

Paleontology series

Fifty millennia of catastrophic extinctions after human contact

David A. Burney¹ and Timothy F. Flannery²¹National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, HI 96741, USA²South 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 uncausal 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).

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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 synchronicity 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.

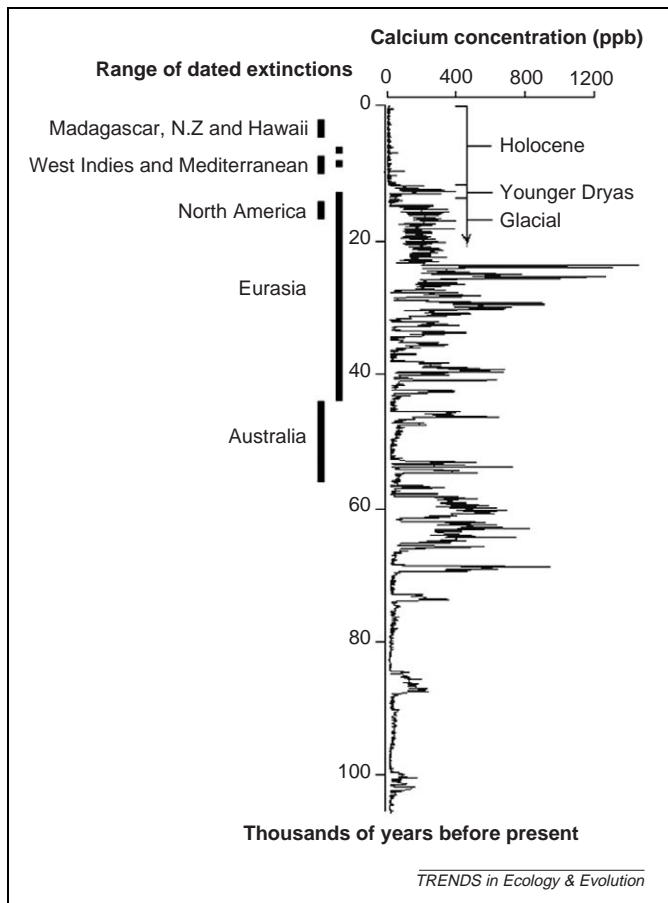


Figure 1. A high-resolution calcium concentration record from the GISP2 Greenland ice core (<http://www.gisp2.sr.unh.edu/DATA/fancy.html>), indicating the relative amount of atmospheric dust, an index for cool and dry versus wet and warm conditions. This proxy measure of the extent of vegetative cover, 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 multi-disciplinary 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 <i>Rattus exulans</i> 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 <i>Cannabis</i> 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 microscopic 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	<i>Sporormiella</i> 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.

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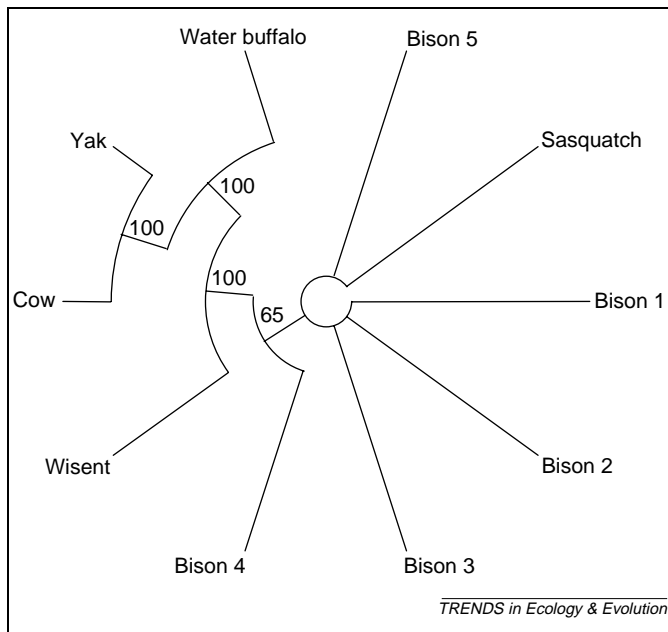


Figure 1. Maximum parsimony tree illustrating the position of the Sasquatch hair sample. Bootstrap support values are given at the nodes. The species and GenBank accession numbers are water buffalo *Bubalus bubalis* (AF197216), yak *Bos mutus* (AY521157), cow *Bos taurus* (AB065127), wisent *Bos bonasus* (AY748759), and North American bison *Bison bison* (1, AY748758; 2, U12947; 3, AY748757; 4, AY748478; 5, AY748620).

offered to shed the hard light of modern science onto this case using a DNA test to eliminate any remaining uncertainty.

We extracted DNA from the hair follicles of ten roots using DNeasy columns (QIAGEN Inc.; <http://www.qiagen.com/>) and amplified the hypervariable region I of the control region (also known as the D-loop) using primers that have conserved sequence in mammals [4]. Alignment of a 429-bp DNA

fragment to DNA databases [5] produced high probability matches to 2058 sequences, all of which were from the infraorder Pecora (horned ruminants). The top 58 matches were from *B. bison*, all with 99–100% sequence identity. A total of 1641 hits were to the Bovinae (mostly to *Bos* spp.) and the remainder to members of the Cervidae (e.g. moose *Alces alces*). The phylogenetic position of the unknown sequence derived from a maximum parsimony analysis of an alignment of representative taxa places the sample in the same clade as North American bison (Figure 1).

There are several possible explanations for these results. First, as suggested from molecular analysis of hair from a suspected Yeti [1], the Sasquatch might be a highly elusive ungulate that exhibits surprising morphological convergence with primates. Alternately, the hair might have originated from a real bison and be unrelated to the Sasquatch. Parsimony would favor the second interpretation, in which case, the identity and taxonomy of this enigmatic and elusive creature remains a mystery.

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Megafaunal extinction: climate, humans and assumptions

Stephen Wroe¹, Judith Field^{1,2} and Donald K. Grayson³

¹Australian Key Centre for Microscopy and Microanalysis, Electron Microscope Unit (F09), University of Sydney, Sydney, NSW 2006, Australia

²School of Philosophical and Historical Inquiry, University of Sydney, Sydney, NSW 2006, Australia

³Department of Anthropology, Box 353100, University of Washington, Seattle, WA 98195, USA

Recently in *TREE*, Burney and Flannery reviewed the role of colonizing humans in prehistoric extinctions [1]. Their treatment is informative and we applaud the broad assertion that realistic explanations will not be found in simple, single-cause paradigms. However, despite some qualification, the authors strive to present human influences as primary in all instances: '...a more interesting

extinction debate lies within the realm of potential human-caused explanations and how climate might exacerbate human impacts' [1]. We question an underlying assumption that evidence from remote islands can be extrapolated to continents, and challenge suppositions underpinning human causation for extinctions in Australia and the Americas, where most megafaunal losses occurred.

Most prehistoric extinctions have been of birds on remote islands within the past few thousand years [2]. The

Corresponding author: Wroe, S. (swroe@bio.usyd.edu.au).

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role of humans in these extinctions is widely accepted [3], but islands are not continents writ small and processes operating at island levels cannot be characterized as scaled-down versions of continental phenomena [2,4]. Extinctions of megafauna center on large Pleistocene mammals from Australia and the Americas, landmasses that exceed even the largest island included in this debate, Madagascar, by more than an order of magnitude [4]. Burney and Flannery touch on this in accepting that each landmass is unique, but these concerns merit much deeper consideration.

Small landmasses are far less likely to provide refugia from human influences [4]. Central to all predation-driven models is prey 'naivety', that is, species not previously exposed to humans lack anti-predator responses and are easily killed. Analogy with remote island taxa is the lynchpin, but such species never knew large terrestrial predators and were pathetically vulnerable to any invading carnivore. On all continents, megafauna were prey to formidable endemics [5] and human-specific antipredator responses have yet to be identified [4]. Continental populations that have been free of predators for generations retain generalized antipredator responses and learn to transfer these to novel or reintroduced carnivores [6]. For example, moose populations initially decline in the face of recolonizing wolves [1], but their populations quickly recover, rapidly learning to deploy antipredator behaviors; this is strongly *contra* the efficacy of 'Blitzkrieg' [4]. Moreover, unlike Pleistocene Australia and the Americas, Holocene island extinctions were accompanied by severe anthropogenic landscape modifications, increased human population densities and the introduction of many non-human predators and competitors [2,4].

Other unproven assumptions underpin anthropogenic causes of Pleistocene extinction events. In Australia, a primary objective has been to demonstrate that extinctions pre-dated 'significant' climate change, but post-dated human arrival [7]. There is inherent supposition that previous glacial maxima were similar to the Last Glacial Maximum (LGM) and caused no major losses. Burney and Flannery place extinctions and human arrival at between 55 000 and 45 000 yr BP, before the LGM. This is misleading given that very few Australian Pleistocene sites are dated. From the data set Burney and Flannery use to argue for continent-wide extinction at 45 000 yr BP [7], we deduce that, of 60 extinct megafaunal species, only 21 can be confidently placed in deposits post-dating the Penultimate Glacial Maximum (PGM) at 130 000 yr BP and only 14 were present 55 000 yr BP. Moreover, some megafauna persisted until the onset of the LGM 30 000 yr BP [8]. It has been suggested that data from Naracoorte in South Australia show minimal faunal turnover during the middle Pleistocene [9] and this has been used to argue against a more recent role for climate; however, this reasoning does not address the crucial middle-late Pleistocene transition at ~130 000 yr BP. This was a time of indisputably extreme climate change, with average

temperatures falling by 8°C or more during the PGM. Of 20 middle Pleistocene species of megafauna found in Naracoorte, only four persisted beyond this crucial point.

That 65% of the species that Aborigines supposedly exterminated cannot be placed within 75 000 years of Aboriginal arrival is conceivably the product of statistical bias. However, adding to the likelihood that this is not a statistical anomaly is mounting evidence that Australia has been subject to stepwise, progressively more extreme aridification and climatic variability over the past 400 000 years [10,11]: '...all Australian records appear to show some trend towards drier climatic conditions superimposed on glacial cyclicality through the Late Quaternary' [10]. This eats deeply into the premise that the PGM and LGM were unremarkable relative to previous glacial maxima. Similarly, in North America, only 45% of genera persisted to within 1000 years of human arrival, leaving open the possibility that extinctions followed a staggered pattern, as evidenced in the better resolved European record [12].

Humans undoubtedly drove recent prehistoric extinctions on remote islands and must take full responsibility for the current biodiversity crisis. However, by prematurely minimizing the role of climatic influences on Pleistocene events, we risk overlooking salient lessons from the past in a world now facing significant climate change.

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A review of the evidence for a human role in the extinction of Australian megafauna and an alternative interpretation

Stephen Wroe^{a,c,*}, Judith Field^{b,c}

^a*School of Biological, Earth and Environmental Sciences (D26), The University of New South Wales, NSW 2052, Australia*

^b*School of Philosophical and Historical Inquiry, The University of Sydney, NSW 2006, Australia*

^c*Australian Key Centre for Microscopy and Microanalysis, The University of Sydney, NSW 2006, Australia*

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Abstract

Arguments that megafaunal extinctions in Australia were anthropogenically mediated have focused on establishing terminal appearance ages. This approach has been underpinned by three principle tenets: (1) if megafauna disappeared before significant climate change, but after human colonisation, then it can be inferred that extinctions were human mediated; (2) climate change within the last glacial cycle was unremarkable relative to previous cycles; and (3) all or most Pleistocene megafauna were present when people arrived on the continent. We review the evidence for human causation and note mounting evidence suggesting that the last 400–300 ka in Australia has been characterised by escalating aridity and climatic variability, culminating in the breach of a hydrological threshold within the last glacial cycle. Only 21 species (35%) of megafauna whose disappearance has been attributed to human activity are known to have persisted after the Penultimate Glacial Maximum, a time of undoubtedly severe climate change. Thus, 39 species of megafauna (65%) cannot be reliably placed within 85,000 years of firm evidence for human arrival, ca 50–43 ka. At most eight species (13%) were clearly present at this time. Four or more persisted until the onset of full glacial conditions at ca 30 ka. We argue for a falsifiable model of staggered extinction in which most megafaunal extinctions predated human arrival and with the influence of people as a minor superimposition on broader trends in train since middle Pleistocene times.

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1. Introduction

In Australia, as elsewhere, the extinction of megafauna in the Late Quaternary has long intrigued scientists from varied disciplines. Historically, because of a lack of data, Australia has played a relatively trivial role in the debate (Martin, 1984). Recently the subject has received intense attention from Australian investigators and a number have concluded that the disappearance of ca 60 large Australian terrestrial species was human mediated (Miller et al., 1999; Roberts et al., 2001a; Brook and Bowman, 2004; Miller et al., 2005). Here we critically review the case for human causation and argue for an alternative model.

2. Defining primary causation

Most Late Quaternary megafaunal extinctions occurred in the Americas and Australia (Martin, 1984). Traditionally, these disappearances have been cast as *either* a human or a climate-driven process, typically described by simple unicausal models (Barnosky et al., 2004). However, it is increasingly clear that the current extinction crisis cannot be explained by single causes and that discerning the relative importance of multiple contributing factors is a major challenge (Didham et al., 2005). This has been reflected in recent discourse regarding Pleistocene extinctions and a growing consensus that causation cannot be assigned to single mechanisms (Barnosky et al., 2004; Burney and Flannery, 2005). Nonetheless, new contributions to the debate continue to be tendered as support for *either* human or climate-driven scenarios.

Regarding North America for example, two recent studies concluded that because some populations of horse

*Corresponding author. School of Biological, Earth and Environmental Sciences (D26), The University of New South Wales, NSW 2052, Australia. Tel.: +61 2 9385 3866; fax: +61 2 9385 1558.

E-mail address: s.wroe@unsw.edu.au (S. Wroe).

and bison were declining prior to the arrival of humans, extinction was climate driven (Guthrie, 2003; Shapiro et al., 2004). Yet, this does not mean that megafauna would have become extinct without human intervention. Alternatively, evidence for late survival of West Indian sloths was presented as supportive of anthropogenic causation in continental North America, where extinctions occurred much earlier (Steadman et al., 2005), but this does not demonstrate that continental extinctions would not have taken place in the absence of climatic change. North American megafaunal extinctions occurred in broad synchrony with both changing climate and human arrival and it will likely remain impossible to convincingly quantify the respective influence of either factor in the near future.

While debate continues over which influence was primary, the definition of ‘primary’ causation remains obscure and consequent semantic differences cloud the discussion. The question can be heavily loaded. Attributing extinctions to prehistoric people has been used to argue against Aboriginal rights (Head, 1996; Wroe et al., 2004b; Hayashida, 2005). Alternatively, accepting that ‘pristine’ hunter–gatherer societies drove extinctions may be seen as a catharsis that energizes conservation efforts (Grayson and Meltzer, 2003; Wroe et al., 2004b; Wroe, 2005).

Potential roles for our own species in these extinctions are tantalizing, but challenge our objectivity. One way to gauge this is to consider analogues involving climate and non-human invasive species. A well-documented example was produced in a recent study of Caribbean Island lizards (Schoener et al., 2001). These authors found that in the wake of a major hurricane an invading lizard (*Leiocephalus carinatus*) greatly elevated the risk of extinction for another (*Anolis sagrei*). Despite population crashes, *A. sagrei* survived on all six islands in which the predator was absent, but became extinct on four of the six islands occupied by *L. carinatus*. Schoener et al. clearly treated predation as the compounding overlay in a climate driven process, but it might also be argued that *A. sagrei* had survived prior hurricanes, consequently the invading species must be considered the primary mediator. Regardless of the position taken, the fact remains that alone neither influence would have resulted in extinction and the question of which was primary may serve no practical purpose.

3. The evidence for human-mediated extinction of Pleistocene megafauna in Australia

Australia has been considered peripheral in this debate because, in addition to the complete absence of direct evidence for either predation or habitat modification (Wroe et al., 2004b), there has been no consensus over the timing of human arrival or megafaunal extinction (Martin, 1984). Central to recent arguments for a human role are claims to have demonstrated concurrence between disappearances of megafauna and human colonisation (Miller et al., 1999;

Roberts et al., 2001a) that were not correlated with significant climate change.

Prior to 1999, the case for anthropogenic causation in Australia was based on extrapolation of evidence from other continents and remote islands (Flannery, 1994). However, human causation of Pleistocene extinctions on other continents is widely disputed and while late Holocene societies clearly drove many island extinctions, islands are not continents writ small. Biogeographic fundamentals preclude their use as direct analogues and the relatively sophisticated, mostly agricultural peoples that colonised islands cannot be directly compared to Pleistocene hunter–gatherers (Grayson, 2001; Grayson and Meltzer, 2002; Wroe et al., 2004b; Wroe et al., 2006).

In 1999 the argument for human mediation in Australia received what some considered its first empirical support with the finding that a large terrestrial bird (*Genyornis newtoni*) disappeared from the central-south at around 50 ka (Miller et al., 1999). Further sampling suggested concurrent dietary shift in sympatric emu populations (Miller et al., 2005). In 2001 the authors of a second study concluded that all Australian megafauna became extinct by ca 46 ka (Roberts et al., 2001a). It was argued that extinctions were human mediated because they predated significant climate change. Computer simulation has also been interpreted as supportive of human causation (Brook and Bowman, 2004).

4. Underlying tenets

Below we address specific issues regarding the works of Miller et al. (1999, 2005), Roberts et al. (2001a) and Brook and Bowman (2004), but we will first consider the broad tenets that underpin arguments for human causation.

4.1. Evidence for long-term climatic deterioration

Implicit in arguments for human mediation is that the last two glacial cycles were no more severe in magnitude or kind than any previous glacial cycles (Barnosky et al., 2004). On the basis of broad climatic proxies at a global scale this is a reasonable assertion. However, sea level data do indicate a sustained shift to greater glacial–interglacial amplitudes from ca 700 ka (Bintanja et al., 2005). More importantly, evidence for escalating aridification in Australia from ca 400 ka has long been alluded to in the literature (Bowler, 1982). Regional evidence suggests that uniquely altered climate forcing produced stepwise, progressively more arid and variable climate in Australia from around 400–300 ka (Nanson et al., 1992; Bowler et al., 2001; Kershaw et al., 2003a; Kershaw et al., 2003b; Nanson et al., 2003). Kershaw et al. (2003b) conclude that all Australian records indicate some trend towards aridification overlaying glacial cyclicity through the Late Quaternary (see Fig. 1).

These trends are evidenced by analyses from a range of localities based on a variety of climate proxies including

pollen, charcoal, hydrology, oxygen isotope and aeolian dust records (Peederman et al., 1993; Hesse, 1994; Bowler et al., 1998; Wang et al., 1999; Bowler et al., 2001; Kershaw et al., 2003a). Progressive increases in oceanic aeolian fluxes reveal a drying trend over the last 500 ka (Hovan et al., 1989; Pye and Zhou, 1989). Pollen and charcoal data from the Lombok Ridge core suggest sustained increases in charcoal and in grasses relative to eucalypts from ca 200 and 185 ka, respectively, suggesting increased aridity (Wang et al., 1999). Stepwise reduction in water levels and increased aridity from ca 300 ka are consistent with the record from Cooper Creek in central Australia (Nanson et al., 1992), progressive decline in mega lake phases in Northern Australia (Bowler et al., 2001), and increasing continental dust levels beginning at ca 35 ka from off the eastern seaboard (Hesse, 1994).

Various models have been advanced to explain this trend, which culminated in the present, particularly dry interglacial (Ayliffe et al., 1998; Hesse et al., 2004). Bowler (1982) suggests that escalating Late Quaternary aridity might have resulted from the cumulative impact of 100 ka cycles. Kershaw et al. (2003b) suggest that the process was tectonically forced: as Australia drifted into southeast Asia

it restricted the transport of warm water through the Indonesian Gateway and resulted in relocation of the world's warmest body of water, the West Pacific Warm Pool. In support the authors cite evidence for a general increase in sea surface temperatures over the last 400 ka as inferred from oxygen isotope data taken from ODP820 (Peederman et al., 1993). Kershaw et al. (2003a, b) argue that this event drove increasing ENSO (El Niño Southern Oscillation) activity after ca 400 ka.

Regardless of the mechanism it has now been widely argued that Australia was subject to increasingly erratic and arid conditions from ca 400 to 300 ka. That the Holocene may be drier than previous interglacials suggests that along this climatic trajectory Australia passed through a hydrological threshold within the last glacial cycle (Ayliffe et al., 1998; Hesse et al., 2004). Human activities cannot account for these long-term trends.

4.2. Significant climate change in the lead up to the Last Glacial Maximum (LGM)

The argument that pre-LGM climate changes were insignificant implies that they were comparable to those

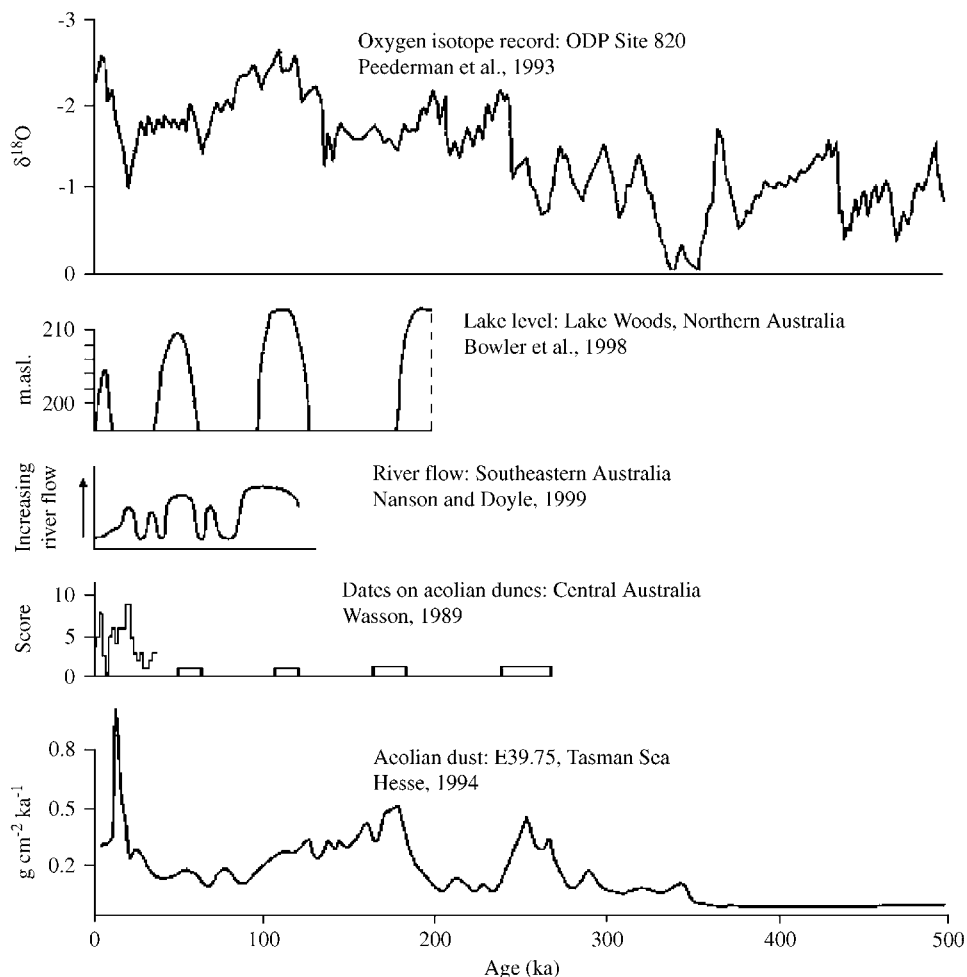


Fig. 1. Proxy records suggesting long-term environmental trends in Late Quaternary Australia (adapted from Kershaw et al., 2003a, b).

of the pre-glacial maxima in previous cycles, which advocates of human causation argue did not cause major extinctions. However, if as the above data suggests, pre-LGM climatic deterioration occurred within a uniquely dry cycle this interpretation is not supported.

Between 50 and 46 ka sea levels fell by ca 30 m (Lambeck and Chappell, 2001). Within the ensuing declining trend were three progressively less significant partial recoveries at around 44, 37 and 33 ka. The latter was the last before descent into full glacial conditions which occurred before ca 30 ka, much earlier than previously supposed (Lambeck et al., 2002).

Regarding hydrology, from ca 50 ka water levels and river flows declined in northern and eastern Australia (Bowler, 1982; Bowler et al., 1998; Bowler et al., 2003). Evidence from Lake George in NSW suggests an increasingly ephemeral system (Bowler, 1982), while data from both Lake George and Lynch's Crater in north Queensland (Kershaw et al., 2003a) indicate a shift toward more sclerophyllous, fire promoting vegetation since the Penultimate Glacial Maximum (PGM). Evidence from northern Australia (Nanson et al., 1992; Bowler et al., 1998) and southeastern Australia (Nanson and Doyle, 1999; Nanson et al., 2003) demonstrate progressively declining water levels and river flow respectively. Nanson et al. (1992) conclude that the last cycle has been marked by stepwise aridification, but that there may have been a secondary pluvial episode between 55 and 35 ka. However, Maroulis, Nanson and colleagues have refined this interpretation since, arguing that at ca 45–40 ka source-bordering dunes on Cooper Creek in central Australia ceased to function because sand-load channels that supplied them dried out and have remained so since (Maroulis et al., unpublished). Further evidence for a sharp decline in the flow conditions in the Cooper basin ~40 ka was identified as the end of a prolonged period of substantially elevated water levels in Lakes Eyre and Frome (Nanson et al., 1998), although this latter interpretation regarding Lake Eyre has been disputed (Magee and Miller, 1998).

Trends were not simple or entirely one-way. Evidence from Lake Mungo in western New South Wales suggests that conditions fluctuated between lake full and lower levels from ca 50 to 40 ka, before entering a period of sustained low levels after 40 ka (Bowler et al., 2003). Also relevant here is the relationship between temperature and evaporation rate. Excluding even lower temperatures during the LGM, average temperatures between 45 and 16 ka were around 6 °C lower than today (Miller et al., 1997) and during cold periods relatively high lake levels or river flows may reflect lower evaporation rates rather than increased actual precipitation (Ayliffe et al., 1998; Hesse et al., 2004).

Modelling suggests a significant increase in ENSO activity beginning at ca 60 ka and peaking before 40 ka (Kershaw et al., 2003a), findings which are corroborated by empirical evidence for ENSO activity in New Guinean corals (Tudhope et al., 2001). These data have been used to

explain sharp rises in charcoal levels at ODP Site 820 (NE Queensland) from 50 ka. Anthropogenic influence has also been advanced by way of explanation, but, the degree to which this overlaps with a human presence is dependent on the accepted ages for human arrival, which vary between ca 62 and 43 ka (O'Connell and Allen, 2004). However, two previous charcoal peaks, including the highest on record at ca 135 ka also correlate with high modelled ENSO activity (Kershaw et al., 2003a).

4.3. *Missing megafauna*

Fundamental to arguments for human causation is that all, or at least most megafauna were present when humans arrived. However, Roberts et al. (2001a, b) observe that their data confirms the presence of only 60% of extinct genera beyond ca 80 ka. The loss of a significant number of genera by 80 ka would predate known human arrival, and coincide with a significant climatic event, descent into the last glacial. Yet these figures are an understatement and based on consideration of ecophysiology and the data presented by Roberts et al. (2001a, b) it has been suggested that extinctions were well in train long before humans arrived (Wroe et al., 2006; Dawson, in press). Ninety two percent of material considered securely dated by Roberts et al. (2001a, b) was identified to species. At this level we note that their data confirms existence of 21 out of ca 60 Pleistocene megafaunal species beyond the end of the PGM at ca 130 ka (Table 1). Thus, 65% of Pleistocene megafauna cannot be placed within ca 85,000 years of firm evidence for human arrival at 45–43 ka (O'Connell and Allen, 2004). Only nine genera and 14 species can be placed within the last 55,000 years and eight species (13%) within 50,000 years (Table 1).

There are two alternative interpretations of these data. The first, which must be accepted by any proponent of a human role in the extinction of most species, is that they reflect differential sampling probabilities rather than actual attenuation in the fossil record, e.g., a Signor-Lipps effect (Kidwell and Holland, 2002).

The argument that statistical bias accounts for the failure of most species to overlap with humans, even to within 85,000 years, can be summarised as follows: uncommon species are usually rare in the fossil record, but if relatively common taxa persist then we might assume that less abundant species, for which there is no direct evidence for temporal overlap with humans, were present but left no palaeontological footprint. However, the possibility of undemonstrated sampling bias is not grounds for assuming that it was so. In the absence of evidence for statistical bias it is more parsimonious to infer that such bias did not exist. Moreover, of the eight species that survived after 50 ka only three are listed as common by Horton (1984), while other species listed as common disappear long before the earliest proposed ages for human arrival.

Consequently, in light of the evidence for unique climatic conditions in the lead up to and since the PGM

Table 1
Last appearances of megafaunal species in sites considered securely dated by Roberts et al. (2001a, b) and Miller et al. (1999)

Species	Last appearance (ka)
* <i>Diprotodon optatum</i>	46.5
* <i>Genyornis newtoni</i>	50
<i>Macropus ferragus</i>	52
<i>Megalibgwilia ramsayi</i>	55
<i>Palorchestes azael</i>	164
<i>Phascolonus gigas</i>	46.5
<i>Procoptodon goliath</i>	46.5
<i>Progyura naracoortensis</i>	164
<i>Propleopus oscillans</i>	164
<i>Protemnodon anak</i>	52
<i>Protemnodon brehus</i>	52
<i>Protemnodon roechus</i>	46.5
<i>Simosthenurus baileyi</i>	164
<i>Simosthenurus brownei</i>	46
<i>Simosthenurus gilli</i>	164
<i>Simosthenurus maddocki</i>	164
<i>Simosthenurus newtoni</i>	164
<i>Simosthenurus occidentalis</i>	46
<i>Simosthenurus pales</i>	164
* <i>Sthenurus andersoni</i>	52
<i>Sthenurus atlas</i>	52
<i>Sthenurus stirlingi</i>	75
<i>Sthenurus tindali</i>	52
<i>Thylacoleo carnifex</i>	46.5
<i>Vombatus hacketti</i>	46
<i>Wallabia kitcheneri</i>	55
<i>Wonambi naracoortensis</i>	55
<i>Zaglossus hacketti</i>	55
<i>Zygomaturus trilobus</i>	55

Of ca 60 Pleistocene spp., 39 are not known from sites post-dating the Penultimate Glacial Maximum, 19 are not found in sites younger than 80 ka, 14 are not found after 55 ka and 8 are found in sites less than 50 ka. Adding data from Cuddie Springs then three species (*) present within 52 ka on the basis of data from Roberts et al. (2001) persisted to 36–30 ka.

the second interpretation of these data should be preferred. In short, the disappearance of megafauna from the fossil record broadly reflects the actual timing of extinctions, with most species disappearing by ca 130 ka in the absence of humans and further staggered extinctions up to and after 50 ka.

On the basis of data from Naracoorte Caves in south-eastern South Australia it has been suggested that there is no evidence for significant rates of extinction or replacement in the middle Pleistocene (Moriarty et al., 2000). These interpretations have been tendered in support of the contention that previous glacial maxima did not drive megafaunal extinctions (Barnosky et al., 2004). That the Naracoorte faunas do not imply major faunal turnover in the middle Pleistocene may be true. However, in light of the climatic data the critical question is how many megafauna survived the PGM, not how many survived previous maxima. Only four out of 20 middle Pleistocene megafaunal species from Naracoorte persist into the late Pleistocene, i.e., 80% do not appear beyond ca 130 ka.

4.4. Naiveté

Most human causation models highlight a prominent role for prey 'naiveté' wherein species not previously exposed to humans lacked anti-predator responses and were therefore easily killed (Martin, 1984). Analogy with remote island taxa is the key. That such taxa are extremely vulnerable to human predation is not disputed. However, most remote island taxa have had no terrestrial predators for geologically significant periods. They are highly vulnerable to any invading species and do not develop anti-predator behaviours even after many generations (Wroe et al., 2004b).

In contrast continental Pleistocene megafauna were prey to large endemic carnivores (Wroe et al., 2004a; Martin et al., in press). No human-specific anti-predator responses have been identified in extant species, which respond to humans as they do to other predators (Wroe et al., 2004b). Continental island populations retain generalised anti-predator responses and learn quickly to transfer these to entirely novel carnivores (Griffin et al., 2000). This also applies to continental marsupials that have not been subject to predation for millennia (Blumstein et al., 2000; Blumstein et al., 2001). Thus extreme naiveté as exemplified in remote island species would not have characterised Australian or American megafauna. Native species may have been more susceptible to colonising humans than Afro-Eurasian taxa, but models assuming complete naiveté greatly overstate the degree and duration of this vulnerability.

Evidence that moose populations initially decline in the face of colonising wolves has been interpreted as supportive of rapid overkill (Berger et al., 2001). However, the authors also demonstrated that moose populations quickly recovered to pre-wolf levels, rapidly learning effective anti-predator behaviours. This is *contra* the validity of predation centred models for continental species because it shows that extinction would only occur if instantaneous and complete losses occurred along expanding colonisation fronts (Wroe et al., 2004b). To accommodate this problem Berger et al. (2001) postulated that extinction-prone species were slow learners, although there is no empirical basis for this assertion. The argument is particularly implausible with respect to proboscideans, but as noted above, even smaller brained marsupials quickly learn to recognise novel carnivores.

4.5. Technology

In the simulation of human impacts, hunting efficiency is the flipside of naiveté. The value of specialised technologies in the dispatch of large prey by hunter-gatherers is widely acknowledged (Smith, 1975; Kusimba, 1999; Ashler and Geib, 2000; Ambrose, 2001; Shea et al., 2001; Shea, 2006). The presence of specialised big-game hunting technology is commonly cited in support of predation-driven extinction

models and its absence considered limiting (Martin, 1984; Flannery, 2001).

We stress that the absence of specialised technologies does not demonstrate that a society did not hunt large animals. Evidence for the taking of large prey extends to around 400 ka in Europe, long before the first appearance of stone projectile points (Thieme, 1997; but see Shea, *in press*). However, technological limitations strongly impact predator–prey modelling (Smith, 1975). On remote islands where megafauna were relatively small, completely lacking anti-predator responses, and characterised by small populations and ranges, technology may not have been limiting, but the argument diminishes when applied to larger, more widely spread, abundant and vigilant continental targets.

In Australia, stone spear points, spear-throwers, and specialised butchery tools widely associated with predation on large game do not appear until post LGM (Flood, 1999; Johnson and Wroe, 2003). Also relevant is the ethnographic evidence suggesting that single animal encounter techniques are favoured by hunter–gatherers that inhabit low latitude grasslands, while strategies that produce mass kills are characteristic of high latitude ecosystems (Marean and Assefa, 1999).

Lastly, the presence/absence of technologies other than those associated with predation on large vertebrates constrain the likelihood that humans drove extinctions. Technologies and knowledge associated with the gathering and processing of plant food, as well as the hunting of small prey, strongly influence human population densities and ranges (Ambrose, 2001). The ability to supplement diet with alternative food sources as megafaunal populations and ranges decline increases the likelihood of extinction, while the expansion of human ranges decreases the likelihood that critical refugia remain (Wroe et al., 2004b).

4.6. Late survival of megafauna

Most recent analyses supporting human causation in Australia accept continent-wide extinction at ca 46 ka and *ipso facto* that younger ages for megafauna-bearing sites are erroneous. Certainly ages for a number of post 40 ka sites have been shown to be either highly equivocal or wrong, however, at least 13 have yet to be clearly validated or dismissed (Johnson, 2005). At present we consider the evidence to be persuasive for ages of ca 36 ka or less regarding at least four. These include Clogg's Cave (Flood, 1974), Seton Rock Shelter (Hope et al., 1977) and one New Guinean site, Nombe Rock Shelter (Flannery et al., 1983). Ages for the fourth site, Cuddie Springs in southeastern Australia, are particularly well supported. This site has yielded evidence of megafauna (including *Genyornis* and *Diprotodon*) and archaeology together in sealed strata dated by luminescence, AMS and radiocarbon determinations on charcoal and sediments between ca 36 and 30 ka (Field et al., 2001; Fifield et al., 2001; Coltrain et al., 2004). Analyses of geomorphology, palynology and archaeology suggest that the deposit is intact (Field and Dodson, 1999;

Field et al., 2002) but it has been argued that the sedimentary sequence at Cuddie Springs is disturbed and that megafauna fossils in archaeological levels are from underlying buried horizons (Roberts et al., 2001b). By demonstrating that the relevant strata have distinct geochemical signatures, rare-earth element analyses have recently further refuted the possibility of mixing, thereby validating the 36–30 ka ages for megafauna (Trueman et al., 2005).

5. Critical review of recent evidence

5.1. Human-mediated ecosystem collapse at 50 ka

Miller et al. (1999, 2005) present analyses of fossil eggshell fragments that document the local disappearance of *Genyornis newtoni* at ca 50 ka and subsequent dietary shift from C4 to C3 plants in surviving emu (*Dromaius novaehollandiae*) populations. Data comprised eggshell fragments retrieved from three locations in south-central Australia. These ranged from 140 ka to recent in age. The authors consider the studied area to be representative of ca 10% of the Australian landmass.

From these data the authors make the following inferences:

- (1) *Genyornis newtoni* was specialised relative to the emu in that C4 plants were an essential part of its diet.
- (2) Evidence for diet change to include a higher proportion of C3 plants in surviving species suggests significant vegetation change.
- (3) These events do not coincide with significant climate change therefore extinction was human mediated.
- (4) The mechanism was human burning which favoured the expansion of C3 and low-quality C4 plants at the expense of high-quality C4 grasses.
- (5) That the disappearance of *Genyornis* in this region at ca 50 ka can be extrapolated to represent extinction of this and the rest of the megafauna over the entire continent.

The data presented by Miller et al. (1999, 2005) is strongly suggestive of vegetation change, but the argument that this was driven by human burning practices is weak:

(1) The assertion that climate change around and after 50 ka was insignificant is *contra* evidence for a long-term drying trend and increased ENSO activity (Kershaw et al., 2003a). Bowler et al. (2003) demonstrates that within the study area Lake Mungo began to fluctuate between lake full and dry conditions from ca 50 ka.

(2) There is no conclusive regional evidence for human occupation until 7–5 ka after 50 ka (O'Connell and Allen, 2004).

(3) There is no evidence of human burning. Palynological and microscopic charcoal evidence from elsewhere (ODP820 and Lynch's Crater) has previously been interpreted as indirect evidence for human-induced burning from ca 45 ka (Kershaw et al., 1997).

However, these authors have revised this interpretation to argue that while humans may have had a compounding effect, the process was essentially climate driven (Kershaw et al., 2003a).

That Aboriginal practices had any influence in these latter instances has been questioned (Bowman, 2000). A much earlier and higher amplitude peak in microscopic charcoal at ca 130 ka from Lake George (NSW) and ODP820 has also previously been interpreted as evidence for human landscape burning (Singh et al., 1981; Kershaw et al., 1997; Kershaw et al., 2003a). Interpretations in line with the consensus view on human dispersal would require that any populations in Australia at this time could not be *Homo sapiens* (Finlayson, 2005).

(4) Regarding vegetation change, plants that remained after 45 ka include common nutritious C4 grass species (e.g., *Themeda triandra*) and C3 chenopods such as saltbush that are susceptible to fire and regenerate slowly (Hodgkinson et al., 1984; Noble, 1989). The persistence of large areas of chenopod shrublands in the arid–semi-arid zones post 45 ka seems inconsistent with the proposal that human firing drove vegetation change. Additionally, the argument that *Spinifex* grasses proliferated due to burning after 45 ka does not sit easily with the fact that for some *Spinifex*, abundance is restricted by regular burning (Noble, 1989).

(5) *Genyornis* and other megafaunal species have been demonstrated to be present at Cuddie Springs at ca 36 ka, refuting the notion of continent-wide extinction prior to this time.

5.2. Continent-wide extinction of the Australian megafauna at 46 ka

Roberts et al. (2001a, b) argued for continent-wide extinction of all megafauna by ca 46 ka. There are >167 Australian Pleistocene sites bearing megafauna (Horton, 1984). Twenty-eight sites were initially dated, but the application of a single selection criterion restricted the data set to 19, ranging from 164 to 46 ka. Post 46 ka deposits were excluded a priori because they did not meet the selection criterion (i.e., that sites contain articulated remains, invoked as an indicator of in situ deposits). Of remaining sites, seven were included in the analysis that predicted disappearance of all megafauna by ca 46 ka.

Selection criteria are arguably useful heuristic devices and in justifying their approach, Roberts et al. (2001a, b) cite a previous work that applied a range of ranked criteria for assessing the ages of megafauna-bearing sites in North America (Meltzer and Mead, 1985). Meltzer and Mead did not include presence/absence of articulated remains as a criterion, but considered the contexts and stratigraphic associations of the dated materials. Their method highlights limitations imposed by the articulated remains approach—which excludes most archaeological and many fossil sites.

Within the scheme of Meltzer and Mead, if the material dated was from stratigraphic layers that were entirely capped on lower and upper layers by different sediments it received the highest possible ranking. This criterion exceeded most forms of direct dating. Among sites dated by Roberts et al. (2001a, b) for which site or excavation details are published, only Cuddie Springs with megafauna dated at 30–36 ka, clearly fits this criterion (Field and Dodson, 1999).

The choice of selection criteria is subjective and can produce very different results for similar research questions. Adherence to any single criterion overlooks contributions from taphonomy, geomorphology, archaeology and many other methods that can establish stratigraphic integrity, site formation processes and associations between the fossil finds and their context.

5.3. The uncertain blitzkrieg of Australian megafauna

The modelling presented by Brook and Bowman (2004) represents an innovative advance over most previous attempts to simulate megafaunal extinction because it incorporates both a role for habitat change and an attempt to allow for variable prey naiveté. The best-supported scenario suggested a significant, albeit lesser role for environmental deterioration as well as predation (Brook and Bowman, 2004). The authors concluded that the process was human mediated and that the extinctions occurred within ca 750 years.

Although such analyses play a role, they remain unconvincing for many, particularly given that they remain largely uncalibrated against empirical data on the population dynamics of hunter–gatherers and megafauna from the only place where such information can be collected, Africa (Barnosky et al., 2004; Wroe, 2005). Brook and Bowman predicted major loss of megafauna in Africa, but this clearly did not happen. Predator hardening in African species was forwarded as the explanation, but there are other possibilities. For example, larger refugia persisted in Africa during periods of climatic stress. This does not exclude a role for humans in Australia, but does suggest that relatively higher rates of extinction would be expected regardless of human activity (Wroe et al., 2004b).

Our greatest concern regarding all computer modelling is the assumption that modern hunter–gatherer societies represent realistic proxies for Pleistocene populations. This is problematic with respect to Clovis Indians in the very latest Pleistocene of North America, but draws a particularly long bow regarding Australian cultures >30,000 years more ancient still.

The archaeology of Australia's first colonisation is sparse, but people clearly utilised an expedient flaked stone tool technology. Regional variations have been noted, but many differences can be related to availability and quality of stone raw material (Bowler et al., 1970; Cosgrove and Allen, 2001). Various colonisation models have been proposed (Birdsell, 1967, 1977; Bowdler, 1977; Horton,

1980), but there is no consensus on rate or timing. Resource breadth is hinted at by functional studies of artefacts (Slack et al., 2004), but dietary breadth and hunting efficiency, critical to predator–prey outcomes is unknown. However, as reflected in the number and range of known archaeological sites from this period, late Pleistocene populations and densities were much lower than those seen at European contact (Johnson and Wroe, 2003). The first Australians arrived with relatively unsophisticated tool kits in a very alien landscape and occupation of the continent may have taken many millennia (Macaulay et al., 2005). Modelling based on ethnographic evidence will seriously overstate actual values for societies >43,000 years more ancient.

6. An alternative model

6.1. An undemonstrated premise

Arguments for human causation categorise evidence for pre-LGM climate change as insignificant on the basis of comparison with glacial maxima. The following rationale is applied:

Change in the lead up to the LGM was relatively insignificant compared with previous glacial maxima and because previous glacial maxima did not cause major extinctions only climatic change of full glacial magnitude can be accepted as significant.

In light of the evidence for a long-term deteriorating climatic trend and no evidence for the survival of most species beyond the PGM, the premise that previous glacial maxima did not cause major losses of megafauna is undemonstrated. Additionally, because the current interglacial appears to be particularly dry it is reasonable to argue that a hydrological threshold was breached in the course of the last glacial cycle. This in itself may explain extinctions.

6.2. The staggered extinction of Australian megafauna

Regarding North America the presence of most genera within 1000 years of the arrival of Clovis people has not been established and this has been raised as an objection to human causation (Grayson and Meltzer, 2002, 2003). These authors suggest that North American extinctions were staggered over many millennia, as was clearly the case in Europe (Grayson, 2001). In Australia, relative to North America, the temporal distance between last appearance of most megafauna and human arrival is vast.

Our analyses make one important fact clear: 65% of extinct Pleistocene megafauna are absent from deposits younger than 130 ka and only eight species were clearly present at the earliest point for which there is broad acceptance for human arrival. At least four of these taxa survived up to 36–30 ka and the onset of full glacial conditions (Table 1).

While we have provided a critique of models that define megafaunal extinction as human driven, we accept that few climate-mediated paradigms have been developed (Barnosky et al., 2004). At present the most comprehensive is that forwarded by Horton (1984), who suggested that in the lead up to the LGM Australian megafauna were restricted to more coastal habitats as increasingly arid conditions expanded outward from the arid core, greatly reducing supplies of free water. There is some evidence to support the broad contention of coastward aridification (Nanson et al., 1992). Horton explained the bias toward larger species on the grounds that they are dependent on freestanding water, while smaller taxa can obtain sufficient water from their food.

A number of amendments must be made to the hypothesis of Horton (1984) in light of more recent evidence. The most obvious are chronological. Growing evidence for a sustained increase in the severity of glacial maxima post 700–600 ka suggests that some taxa often considered ‘late Pleistocene’ may have disappeared at this point. More importantly, Australian evidence for increasingly arid and erratic conditions since 400–300 ka and the lack of evidence for 65% of species post 130 ka suggests that most extinctions occurred during, or in the immediate lead up to the PGM. Further staggered extinctions then occurred with a general trend toward increased aridity from ca 100 ka.

Additional evidence testifying to the disappearance of megafauna prior to human arrival has been tendered in an analysis of Tasmanian rockshelters (Cosgrove and Allen, 2001). Humans are not thought to have arrived in Tasmania until the development of a significant land-bridge at ca 37 ka (Cosgrove and Allen, 2001; O’Connell and Allen, 2004). Consequently, any anthropogenic model would predict the survival of Tasmanian megafauna to after 37 ka. However, no megafauna have been found post 46 ka in Tasmania and among >600,000 bones from the eight earliest Tasmanian archaeological sites, none represent extinct Pleistocene species (Cosgrove and Allen, 2001). Similarly, a recent analysis of Late Quaternary deposits in the Darling Downs found no evidence of human occupation until long after the loss of megafauna (Price and Sobbe, 2005).

Low fecundity and low population densities render large mammal species more vulnerable to extinction (Cardillo et al., 2005). These traits can expose large species to a higher risk of extinction through human influence (Martin, 1984). However, these same characteristics also increase extinction risk due to climate-driven habitat loss. Geographic range size affects large species more strongly and they are less resilient in the face of population crashes (Cardillo et al., 2004, 2005).

Increasing body size is commonly a response to low quality food and/or seasonal conditions (Owen-Smith, 1988). Consequently, the gigantism apparent in many Pleistocene lineages is likely an adaptation to increasingly arid/erratic climate. It has been argued that because

some Pleistocene megafauna were adapted to relatively arid conditions we might expect their ranges to expand rather than contract with further aridification (Prideaux, 2004). However, there is tension between large size as an effective response to aridification and the negative consequences of greater body mass, which demand greater habitat area to maintain viable populations (Webb, 1998). Although some degree of aridification would benefit large species adapted to semi-arid conditions it is simplistic to argue that ever escalating aridity would result in the expansion or maintenance of their geographic ranges. Even extinct megafauna best equipped to deal with relatively low/erratic rainfall were adapted to semi-arid conditions, not arid conditions in the strict sense (i.e., <250 mm/yr). As habitat declines beyond minimum thresholds, large species are likely to become extinct first (Cardillo pers. comm., 2005). This is consistent with demonstrated positive relationships between body mass and landmass area (Burness et al., 2001; Wroe et al., 2004a) and modelling that suggests high species losses among extant large mammals as habitat area decreases (Soule et al., 1979).

Temperature and rainfall fell during the PGM and through the last glacial cycle. During the LGM falls in average temperature of ca 8 °C were achieved across much or all of Australia (Hesse et al., 2004), broadly in line with results from analysis of the Vostok ice core, Antarctica (Petit et al., 1999). These data suggest similarly low temperatures during the PGM, that through most of the last glacial temperatures were around 3–6 °C lower than today. While specific influences are not well understood it is clear that primary productivity would have been depressed by lower temperatures and rainfall, an effect further amplified by falling CO₂ levels, which were 20–40% lower (Petit et al., 1999; Hesse et al., 2004). CO₂ availability influences competitive regimes between C3 and C4 grasses (Hughes, 2003) and impacts the distribution of flora and fauna. This would not simply effect redistribution of ranges because many plants are constrained by drainage and nutrient requirements (Hughes, 2003). Analysis of Australian plant endemism suggests that falling temperatures and CO₂ exerted a powerful limit on refugia, restricting many plants to more mountainous coastal regions (Crisp et al., 2001).

It is probable that the ranges of megafauna were repeatedly limited to small refugia through successive glacial cycles as occurred in Europe and North America (Hewitt, 2000). Isolation, low relief, landmass area and low rainfall further restrict the size and distribution of refugia in Australia relative to those of other continents, compounding the potential for extinctions (Wroe et al., 2004b). The distinction between range contraction and extinction is fine. In a continent as arid as Australia, relatively minor changes in rainfall patterns can profoundly impact the environment (Ayliffe et al., 1998). Further progressive and stepwise reduction in rainfall and/or the onset of more variable, erratic climate, as has been suggested for the last

few glacial cycles, would have had catastrophic impacts with refugia becoming too small and disjunct to maintain viable populations of species that require large ranges. We argue that the critical factors separating surviving from extinct species were abilities to subsist on less food per individual within restricted and/or fragmented geographic ranges and/or to move rapidly and efficiently to ephemeral patches of viable habitat.

It has recently been suggested that even if we accept late survival for some megafauna, the evidence still supports human causation, although this would obviously eliminate blitzkrieg (Johnson, 2005). This is because in Johnson's view the evidence still points to a major suppression of megafaunal populations before significant climate change and the lack of articulated material after 46 ka can be explained by human butchery practices.

Operating on the assumption that 13 sites younger than 46 ka without articulated remains were correctly dated, Johnson (2005) regressed last appearances against distance from the coast. He found no correlation between distance from the sea and late survival and interpreted results as *contra* Horton's hypothesis.

We have several reservations with respect to Johnson's conclusions:

1. The validity of ages for some of these 13 sites is highly questionable. At present, among Australian sites strong cases can only be made for Cuddie Springs (36–30 ka), Clogg's Cave (22 ka) and Seton Rock Shelter (16 ka) (Field, 2004; Trueman et al., 2005).
2. Human butchering activities typically do leave disarticulated remains, but this is true of fossilization in general. Moreover, humans do not always disarticulate the remains of animals they are butchering (Pickering, 1995). In the absence of any direct evidence for human intervention the more likely explanation for the paucity of articulated remains (which are always rare) in the latest Pleistocene, is that this reflects decreasing population sizes and opportunities for fossilisation under increasingly arid/erratic conditions.
3. Horton's hypothesis centres on declining rainfall as the actual limiting factor and distance from the coast is offered only as a descriptive proxy. In much of Australia arid–semi-arid conditions persist to the continental margins. A better test of Horton's model is one that correlates last appearance with relative rainfall. If we include the three Australian sites mentioned above, the two youngest are within the well-watered south east of the continent, while one falls marginally within the current arid–semi-arid zone. The two post 50 ka sites considered securely dated by Roberts et al. (2001a, b), Ned's Gully, Queensland (46.5 ka) and Kudjal Yolga Cave, Western Australia (46 ka), were well outside the current arid–semiarid zone. Consequently, insofar as this meagre dataset can be analysed, it is consistent with Horton's model.

7. Conclusions

Arguments for human causation in Australia have focused on terminal appearance ages, operating on the premises that disappearance ages of the last species broadly represent those of most megafauna, that the great majority if not all species were present when humans arrived and that climates during the penultimate and last glacial cycles did not differ significantly from those that preceded them. We conclude that the evidence does not support these underlying tenets of anthropogenic mediation.

Most species do not appear within 95,000 years of human arrival and in light of evidence for progressive, long-term aridification of the continent the most parsimonious conclusion is that the process was staggered, with major losses occurring by 130 ka and further range contractions and extinctions throughout the last glacial cycle. To this extent our interpretation is falsifiable on the basis of further dating.

Anthropogenic influence cannot be excluded. The proposition that people could have had no interaction with megafauna is inconceivable, especially considering the Cuddie Springs evidence (Field, 2004; Wroe et al., 2004b), but the maximum extent of human culpability is currently constrained to the 13% of species that can be placed at the scene. While it may yet be demonstrated that human activities combined with climate change to press surviving populations to extinction, in such instances attempts to determine which was ‘primary’ will likely remain futile.

In circumstances where climate change presents a major threat to biodiversity, premature acceptance of human causation for Pleistocene faunal extinctions may divert energy from potentially informative lines of investigation. In addition to the development of more comprehensive chronologies, future tests of ours and other competing explanations include the use of programmes currently used to predict the influences of future climate change to reconstruct past vegetation distributions, and the study of ecophysiology among extinct species. Further investigation of the archaeological record will provide information about human behaviour and subsistence strategies during a period of climatic flux and habitat reconfiguration.

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