

Human Dispersal and Late Quaternary Megafaunal Extinctions: the Role of the Americas in the Global Puzzle

Fernando A. S. Fernandez

Departamento de Ecologia – Universidade Federal do Rio de Janeiro – Brazil

Abstract

As Alfred Russell Wallace once wrote, we live in a zoologically impoverished world, from which most of the largest, strangest and most spectacular animals disappeared quite recently. About two thirds of all animal species larger than 50 kg (the so-called megafauna) were extinct from the late Pleistocene onwards, starting in Australia at about fifty thousand years ago and following humans' footsteps is their expansion throughout Eurasia and the Americas. The extinctions went on through the Holocene, reaching islands all around the globe, that can be seen as 'time machines' where megafauna survived for millennia after the continental extinctions, such as the Caribbean, the islands off Alaska, and Wrangel Island in the Arctic Ocean. In Madagascar and New Zealand, extinctions are but a few centuries old. These late Quaternary extinctions were a global phenomenon that begs for a global explanation. Climatic hypotheses fail to explain these patterns for several reasons, for example, there were dozens of other glacial cycles throughout the Pleistocene, without associated mass extinctions; extinctions in Australia and the islands did not coincide with glacial peaks; and climate changes cannot explain why extinctions were systematically more recent on islands. However, the pieces of the puzzle immediately fit together when we observe the clear correspondence between the dates of humans' arrival and of megafaunal extinction in each landmass. Bernardo Araujo recently analysed the chronology of extinctions of megafaunal genera around the world. He found that extinctions took place closer than expected by chance to periods of high climatic variation alone in only two of the analysed cases, to dates of human arrival alone in seventy-four cases, and to both in eight cases, with 40 cases unexplained. Thus, anthropogenic impact is the most plausible and parsimonious main cause of the late Quaternary extinctions. In a modern view, the extinctions were a long process that took several millennia to occur in most continents, with a few stragglers like the Irish elk and the North American mastodons. Low reproductive potential was the main determinant of the extinct species; the apparent selection by size is an artefact of the inverse correlation between the two variables. The absence of evolved instincts against newly arrived humans, the difficulty of conserving meat and the lack of perception of the world's finitude must have contributed to the outcome. Thus, human-megafauna interactions are an important and undervalued part of human history that merits being represented on the UNESCO World Heritage List. Furthermore, learning from the extinctions of the past is crucial to allow us to minimise extinctions in the future. Candidate sites in the Americas might include those that show consumption of megafauna (such as Monte Verde), remarkable rock paintings (such as Serra da Capivara, Brazil) and the latest American megafauna (such as Las Breas de San Felipe, Cuba).

Introduction - the late Quaternary extinction sequence

In 1876, Alfred Russel Wallace wrote: 'we live in a biologically impoverished world, from which all the hugest, and the fiercest, and the strangest forms have recently disappeared' (Wallace, 1876, p. 150; quoted in Grayson, 1984). The sense of incompleteness felt by Wallace, at a time when palaeontology was still a young science, is well justified. In the last 50,000 years - the blink of an eye in geological times - the planet has lost an impressive array of large animals, including mammoths, mastodons, woolly rhinos, sabertooth tigers, giant ground sloths, gliptodonts, moas, elephant birds, marsupial lions and many others. These recently lost beasts represented about two thirds of all the world's megafauna - here defined as animals with adult body weight above 50 kg. For example, at least 97 of 150 genera of large mammals were lost between 50 thousand years ago (henceforth ky) and 500 years ago (Turvey and Fritz, 2011). When trying to understand the causes of this huge 'prehistoric revolution' (Martin and Klein, 1984), it is crucial to note that these extinctions were not an event well-defined in time, but rather a process: the megafauna disappeared at markedly different times in different parts of the planet. We will briefly review this dramatic sequence.

The extinctions first reached Australia, around 50 ky. By that time, the spectacular Australian fauna included the diprotodonts (genus *Diprotodon*), giant marsupial browsers that could weigh almost three tons; *Palorchestes*, ecological equivalents to tapirs; *Thylacoleo carnifex*, the 'marsupial lion' (actually a leopard-sized large carnivore) and a whole family of giant short-nosed kangaroos, the Sthenurinae (Murray, 1984; Johnson, 2006). Aside from the mammals, there were gigantic reptiles such as *Megalania prisca* that resembled an oversized Komodo dragon, *Wonambi naracoortensis*, similar to a large anaconda, plus some huge terrestrial birds, *Genyornis newtoni*. The Tasmanian 'wolf' or thylacine, *Thylacinus cynocephalus*, often considered endemic of Tasmania (where it survived until 1936), was also found throughout Australia at that time. In continental Australia, the extinctions took place during an 'extinction window' that went from 50 to 40 ky, with a peak at around 46 ky (Roberts et al., 2001). A recent claim by Wroe et al. (2013) that the extinctions in Australia were spread in time since the Middle Pleistocene does not seem consistent, because the species at that time were nearly all from the same genera as the ones that disappeared during the 'extinction window', and thus they are likely to represent taxonomical splitting rather than a truly different species set. An interesting point is that in Tasmania the extinctions happened distinctly later than in continental Australia, around 41 to 40 ky (Turney et al., 2008).

In Eurasia, the extinctions were quite spread out in time, roughly presenting two pulses (Turney and Fritz, 2011). In the southern latitudes, around the Mediterranean Basin, most species vanished between 45 and 20 ky. The extinctions in the northern latitudes came much later, from 14 to about 9 ky. Some stragglers survived even later, such as the 'Irish elk' (*Megaloceros*) in the Ural Mountains until some 7,700 years ago (Stuart et al., 2004). Among the main losses suffered in Eurasia were the Eurasian mammoths (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*) and cave bears (*Ursus spelaeus*). The coexistence of humans with this striking fauna, including the hunting activity, is richly documented in the superb Cro-Magnon rock paintings, in sites such as Altamira, Lascaux and El Pindal. This coexistence lasted until the big animals became extinct, soon followed by their artistic representations.

In North America, the extinction process was comparatively 'quick', as it took place mostly between 13.5 ky and approximately 11 ky. Again, some stragglers survived until more recent times, such as the mastodons (*Mammuthus americanum*), whose last records, in the region of the Great Lakes, are dated to 9,900 years ago (Woodman and Athfield, 2012). The North American megafauna at this time was very rich and much more similar to Africa's present fauna than we could imagine, based on the remaining species there (Anderson, 1984). Among others, there were North American mammoths (*Mammuthus columbi*), mastodons, giant ground sloths (see next paragraph) and also camels (*Camelops hesternus*), horses and bison, including the huge long-horned bison (*Bison latifrons*). Furthermore, North America was home to an exceptionally rich carnivore fauna, including the giant bear (*Arctodus simus*), the sabertooth tiger (*Smilodon fatalis*), the only slightly smaller scimitar cat (*Homotherium serum*), lions (*Panthera leo atrox*), oversized wolves (the dire wolf, *Canis dirus*) and cheetahs (*Miracinonyx trumani*) (Flannery, 2001).

In South America, the extinctions were spread along a longer period of time than in North America, from about 13 ky to 7.8 ky (Barnosky and Lindsey, 2010). This means that, although there is a considerable overlap in time between the continents, many of the South American extinctions took place after the process was mostly completed in North America. The South American megafauna, like their North American counterparts, also included at least two species of elephants (from the genera *Haplomastodon* and *Cuvieronius*), sabertooth tigers (*Smilodon populator*) and a rich diversity of ground sloths (families Megatheriidae, Megalonychidae, Milodontidae and Nothotheriidae). The largest ground sloths (genera *Megatherium* and *Eremotherium*) were huge, slow animals that could weigh more than five tons. Besides, there were large native grazers similar to hippos called toxodonts (*Toxodon platensis*), many gigantic armadillo-like gliptodonts and a rich diversity of roofed beasts including highly peculiar animals like *Macrauchenia* as well as more familiar horses (*Equus*). Although today South America is relatively poor in megafauna - the tapirs, jaguars and marsh deer are the few remaining large mammals - this was not by any means true about 15 thousand years ago.

The extinctions were not limited, by any means, to the Pleistocene-Holocene boundary - on the contrary, they went on through the Holocene. That is why it is more correct to talk about 'late Quaternary extinctions' rather than using the misleading expressions 'Pleistocene extinctions' or 'Pleistocene-Holocene extinctions', the latter seeming to imply that they happened in the boundary between the two epochs. It was indeed well into the Holocene that the extinctions finally reached some 'time machines' where some last members of the vanished megafauna still survived. These time machines - places where intact Pleistocene ecosystems could still be found well into the Holocene - were the islands.

In the Caribbean, all several dwarf giant ground sloths became extinct from about 6 ky to 4.7 ky, at least some 4,500 years later than anywhere in the mainlands of either North or South America (Barnosky et al., 2004; Steadman et al., 2005). The most recent records are from Cuba, the largest island in the Caribbean. In Beringia, mammoths (*Mammuthus primigenius*) survived on the island of St Paul (near Alaska) (Guthrie, 2004) and Wrangel (to the north of Siberia) until some 5 ky and 4 ky respectively. The last date (Vartanyan et al., 1993) is more than seven thousand years after the Younger Dryas, the last cold event of the last glacial cycle. In the Mediterranean, at least five species of dwarf elephants of the genera *Elephas* (*Palaeoloxodon*) and

Mammuthus became extinct over twenty islands. Most of these findings are not dated; the few existing dates are not quite reliable but if correct they would point to the survival of elephants until as recently as 4 ky in the Aegean islands (Theodorou et al., 2007 in Liscaljet 2012). A dwarf elephant is also present in Egyptian wall paintings of the eighteenth dynasty (near 3.5 ky), suggesting that the Egyptians coexisted with these now extinct animals in historical times (Masseti, 2001). Other quite recent - possibly Holocene - losses in the Mediterranean islands included several species of dwarf hippopotamus (genus *Hippopotamus*) from Crete, Sicily, Malta and Cyprus (Petronio, 1995).

Two of the most spectacular cases, however, were Madagascar and New Zealand -where the disappearance of the megafauna was most recent. In Madagascar, a dozen species of spectacular giant lemurs became extinct between 2,000 and less than 400 years ago, when the last of them, the man-sized *Megaladapis edwardsi*, was seen by the French governor, Etienne de Flacourt (Flacourt, 1658). Flacourt may also have seen the last of the half-ton elephant birds (*Aepyornis maximus*). When the European colonizers arrived, huge elephant bird eggshells still littered the beaches of the island's south and south-eastern coasts, pointing to a very recent extinction indeed. Furthermore, Madagascar also lost pigmy hippos and giant fossas (Dewar, 1984). In New Zealand, there was an equally spectacular fauna of a dozen species of moas, large terrestrial birds up to three metres tall, plus the gigantic Haast's eagle *Harpagornis moorei*. All these huge animals went extinct as recently as between 900 and 500 years ago (Trotter and McCulloch, 1984).

Unlike any other extinction wave in the geological past, this one appeared to be size-selective: only the largest animals were extinct (Lyons et al., 2004). The Quaternary extinctions deprived the planet of most of its large animals, but had little effect on the small ones.

The aim of this article is to briefly discuss how the late Quaternary extinctions relate to human dispersal across the planet, how this affects our views of human history, and the role of American sites in conserving this memory.

Pitfalls of the climatic explanations for the late Quaternary extinctions

Ever since Wallace, there has been much controversy on what caused the Quaternary extinctions, a dramatic revolution in the history of life so close to our time. The hypothesis that the demise of the big animals had been caused by climate changes was a favourite for near a century after Wallace (Grayson, 1984); it is still popular and has been proposed in many regional studies to explain the disappearance of Pleistocene faunas (review in Koch and Barnovsky, 2006). From a global perspective, however, the climatic hypothesis fails to explain too many of the extinction patterns; six of its main pitfalls are briefly pointed out below.

Firstly, climatic hypotheses do not explain the regional asynchrony of the extinctions. Climatic events linked to the last glacial cycles were planetary events that affected the whole planet at the same time, for example, cold peaks were also linked to dry periods in tropical regions. Nevertheless, as we saw, the extinctions took place at completely different times in different places around the world.

Secondly, the chronology of the last glacial cycle does not explain the timing of extinctions in several parts of the world. For instance, in Australia the extinctions occurred mostly within a relatively mild period about twenty thousand years before the Last Glacial Maximum that lasted from about 23 to 18 ky. On the other extreme of the time scale, the insular extinctions all occurred several thousand years after the end of the Younger Dryas, the last cold event of the glacial cycle, at about 13 to 11.5 ky (Burney and Flannery, 2005).

Thirdly, in the Pleistocene there were at least 31 other glaciations before the last, without any wave of extinctions associated to them (Cione et al., 2003; Barnosky et al., 2004; Johnson, 2006). The recent suggestion by Wroe et al. (2013) that the last glacial cycle was notably more intense than the previous ones, at least in the Sahul, is not convincing because intensification can be observed only in the warm (interglacial) phases that which are not implied in the extinctions in the climatic hypothesis. On the other hand, there is little difference where it matters, that is, among the cold extremes of the last cycles (see Wroe et al.'s own figure 5).

Fourthly, climatic hypotheses cannot explain why the extinctions on islands all over the world, independent of their latitudes and longitudes, were systematically more recent than in the continents - all of them in the Holocene, a period of relatively stable climate.

Fifthly, climatic hypothesis would predict many extinctions among plants that are usually more affected by climate changes than animals, but this prediction conspicuously fails: there was no wave of floristic extinctions in the Quaternary.

Sixthly, the climatic hypothesis predicts that small warm-blooded animals would be more affected than large ones, because the former have higher surface/volume ratios and thus less efficient homeothermy (Thompson, 1917). But what happened was exactly the opposite: the large animals were the ones that disappeared.

The Quaternary extinctions are a global phenomenon that begs for a global explanation. Arguably, a major reason why the subject still seems puzzling is that many studies have tried to explain the extinctions using regional approaches, thus losing sight of the immense explanatory power of a comparative, global analysis. The pieces of the puzzle indeed immediately fit together when we observe the close similarity between the dates of human arrival and the extinctions in each land mass. A quick review of modern man's spread across the globe may be useful here. I make no claim to present a detailed appraisal of the complex process of colonization of our planet; rather, I intend to provide only a brief sketch of the main events.

Man's dispersal across the planet

Modern humans originated in eastern Africa and had most of their existence restricted to a relatively small part of the world. The oldest dates for our species are at least 160 ky and the oldest ones out of Africa - in the Middle East - are about 120 ky. From the Middle East, modern humans dispersed to Tropical Asia and remained restricted to these regions until about 50 ky (Stringer and Andrew, 2005).

From there, the first new land mass to be colonized was Australia, reached by humans at about 50 ky. As the colonizers came from the north, the last part of Australia to be reached was the southern tip, where Tasmania lies. At the time, Tasmania was connected to Australia, New Guinea and smaller islands forming a single landmass, Sahul.

The expansion of humans towards the temperate parts of Eurasia started at a roughly similar time, at over 40 ky, but this was a much longer process as humans seemed to have reached the cold areas of the gigantic Eurasian continent, such as northern Siberia, by less than 20 ky. It was the first time humans had to colonize a continent against a temperature gradient - from warm to cold - and possibly this factor helps to explain why it took so long (Araujo, 2013).

However, once reaching the eastern tip of Eurasia, humans had free access to the Americas, as Eurasia and North America were then connected through Beringia. North America was reached around 15 ky or a little before this. At the time, northern North America was still covered by a thick ice cover, because the deglaciation following had still not finished. Progression through this part of the continent seems to have been slow, but at about 13.5 ky is the first evidence that humans had reached North America's central plains.

Within the Americas, and especially in South America, the colonization frontier seems to have expanded at quite different speeds in different directions. The oldest reliable archaeological dates in South America are from Monte Verde, near Puerto Monte, in southern Chile, at over 14 ky. This striking date seems consistent with the hypothesis of a faster colonization route along South America's Pacific coast. For pre-technological people, the Andes were surely an imposing geographical barrier and this may have conditioned a 'fast' (lasting a few hundred years) movement southwards through the narrow land strip between the Pacific and the gigantic mountain chain. To the east of the Andes, with a more complex geography and dense forests, human expansion seems to have been much slower than on the west coast.

The last places to be reached by humans were the islands, all around the world, for the obvious reason that reaching them only became possible after the invention of efficient watercrafts, capable of traversing extensions of saltwater (with the exception of land-bridge islands such as Tasmania, which were connected to the continents at times of low sea levels during the late Pleistocene). The first important oceanic islands in the Americas that were reached by humans were the Caribbean islands, at nearly 6 ky. The Mediterranean islands seem to have been reached slightly later, and Wrangel, the home to the last mammoths, was occupied at about 4 ky. Madagascar, one of the world's largest islands, was first reached by humans only about 2,300 years ago and surprisingly, the first colonizers came from south Asia rather than Africa. Finally, New Zealand was the world's last large landmass to be reached by humans, just about 900 years ago.

A quantitative, global analysis making use of improved dating

The striking similarity between these dates of human arrival and the dates of the extinctions at the different landmasses across the world has been pointed out by many authors, including Martin (1984, 2005), Fernandez (2000), Lyons et al. (2004), Burney and Flannery (2005), Johnson (2006) and Gillespie (2008). However, Bernardo Araujo (2013) provided the first global

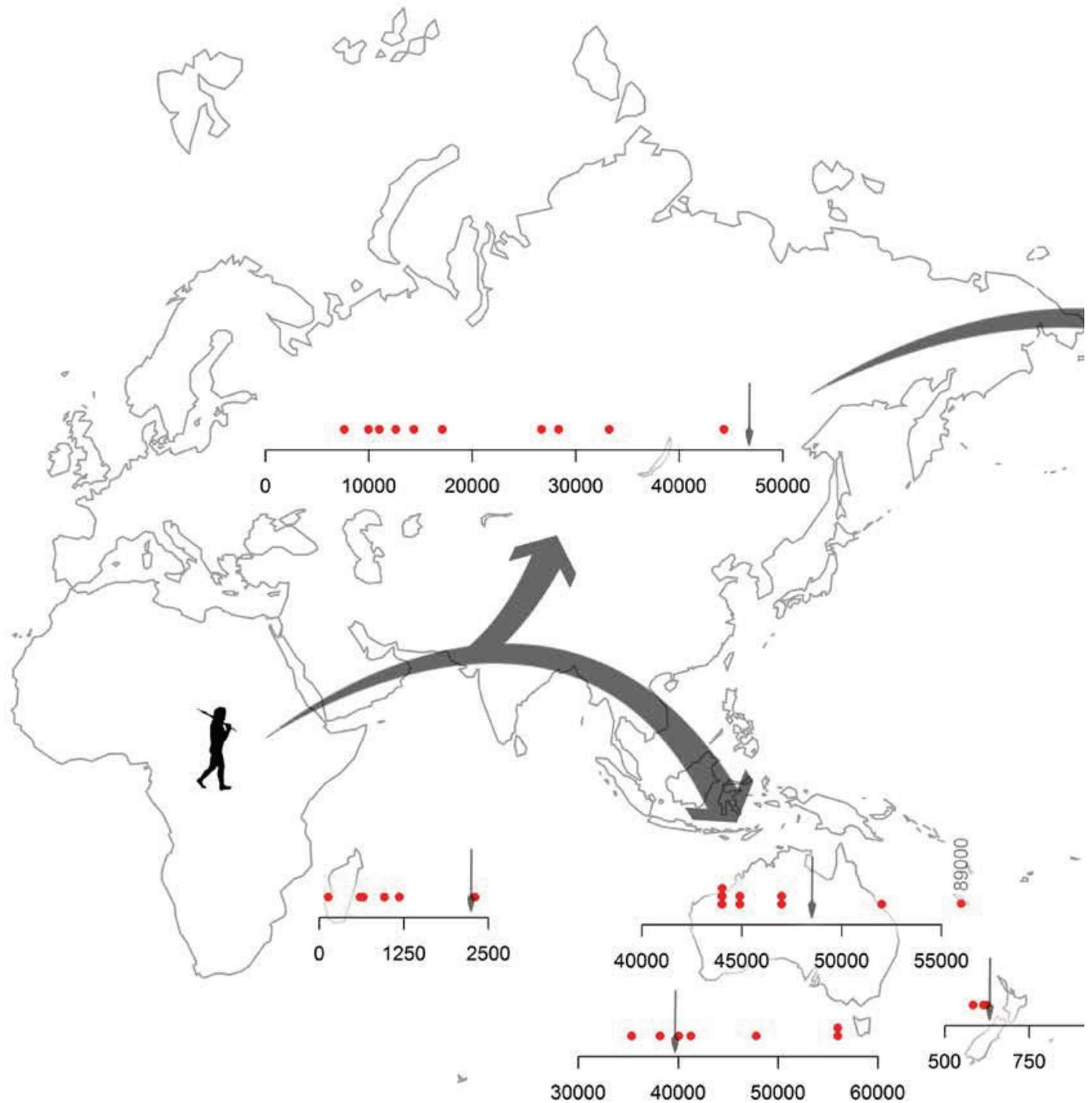
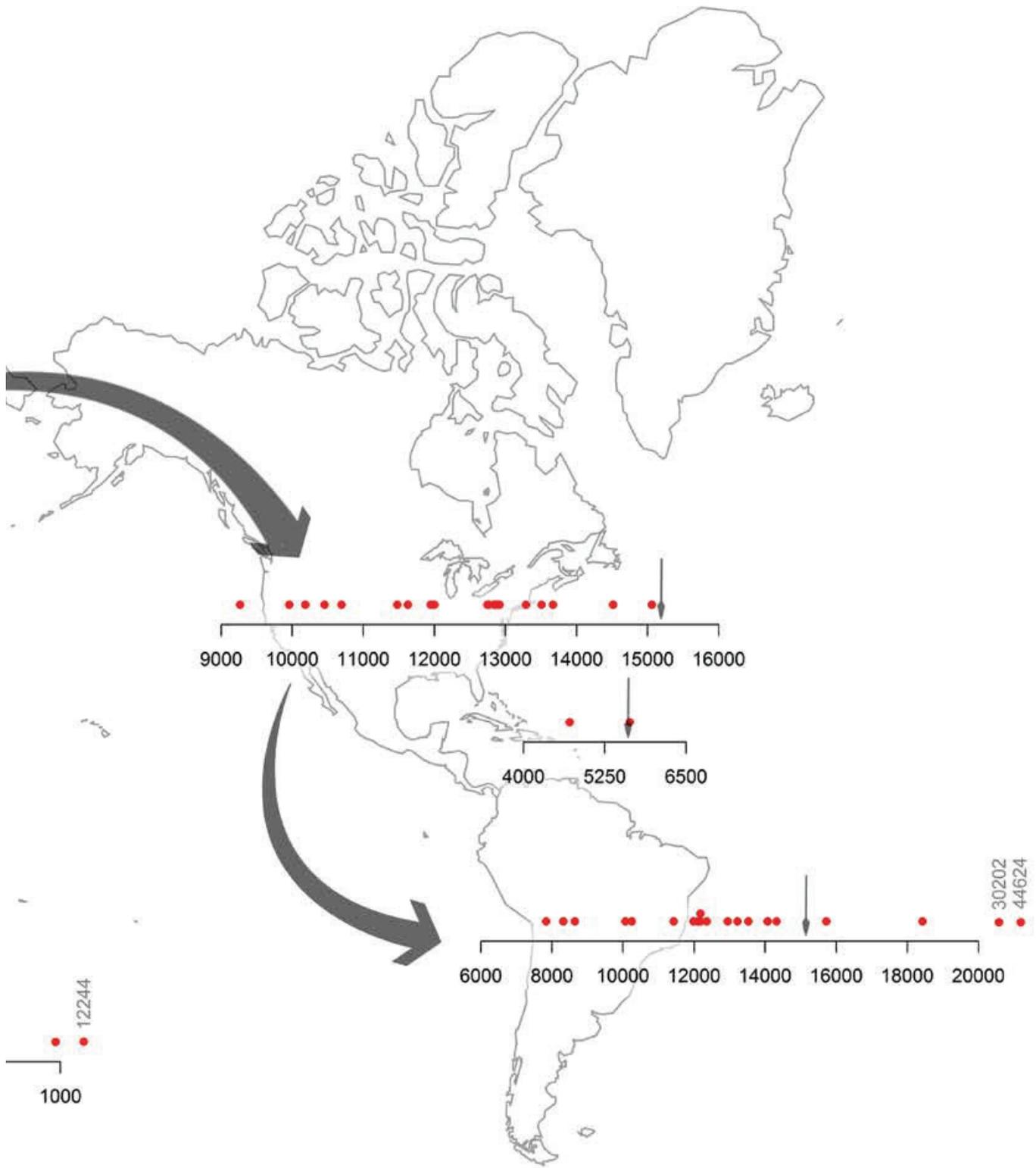


Figure 1. The timing of human arrival and megafaunal genera extinction across the world in the late Pleistocene and Holocene, as analyzed by Bernardo Araujo (2013). The displayed quantitative axes show the last known dates of occurrence at each landmass (calibrated dates, in years before past) of megafaunal genera (red dots). Grey spears point to the time of first known dates of human presence at each landmass. The large grey arrows show the main routes of human dispersal across the globe. © Bernardo Araujo.



quantitative analysis of the relations between the timing of the megafaunal extinctions, climatic changes and human arrivals to each of the world's land masses, taking advantage of the massive recent progress in dating methods. Using inaccurate time frames in quantitative analyses (for example, as in Prescott et al., 2012, for human arrival), it would be difficult to disentangle the effects of different putative causes for the extinctions (Lima-Ribeiro et al., 2012).

In Araujo's (2013) analysis, the intensity of climatic variation in the late Pleistocene and Holocene was assessed through the North Greenland Ice Core Project data on oxygen isotopic composition on ice cores (Andersen et al., 2004). This database comprises $\delta^{18}\text{O}$ data (a temperature proxy) for the last 122 ky. Megafaunal dates and human dates were obtained from literature for nineteen regions of the world where these events took place at markedly different times. The regions considered in the analysis were Australia, the Caribbean, Japan, Madagascar, New Zealand, Tasmania, Wrangel Island, Beringia (north-westernmost North America and north-easternmost Eurasia), central North America, eastern North America, western North America, northern Europe, southern Europe, west Siberia, central Russia, northern South America, central South America, Patagonia and the Andean region (the Andes and South America's western coast). Only calibrated dates, regarded as reliable according to the Mead-Melzer modified scale (Barnosky and Lindsey, 2010) were used. The database included 2,088 megafaunal dates (for 67 genera) and 762 archaeological dates.

Araujo's (2013) main results are summarised in Figure 1. The dates shown are the last known occurrences of each megafaunal genus and the first known human presence in each landmass. For sampling reasons, the last known date of a fossil genus tends to overestimate how long ago the extinction occurred and the first known human date tends to underestimate how old is the arrival (Signor and Lipps, 1982; Buck and Bard, 2007). Taking this in account, the clustering of the extinctions dates around the times of human arrival can be clearly seen. Comparing the two variables (human arrival and climate variation), the extinction times were nearer than expected by chance only to the time of human arrival in 76 cases (each case being the extinction of a genus in one of the 19 regions). On the other hand, the time of the extinction was closer than expected by chance only to the times of intense climate change in just 2 cases (a value close to the expected by a random placement of the extinctions along time). Extinctions were closer than expected by chance to both human arrival and times of intense climatic variation in 8 cases, and to neither of these variables in 40 cases, out of a total of 126 cases. These findings provide clear support for the hypothesis that anthropogenic impacts, rather than climate variation, were the main driver of the late Quaternary extinctions.

The eight cases where the extinctions were close in time both to human arrival and to climatic variation were mostly in the Americas. In these continents, human arrival approximately coincided in time with the events linked to the Younger Dryas, the last cold phase of the last glacial cycle. This finding is consistent with the view that climate changes actually played a role in the late Quaternary extinctions. But what role was this? Several authors have interpreted this kind of result as a 'synergy', for the Americas (Barnosky et al., 2004; Lima-Ribeiro and Diniz Filho, 2013) and elsewhere (for example, Nogués-Bravo et al., 2008, Lorenzen et al., 2011). However, this terminology can be misleading, by seeming to attribute similar roles to both factors: climate and humans. Synergy refers to an interaction between two or more factors that, when acting together, produce an effect that is larger than or different from the sum of their individual effects. However, the global approach provides 'natural experiments' in time and space that allow us to separate the factors: the megafauna survived through many other intense glacial cycles throughout the whole Pleistocene and it also persisted well into the Holocene in islands not yet reached by people. Both lines of evidence show that if it were not for the anthropogenic impacts, it is unlikely that the megafauna would have become extinct. Thus, climate changes seemed to have acted mostly as intensifiers, when they coincided with humans' arrival in a given landmass. In the context of logic, one could say that human arrival was the necessary cause of the extinctions - without it, the megafauna would not have disappeared - while climate change was just a contributory cause - by itself it would have little effect, but once present it played a role as well.

The associational critique and why it does not refute the anthropogenic hypothesis

Within archaeological contexts, a question often raised regarding the anthropogenic hypothesis is, if it is correct, then why there are relatively few sites showing associations between humans and megafauna? This has been called the 'associational critique' (Meltzer, 1986). Is this pattern incompatible with the hypothesis of anthropogenic impacts?

To answer this question, let's suppose just for a moment, that the anthropogenic hypothesis is correct. If so, using the mammoths as an example, in which proportion of mammoth sites would we expect to find associated archaeological remains? First, we must keep in mind that the time of coexistence of mammoth and humans, until mammoths became extinct, was a tiny part of the geological time range of mammoth records (Lister and Bahn, 2009). But this is still not the point. About twenty centuries in North America was the time of coexistence of mammoths and humans in the same continent, but *in any one locality the coexistence was much shorter still*. Thus, one would have to be very lucky indeed to find an archaeological site from precisely the few decades or so when mammoths and humans coexisted in *that given locality*. In any other case, he (she) would

find only mammoths without humans (before coexistence) or humans without mammoths (after coexistence). The expected pattern would be that a small fraction of megafaunal sites would have archaeological remains, and that is what is found.

Recently, Surovell and Grund (2012) presented another, complementary, refutation of the associational critique. They compared the relative temporal depths of coexistence (time spans between human arrival and megafaunal extinction, in proportion of the whole length of the archaeological record) among Australia, North America and New Zealand. Furthermore, they modelled taphonomic biases and also human demography to estimate how long it would take for humans to become abundant in a given landmass after their first arrival. Their results show that kill sites would be expected to be very common in New Zealand, to have intermediate frequency in North America and to be extremely rare or absent in Australia. This order of frequency of kill sites again is similar to the patterns we observe in the real world.

A modern view of the anthropogenic hypothesis

It is interesting to think about the process that resulted in these patterns. The hypothesis that the late Quaternary extinctions were caused by anthropogenic impacts has been considerably improved, in light of more recent knowledge, since it was put forward by Paul Martin (1967, 1984). A modern view of the anthropogenic extinctions as part of our early history would be as follows.

Except where megafauna co-evolved with early hominids (in Africa and south Asia, where there were few extinctions, and northern Eurasia, where they were quite spread across time), there is no reason to expect that big animals would have evolved instincts to avoid man. This is the phenomenon of 'island naivety', well known from many historical examples (Diamond, 1984). In the most plausible scenario, big beasts in the newly-colonized lands were quite unaware that humans could be dangerous hunters - to their downfall.

Putting the extinctions in the perspective of the time in which they happened, at least in three aspects, helps us understand that crucial period of human history. First, there was neither agriculture nor livestock - probably not a coincidence, as they were invented only after the megafauna disappeared. Thus, consumption of meat from large animals was probably indispensable for feeding a growing human population and if humans had any access to this resource - and technologically they had - one would hardly expect that they would not have used it. Second, once a large beast was killed, there was no efficient way to conserve vast amounts of meat. There were some valiant attempts such as underwater meat caching, first discovered in the Heisler site in Michigan (Fisher, 1995), and possibly the use of salt as well - but this was hardly enough. Therefore, a highly efficient use of megafaunal meat is unlikely. Third, people living at the time of our species' dispersal did not even know that the world had an end. They went on finding virgin hunting fields, until one day - in the Americas, probably the day when the southernmost tip of Tierra del Fuego was reached - there were no more. Given these three points, if we put ourselves in the shoes of a Clovis or any other people of the time, how could we expect them to use the megafauna in a cautious, sparing way? What for, not knowing that the world had an end? Such restraint may make sense from our perspective, but not from theirs.

Although in its original modern formulation (for example, Martin, 1967, 1973), the hypothesis of anthropogenic impacts puts much emphasis on hunting as the main extinction mechanism (hence its common label the 'overkill hypothesis'), more modern views have highlighted a diversity of anthropic impacts, all of which must have affected megafauna to different extents. Among these factors are introduced diseases (MacPhee and Marx, 1997) and fire. The later process is well documented, especially in Australia (Flannery, 1994; Johnson, 2006; Rule et al., 2012) and in North America (Flannery, 2001; Kerr, 2003; Gill et al., 2009). Increased frequency of fire actually seems to have been a consequence of the decline of plant-eating beasts, but it may have further affected the megafauna through habitat changes. Besides, some of the extinctions must have been caused indirectly through cascading ecological effects, especially the demise of large carnivores and scavengers. It is unlikely that the Clovis extinguished sabertooth tigers through hunting them for meat; there must have been easier sources of protein around. However, after all their big prey species were gone, sabertooths were doomed as well. The same must have applied to the huge North American teratorn birds and other large scavengers that depended on megafauna. The California condor's habit of scavenging on stranded marine mammals must have emerged as a much-needed ecological niche shift after its usual food sources had all but disappeared.

Another point is that it was not a 'quick' extinction at all, as had been proposed by Martin's 'blitzkrieg' version of his hypothesis (Martin, 1973). The extinctions were a long historical process that lasted several thousand years in each continent, with a few stragglers left even after that, as expected - the last on the islands. A comment here about the time scale involved in the events here described could be useful. Palaeontologists work with so-called 'geological time', which comprises very long time scales, often in the order of millions or billions of years. Besides, the farther away we look to a given time span in the past, the shorter it seems. There seems to be little difference between 40,500 to 40,000 years ago, but from Columbus to us it seems a long time. This trap of our perception and Martin's unfortunate expression help to explain many misunderstandings about the anthropogenic hypothesis. 'Blitzkrieg' means lightning war, but it was not a war at all, nor was it quick. As far as we know, the

animals were hunted not because of our species' urge for killing, but because they provided valuable resources for which there were no substitutes at the time. It was a very long process that took several millennia in continents and centuries in large islands.

The Quaternary extinctions do not imply that humans were terrible hunters. Big, slow-breeding animals are the most vulnerable to hunting. The species that became extinct had low fecundity, usually approximately less than one young per female per year (Johnson, 2002). Wallace's first impression - that the extinctions affected preferentially large animals - is an artefact of the negative correlation in nature between body size and breeding rates. Big animals might not have even been a major component of the diet and even so, they would be expected to become extinct. For example, Johnson (2006) estimated that a group of ten Australian aborigines needed to kill only about two diprotodonts per year to extinguish a population of these huge marsupials. The point with the late Quaternary extinctions was not the intensity of the hunting - it was the fragility of the hunted.

Altogether, from an ecologist's point of view, it is not surprising that humans' arrival in the new continents would have extinguished megafauna - it would be surprising if it had not.

The conservation of the memory of the human-megafauna interactions and the south-central American sites

In light of the evidence now available, without the anthropogenic impacts following human dispersal, nobody would be talking of 'Quaternary extinctions' today. It remains quite plausible that anthropogenic impacts were magnified by climatic events in some places, but climate change does not seem to be a major cause. However, regardless of whether anthropogenic impacts were the main cause or 'just' one of the major causes, what we know today is more than enough to show that these extinctions were one of the main events in the history of man's interactions with natural environments, as our species dispersed across the planet. Yet, perhaps because of the relative recency of Martin's hypothesis, or perhaps because the extent of humans' role is still debated, these are undervalued pages of our history. The late Quaternary extinctions are a fascinating subject that have seldom received the attention they deserve in education or in the media. The UNESCO World Heritage Convention can have an important role in changing this scenario.

The Americas must play a special role in the effort for changing this scenario. After all, the Americas were the New World, not just in the familiar, Eurocentric, cultural way - they were also the biological New World. The Americas were the last continents to be reached by modern humans and therefore the continents where megafaunal extinctions as a whole were the most recent. They therefore have a crucial role in preserving the memory of our interactions with the extinct large animals. Herein, we would like to tentatively propose three American sites which can be particularly valuable for this goal.

The first is Monte Verde in southern Chile. With its very old dating, Monte Verde is of course a key site in understanding human dispersal into the continent. But there is more to it; Monte Verde also illustrates particularly well the use of megafauna by humans, with a chunk of gomphothere meat found in an archaeological context. As Monte Verde is likely to reflect the oldest colonization of the continent, this finding may well represent a snapshot of the early utilisation of the just discovered South American megafauna.

The second site is Serra da Capivara, within Serra da Capivara National Park, in Piauí state in north-eastern Brazil. This is also a highly valuable site, not because of its unreliable claims to greater antiquity, but for its richness in rock paintings, many of which represent extinct species and their interactions with the early settlers. To our knowledge, there is no other site which represents so well human-megafauna interactions in Brazil. Besides, these paintings unfortunately are threatened by vandalism, which increases the urgency of efforts to conserve them.

The third site proposed is Las Breas de San Felipe, in Cuba. It would be important to represent the last of the American extinct megafauna and its interactions with humans. Hence, Cuba was home to the last surviving megafauna in the Americas. The most recent records are from the sites of Las Breas de San Felipe and Solapa de Silex, with human artefacts associated to dwarf giant ground sloths (genera *Parocnus* and *Megalocnus* respectively), dated to 5.7 and 4.7 ky respectively (reliable calibrated dates). Las Breas de San Felipe is a tar pit, a kind of miniature Rancho Las Breas, the famous Californian tar pit site (Iturralde-Vinent et al., 2000). Among Cuban sites, Las Breas de San Felipe is the richest, with easiest access and thus the one that presents more potential to be nominated to the UNESCO World Heritage List, despite the slightly younger dating of Solapa de Silex's ground sloths (MacPhee et al., 2007).

Conserving evidence of human-megafauna interactions is important for us to learn from our history - about when our impacts on nature were severe, when they were not, and what caused the different outcomes. It is also a useful reminder of the fragility of nature - especially of the big animals - to our actions, in a time when so many people still deny the full magnitude of our impacts on the natural systems. Now that we are extinguishing species at unprecedented rates, more than ever we need to learn from the past. As Paulinho da Viola (1972) sang in '*Dança da Solidão*', '*Meu pai sempre me dizia / Meu filho tome*

cuidado / Quando eu penso no futuro / Não me esqueço do passado ('My father always told me / My son, be careful / When I think about the future / I don't forget the past').

Acknowledgements

First and foremost, I would like to thank Bernardo Araujo for all his help and discussions, for preparing Figure 1 and for allowing me to use some of his unpublished data in this paper - which is also his. I am grateful to Nuria Sanz for her invitation to contribute to this volume. These ideas owe much to discussions with José Alexandre Diniz-Filho, Matheus Lima-Ribeiro, Leonardo Ávila, Leopoldo Soibelzon, Joaquín Hortal and the late Ibsen de Gusmão Câmara and Paul Martin, among others. I also thank the participants of the 'The First Peopling of the Americas and the World Heritage Convention' in Puebla, Mexico, especially Antonio Gilman, Chris Scarre, Dennis O'Rourke, Ian Kuijt, James Chatters, Joaquín Arroyo-Cabrales and Tom Dillehay for their comments. Finally, I thank Anjelica Young and Chantal Connaughton for their logistical support all along and for their careful review of the manuscript.

Bibliography

Andersen, K. K., Azuma, N., Barnola, J.-M., Bigler, M., Biscaye, P., Caillon, N., Chappellaz, J., Clausen, H. B., Dahl-Jensen, D., Fischer, H., Flückiger, J., Fritzsche, D., Fujii, Y., Goto-Azuma, K., Grønbold, K., Gundestrup, N. S., Hansson, M., Huber, C., Hvidberg, C. S., Johnsen, S. J., Jonsell, U., Jouzel, J., Kipfstuhl, S., Landais, A., Leuenberger, M., Lorrain, R., Masson-Delmotte, V., Miller, H., Motoyama, H., Narita, H., Popp, T., Rasmussen, S. O., Raynaud, D., Rothlisberger, R., Ruth, U., Samyn, D., Schwander, J., Shoji, H., Siggard-Andersen, M.-L., Steffensen, J. P., Stocker, T., Sveinbjörnsdóttir, A. E., Svensson, A., Takata, M., Tison, J.-L., Thorsteinsson, Th., Watanabe, O., Wilhelms, F. and White, J. W. C. 2004. High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature*, Vol. 431, pp. 147-51.

Anderson, E. 1984. Who's who in the Pleistocene: a mammalian bestiary. P. S. Martin and R. G. Klein (eds), *Quaternary Extinctions: A Prehistoric Revolution*. Arizona, University of Arizona Press, pp. 40-89.

Araujo, B. 2013. Pleistocene-Holocene extinctions: distinguishing between climatic and anthropic causes. Master's thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro.

Barnosky, A. D. and Lindsey, E. L. 2010. Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quaternary International*, Vol. 217, pp. 10-29.

Buck, C.E. and Bard, E. 2007 A calendar chronology for Pleistocene mammoth and horse extinction in North America based on Bayesian radiocarbon calibration. *Quaternary Science Reviews*, Vol. 26, pp. 2031-035.

Burney, D.A. and Flannery, T. F. 2005. Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology and Evolution*, Vol. 20, pp. 395-401.

Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L. and Shabel, A. B. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science*, Vol. 306, pp. 70-75.

Cione, A. L., Tonni, E. P. and Soibelzon, L. 2003. The broken zig-zag: late Cenozoic large mammal and tortoise extinction in South America. *Revista del Museo Argentino de Ciencias Naturales*, Vol. 5, pp. 1-19.

Dewar, R. E. 1984. Extinctions in Madagascar: the loss of the subfossil fauna. P. S. Martin and R. G. Klein (eds), *Quaternary Extinctions: A Prehistoric Revolution*. Arizona, University of Arizona Press, pp. 574-99.

Diamond, J. M. 1984. Historic extinction: a Rosetta stone for understanding prehistoric extinctions. P. S. Martin and R. G. Klein (eds), *Quaternary Extinctions: A Prehistoric Revolution*. Arizona, University of Arizona Press, pp. 824-66.

Fernandez, F. A. S. 2000. *O poema imperfeito - crônicas de biologia, conservação da natureza e seus heróis*. Curitiba, Universidade Federal do Paraná.

Flacourt, E. 1658. *Histoire de la Grande Isle Madagascar*. Available for download at <http://gallica.bnf.fr/ark:/12148/bpt6k1047463/f3.image>.

Flannery, T. 1994. *The Future Eaters: An Ecological History of the Australasian Lands and People*. Australia, Grove Press.

A Genetic and Biological Perspective of the First Settlements of the Americas

Flannery, T. 2001. *The Eternal Frontier: An Ecological History of North America and its People*. Melbourne, Australia, The Text Publishing Company.

Fisher, D.C. 1995. Experiments on subaqueous meat caching. *Current Research in the Pleistocene*, Vol. 12, pp. 77-80.

Gill, J. L., Williams, J. W., Jackson, S. T., Lininger, K.B. and Robinson, G. S. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science*, Vol. 326, pp. 1100-103.

Gillespie, R. 2008. Updating Martin's global extinction model. *Quaternary Science Reviews*, Vol. 27, pp. 2522-529.

Grayson, D. K. 1984. Nineteenth-century explanations of Pleistocene: a review and analysis. P. S. Martin and R. G. Klein (eds), *Quaternary Extinctions: A Prehistoric Revolution*. Arizona, University of Arizona Press, pp. 5-39.

Guthrie, R. D. 2004. Radiocarbon evidence of mid-Holocene mammoths stranded on an Alaskan Bering Sea island. *Nature*, Vol. 429, pp. 746-49.

Iturralde-Vinent, M. A., MacPhee R. D. E., Díaz-Franco S., Rojas-Consegra R., Suárez W. and Lomba, A. 2000. Las Breas de San Felipe, a Quaternary fossiliferous asphalt seep near Martí (Matanzas Province, Cuba). *Caribbean Journal of Science*, Vol. 36, pp. 300-13.

Johnson, C. N. 2002. Determinants of loss of mammal species during the late Quaternary megafauna extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society of London B*, Vol. 269, pp. 2221-227.

Johnson, C. N. 2006. *Australia's Mammal Extinctions: A 50000 Year History*. Cambridge, Cambridge University Press.

Koch, P. L. and Barnosky, A. D. 2006. Late Quaternary extinctions: state of the debate. *Annual Review of Ecological Evolution Systems*, Vol. 37, pp. 215-50.

Kerr, R. A. 2003. Megafauna died from big kill, not big chill. *Science*, Vol. 300, p. 885.

Lima-Ribeiro, M. S. and Diniz-Filho, J. A. F. 2013. *Modelos Ecológicos e a Extinção da Megafauna: Clima e Homem na América do Sul*. São Carlos, Editora Cubo.

Lima-Ribeiro, M. S., Nogués-Bravo, D., Marske, K., Fernandez, F. A. S., Araujo, B. and Diniz-Filho, J. A. F. 2012. Human arrival scenarios have a strong influence on interpretations of the late Quaternary extinctions: a comment on Prescott's et al. [2012] analyses. *Proceedings of the National Academy of Sciences USA*, Vol. 109, E2409-10.

Liscaljet, N. 2012. *Napakaliit trompa*: new pigmy proboscidean from the Cagayan valley (Philippines). *Quaternary International*, Vol. 276, pp. 278-286.

Lister, A. and Bahn, P. 2009. *Mammoths: Giants of the Ice Age*. Berkeley, University of California Press.

Lorenzen, E. D., Nogués-Bravo, D., Orlando, L., Weinstock J., Binladen, J., Marske K.A., Ugan, A., Borregaard, M. K., Gilbert M. T. P. and Nielsen, R. 2011. Species-specific responses to Late Quaternary megafauna to climate and humans. *Nature*, Vol. 479, pp. 359-65.

Lyons, S. K., Smith F. A. and Brown, J. H. 2004. Of mice, mastodon and men: human-mediated extinctions on four continents. *Evolutionary Ecology Research*, Vol. 6, pp. 339-58.

MacPhee, R. D. E. and Marx, P. A. 1997. The 40,000 year plague - humans, hyperdisease and first contact extinctions. S. Goodman and B. Patterson (eds), *Natural Change and Human Impact in Madagascar*. Washington D.C., Smithsonian Institution Press, pp. 169-217.

MacPhee, R. D. E., Iturralde-Vinent, M. A. and Vázquez, O. J. 2007. Prehistoric sloth extinctions in Cuba: implications of a new 'last' appearance date. *Caribbean Journal of Science*, Vol. 43, pp. 94-98.

Martin, P. S. 1967. Prehistoric overkill. P. S. Martin and H. E. Wright Jr. (eds), *Pleistocene Extinction: The Search for a Cause*. New Haven, Yale University Press, pp. 75-120.

Martin P. S. 1973. The discovery of America. *Science*, Vol. 179, pp. 969-74.

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

Martin, P. S. 2005. *Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of America*. Berkeley, University of California Press.

Martin, P. S. and Klein, R. G. (eds). 1984. *Quaternary Extinctions: A Prehistoric Revolution*. Arizona, University of Arizona Press.

- Masseti, M. 2001. Did endemic dwarf elephants survive on Mediterranean islands up to prehistorical times? *The World of Elephants - International Congress, Rome*.
- Meltzer, D. J. 1986. Pleistocene overkill and the associational critique. *Journal of Archaeological Science*, Vol. 13, pp. 51-60.
- Murray, P. 1984. Extinctions downunder: a bestiary of extinct Australian late Pleistocene monotremes and marsupials. P. S. Martin and R. G. Klein (eds), *Quaternary Extinctions: A Prehistoric Revolution*. Arizona, University of Arizona Press, pp. 600-28.
- Nogués-Bravo, D., Rodríguez, J., Hortal, J., Batra, P. and Araújo, M. B. 2008. Climate change, humans, and the extinction of the woolly mammoth. *Plos Biology*, Vol. 6, e79.
- Petronio, C. 1995. Note on the taxonomy of Pleistocene hippopotamuses. *Ibex*, Vol. 3, pp. 53-55.
- Prescott, G. W., Williams, D. R., Balmford, A., Green, R. E. and Manica, A. 2012. Quantitative global analysis of the role of climate and people in explaining late Quaternary megafaunal extinctions. *Proceedings of the National Academy of Sciences USA*, Vol. 109, pp. 4527-531.
- Roberts, R. G., Flannery, T. F., Ayliffe, L. K., Yoshida, H., Olley, J. M., Prideaux, G. J., Laslett, G. M., Baynes, A., Smith, M. A., Jones, R. and Smith, B.L. 2001. New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. *Science*, Vol. 292, pp. 1888-892.
- Rule, S., Brook, B. W., Haberle, S. G., Turney, C. S. M., Kershaw, A. P. and Johnson, C. N. 2012. The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. *Science*, Vol. 335, pp. 1483-486.
- Signor, P. W. and Lipps, J. H. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. *Geological Society of America*, Vol. 190, pp. 291-96.
- Steadman, D. W., Martin, P. S., MacPhee, R. D. E., Jull, A. J. T., McDonald, H. G., Woods, C. A., Iturralde-Vinent, M. and Hodgins, G. W. L. 2005. Asynchronous extinction of late Quaternary sloths on continents and islands. *Proceedings of the National Academy of Sciences*, Vol. 102, pp. 11763-768.
- Stringer, C. and Andrew, P. 2005. *The Complete World of Human Evolution*. London, Thames & Hudson.
- Surovell, T. A. and Grund, B.G. 2012. The associational critique of Quaternary overkill and why it is largely irrelevant to the extinction debate. *American Antiquity*, Vol. 77, pp. 673-88.
- Stuart, A.J., Kosintsev, P.A., Higham, T.F.G., and Lister, A.M. 2004. Pleistocene to Holocene extinctions dynamics in giant deer and woolly mammoth. *Nature*, Vol. 431, pp. 684-89.
- Trotter, M. M. and McCulloch, B. 1984. Moas, men, and middens. P. S. Martin and R. G. Klein (eds), *Quaternary Extinctions: A Prehistoric Revolution*. Arizona, University of Arizona Press, pp. 708-27.
- Thompson, D. W. 1917. *On Growth and Form*. Cambridge, Cambridge University Press.
- Theodorou, G.E., Symeonides, N.K., Stathopoulou, E. 2007. *Elephas tiliensis* n. sp. from Tilos island (Dodecanese, Greece). *Hellenic Journal of Geosciences*, Vol. 42, pp. 19-32.
- Turney, C. S. M., Flannery, T., Roberts, R. G., Reid, C., Fifield, L. K., Higham, T. F. G., Jacobsa, Z., Kempf, N., Colhouni, E. A., Kalinj, R. M. and Ogle, N. 2008. Late-surviving megafauna in Tasmania, Australia, implicate human involvement in their extinction. *Proceedings of the National Academy of Sciences*, Vol. 105, pp. 12150-153.
- Turvey, S. T. and Fritz, S. A. 2011. The ghost of mammals past: biological and geographical patterns of global mammalian extinction across the Holocene. *Philosophical Transactions of the Royal Society of Sciences B*, Vol. 366, pp. 2564-576.
- Vartanyan, S. L., Garutt, V. E. and Sher, A. V. 1993. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. *Nature*, Vol. 362, pp. 337-340.
- Wallace, A. 1876. *The Geographical Distribution of Animals*. London, Harper and Brothers.
- Woodman, N. and Athfield, N.B. 2012. Post-Clovis survival of American Mastodon in the southern Great Lakes Region of North America. *Quaternary Science Reviews*, Vol. 72, pp. 359-63.
- Wroe, S., Field J. H., Archer M., Grayson D. K., Price G. J., Louys J., Faith J. T., Webb G. E., Davidson I. and Mooney S. D. 2013. Climate change frames debate over the extinction of megafauna in Sahul (Pleistocene Australia-New Guinea). *Proceedings of the National Academy of Sciences USA*, Vol. 110, pp. 8777-781.