negatively affect simultaneously population sizes of many different species, often with contrasting habitat preferences. Perhaps the most promising role for climate in our understanding of the extinctions lies in better elucidating how it might have interacted with human impacts to help seal the fate of so many taxa.

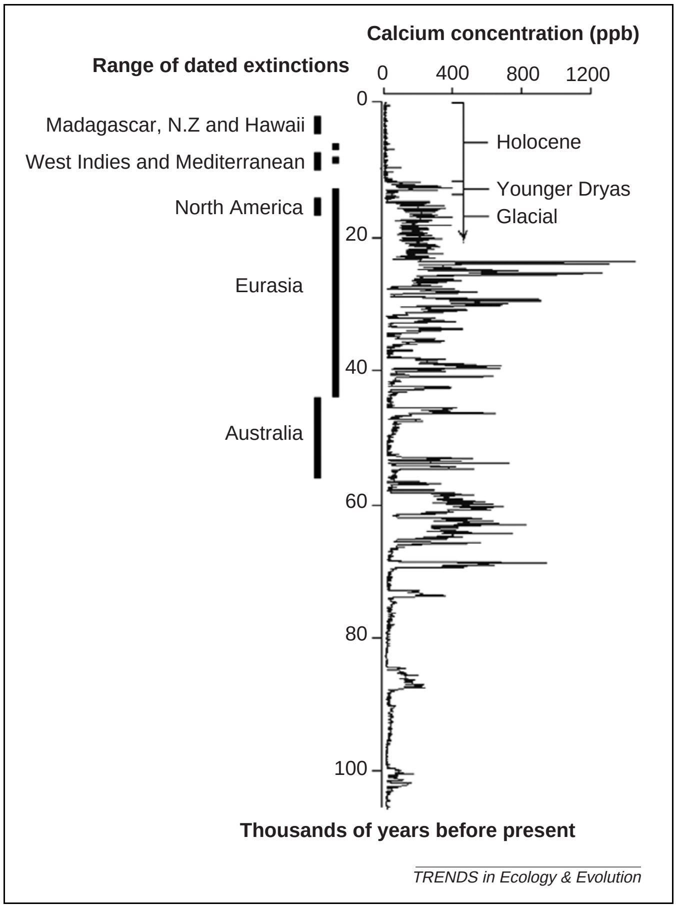

Figure 1. A high-resolution calcium concentration record from the GISP2 Greenland ice core (http://www.gisp2.sr.unh.edu/DATA/fancy.html), indicating the relative amount of atmospheric dust, an index for cool and dry versus wet and warm conditions. This proxy measure of the extent of vegetative cover, as well as other Pleistocene climatic indices, shows no correlation with the distribution of 'last occurrence' dates for extinct fauna in key regions (vertical bars). Climate data adapted from [67], with extinction ranges from [1,64].

factors, such as climate change and extreme events?; and (iii) Are there any extractable lessons from the past concerning present challenges to restore damaged ecosystems and to design more sustainable human environments? Here, we focus on another question, however, which is not whether humans have transformed living landscapes and contributed heavily to the extinction patterns in the time frame of interest, but rather, how they could have done it.

Measurement techniques in human paleoecology

Although Table 1 lists many human-agency hypotheses, most invoke overkill, habitat transformation, biological invasion, or disease. If any one of these could be shown to be a sufficient explanation for a well studied example, this would help clarify what it is that humans do that is potentially most destructive to the largest number of places in the long run, and would also cast doubt indirectly on climatic explanations. A key theoretical problem, however, is that each landmass is a unique configuration. Similar to other important generalizations in the field of biogeography, such as species–area relationships, even the hundreds of replicates that the global record provides for the ecological impacts of humans must be viewed cautiously, because colonizations of new lands by humans do not represent controlled treatments in the sense of a laboratory experiment. Nevertheless, insights can be gleaned from historical narratives generated from multidisciplinary analysis of the key time frame that includes: (i) a sufficiently long baseline before human arrival to demonstrate the prevailing ecological trends; (ii) the reasonably precise determination of when humans arrived and what they were doing during the early days of colonization; and (iii) what has changed subsequently in the living landscapes; that is, the interaction of biota with soils, water, climate and exotic taxa, including humans.

The history of science provides some clues as to how progress can be made at a theoretical impasse. New types of data and more refined measurements can, and often have, reduced the muddle in a scientific controversy, and the consilience of an array of different types of information, collected as independently as possible, might point the way to new insights [10–12].

Notions of chronology in long-debated extinction events of the late Quaternary were so improved by the advent of ^{14}C dating that serious scientific discussion regarding the cause of these extinctions made significant advances only after the advent of the method. Overkill hypotheses have depended heavily on the fact that, except for the early Australian case, key stratigraphic events (recognizable horizons in sedimentary layers and their associated fossils) have been determined with the use of radiocarbon dating. These dates generally show the close timing of key events, such as incontrovertible evidence for a human presence, and decline of megafaunas (see [13] for examples). In the past decade, great progress has been made in refining chronologies by use of Accelerator Mass Spectrometry (AMS) of microgram-range carbon samples that have been subjected to a battery of pretreatments to remove contaminating exogenous carbon. This has led to recent chronologies for extinction events and related environmental changes, suggesting that megafaunas have been brought down quickly not only in North America [14], but also in Madagascar [15] and the islands of the South Pacific [16,17]. This is in contrast to the more protracted and stepwise extinctions in Eurasia, for which dating evidence shows that hominins have evolved physically and culturally alongside a megafauna that experienced losses spread out over the past several tens of thousands of years [18,19].

Especially in Australia and the previously attached shelf island of New Guinea, the events surrounding human arrival and megafaunal extinction have been clarified temporally by resorting to a range of dating methods, because conventional radiocarbon dating does not reach back far enough to provide the necessary precision. Recent refinements in pretreatment of samples for AMS, and particularly the use of optical thermoluminescence and Uranium-series techniques for dating, show that human arrival, an increase in burning in the environment and megafaunal decline all cluster around 45 000–55 000 years ago [20–22] (but see [23]).

A second area of recent major progress provides refined tallies of the faunal losses in less-studied areas that could provide insight to the overall process. On islands of the Pacific [16,24], the West Indies [25] and the

Mediterranean [26], the full extent of the losses is now more apparent as a result of dogged efforts by paleontologists. For instance, it has been estimated that >2000 species of flightless rails might have been lost from South Pacific islands alone, based on extrapolation from well-known cases [16].

A third avenue for increased perspective on the time period of interest has been in the area of reconstruction of the feeding behavior, ecology and life-history parameters of creatures lost in these extinctions. These include information about the diet of bizarre extinct creatures, such as the giant lemurs of Madagascar [27] and the large flightless ducks of Hawaii [28], from coprolites, stable isotopes and other evidence. Similarly, studies of more familiar North American Pleistocene megafauna, particularly elephants and their relatives (e.g. [29]) have helped scientists better visualize the role of these creatures in the environment (e.g. the importance of megaherbivory in moderating wildfire occurrence).

Proxies for humans and megafauna

Archaeology should, in theory, provide the necessary information concerning human arrival and transformation of biotas, but conventional methods of excavation have had mixed success in detailing events surrounding the initial coupling of prehuman natural systems and subsequent human-dominated landscapes.

Evidence from 'kill' sites

A highly conservative estimate of 14 definite 'kill' sites in North America (archaeological sites containing evidence for butchery of extinct megafauna by humans) was published recently [30], most of them mammoth sites in the southwestern USA. This scarcity of evidence is predicted by the Blitzkrieg model of Martin and many subsequent overkill models, because a rapid killing-off would leave little trace of interactions between humans and their prey owing to the short time-frame of the period of interaction at any given location. Moas were apparently extinguished within just a few centuries after the arrival of the Maori in New Zealand ~1200 AD [31,32], yet abundant evidence of moa butchery is present in >100 sites on the South Island. Evidence is much scarcer on the warmer north island, where the higher human population density is believed to have driven the extinction much faster, leaving fewer traces [32].

In Madagascar, late Holocene evidence for butchery of pygmy hippos, elephant birds and giant lemurs is scarce, but dating of these bones agrees well with other types of evidence for human colonization from palynology and other indirect indicators [15]. Much work remains to be done everywhere, with South America, Beringia and the West Indies obvious areas for seeking out and analyzing the earliest archaeological sites for evidence concerning the extinctions.

It is quite relevant to the issue of a climatic versus human role that the preliminary evidence suggests that the megafauna of South America died out roughly a millennium later than in North America, although the argument continues as to whether Monte Verde [33] and perhaps other sites in South America indicate a human presence there *ca.* one millennium earlier than the evidence for Clovis culture (earliest well documented Paleoindian) big-game hunters in North America. On an uninhabited Alaskan Bering Sea Island, mammoths persisted until mid-Holocene times, in spite of climate change [34].

Meanwhile, in the Greater Antilles, it appears that at least some of the insular megafauna of 'dwarf giant' ground sloths, giant rodents and insectivores, and flightless birds persisted well into the Holocene, long after the drastic climate changes at the end of the Pleistocene that obscure issues in North America. Although more dates are needed, it looks as though, in the West Indies, megafaunal extinctions and transformation of the landscape by burning approximately coincide with the earliest evidence for humans from archaeological sites [35].

Founding human populations, especially those that find themselves on larger landmasses (or perhaps grow slowly owing to disease or other factors) thus might be impossible to detect with the use of customary archaeological techniques, such as surface survey and excavation of artifacts. Recent years have seen an increasingly important role for proxies for a human presence (Table 2). Bones of rats introduced to Pacific Islands by Polynesians, for instance, serve as a stratigraphic marker for human arrival in Hawaii [24], the South Pacific [16] and elsewhere. In New Zealand, a few sites [36] have been interpreted as containing rats well before human establishment, perhaps suggesting an initial failed colonization, or a temporary visit by voyaging canoes that moved on but left rat passengers behind. The more conventional pattern, however, is for rats or any other human-introduced microfauna (such as lizards) to proliferate rapidly enough to provide a marker horizon in cave sediments, owl roost deposits and stratified dune deposits almost instantaneously on stratigraphic timescales. The low number of founding humans might take a few centuries to fill up the new landscape with archaeological evidence that can rarely, if ever, be subsequently detected before some critical level of human density is achieved.

Palynological evidence

Even low-density human populations do things to the environment other than killing the biggest animals. Some of these can be detected at the microscopic level. Palynology, the study of fossil pollen grains and other microfossils, has become increasingly important in understanding the changes in the biotic landscape that are apparently contemporaneous with initial human activity. Pollen analysts have long noted that the presence of humans can be detected in such prehistoric vegetation changes as the 'landnam' phenomenon (decline in elm pollen, probably from overharvesting by neolithic pastoralists) in early Holocene Europe [37] and the deforestation of late Holocene New Zealand [38] and Madagascar [39]. Microscopic charcoal particles have now been used worldwide to detect a human-induced change in fire regime (for a recent review see [40]).

The Sporormiella example

There is a less familiar proxy relevant to the extinction story. *Sporormiella* spp. are fungi that grow on animal

Table 2. Proxy evidence for human arrival to a new land

Method of detection	Rationale	Examples	Refs
Bones of introduced micro-vertebrates	Because of high reproductive rates, small animals brought by humans will be highly visible in the stratigraphic record soon after human arrival	Pacific rat *Rattus exulans* in Hawaii	[45]
Increase in ruderal pollen and spore types	Vegetation disturbance by humans leads to large increase in pioneer species	Increase in bracken fern spores after Maori colonization in New Zealand	[38]
Appearance of exotic pollen types	Plant brought by first colonists might naturalize and produce a distinctive pollen horizon	Appearance of *Cannabis* pollen in Madagascar	[15]
Paleolimnological traces of cultural eutrophication	Arriving humans might transform watersheds, releasing nutrients to water bodies that change the fossil plankton flora	Increase of eutrophic algae after local human settlement in western Madagascar	[66]
Sudden increase of micro-scopic charcoal particles	Use of fire by humans leads to an increase in soot particles above normal background values	Detection of human arrival in Australia from microscopic charcoal in Lynch's Crater	[21]
Drastic decline in dung-fungus spores	*Sporormiella* spp. grow primarily on megafaunal dung; thus, distinctive fungal spores might provide a proxy for large mammal density; sudden decline might indicate transformation of mammal biota by humans	Spore decline before Younger Dryas and charcoal increase in upstate New York	[44]

dung. Pioneer studies by Davis [41] showed that these spores occur at high frequency in megafaunal dung deposits, and are well represented in some lake sediment cores until ~12 000 radiocarbon years ago. They almost disappear from Holocene sediments, only to reappear with the advent of cattle following European settlement.

In Madagascar, *Sporormiella* declines in sediment cores within a few centuries of human arrival, and reappears with the introduction of cattle about a millennium later. A key point for further discussion is that microscopic charcoal shows a drastic increase within one to a few centuries following the *Sporormiella* decline [42]. This suggests that (as first noted as a possibility for Australia by Flannery [43]) vegetation change and an increase in fire frequency were more of a consequence than a cause of the megafaunal decline. AMS dating of pretreated bone collagen from a wide array of the extinct fauna shows, however, that most species held on at least tenuously for centuries after the initial (*Sporormiella*-inferred) population crash, to go extinct after the environment had already been transformed in many areas and human populations had become archaeologically visible. A similar pattern, but >10 000 years earlier, has been inferred from spore, charcoal and pollen analysis in upstate New York [44].

Integrated site analysis

Studying the past at the landscape level, and achieving a high degree of site integration in terms of the widest array of consilient evidence from fossils, microfossils and artifacts, are parallel ideas that are not new. Recent years have seen the emergence of multidisciplinary teams focusing landscape-level paleoecology and integrated site analysis specifically on the sites that are judged to best preserve the key events in human arrival and biotic transformation [16,24,44,45]. From the linked perspectives of dating accuracy and hypothesis testing, one of the key finds is a site with interpretable stratigraphy, well dated to the time just before, during, and after human arrival, that preserves vertebrate bones, invertebrate shells, plant macrofossils, pollen, diatoms, charcoal and human artifacts. Such sites offer opportunities for evaluating cause and effect in a stratigraphic record (always a risky enterprise). For instance, this type of site might enable the comparison of the last occurrences of extinct taxa and the first evidence for an array of human impacts that are detectable and potentially separable in the fossil and archaeological record. Such integrated sites have a key role in resolving questions about stratigraphic events that are too close in time, too recent, or too old to resolve directly with the use of ^{14}C analysis [39,42].

Suitable sites for such broad-scale analysis are rare, although some degree of integration of this type has been achieved in both dry and wet cave sediments, open wetland sites with approximately neutral sediment pH and, to some degree, dung deposits in dry caves. In each of these site types, sequences of ancient DNA have also been recovered, revealing taxonomic relationships of extinct creatures and the identity of dietary items [17,46].

Future directions for research

Much progress has been made during the past five years in the chronometry, hypothesis testing, modeling, site integration and landscape reconstruction necessary to better understand the extinction patterns of the past few tens of millennia. New models have been generated that incorporate ever more precise estimates of key parameters, and attempt to integrate many relevant ecological factors. One clear need is to generate stronger and more rapid integration between hypothesis generation, modelers, and data-gatherers. An example of this in practice is the evaluation of the Hypervirulent Disease Hypothesis [25] by a team currently studying West Nile Virus and modeling its spread [47]. Similarly, there is a great need for more rigorous, multi-technique dating programs focusing on key contentious sites.

More scientific and technical attention also should be devoted to finding and developing practical applications of this area of research. For more than a decade, conservation organizations and government agencies have occasionally sought background information concerning baseline paleoecological conditions and past ranges of presently endangered species. Organizations in Hawaii, such as the National Tropical Botanical Garden (http://www.ntbg.org), routinely use paleoecological studies to guide plant restoration projects in areas heavily invaded by exotics and currently lacking most native plants [48].

Epilogue: so, what caused all these extinctions, anyway, and why does it matter?

Just as scientists who study these extinctions are still divided on the exact cause, they are also divided on the more philosophical issue in the background: does it matter in any practical sense what caused these extinctions? No one has tried to argue recently that humans have not had negative impacts on ecosystems. Historically documented extinctions show this clearly in some cases [11] and provide a 'Rosetta Stone' for prehistoric extinctions highlighting a multiplicity of human-derived causes. Proponents of climatic explanations freely acknowledge that humans have also changed environments [40].

Perhaps there are moral arguments that could be relevant. There might be more obligation to try to slow present extinction rates or re-introduce extirpated species (or close relatives and ecological surrogates, such as elephants, camelids and cheetahs to North America) to former habitats if humans caused the extinctions in the first place [14,49–51]. It could be argued, however, that ecological restoration, including this type of species translocation, should be undertaken with the same vigor regardless of the original cause of the extinctions. This would include climate, because whatever climate catastrophe one chooses to explain the late prehistoric extinction pattern, it must have been rare and somehow often restricted to a single landmass at any given time (but see [52]). Such a bizarre climate catastrophe, (such as an asteroid impact or Noah's Flood, at least figuratively, but apparently restricted to one or a few landmasses at a time) would be something that humans would feel automatically inclined to hasten nature's recovery from, if only out of self-interest.

If humans had a key role in most of these extinctions, or if biotic catastrophes loom ahead that are beyond our capacity to even imagine (both are likely), it makes basic survival sense to understand as much as we can about the last great revolution in the history of life, one that began at least 50 millennia ago and continues to the present.

Acknowledgements

We thank M. Bell for encouraging us to review this topic; P. Martin, M. Soulé, J. Berger, J. Donlan, G. Robinson and D. Foreman shared thoughtful discussions concerning the practical significance of the global extinction pattern; L. Godfrey, P. Martin, A. Barnosky and L. Burney provided helpful comments on the article. This publication was written under support from NSF BCS-0129185.

References

1 Martin, P.S. and Steadman, D.W. (1999) Prehistoric extinctions on islands and continents. In *Extinctions in Near Time: Causes, Contexts, and Consequences* (MacPhee, R.D.E., ed.), pp. 17–55, Kluwer Academic/Plenum

2 Lyons, S.K. *et al.* (2004) Of mice, mastodons, and men: human-mediated extinctions on four continents. *Evol. Ecol. Res.* 6, 339–358

3 Alroy, J. (1999) Putting North America's end-Pleistocene megafaunal extinction in context: large-scale analyses of spatial patterns, extinction rates, and size distributions. In *Extinctions in Near Time: Causes, Contexts, and Consequences* (MacPhee, R.D.E., ed.), pp. 105–144, Kluwer Academic/Plenum

4 Martin, P.S. (1984) Prehistoric overkill: the global model. In *Quaternary Extinctions: A Prehistoric Revolution* (Martin, P.S. and Klein, R.G., eds), pp. 354–403, University of Arizona Press

5 Alroy, J. (2001) A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292, 1893–1896

6 Zimov, S.A. *et al.* (1995) Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.* 146, 765–794

7 Fiedel, S.J. and Haynes, G. (2004) A premature burial: comments on Grayson and Meltzer's 'Requiem for Overkill'. *J. Archaeol. Sci.* 31, 121–131

8 Guthrie, D. (2003) Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature* 426, 169–171

9 Shapiro, B. *et al.* (2004) Rise and fall of the Beringian steppe bison. *Science* 306, 1561–1565

10 Wilson, E.O. (1998) *Consilience: The Unity of Human Knowledge*, Alfred A. Knopf

11 Diamond, J.M. (1997) *Guns, Germs, and Steel: The Fates of Human Societies*, Jonathan Cape

12 Pimm, S.L. (2001) *The World According to Pimm: A Scientist Audits the Earth*, McGraw-Hill

13 Martin, P.S. and Wright, H.W., eds (1967) *Pleistocene Extinctions: The Search for a Cause*, Yale University Press

14 Flannery, T.F. (2001) *The Eternal Frontier: An Ecological History of North America and Its Peoples*, Atlantic Monthly Press

15 Burney, D.A. *et al.* (2004) A chronology for late prehistoric Madagascar. *J. Hum. Evol.* 47, 25–63

16 Steadman, D.W. (1995) Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science* 267, 1123–1131

17 Slikas, B. (2004) Hawaiian birds: lessons from a rediscovered avifauna. *Auk* 120, 953–960

18 Stuart, A.J. (1999) Late Pleistocene megafaunal extinctions: a European perspective. In *Extinctions in Near Time: Causes, Contexts, and Consequences* (MacPhee, R.D.E., ed.), pp. 257–269, Kluwer Academic/Plenum

19 MacPhee, R.D.E. *et al.* (2002) Radiocarbon chronologies and extinction dynamics of the late Quaternary mammalian megafauna of the Taimyr Peninsula, Russian Federation. *J. Archaeol. Sci.* 29, 1017–1042

20 Roberts, R.G. *et al.* (2001) New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. *Science* 292, 1888–1892

21 Turney, C.S.M. *et al.* (2001) Redating the onset of burning at Lynch's Crater (North Queensland): implications for human settlement in Australia. *J. Quat. Sci.* 16, 767–771

22 Bird, M.I. *et al.* (2002) Radiocarbon analysis of the early archaeological site of Nauwalabila I, Arnhem Land, Australia: implications for sample suitability and stratigraphic integrity. *Quat. Sci. Rev.* 21, 1061–1075

23 Wroe, S. *et al.* (2004) Megafaunal extinction in the late Quaternary and the global overkill hypothesis. *Alcheringa* 28, 291–331

24 Burney, D.A. *et al.* (2001) Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecol. Monogr.* 71, 615–641

25 MacPhee, R.D.E. and Marx, P.A. (1997) The 40,000-year plague. In *Natural Change and Human Impact in Madagascar* (Goodman, S. and Patterson, B., eds), pp. 169–217, Smithsonian Press

26 Alcover, J.A. *et al.* (1999) Una aproximació a la paleoecologia de les illes. In *Ecologia de les Illes* (Alcover, J.A. and Del Hoyo, X., eds), pp. 169–204, Monografies de la Societat d'Història Natural de les Balears 6

27 Godfrey, L.R. *et al.* (2004) Dental use wear in extinct lemurs: evidence of diet and niche differentiation. *J. Hum. Evol.* 47, 145–169

28 James, H.F. and Burney, D.A. (1997) The diet and ecology of Hawaii's extinct flightless waterfowl: evidence from coprolites. *Biol. J. Linnean Soc.* 62, 279–297

29 Fisher, D.C. (1997) Extinction of proboscideans in North America. In *The Proboscidia: Evolution and Paleoecology of Elephants and Their Relatives* (Shoshani, J. and Tassy, P., eds), pp. 296–432, Oxford University Press

30 Grayson, D.K. and Meltzer, D.J. (2003) A requiem for North American overkill. *J. Archaeol. Sci.* 30, 585–593

31 Holdaway, R.N. and Jacomb, C. (2000) Rapid extinction of the moas (Aves: Dinornithiformes): model, test, and implications. *Science* 287, 2250–2254

32 Worthy, T.H. and Holdaway, R.N. (2002) *The Lost World of the Moa*, Indiana University Press

33 Meltzer, D.J. (1997) Monte Verde and the Pleistocene peopling of the Americas. *Science* 276, 754–755

34 Guthrie, R.D. (2004) Radiocarbon evidence of mid-Holocene mammoths stranded on an Alaskan Bering Sea Island. *Nature* 429, 746–749

35 MacPhee, R.D.E. (1999) "Last occurrence" of the Antillean insectivore *Nesophontes*: new radiometric dates and their reinterpretation. *Am. Mus. Novitates* 3261, 1–20

36 Holdaway, R.N. (1996) The arrival of rats in New Zealand. *Nature* 384, 225–226

37 Faegri, K. *et al*. (1989) *Textbook of Pollen Analysis*, John Wiley & Sons

38 McGlone, M.S. and Wilmshurst, J.M. (1999) Dating initial Maori environmental impact in New Zealand. *Quat. Internat.* 59, 5–16

39 Burney, D.A. (1999) Rates, patterns, and processes of landscape transformation and extinction in Madagascar. In *Extinctions in Near Time: Causes, Contexts, and Consequences* (MacPhee, R.D.E., ed.), pp. 145–164, Kluwer Academic/Plenum

40 Grayson, D.K. (2001) The archaeological record of human impacts on animal populations. *J. World Prehist.* 15, 2–68

41 Davis, O.K. (1987) Spores of the dung fungus *Sporomiella*: increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quat. Res.* 28, 290–294

42 Burney, D.A. *et al*. (2003) *Sporormiella* and the late Holocene extinctions in Madagascar. *Proc. Natl. Acad. Sci. U. S. A.* 100, 10800–10805

43 Flannery, T.F. (1994) *The Future Eaters*, Reed Press

44 Kerr, R.A. (2003) Megafauna died from big kill, not big chill. *Science* 300, 885

45 James, H.F. *et al*. (1987) Radiocarbon dates on bones of extinct birds from Hawaii. *Proc. Natl. Acad. Sci. U. S. A.* 84, 2350–2354

46 Poinar, H.N. *et al*. (1998) Molecular coproscopy: dung and diet of the extinct ground sloth *Nothrotheriops shastensis*. *Science* 281, 402–406

47 Lyons, S.K. *et al*. (2004) Was a "hyperdisease" responsible for the late Pleistocene megafaunal extinction? *Ecol. Lett.* 7, 859–868

48 Ernst, C. (2001) Discovering Kauai's real 'Lost World'. *Malamalama* 3, 8–10

49 Martin, P.S. and Burney, D.A. (1999) Bring back the elephants! *Wild Earth* Spring, 57–64

50 Martin, P.S. (2002) Prehistoric extinctions: in the shadow of man. In *Wilderness and Political Ecology: Aboriginal Influences and the Original State of Nature* (Kay, C.E. and Simmons, R.T., eds), pp. 1–27, University of Utah Press

51 Foreman, D. (2004) *Rewilding North America: A Vision for Conservation in the 21st Century*, Island Press

52 Guthrie, R.D. (1984) Mosaics, allelochemicals and nutrients: an ecological theory of Late Pleistocene megafaunal extinctions. In *Quaternary Extinctions: A Prehistoric Revolution* (Martin, P.S. and Klein, R.G., eds), pp. 259–298, University Arizona Press

53 Graham, R.W. and Lundelius, E.L. (1984) Coevolutionary disequilibrium and Pleistocene extinctions. In *Quaternary Extinctions: A Prehistoric Revolution* (Martin, P.S. and Klein, R.G., eds), pp. 223–249, University Arizona Press

54 Berger, W.H. (1991) On the extinction of the mammoth: science and myth. In *Controversies in Modern Geology* (Muller, D. *et al*., eds), pp. 115–132, Academic Press

55 King, J.E. and Saunders, J.A. (1984) Environmental insularity and the extinction of the American mastodon. In *Quaternary Extinctions: A Prehistoric Revolution* (Martin, P.S. and Klein, R.G., eds), pp. 315–339, University Arizona Press

56 Whittington, S.L. and Dyke, B. (1984) Simulating overkill: experiments with the Mosimann and Martin model. In *Quaternary Extinctions: A Prehistoric Revolution* (Martin, P.S. and Klein, R.G., eds), pp. 451–465, University Arizona Press

57 Janzen, D.H. (1983) The Pleistocene hunters had help. *Am. Nat.* 121, 598–599

58 Whitney-Smith, E. (2004) Late Pleistocene extinctions through second-order predation. In *The Settlement of the American Continents: A Multidisciplinary Approach to Human Biogeography* (Barton, C.M. *et al*., eds), p. 177, University Arizona Press

59 Haynes, C.V. (1991) Geoarchaeological and paleohydrological evidence for a Clovis-age drought in North America and its bearing on extinction. *Quat. Res.* 35, 438–450

60 Owen-Smith, N. (1987) Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* 13, 351–362

61 Schüle, W. (1990) Landscapes and climate in prehistory: interactions of wildlife, man and fire. In *Fire in the Tropical Biota* (Goldhammer, J.G., ed.), pp. 273–318, Springer-Verlag

62 Humbert, H. (1927) La destruction d'une flore insulare par le feu. *Mem. Acad. Malgache* 5, 1–80

63 Miller, G.H. *et al*. (1999) Pleistocene extinction of *Genyornis newtoni*: human impact on Australian megafauna. *Science* 283, 205–208

64 Barnosky, A.D. *et al*. (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306, 70–7559 Owen-Smith, N. (1987) Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* 13, 351–362

65 Fiedel, S.J. (1999) Older than we thought: implications of corrected dates for Paleoindians. *Am. Antiq.* 64, 95–115

66 Matsumoto, K. and Burney, D.A. (1994) Late Holocene environments at Lake Mitsinjo, northwestern Madagascar. *Holocene* 4, 16–24

67 Mayewski, P.A. *et al*. (1994) Changes in atmospheric circulation and ocean ice cover over the North Atlantic during the last 41,000 years. *Science* 263, 1747–1751