

Late Quaternary megafaunal extinctions on the continents: a short review

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This paper provides an overview of the contentious issue of global megafaunal extinctions in the Late Quaternary. The main proposed causes are 'overkill', environmental change or a combination of both. There are major objections to the other suggested causes. Extinctions were highly variable in their severity between different zoogeographical regions, with the greatest impact in North America, South America and Australia, but also substantial in northern Eurasia. Sub-Saharan Africa and Southern Asia were much less affected. For northern Eurasia, detailed chronologies show a staggered extinction pattern, in which each megafaunal species exhibits unique and complex distributional shifts, culminating in extinction for some species and survival in others. Environmental drivers were clearly very important, although the possible role of humans is not yet clear. Alaska/Yukon also has a good radiocarbon record which also suggests a staggered extinction pattern. However, the available data for the rest of North America are largely unsatisfactory. South America also boasted spectacular extinct megafauna, but again the currently available dates are insufficient to reliably discern patterns or possible causes. Australia and New Guinea also suffered major losses, but extinctions probably occurred much earlier than elsewhere, so that establishing a chronology is especially difficult. Africa and Southern Asia have the least available data. In order to make meaningful progress, it is vital to establish a large database of reliable radiocarbon dates for each region made directly on securely identified megafaunal remains. The need is for much more high quality data, not more debate based on imperfect evidence. Copyright © 2014 John Wiley & Sons, Ltd.

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1. INTRODUCTION

This review aims to provide an overall picture of this complex and fascinating subject which has given rise to a vast literature, and continuing lively debate and controversy. It is not my intention here to promote a particular hypothesis for the cause or causes of extinctions, but to provide a useful summary of the current state of knowledge. However, as will be abundantly clear from the text, I strongly believe that accurate dating is the key to resolving this very important issue which is highly relevant to the fate of the megafauna that we still have today.

The faunas, extinct and extant, are treated here by zoogeographical region (ecoregions) (e.g. as in Olson *et al.*, 2001). In view of the quality of the available evidence, I have paid particular attention to northern Eurasia, whereas North America, Australia and South America receive rather less coverage, and Africa and Southern Asia are only considered briefly. I have restricted this review to continental faunas,

including some islands which were connected to the mainland at times of lower sea level.

The Late Quaternary featured accelerated losses of large terrestrial vertebrates (megafauna) over most of the globe. The term 'megafauna' is used here for species with mean adult body weights of *ca.* 45 kg or over. In general, the larger the animal, the more it was at risk of extinction as large size usually correlates with slower breeding and a smaller number of individuals in the population (Johnson, 2002). Earlier extinctions in the Pleistocene affected small as well as large species, and many megafaunal losses were replaced by the evolution or immigration of ecologically similar forms. In contrast, Late Quaternary extinctions (except those within the last few hundred years: Dulvy *et al.*, 2009; Turvey, 2009a, b) primarily affected terrestrial large mammals, together with a few large birds and reptiles, leaving marine biotas largely unscathed.

That there had been a major extinction of megafauna in the recent geological past was recognized by 19th-century researchers, including Alfred Russel Wallace and Charles Darwin. Wallace's much-quoted observation (Wallace, 1876, p. 150) bears repeating for its remarkable insight: 'we live in a zoologically impoverished world from which

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all the hugest and fiercest and strangest forms have recently disappeared. It is surely a marvellous fact and one that has hardly been sufficiently dwelt upon, this dying out of so many large Mammalia, not in one place only, but over half the land surface of the globe'.

Today, renewed interest in the topic is fuelled by concerns for the future of global ecosystems and the threatened extinction of many living species. Much credit for this must go to the late Paul Martin (1928–2010) for his enthusiastic advocacy of the subject over a period of more than 40 years (e.g. Martin, 1967, 2005; Martin and Klein, 1984; Martin and Stuart, 1995; Martin and Steadman, 1999). From a geological perspective, Late Quaternary extinctions (large and small species) can be seen as either a relatively minor episode or just the beginning of a major mass extinction—the so-called 'Sixth Extinction'—that is in progress at the present day and shows every indication of accelerating into the future (Leakey and Lewin, 1996; Barnosky *et al.*, 2011).

Major advances in tracking the geographical and temporal patterns of extinctions have been made principally due to the extensive application of radiocarbon dating to the issue. The technique can be used to directly date megafaunal material, namely bones, teeth, antlers and, more rarely, various soft tissues and dung. In this paper, all radiocarbon dates are given as median calibrated years before present ('present' defined by convention as the year 1950). The rigorous application of objective criteria both in submitting material for radiocarbon dating and in assessing published dates (Lister and Stuart, 2013) is vitally important for establishing reliable chronologies for each species and each geographical region. All dating should be made directly on securely identified material of the species in question. Experience has shown that dates made on associated material such as charcoal (context dates) are often incorrect (usually too young), sometimes by a wide margin. Published dates should be rejected if they lack laboratory identification; the material dated is not specified, comprises more than one skeletal element or comes from more than one individual. Dates on apatite or bone carbonate should also be rejected as these have been shown to be unreliable. Lister and Stuart (2013) also advocate disregarding dates which were done pre-1980 (an arbitrary, but convenient, cut-off point) as laboratory methods have improved considerably in recent decades. Important or unexpected results, for example indicating Holocene survivals, should be subject to independent repeat dating by another laboratory. Similarly, if a date is an outlier (i.e. in comparison with a reasonably large set of dates, it significantly extends a species' range in time and/or space), it also should be corroborated by repeat dating in another laboratory before it can be accepted.

Other methods of dating, such as uranium–thorium, optically stimulated luminescence (OSL), electron spin resonance (ESR) and amino acid racemization (AAR), can be

used for material beyond the practical radiocarbon limit of about 50 000 years. An increasingly important tool for unravelling the complexities of extinction dynamics is ancient DNA (aDNA), extracted from bones, teeth or other organic remains (e.g. Shapiro *et al.*, 2004; Campos *et al.*, 2010b; Lorenzen *et al.*, 2011; Stiller *et al.*, 2014). In addition, stable isotope analyses are used to provide important information on the diets and community structure of Quaternary megafaunal species (e.g. Stevens and Hedges, 2004; Bocherens *et al.*, 2011a, b).

Analyses of ancient DNA in megafaunal remains, in combination with radiocarbon dating, are producing exciting results, including the estimation of changing past population sizes. During the Last Glacial period in northern Eurasia and North America, several extinct megafaunal species (e.g. *Panthera spelaea*, *Mammuthus primigenius*) declined in genetic diversity (Lorenzen *et al.*, 2011). However, to what extent this contributed to their eventual extinction is less clear, as other species such as *Ovibos moschatus* and *Saiga tatarica* also experienced similar bottlenecks but nevertheless have survived to the present day (Campos *et al.*, 2010a, b). Another significant development in the last few years is niche modelling, in which geographical ranges of megafauna at different times in the past are related to climate and vegetation (Nogués-Bravo *et al.*, 2008, 2010; Lorenzen *et al.*, 2011). These niche models are used to simulate the changing potential range of each taxon and thus determine whether species became extinct as a result of habitat loss or whether other factors such as human hunting might have been involved.

As will be very apparent from this review, megafaunal extinctions were highly variable in their severity between different zoogeographical regions, with the greatest impact in North America (Nearctic Ecoregion), South America (Neotropic Ecoregion) and Australasia (Australasia Ecoregion) (Lyons *et al.*, 2004a). However, they were also substantial in northern Eurasia (Palaeartic Ecoregion). In contrast, sub-Saharan Africa (Afro-tropic Ecoregion) and Southern Asia (Indo-Malay Ecoregion) were less affected, so that, for example, elephants and rhinos survive in both regions, albeit precariously, to the present day. One of the major challenges in Quaternary palaeontology is to understand the reasons for these differences.

2. THE SEARCH FOR A CAUSE

Nearly half a century after Paul S. Martin reignited interest in this fascinating topic, the cause or causes of the Late Quaternary extinctions remain highly controversial and continue to generate a large amount of literature and debate. The well-established contending hypotheses are 'overkill' by human hunters, climatic/environmental change or a combination of

both. Both hypotheses have their merits and demerits; see, for example, Grayson (1984), Stuart (1991), Lyons *et al.* (2004a) and Koch and Barnosky (2006). More recently proposed explanations, such as ‘hyperdisease’, extraterrestrial impact and solar flare, all have serious shortcomings (see further discussion below).

2.1. ‘Overkill’ hypothesis

It is almost universally accepted that the numerous extinctions of terrestrial vertebrates (large and small) on oceanic islands were entirely or mostly a direct consequence of human colonization in the Holocene, mostly in the last 1000–2000 years (Alcover *et al.*, 1998; Martin and Steadman, 1999; Turvey, 2009a, b; Crowley, 2010). Ecosystems that had evolved essentially in isolation were severely impacted by habitat destruction, hunting and the introduction of alien species such as rats, dogs, pigs and goats. For example, before human arrival in the late 13th century AD, New Zealand (separated from Australia by about 1500 km of sea and by similar distances from major Pacific islands) had no mammals, except bats, but instead a rich avifauna, including nine species of moa on North and South Islands. Within a century of colonization by Polynesians (ancestral Maori), all species of moa were probably extinct (Rawlence *et al.*, 2012; Rawlence and Cooper, 2013; Allentoft *et al.*, 2014), and the abundance of moa remains in early archaeological sites provides compelling corroborative evidence that they were extensively hunted and eaten. In combined genetic and dating analyses, Allentoft *et al.* (2014) concluded that populations of the four moa species studied were large and viable for at least 4000 years prior to human arrival and that their subsequent demise was sudden—‘a striking example of human overexploitation of megafauna’ (Allentoft *et al.*, 2014, p. 4922). However, the role of humans in continental extinctions is much less clear.

Paul Martin (1967, 1973, 1984) energetically championed the ‘Prehistoric overkill’ hypothesis, according to which major extinctions of terrestrial vertebrates in the Late Quaternary, on both continents and oceanic islands, resulted from the same process, namely, the global spread of modern humans (*Homo sapiens*) who indulged in unsustainable levels of hunting. The larger ‘big game’ species are thought to have been especially vulnerable because they were slow-breeding and existed in relatively low populations. However, with his well-known ‘Blitzkrieg’ (literally ‘lightning war’) hypothesis—a special case of ‘overkill’—Martin (e.g. 1973, 1984) went much further and postulated that when modern humans first colonized North America, South America and Australia in the Late Pleistocene, they encountered naive prey lacking behavioural and evolutionary adaptations to the novel and aggressive human predator. Megafaunal losses in Eurasia and especially Africa

supposedly were less severe because of the long co-existence of humans and megafauna in these continents. In contrast, he envisaged that in ‘continents of colonization’ human arrival was followed by catastrophic collapse of megafaunal populations and that the human populations initially underwent a population explosion fuelled by super-abundant food (Mosimann and Martin, 1975). Largely in response to a perceived problem that in North America there were too few ‘kill sites’ (i.e. sites with direct association of projectile weapons and megafaunal remains), Mosimann and Martin (1975) and Martin (e.g. 1984, 2005) proposed that the slaughter had occurred so rapidly as to leave little trace in the fossil record.

Computer modelling by Alroy (2001) and others lends some support to the idea that hunting by humans could have resulted in extinctions, especially if the model allows the hunters to switch to other more abundant prey but still continue opportunistic hunting of the increasingly rare slow-breeding species. The later survival of some megafaunal taxa on islands than on the continents, for example, Holocene mammoths on Wrangel Island and ground sloths in the West Indies, appears consistent with ‘overkill’, as extinctions only seem to have occurred around the time of the first human arrivals.

With variations, the basic ‘overkill’ hypothesis continues to enjoy considerable support, especially with many researchers in North America and Australia (see below). In marked contrast, ‘Blitzkrieg’ generally has not been well-received. Problems with ‘overkill’ include the following:

- (a) How could humans in low population densities and with relatively simple technologies have exterminated so many varied large animals and over their entire geographical ranges?
- (b) In northern Eurasia, most, or all, extinctions occurred many millennia after the appearance of modern humans (see below).
- (c) Late Pleistocene extinctions, especially in the Americas, affected a number of smaller mammalian and avian species that are unlikely to have featured significantly in the human diet.
- (d) Many extinct carnivores were also very unlikely to have been extensively hunted (Grayson, 1984).
- (e) For most of the subsequent Holocene period, very few megafaunal species on the continents have disappeared, although faced with very much higher human populations.
- (f) Many species which are known to have been extensively hunted, such as reindeer and horse in northern Eurasia, survive to the present day.

Major objections to ‘Blitzkrieg’ also include the supposed extreme rapidity of the process with the paucity of fossil and archaeological evidence paradoxically cited as supporting

the hypothesis and the improbability that prey remained naive long enough to be wiped out (Berger *et al.*, 2001). An obvious chronological test of 'overkill', by means of radiocarbon or other dating methods, is that, for a given region, a marked increase in extinctions should follow extensive human colonization, as has been suggested for North America (see below).

2.2. Environmental change hypothesis

The profound climatic changes and resulting disruption of biota that occurred globally around the Last Glacial–Holocene transition offer a compelling cause of extinctions. Major changes in North America and northern Eurasia included the replacement of vast areas of open vegetation with grasses and herbs—the 'mammoth steppe'—by forests, mainly boreal conifer forest and temperate deciduous forest (e.g. Guthrie, 1984, 2001; Allen *et al.*, 2010; Huntley *et al.*, 2013). In Alaska/Yukon and northern Eurasia, many species supposed to have been highly adapted to the 'mammoth steppe' biome are thought to have become extinct because their habitat disappeared. Different kinds of vegetational changes also occurred on other continents, although generally these changes are less well known.

However, the geological record shows a complex pattern of climatic/environmental changes during most of the last 780 ka (Middle and Late Pleistocene), which featured repeated glacial–interglacial transitions broadly resembling the most recent Last Glacial–Holocene transition, yet no such catastrophic extinction occurred previously. Accordingly, several authors have proposed that the Last Glacial–Holocene cycle had unique characteristics which resulted in unprecedented major extinctions (e.g. Graham and Lundelius, 1984; Guthrie, 1984), a hypothesis which has yet to be tested by detailed comparisons with earlier cycles.

Another issue is why were the animals that went extinct not able to find suitable habitat somewhere, as happened for example with survivors such as reindeer, saiga and musk ox in northern Eurasia? In the case of those that went extinct, such as woolly rhinoceros, possibly, the remaining areas were too small and fragmented, and/or topographical or vegetational barriers prevented migration.

The environmental change hypothesis predicts close temporal correlations between environmental changes and extinctions and so is testable by comparison with climatic and vegetational proxies. These show convincing correlations for northern Eurasia and Alaska/Yukon (see below) but need more data for testing in other ecoregions.

2.3. Combined hypothesis

Since the above hypotheses appear inadequate to explain all the facts, a number of authors (e.g. Stuart, 1991, 1999;

Barnosky *et al.*, 2004; Koch and Barnosky, 2006; Nikolskiy *et al.*, 2011) have suggested a combination of 'overkill' and environmental change, in which extinctions resulted from human hunting of megafaunal populations also subject to habitat fragmentation and other stresses in response to climatic and resulting vegetational changes. Hunting pressure became critical only when populations were already reduced in both numbers and geographical range by environmental changes, and additionally, the presence of humans in an area might have inhibited the natural migration of megafaunal species responding to environmental changes. This scenario provides a plausible explanation as to how a widespread species such as woolly mammoth could disappear over its entire range. The combined hypothesis predicts a temporal and geographical pattern of range shrinkage for each megafaunal species—attributable to environmental changes—together with archaeological evidence that human populations were present in the refugial areas prior to extinction.

2.4. Hyperdisease hypothesis

MacPhee and Marx (1997) postulated that extinctions could have been driven by a lethal pathogen introduced by humans (or their dogs) as they spread around the globe. However, there is no known disease at the present day that would preferentially select larger mammalian species or be infectious across a range of orders (see comparison with modern West Nile Virus; Lyons *et al.*, 2004b).

2.5. Extraterrestrial impact hypothesis

A sensational proposal was made by Firestone *et al.* (2007). They described a range of features in sediment profiles across North America dating from the onset of the Younger Dryas stadial (*ca.* 12.9 ka) which they attributed to the impact of a comet or other extraterrestrial bodies. The event is supposed to have been a major contributor to megafaunal extinction in North America and also to the release of vast quantities of meltwater from the North American (Laurentide) ice sheet, which in turn triggered the Younger Dryas cold episode.

Although it has attracted a great deal of media attention, this idea has not been well received by most of the scientific community (Pinter *et al.*, 2011). Other researchers have been unable to find corroborative evidence, from either the originally studied localities or elsewhere, that such an impact event actually occurred (Kerr, 2008; Surovell *et al.*, 2009). For a recent detailed critique of this hypothesis, see Holliday *et al.* (2014). Since the impact hypothesis implies sudden extinction of North American megafauna at *ca.* 12.9 ka, it should be eminently testable by an extensive programme of direct radiocarbon dating of megafaunal remains. Significantly, the well-evidenced extinction chronology for Alaska/Yukon does not coincide with the onset of the Younger Dryas (see below).

2.6. Solar flare hypothesis

Another dramatic hypothesis postulates that *ca.* 12.8 cal ka a massive increase in radiation from a solar flare caused global mass extinctions (LaViolette, 2011). This idea can be refuted easily because the extinctions were demonstrably not synchronous on a global scale, as would have been expected from such a catastrophic event. Moreover, if the radiation dose were sufficiently high to wipe out mammoths and other megafauna, then many other terrestrial species and humans would also have been seriously affected, which clearly did not happen (Van der Plicht and Jull, 2011).

3. NORTHERN EURASIA (PALAEARCTIC ECOREGION)

During the Last Glacial, especially around the Last Glacial Maximum (LGM), an ice sheet covered a large area of north-western Eurasia, and there was also extensive glaciation of the Alps and other mountain areas (Ehlers and Gibbard, 2004a). Broadly speaking, for much of the Last Glacial, areas today covered by tundra or boreal, temperate and mixed forest supported herb-dominated steppe-tundra vegetation (so-called 'mammoth steppe'), while reduced areas of forest persisted in southern refugia (Allen *et al.*, 2010).

Northern Eurasia (the largest ecoregion) is an especially fruitful region for the study of Late Quaternary extinctions, not only because of the wealth of available archaeological, palaeontological and environmental data, but also because it has by far the largest number of available radiocarbon dates made directly on megafaunal remains. These have made it possible to construct detailed chronologies for most of the extinct species and also many of the survivors (Sulerzhitsky and Romanenko, 1997; MacPhee *et al.*, 2002; Stuart *et al.*, 2002, 2004; Stuart and Lister, 2007, 2011, 2012, 2014; Lister and Stuart, 2008; Pacher and Stuart, 2009; Nikolskiy *et al.*, 2011).

The importance of megafaunal extinctions in this region has been downplayed by some authors as fewer species disappeared here compared with, for example, North America. However, losses in northern Eurasia were substantial. In the areas for which we have good information (Europe, Russian Federation, Kazakhstan, Mongolia, northern China and Japan), approximately 18 mammalian species including *Homo neanderthalensis* (19 if Denisovans are regarded as a distinct hominin species, see below) out of a total of 49 with body weights greater than 45 kg disappeared, that is about 37%. Moreover, as elsewhere, the largest animals were most affected, so that three species of elephant, two rhinos (all exceeding 2 t) and most other large mammals weighing over 500 kg disappeared (Fig. 1).

The inferred extinction dates for northern Eurasia megafaunal species fall into four broad chronological phases: (1) early Last Glacial, pre-40 ka; (2) close to the onset of the LGM; (3) Late Glacial and Early Holocene; and (4) Late Holocene. The youngest direct radiocarbon dates are listed in Stuart and Lister (2012, table 2).

3.1. Early Last Glacial (*ca.* 117–40 ka)

This first wave of extinctions occurred mostly beyond the range of radiocarbon dating and, moreover, has received relatively little attention, so that the existing chronology is very approximate. During the Last Interglacial (*ca.* 130–117 ka), the range of *Hippopotamus amphibius* (hippopotamus) extended from Africa as far north as Britain (Stuart, 1982), from which the fossil remains are significantly larger than those of modern African animals. Hippos were probably also present at this time in parts of southern Europe, France and the Rhine Valley (Stuart, 1991; Van Kolfschoten, 2000; Stuart and Lister, 2007), although there is uncertainty because some putative Last Interglacial finds may be early Middle Pleistocene or older (van Kolfschoten, 2000). Intolerant of cold, hippopotamus was probably extirpated from mainland Europe at the beginning of the Last Glacial and did not return in the Holocene. However, (dwarf) hippos probably survived much later on some Mediterranean islands, notably Cyprus (Simmons, 1999). Moreover, hippos were present in the Holocene in North Africa (Mauritania, Algeria and Egypt), surviving until the early 1800s in Egypt (Manlius, 2000).

Palaeoloxodon antiquus (straight-tusked elephant) was widespread in Europe in the Last Interglacial period (Eemian) in association with regional temperate and Mediterranean forests but may have retreated south of the Pyrenees and Alps in response to cooler temperatures and the spread of open vegetation in the early part of the Last Glacial (Stuart, 2005). There is some indication that it survived in Iberia to *ca.* 70–50 ka (Stuart, 2005; Stuart and Lister, 2007). However, two radiocarbon dates in the range *ca.* 37–40 ka were obtained on unstratified *P. antiquus* molars from the Netherlands and North Sea (Bosscha Erdbrink *et al.*, 2001; Mol *et al.*, 2007), which suggest much later survival of this species in north-west Europe. In view of the potential importance of these records, it is desirable to attempt to corroborate them by independent dating of the same specimens and/or of additional material. *Stephanorhinus hemitoechus* (narrow-nosed rhino) was also widespread during the Last Interglacial and apparently survived into the early part of the Last Glacial in southern Europe, to perhaps *ca.* 45 ka (Stuart and Lister, 2007).

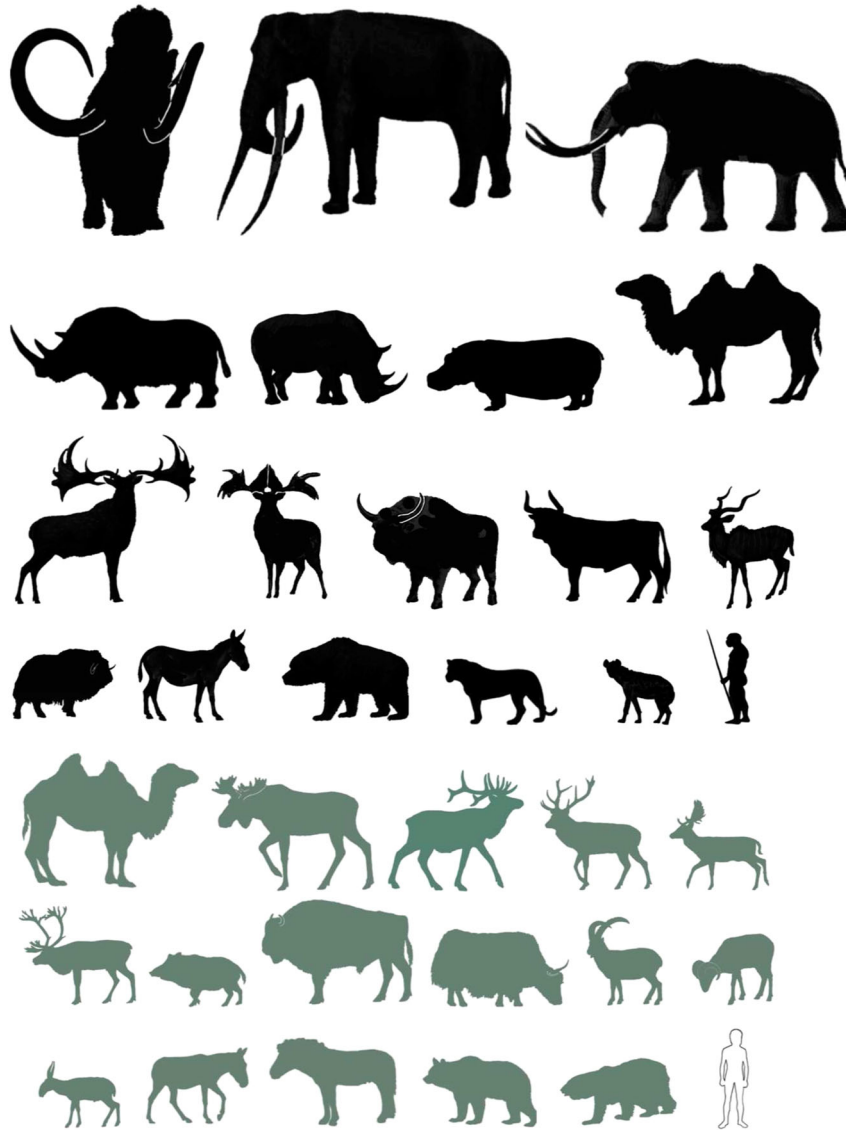


Figure 1. Northern Eurasia (Palearctic Ecoregion). Selected extinct species (black): *Mammuthus primigenius*^H, *Palaeoloxodon antiquus*, *Palaeoloxodon naumanni*, *Coelodonta antiquitatis*, *Stephanorhinus hemitoechus*, *Hippopotamus amphibius*^{*}, *Camelus knoblochi*, *Megaloceros giganteus*^H, *Sinomegaceros yabei*, *Bison priscus*, *Bos primigenius*^H, *Spiroceros kiakhtensis*, *Ovibos moschatus*^H, *Equus hydruntinus*^H, *Ursus spelaeus*, *Panthera spelaea*, *Crocota crocuta*^{*}, *Homo neanderthalensis*. Selected living species: *Camelus bactrianus*, *Alces alces*, *Cervus canadensis*, *Cervus elaphus*, *Dama dama*, *Rangifer tarandus*, *Sus scrofa*, *Bison bonasus*, *Bos mutus*, *Capra ibex*, *Ovis canadensis*, *Saiga tatarica*, *Equus hemionus*, *Equus ferus*, *Ursus arctos*, *Ursus maritimus*. Outline *Homo sapiens* gives approximate scale. ^{*}Extirpated in Last Glacial, ^Hextirpated in Holocene, ^Hextinct in Holocene. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

3.2. Extinctions close to the onset of the LGM (ca. 30–27 ka)

The extinction of cave bear *Ursus spelaeus* and related species occurred at around 27.5 ka, near to the onset of the LGM (Pacher and Stuart, 2009; Stiller *et al.*, 2014). Assuming that cave bears were predominantly vegetarian, their demise can be reasonably attributed to decreased temperatures and concomitant deterioration in vegetational quality and productivity. The contrasting survival to the present day of the brown bear *Ursus arctos* could well be related to its less restricted omnivorous diet.

Recent research on the mitochondrial DNA of cave bears has revealed marked genetic diversity (Stiller *et al.*, 2014), presumably reflecting their fragmented geographical distribution and complex migrational history. *Ursus kudarensis* was a distinct species restricted to the Caucasus. *Ursus spelaeus* (including subspecies) is known only from Western Europe, whereas the genetically distinct *Ursus ingressus* (perhaps also of specific status) had a more easterly distribution, including the Balkans and Urals. There was a narrow band of overlap with *U. spelaeus* in Central Europe.

Crocota crocuta (spotted hyaena), which still occurs in sub-Saharan Africa today, seems to have been extirpated from northern Eurasia at a broadly similar time. It probably disappeared from most of its range about 40 ka but persisted until ca. 31 ka in the south and west of Europe (Stuart and Lister, 2014). This pattern suggests that the main drivers were decreasing temperatures, and probably also decreased availability of prey and scavenging opportunities. Other species, such as *Panthera spelaea* (cave lion) (Stuart and Lister, 2011) and *Megaloceros giganteus* (giant deer) (Stuart *et al.*, 2004), withdrew from Europe during the LGM but survived farther east. A short series of direct dates on *Palaeoloxodon naumanni* (Naumann's elephant) from Japan terminates at around 28 ka (Takahashi *et al.*, 2006; Iwase *et al.*, 2012), so perhaps this species also disappeared at around the onset of the LGM.

Calibrated dates of ca. 32 ka on a mandible of *Homotherium latidens* (a sabretooth cat) dredged from the bed of the North Sea (Reumer *et al.*, 2003) are potentially very significant as otherwise all the youngest sabretooth records from Europe are of Middle Pleistocene age. However, as this record appears anomalous, the two radiocarbon dates on this find need to be corroborated either by independent dating of the same specimen by another laboratory or by the discovery and dating of further material.

The timing of and causes of *Homo neanderthalensis* extinction have been much debated. A recent paper by Wood *et al.* (2013) concluded that Neanderthals had gone from western Europe ca. 40 ka. The latest and most comprehensive study, using improved AMS dating of key sites covering the Middle to Upper Palaeolithic transition (Higham *et al.*, 2014), indicates that Neanderthals disappeared from different areas at different times but had gone from all of Europe ca. 41–39.3 ka. The related Denisovans are known only from very sparse material found in a single cave in southern Siberia (Reich *et al.*, 2010), and their extinction chronology is unknown. The earliest anatomically modern humans in Europe may be represented by the Uluzzian technocomplex in Italy and the Balkans, dating between 45 and 43 ka, indicating that there was an overlap of several millennia between Neanderthals and modern humans, which would have allowed ample time for cultural exchanges between a mosaic of populations. Recent studies, which demonstrate that a small amount of Neanderthal DNA is present in the genome of modern non-African humans, indicate that some interbreeding occurred between the two species (Sankararaman *et al.*, 2014), probably between 50 and 60 ka in Asia. These recent findings suggest that the final disappearance of Neanderthals might relate to the onset of Greenland Stadial 9 (GS 9, ca. 40 ka) but clearly occurred well before the extinction of *Crocota crocuta* and *Ursus spelaeus* at around the onset of Greenland Stadial 3 (GS 3, ca. 28 ka) (see above). It seems likely that Neanderthals

gradually succumbed to competition from modern humans, possibly in combination with climatic deterioration.

3.3. Late Glacial and Early Holocene extinctions (ca. 15–4 ka)

Both *Coelodonta antiquitatis* (woolly rhino) (Stuart and Lister, 2012) and *Panthera spelaea* (cave lion) (Stuart and Lister, 2011) went extinct during the Late Glacial at about 14 ka, probably as a result of the replacement of vast areas of open herb-dominated vegetation ('mammoth steppe') by shrubs and trees from ca. 14.7 ka, in response to increased temperatures. In the case of the cave lion, there was possibly a concomitant reduction in the abundance of available prey. The range of *Mammuthus primigenius* (woolly mammoth) was also drastically reduced at this time, but it survived into the Early Holocene in restricted areas of northern Siberia; until ca. 11.1 ka in Taimyr and to ca. 10.7 ka in the New Siberian Islands (then connected to the mainland) (Nikolskiy *et al.*, 2011). Research led by Sergey Vartanyan (Vartanyan *et al.*, 1993, 1995; Long *et al.*, 1994), based on a large number of radiocarbon dates from several laboratories, sensationally demonstrated that woolly mammoths had survived on Wrangel Island, off north-eastern Siberia, to ca. 4.0 ka (contemporary with early Egyptian civilization). However, attempts to find such late records from mainland Siberia have been unsuccessful so far (Vartanyan, 2013). There are rather few available dates for the northern Eurasia species *Bison priscus* ('steppe bison'), but it evidently survived into the Late Glacial in Siberia and European Russia and to the early Holocene (ca. 9.8 ka) in Taimyr (MacPhee *et al.*, 2002) and western Chukotka (ca. 8.9 ka; Kirillova *et al.*, 2013). Another Holocene survivor, *Megaloceros giganteus* (giant deer, or so-called 'Irish elk'), disappeared from Western Europe within the early part of the Younger Dryas cold phase, ca. 12.4 to 12.8 ka, and previously was thought to have gone extinct at that time. However, research in the last few years has revealed that it persisted until at least 7.7 ka in western Siberia and European Russia (Stuart *et al.*, 2004).

3.4. Extinctions ca. 4 ka to present

Ovibos moschatus (musk ox), now restricted to Arctic North America and Greenland, survived until at least 3 ka in the tundra of northern Siberia (Taimyr) (Campos *et al.*, 2010a). In the Late Pleistocene (based on associated dates), *Equus hydruntinus* ('European ass'), although rare, was widespread across western Eurasia, but during the Holocene, its distribution became highly fragmented and restricted to southern Europe and south-west Asia, with the latest record estimated at approximately 3 ka from the Caucasus (Crees and Turvey, 2014). These authors suggest that its extinction was primarily due to climate-driven reduction of open

habitats and vulnerability of fragmented populations to human exploitation.

Other species have disappeared within the last few hundred years, almost certainly because of hunting by humans. The last recorded individual of *Bos primigenius* (aurochs), the wild ancestor of domestic cattle, died in 1627 in Jaktorów Forest, Poland. *Panthera leo* (lion) had probably disappeared from its foothold in South-eastern Europe by around 2000 years ago, although it was still present to within the last 200 years in the Middle East and North Africa (Sommer and Benecke, 2006). *Panthera pardus* (leopard) was extirpated from Southern and Central Europe during the Holocene (Sommer and Benecke, 2006, fig. 5) but survives to the present day within northern Eurasia in North-east China and North Korea. It also occurs widely in Africa and Southern Asia.

3.5. Other extinctions

In addition to those with good radiocarbon coverage (discussed above), there are a few megafaunal species for which available information is inadequate to infer the time of extinction. These include *Camelus knoblochi* (extinct camel) (Titov, 2008) and *Spiroceros kiakhtensis* (spiral-horned antelope), both from southern Siberia. A single metatarsal of *S. kiakhtensis* from the Baikal region gave a date of ca. 37 ka (Stuart and Lister, 2012, table 2), consistent with the stratigraphy (Shchetnikov *et al.*, 2012), which strongly suggests that the extinction of this species occurred in the Late Quaternary. Of the few available dates on the giant deer *Sinomegaceros yabei*, known from China and Japan, the youngest reported date (Japan) is ca. 44.6 ka (material not stated) (Iwase *et al.*, 2012).

3.6. Survivors

The larger surviving mammals of the region include (Fig. 1) *Ursus maritimus* (polar bear), *Ursus arctos* (brown bear), *Panthera tigris* (tiger), *Panthera pardus* (leopard), *Equus ferus* (Przewalski's horse), *Equus hemionus* (onager), *Sus scrofa* (wild boar), *Alces alces* (Eurasia elk or moose), *Cervus elaphus* (red deer) (western Eurasia), *Cervus canadensis* (wapiti) (north-eastern Eurasia and North America), *Cervus nippon* (sika deer), *Dama dama* (fallow deer), *Rangifer tarandus* (reindeer or caribou), *Saiga tatarica* (saiga antelope), *Ovis canadensis* (bighorn sheep), *Capra pyrenaica* (Spanish ibex), *Bison bonasus* (European bison), Bactrian camel (*Camelus ferus*) and *Bos mutus* (yak). The 2011 Red List of Threatened Species of the International Union for Conservation of Nature (IUCN) classifies the saiga and Bactrian camel as 'critically endangered' and tiger, Przewalski's horse and onager as 'endangered'.

3.7. Extinction patterns in northern Eurasia

The pattern of northern Eurasia extinctions, summarized in Figure 2, is conspicuously staggered over many millennia (Stuart, 1991; Stuart and Lister, 2007), contrasting with North America where most extinctions seem to have occurred in the Late Glacial, perhaps within less than 1000 years (see below). In northern Eurasia, each megafaunal species exhibits a unique and complex pattern of distributional shifts, culminating in extinction for some species and survival in others. For example, comparing woolly mammoth with giant deer, Stuart *et al.* (2004) and Lister and Stuart (2008) noted their very different responses to environmental change, probably related to their different ecologies. Both, however, suffered range contraction during the LGM, followed by partial re-expansion, but eventually became restricted to smaller, but geographically very different, refugial areas, where they persisted for several millennia before disappearing completely. A third megaherbivore, the woolly rhinoceros, shows yet another pattern, with complex range shifts at various times, much less marked response to the LGM and a progressive contraction of range, with the last populations probably surviving in north-eastern Siberia prior to global extinction. So far, there is no evidence of longer-term refugial survival (Stuart and Lister, 2012). Modern humans seem to have arrived in Europe ca. 45 ka, from Africa via the Middle East, replacing the Neanderthals, who preceded them within a few thousand years (see above). However, by far, the majority of extinctions in northern Eurasia occurred many millennia after this event, thus precluding any rapid 'overkill' model. Significantly, there is no evidence whatsoever that the extinction of carnivores (*C. crocuta*, *Panthera spelaea*) followed on from the extinction of their herbivore prey. There is abundant evidence that climatic and vegetational changes had major impacts on the ranges of species, which would have increased their vulnerability to extinction. Moreover, the strongly differing timescales and geographical patterns of species' range contractions are more consistent with environmental drivers in relation to their differing ecologies than any obvious pattern of human expansion or exploitation. However, the possible role of humans in this process, especially in inhibiting natural range expansion of megafaunal species and in precipitating the extinction of terminal populations, has yet to be satisfactorily explored.

4. NORTH AMERICA (NEARCTIC ECOREGION)

During the Last Glacial period, North America had a rich and diverse large mammal fauna (Figs. 3 and 4). In part, this was a legacy of the 'Great American Biotic Interchange' in the Late Pliocene about three million years ago when, after

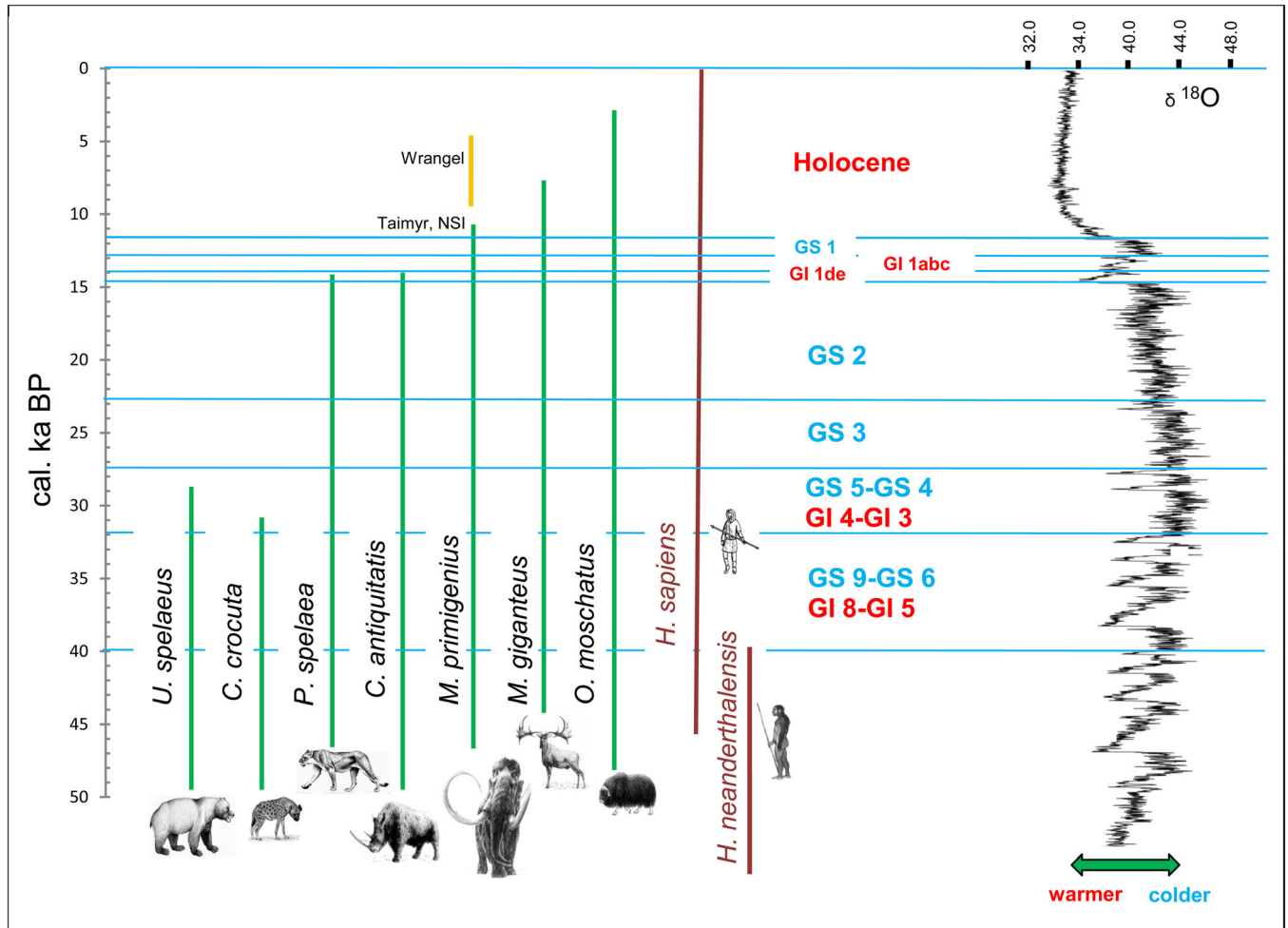


Figure 2. Summary extinctions chart for northern Eurasia. Green bars show the known time-span (from 50 ka) of a range of species with good radiocarbon dated records. *C. crocuta* survives today in Africa and *O. moschatus* in Greenland and the far north of Canada and Alaska; the other species are globally extinct. Time-ranges for Neanderthals. *Homo neanderthalensis* and modern humans *H. sapiens* are also shown. Greenland stadials and interstadials are indicated (NGRIP Dating Group, 2008); cold phases in blue, warm phases red. Latest survivals for woolly mammoth shown: NSI, New Siberian Islands, Wrangel, Wrangel Island. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

millions of years of isolation, North and South America became connected via the Isthmus of Panama (Marshall, 1988). This event allowed endemic South American animals such as ground sloths, glyptodonts and capybaras to colonize North America (and many North American animals to migrate in the opposite direction). Another factor was the lower rate of extinction throughout the earlier Pleistocene, compared with northern Eurasia, so that by the Late Quaternary, there were many more megafaunal species in total (Stuart, 1991). The extent of the Late Quaternary extinctions was correspondingly great. Out of about 54 species with a body weight greater than 45 kg, around 37 went extinct, or about 69%. Remarkably, all species of horse in both North and South America died out in the Late Pleistocene, whereas they survived into the Holocene in northern Eurasia. Even more remarkably, horses—descended from domesticated

animals introduced by the Spanish in the 16th century—subsequently thrived as feral populations (mustangs) in large areas of North America.

During the Last Glacial, North America experienced rather similar climatic and vegetational changes to those of northern Eurasia, with the important difference that during the LGM, the ice sheet was much more extensive in the former. This vast ice sheet covered most of the northern half of the continent but left the interior of Alaska and part of the Yukon ice free (Ehlers and Gibbard, 2004b). For many millennia, this ice sheet prevented most biotic interchange between Alaska/Yukon and what is now the contiguous United States. However, in the Late Glacial, a corridor opened between the western Cordilleran and eastern Laurentide ice sheets, allowing animals and humans to migrate in both directions. Analyses of 700 pollen records from northern and eastern North America show a complex

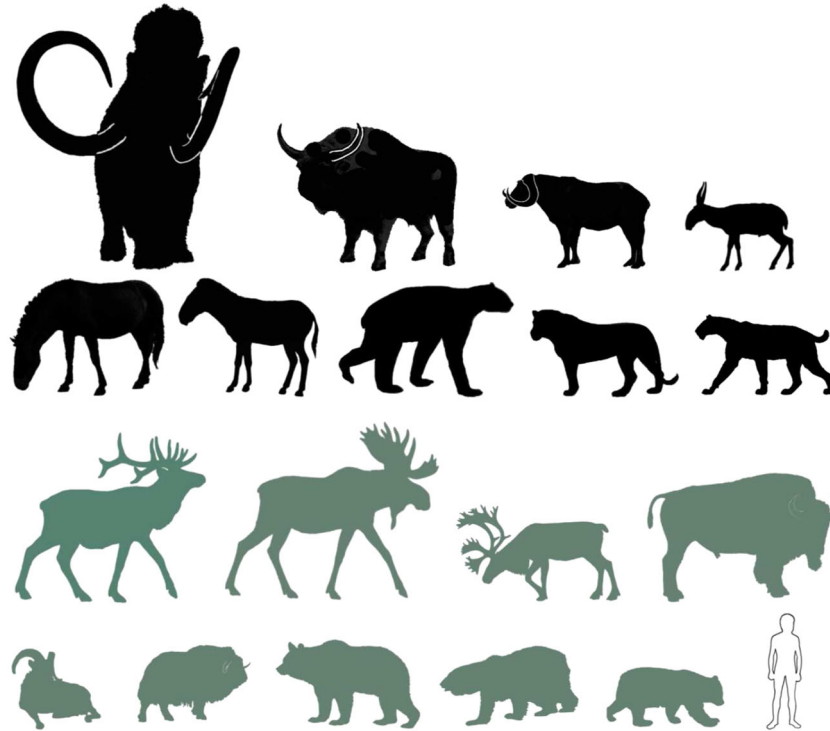


Figure 3. Alaska/Yukon (Nearctic Ecoregion). Selected extinct species (black): *Mammuthus primigenius*, *Bison priscus*, *Bootherium bombifrons*, *Saiga tatarica*^{*}, *Equus* sp. (caballine horse), *Equus* sp. ('hemion-like' ass), *Arcodus simus*, *Panthera spelaea*, *Homotherium serum*. Selected living species: *Cervus canadensis*, *Alces alces*, *Rangifer tarandus*, *Bison bison*, *Ovis dalli*, *Ovibos moschatus*, *Ursus arctos*, *Ursus maritimus*, *Ursus americanus*. Outline *Homo sapiens* gives approximate scale. ^{*}Extirpated in Last Glacial. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

vegetational history (Williams *et al.*, 2004), although this paper details the difficulties and inherent inaccuracies in reconstructing biomes. Vegetational conditions were relatively stable during the LGM 21–17 ka, changed rapidly during the Late Glacial (16–11.5 ka) and Early Holocene (11.5–8 ka) and thereafter showed little change until 0.5 ka. The extensive spread of taiga after *ca.* 12 ka as the ice sheets retreated is striking.

Humans did not reach the Americas until late in the Pleistocene, almost certainly entering Alaska from north-eastern Siberia. There is archaeological evidence for humans in Alaska *ca.* 13.5 ka, and initial colonization may have occurred *ca.* 14 ka (Potter, 2008), although, until the opening of the ice-free corridor, they may have been unable to migrate southwards to the present contiguous United States. However, some authorities suggest that people could have found an earlier route, presumably using boats, along the islands of the Pacific coast following deglaciation of this area at *ca.* 15 ka (e.g. Goebel *et al.*, 2008). The Monte Verde site in South America argues for human colonization before the opening of the ice-free corridor (see below). There is abundant evidence for rather later human presence in North America south of the ice sheets in the form of distinctive Clovis fluted stone projectile points that occur across much of the United States. The age

(associated dates) of the Clovis culture at a number of sites has been estimated by Waters and Stafford (2007) to range from *ca.* 13.2 to 12.8 ka, but this 'window' may be too narrow (Meltzer, 2010). The timing of human arrival in the southern half of North America is much debated. However, to put it into perspective, the arguments only concern whether or not people arrived a few thousand years earlier than the Clovis culture, as is suggested by a few plausibly older sites (Meltzer, 2010). For example, at Buttermilk Creek, Texas, numerous stone artefacts have associated dates from 13.2 to 15.5 ka and underlie a Clovis level dated at *ca.* 12.8 to 13.1 ka (Waters *et al.*, 2011).

4.1. Alaska/Yukon

Because for much of the Last Glacial Alaska/Yukon (eastern Beringia) was isolated from the rest of North America by ice sheets, it can be treated as a separate entity. There are many available radiocarbon dates made directly on megafauna from this region so providing good chronologies for several species (Harrington, 2003; Guthrie, 2004, 2006; Shapiro *et al.*, 2004; Fox-Dobbs *et al.*, 2008; Campos *et al.*, 2010b; Stuart and Lister, 2011; Mann *et al.*, 2013). These indicate that *Equus* species (caballine horses) survived in this

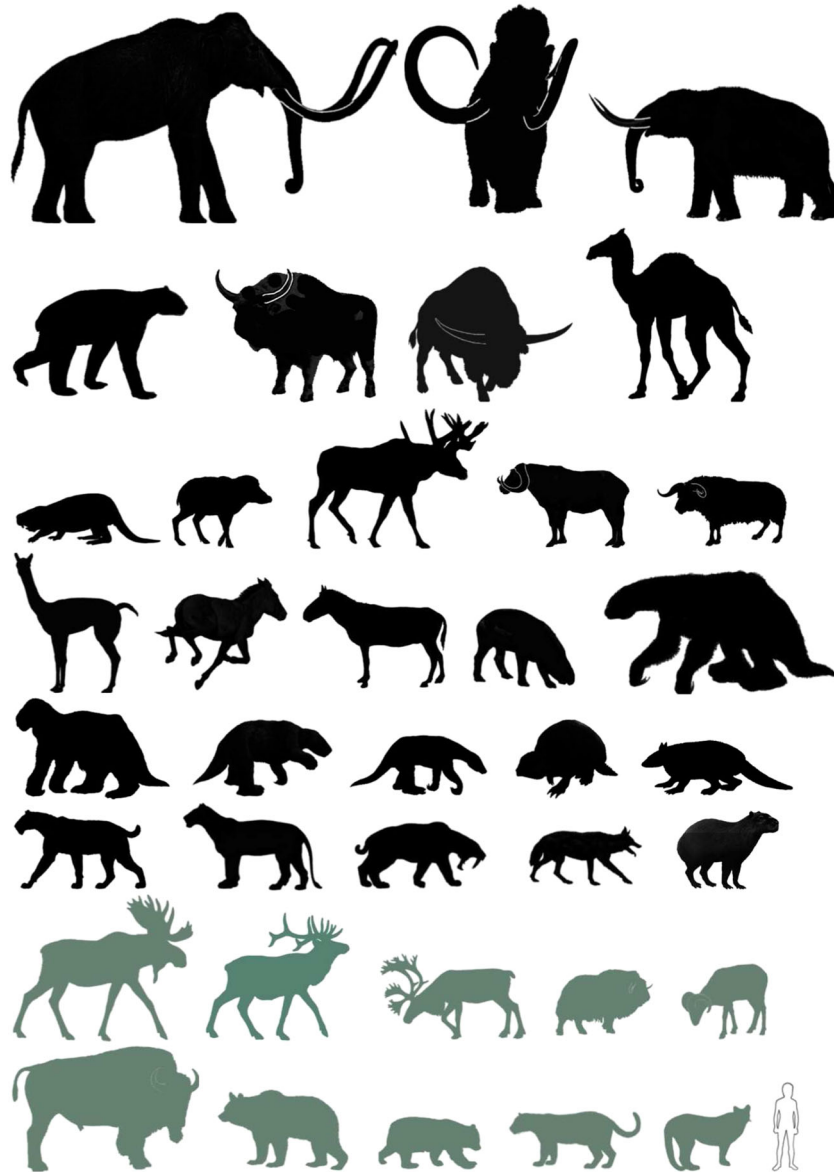


Figure 4. North America, south of 60° latitude (Nearctic Ecoregion). Selected extinct species (black): *Mammuthus columbi*, *Mammuthus primigenius*, *Mammuthus americanus*, *Arctodus simus*, *Bison priscus*, *Bison latifrons*, *Camelops hesternus*, *Castoroides ohioensis*, *Platygonus compressus*, *Cervalces scotti*, *Bootherium bombifrons*, *Euceratherium collinum*, *Hemiauchenia macrocephala*, *Equus occidentalis*, *Equus scotti*, *Tapirus veroensis*, *Eremotherium laurillardii* (*E. rusconi*), *Megalonyx jeffersonii*, *Paramylodon* (*Glossotherium*) *harlani*, *Nothrotheriops shastensis*, *Glyptotherium floridanum*, *Holmesina septentrionalis*, *Homotherium serum*, *Panthera atrox*, *Smilodon fatalis*, *Canis dirus*, *Neochoerus pinckneyi*. Selected living species: *Alces alces*, *Cervus canadensis*, *Rangifer tarandus*, *Ovibos moschatus*, *Ovis canadensis*, *Bison bison*, *Ursus arctos*, *Ursus americanus*, *Panthera onca*, *Puma concolor*. Outline *Homo sapiens* gives approximate scale. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

region until *ca.* 14.6 ka, *Mammuthus primigenius* (woolly mammoth) until 13.4 ka, *Panthera spelaea* (cave lion) until 13.3 ka and *Saiga tatarica* (saiga antelope) until 14.5 ka. Today, saiga is entirely absent from North America and occurs only in a limited area of northern Eurasia (mainly Kazakhstan). *Mammuthus primigenius* survived on St Paul Island in the Bering Sea until at least 6.5 ka (Guthrie, 2004; Veltre *et al.*, 2008), an interesting parallel to the Holocene survival of the same species on Wrangel Island.

A number of calibrated radiocarbon dates on *Arctodus simus* (short-faced bear) terminating at 40.1 ka, *Homotherium serum* (a sabretooth cat) at 24.7 ka and *Equus* sp. ('hemionelike' ass) at 35.7 ka together suggest that all three were extirpated from this region before the LGM (Guthrie, 2003; Fox-Dobbs *et al.*, 2008). These results are consistent with a staggered pattern of losses, much as seen in northern Eurasia (see above) and suggest that significant megafaunal disappearances occurred here well before the arrival of humans. There is

no evidence from this region for an extinction event *ca.* 12.9 ka as predicted by the impact hypothesis (see above).

In addition *Camelops hesternus* (western camel) is recorded from a Last Interglacial site in the Yukon (Zazula *et al.*, 2011), while finds of *Megalonyx jeffersonii* (Jefferson's ground sloth), *Mammuthus americanum* (American mastodon) and *Castoroides ohioensis* (giant beaver) are probably also of Last Interglacial age (Harrington, 2011; Mann *et al.*, 2013). It is likely that the warmer climate of this period allowed these species to extend their ranges much further northwards. Presumably, they were subsequently extirpated from this region because of deteriorating climate.

4.2. Canada south of 60° latitude, contiguous United States and northern Mexico

The scale of megafaunal extinctions in North America is very impressive with the disappearance of around 35 genera in the Late Pleistocene (Steadman *et al.*, 2005; Faith and Surovell, 2009; Haynes, 2009, 2013). Direct evidence of predation by humans is available in a few cases, where megafaunal remains (Columbian mammoth, mastodon) occur in direct association with Clovis spear points (e.g. Haury, 1953; Haury *et al.*, 1959; Graham *et al.*, 1981; Haynes and Haury, 1982). Remains of two gomphotheres (*Cuvieronius* sp.) accompanied by Clovis points and flakes (with associated dates on charcoal of *ca.* 13.4 ka) have been described recently from a site in Sonora, Mexico (Sanchez *et al.*, 2014).

Compilations by Haynes (2013) and Fiedel (2009) summarize youngest dates (direct and context dates) for a range of species. Those with youngest (calibrated) dates before *ca.* 24 ka, that is, falling before the LGM, include *Eremotherium rusconii* (*E. laurillardii*) (a ground sloth), *Glyptotherium floridanum* (a glyptodont), *Holmesina septentrionalis* ('giant armadillo') and *Paramylodon (Glossotherium) harlani* (Harlan's ground sloth). *Miracinonyx trumani* (American cheetah) and *Homotherium serum* (a sabretooth) have youngest dates in the range 17–18 ka. The recently published ultrafiltered radiocarbon dates from Rancho La Brea, California, include a date of *ca.* 17.4 ka on *Canis dirus* (dire wolf) (Fuller *et al.*, 2014).

Most have youngest dates in the range 11.5 to 15 ka, including *Panthera atrox* (American lion), *Arctodus simus* (short-faced bear), *Megalonyx jeffersonii* (Jefferson's ground sloth), *Mammuthus columbi* (Columbian mammoth), *Mammuthus primigenius* (woolly mammoth), *Mammuthus americanum* (mastodon), *Equus* spp. (horses), *Platygonus compressus* and *Mylohyus nasutus* (extinct peccaries), *Palaeolama mirifica* (extinct lama), *Hemiauchenia macrocephala* (large-headed lama), *Cervalces scotti* (extinct moose), *Bootherium bombifrons* (Harlan's musk ox), *Navahoceros fricki* (American mountain deer), *Stockoceros*

onusrosagris (a pronghorn), *Camelops hesternus* (western camel) and *Castoroides ohioensis* (giant beaver). In addition, the ultrafiltered radiocarbon dates from Rancho La Brea include an averaged date of *ca.* 13.7 ka for *Smilodon fatalis* (a sabretooth) (Fuller *et al.*, 2014). For date lists on *Nothrotheriops shastensis* (Shasta ground sloth), see Steadman *et al.* (2005, table 1), and *Oreamnos harringtoni* (extinct mountain goat), see Mead *et al.*, 1986). Several dates in the range 11.5 to 15 ka, notably on *H. macrocephala*, *C. hesternus*, *N. shastensis*, *S. onusrosagris*, *N. fricki* and *O. harringtoni*, were done more than 25 years ago and have very large standard errors; therefore, re-dating would be very desirable.

An extinct giant tortoise, *Geochelone crassiscutata*, is recorded from the Last Interglacial (Sangamonian) of North America as far north as Illinois (King and Saunders, 1986), indicating a climate significantly warmer than today, and presumably disappeared in the face of decreasing temperatures in the Last Glacial. The history of this southern thermophile invites comparison with *Hippopotamus* in Europe (see above). Other extinctions in the Late Pleistocene of North America, although lacking reliable dating evidence, include *Tapirus veroensis* (a tapir), *Hydrochoerus holmesina* and *Neochoerus pinckneyi* (capybaras).

Taken at face value, these data could be interpreted in two radically different ways.

- Most or all megafauna went extinct within a very short time, around 12.5 to 13.5 ka, or perhaps a much shorter period within that time span, as advocated by Faith and Surovell (2009; see below), and that more dating work would show that most or all apparent earlier extinctions (with few dates) are an artefact of inadequate sampling.
- The observed pattern of extinctions in two or more phases, pre-LGM and Late Glacial, is real, much as in northern Eurasia. The second interpretation would imply that the earlier extinctions most likely occurred before the arrival of humans and, therefore, probably resulted from environmental changes.

A series of eight additional dates made directly on *Arctodus simus* material were published by Schubert (2010). The youngest (calibrated) are *ca.* 12.8 ka (Kansas) and *ca.* 12.7 ka (Texas), indicating that the short-faced bear co-existed with humans of the Clovis culture and that it was one of the last megafaunal species to go extinct in North America.

Faith and Surovell (2009) interpreted the available Late Pleistocene North American record of extinctions as a sudden event. They recognized the last appearance dates of 16 of 35 genera of mammals as securely falling between *ca.* 13.8 and 11.4 ka (12 000 to 10 000 radiocarbon years BP). Although the latest dates on the other 19

genera could indicate that they disappeared earlier, they believe that this is an artefact of sampling ('Signor-Lipps effect') and that the evidence is consistent with 'an extinction mechanism that is capable of wiping out up to 35 genera across a continent in a geologic instant' and 'North American Late Pleistocene extinctions are best characterized as a synchronous event, [a] sudden surge in extinction rates consistent with overkill or extra-terrestrial impact' (Faith and Surovell, 2009, p. 20641).

I would argue that the dates available at present from North America outside Alaska/Yukon are inadequate, not only in number but in many cases also in quality, for constructing a reliable chronology. There is an overwhelming need for an extensive programme of direct radiocarbon dating of a wide range of North American megafaunal species. Only then will we have a sound basis for solving the problem of cause or causes of megafaunal extinctions in this region. On rather similar lines, Grayson (2007) argued that the continuing debate over the causes of North American losses is not likely to be resolved unless the history of each species is analysed individually, as is being done for Europe and northern Asia. 'Recent advances in understanding Eurasia extinctions provide a research guide for extracting ourselves from the explanatory morass that now characterizes the North American situation' (Grayson, 2007, p. 185).

4.3. *Sporormiella*

Additional evidence is provided by studies of the changing abundance of a dung fungus *Sporormiella* in lake sediments (Davis and Shafer, 2005; Gill *et al.*, 2009; Gill, 2014). Marked declines in the abundance of *Sporormiella* at Appleman Lake, Indiana, and several New York sites have been interpreted as reflecting a megafaunal decline at 14.8 to 13.7 ka, during the Bølling–Allerød warm period, before both the Younger Dryas cooling and the proposed extraterrestrial impact event at 12.9 ka (Gill *et al.*, 2009). This inferred decline in megafaunal populations occurred a few millennia before their final extinction and closely preceded enhanced fire regimes and the development of plant communities with no modern analogues.

4.4. *Survivors*

The larger surviving mammals of the region include (Figs. 3 and 4) *Ursus maritimus* (polar bear), *Ursus arctos* (grizzly or brown bear), *Ursus americanus* (black bear), *Puma concolor* (mountain lion), *Panthera onca* (jaguar), *Antilocapra americana* (pronghorn), *Cervus canadensis* (wapiti or North American elk), *Rangifer tarandus* (caribou), *Odocoileus hemionus* (mule deer), *Odocoileus virginianus* (white-tailed deer), *Alces alces* (moose), *Ovibos*

moschatus (musk ox), *Ovis canadensis* (bighorn sheep), *Ovis dalli* (Dall sheep), *Oreamnos americanus* (mountain goat) and *Bison bison* (American bison). None of these is listed as endangered in the IUCN Red List. However, the American bison was brought close to extinction during the 19th century as a result of indiscriminate and commercial hunting, but the species' numbers have now substantially increased following active conservation efforts.

5. SOUTH AMERICA (NEOTROPIC ECOREGION)

In the Late Pleistocene, South America exhibited a rich and varied fauna (Fig. 5), resulting from the admixture of (what appears to us) bizarre endemic animals that had evolved during millions of years when it was an isolated island continent and the immigration of North American forms from the Late Pliocene onwards. As recognized by Martin (1984), Late Quaternary megafaunal extinction in South America appears to have been more extensive than on any other continent. Taxonomic uncertainties for the extinct species preclude an accurate estimate of losses, but at a generic level, approximately 80% became extinct. Interestingly, as in North America, all species of horse disappeared. The severity of the extinctions is strikingly illustrated by the fact that today the largest native South American mammals are Baird's tapir (*Tapirus bairdii*) and the lowland tapir (*Tapirus terrestris*), which average only about 350 and 250 kg, respectively.

Unlike the northern continents, South America was not extensively glaciated in the Pleistocene, although there were mountain glaciers in the Andes (Ehlers and Gibbard, 2004c). However, the Last Glacial may have seen some expansion of open herb-dominated vegetation, no doubt well suited to grazing herbivores, at the expense of tropical forests (Haberle and Maslin, 1999; González *et al.*, 2008). An intriguing question is why South America had major extinctions whereas sub-Saharan Africa had very few (see below), when both have a broadly similar range of climate and vegetation at the present day (although in very different proportions). The answer might be related to the fact that most South American extinct megafauna is from the southern part of the continent, which extends considerably further south than Africa.

Although much good research has been done and is in progress, the number of dates available at present is inadequate for constructing a reliable chronology for extinctions. Undoubtedly, however, there is a very exciting and important story to be uncovered here. Fortunately, as most of the South American extinctions seem to have occurred within the range of radiocarbon dating, the prospects for future research are excellent. The brief account given here is based largely on Barnosky and Lindsey (2010), in which they

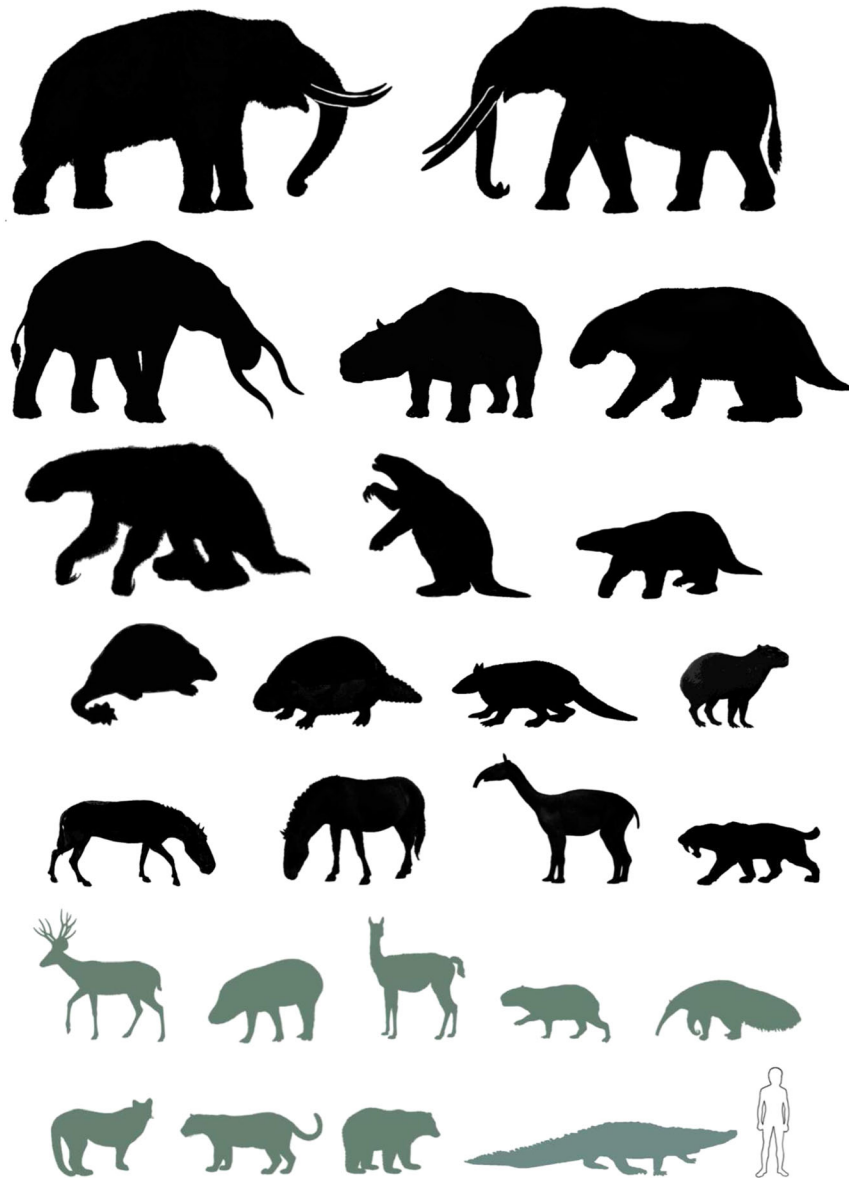


Figure 5. South America (Neotropic Ecoregion). Selected extinct species (black): *Haplomastodon waringi*, *Notiomastodon (Stegomastodon) platensis*, *Cuvieronius hyodon*, *Toxodon platensis*, *Megatherium americanum*, *Eremotherium laurillardi*, *Catonyx cuvieri*, *Mylodon darwini*, *Doedicurus clavicaudatus*, *Glyptodon clavipes*, *Holmesina septentrionalis*, *Neochoeerus pincneyi*, *Hippidion saldiasi*, *Equus* sp., *Macrauchenia patachonica*, *Smilodon populator*. Selected living species: *Blastoceros dichotomus*, *Tapirus baurdii*, *Lama guanicoe*, *Hydrochoerus hydrochaeris*, *Myrmecophaga tridactyla*, *Puma concolor*, *Panthera onca*, *Tremarctos ornatus*, *Crocodylus acutus*. Outline *Homo sapiens* gives approximate scale. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

evaluate the available radiocarbon dates on the megafauna and early human settlement of South America.

Most South American archaeological sites have dates *ca.* 13 ka or younger, yet there is one major site, Monte Verde in southern Chile, dated to *ca.* 14.8 ka (Dillehay and Collins, 1991; Dillehay, 1997; Meltzer, 2010). This site is widely recognized as the earliest archaeology in the Americas, significantly older than Clovis or even the oldest-known archaeology from Alaska, although some archaeologists remain unconvinced (e.g. Fiedel, 1999). Excluding the

highly unlikely possibility that Palaeolithic people somehow crossed the Atlantic from Africa or Europe or the Pacific from Asia, the only possible route for human entry is via North and Central America. The problem is how did people get so far south without leaving archaeological traces en route?

Barnosky and Lindsey (2010) listed 93 dates for 15 megafaunal genera. However, their compilation does not include dates for one of the most extraordinary endemic mammals, the litoptern *Macrauchenia* (which could be described as

resembling a humpless camel with a short trunk); possibly, it had disappeared earlier. At face value, the latest radiocarbon-dated occurrences fall into the following three groups:

- (a) Those dating from earlier than 18 ka—*Holmesina* (giant armadillo), *Glyptodon* (a glyptodont) and *Haplomastodon* (a mastodon)
- (b) Those dating from between 18 and 11 ka—*Cuvieronius* (a gomphothere mastodont), *Mylodon*, *Glossotherium*, *Nothrotherium* and *Eremotherium* (ground sloths), *Toxodon* (a notoungulate), and *Hippidion* and *Equus* (horses)
- (c) Those dating from between 11.5 and 8 ka—*Smilodon* (a sabretooth cat), *Megatherium* (giant ground sloth), *Catonyx* (a ground sloth) and *Doedicurus* (a glyptodont)

However, much further research is required to see whether there is any reality to this apparent chronological pattern. The intriguing possibility that *Doedicurus*, *Catonyx*, *Megatherium* and *Smilodon* survived into the Holocene, that is later than *ca.* 11.7 ka, may or may not be corroborated as more radiocarbon dates become available.

Since the above paper appeared, more megafaunal dates have been published. Dantas *et al.* (2013) listed radiocarbon dates made directly on megafaunal material from Brazil. Latest (UMAS laboratory, median calibrated) dates on *Eremotherium* are 18.75 and 19.0 ka, *Notiomastodon ca.* 17 ka and *Toxodon ca.* 11.6 and *ca.* 12.7 ka. Hubbe *et al.* (2013) presented direct megafaunal dates from South-eastern Brazil, the latest of which are *Catonyx ca.* 12.7 ka, *Toxodon ca.* 13.7 ka, *Eremotherium ca.* 14.9 ka and *Smilodon ca.* 17.8 ka.

It is evident that a substantial number of extinct South American megafaunal species survived into the Late Glacial and some possibly into the Early Holocene. However, in view of the unsatisfactory dating evidence, it is premature to attempt correlations with either environmental changes or human arrival in South America. Barnosky and Lindsey (2010) concluded, very reasonably, that 'These results highlight the need for future intensive dating efforts on South American megafauna and archaeological remains' (p. 10).

5.1. Survivors

The larger surviving mammals of the region include (Fig. 5) *Panthera onca* (jaguar), *Puma concolor* (mountain lion), *Tremarctos ornatus* (spectacled bear), *Tapirus bairdii* (Baird's tapir), *Tapirus terrestris* (lowland or Brazilian tapir), *Tapirus pinchaque* (mountain tapir), *Myrmecophaga tridactyla* (giant anteater), *Hydrochoerus hydrochaeris* (capybara), *Vicugna vicugna* (vicuña), *Lama guanicoe* (guanaco), *Blastocerus dichotomus* (marsh deer), *Hippocamelus antisensis* (taruca or North Andean deer), *Hippocamelus*

bisulcus (huemul or South Andean deer), *Crocodylus acutus* (American crocodile) and *Eunectes murinus* (anaconda). The IUCN Red List classifies mountain and Baird's tapirs as 'endangered'. Remarkably, the discovery of a 'new' tapir species *Tapirus kabomani*, the smallest of the genus (110 kg), was announced in 2013 (Cozzuol *et al.*, 2013). It is also listed as 'endangered'.

6. AUSTRALASIA (AUSTRALASIA ECOREGION)

Australia, Tasmania and New Guinea constituted a single land mass ('Sahul') at times of lowered sea levels during the Pleistocene. Unlike the northern continents, Australia was glaciated only to a very limited extent, but there were climatic fluctuations between more arid and wetter periods (Johnson, 2006). For example, at Lynch's Crater in Queensland (Rule *et al.*, 2012), tropical rain forest taxa predominate from *ca.* 130 to *ca.* 78 ka (broadly Last Interglacial), replaced by sclerophyll taxa with eucalypts and acacia from about 46–11 ka (Last Glacial), followed by re-establishment of rain forest taxa thereafter (Holocene).

The first humans (*Homo sapiens*—the ancestors of the modern aborigines) are estimated to have arrived, via South-east Asia, around 62 to 43 ka. Although sea levels were lower at this time, they would have needed boats to cross several intervening water gaps.

In the Late Quaternary, as today, the terrestrial mammalian faunas were dominated by marsupials (Fig. 6). There were also a few monotremes (egg-laying mammals unique to this continent in the Quaternary, although also present in South America in the Palaeocene), some endemic placental rodents and bats, and the dingo, which originated in South-east Asia and was introduced by human agency sometime before 3.5 ka, when it first appears in the archaeological record (Oskarsson *et al.*, 2012).

Johnson (2006) estimated that about 55 species of mammals were lost from Australia and New Guinea during the Late Pleistocene, of which around 40 were megafauna (i.e. 45 kg or more), and Webb (2008) listed a total of 29 mammals of 50 kg or more from the Late Pleistocene in Australia alone. Because of stratigraphic uncertainties and problems of direct dating, it is very difficult to be sure that all of the species that are supposed to have occurred in the Late Pleistocene actually did so. Moreover, several megafaunal species are imperfectly known as they are based only on fragmentary material.

Uniquely, in Australasia, most extinctions seem to have taken place close to or beyond the range of radiocarbon dating, so that other less precise methods of absolute dating have to be used. Establishing a robust chronology for extinctions is hampered at present because of these difficulties, but future improvements in dating techniques could radically

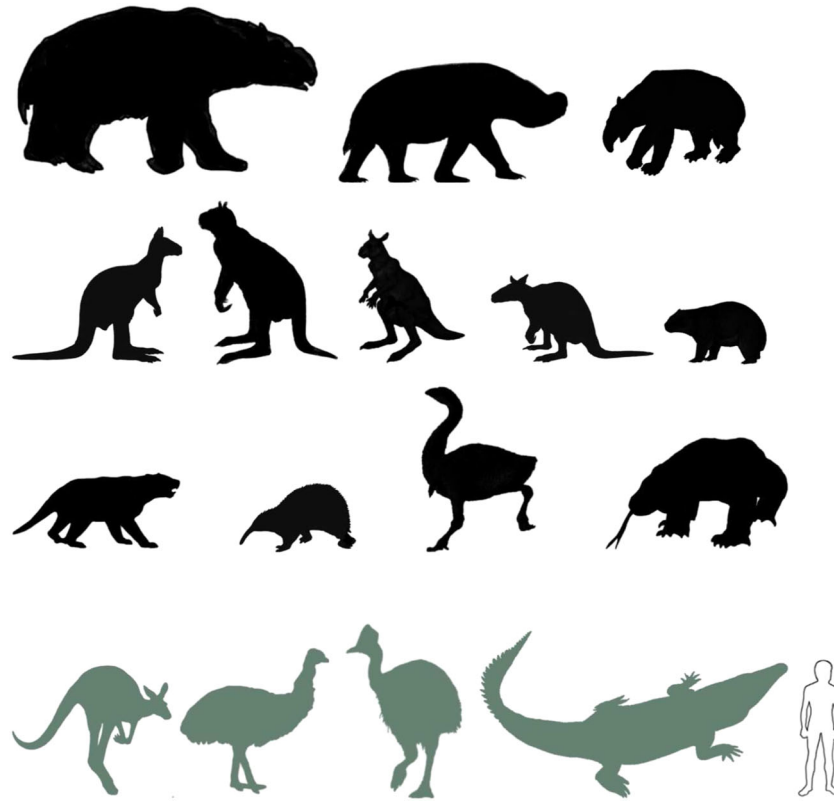


Figure 6. Australasia (Australasian Ecoregion). Selected extinct species (black): *Diprotodon optatum*, *Zygomaturus trilobus*, *Palorchestes azeal*, *Macropus ferragus*, *Procoptodon goliath*, *Sthenurus* sp., *Protemnodon brehus*, *Phascolonus gigas*, *Thylacoleo carnifex*, *Zaglossus hacketti*, *Genyornis newtoni*, *Varanus priscus* (*Megalania prisca*). Selected living species: *Macropus giganteus*, *Dromaius novaehollandiae*, *Casuarius casuarius*, *Crocodylus porosus*. Outline *Homo sapiens* gives approximate scale. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

change this situation. Nevertheless, it is very clear that Australia suffered spectacular extinction in the Late Pleistocene, with the loss of perhaps 91% of its mammalian megafaunal species.

As pointed out by several workers (e.g. Murray, 1991), a curious and unique characteristic of Australian Pleistocene mammal faunas, in comparison with those from other continents, was as a whole the size spectrum was shifted towards the smaller end. This phenomenon probably relates to the general environmental depletion in nutrients and the restricted area habitable by large mammals because of the extensive arid continental interior. The largest known Australian mammal of all time was the giant wombat-like *Diprotodon optatum*, of which some individuals probably weighed as much as 2 t (roughly comparable to a white rhinoceros or a hippopotamus), but there was no marsupial equivalent in size to an elephant or mastodon. Other large mammals related to *Diprotodon* were the cow-sized *Palorchestes azeal* ('marsupial tapir'), which had long claws and likely a moderately long trunk, and *Zygomaturus trilobus*, which probably had a smaller trunk. The extinct mammalian megafauna also included *Macropus ferragus* (a large kangaroo), *Phascolonus gigas* (giant wombat),

several species of *Sthenurus* and *Simosthenurus* (short-faced kangaroos), *Procoptodon goliath* (giant short-faced kangaroo), *Protemnodon* species (large wallaby-like kangaroos), *Thylacoleo carnifex* ('marsupial lion') and the monotreme *Zaglossus hacketti* (giant echidna) (Murray, 1984, 1991; Johnson, 2006).

Extinctions also occurred in some non-mammalian megafauna. The timing of the disappearance of a large (non-ratite) bird, the giant flightless goose *Genyornis newtoni*, has been extensively studied (see below). *Varanus priscus* (formerly *Megalania prisca*), a giant goanna or monitor lizard, is also thought to have gone extinct in the Late Pleistocene (Molnar, 1991). At perhaps 700 kg, much larger than its close living relative, the komodo dragon, it would have been a formidable predator, able to tackle even the largest marsupials. Additional possible Late Pleistocene reptilian extinctions include a giant snake *Wonambi naracoortensis*, perhaps 5 m long, and a terrestrial ziphodont crocodile *Quinkana fortirostrum* (Molnar, 1991; Wroe and Field, 2006).

Most authorities believe that all, or nearly all, of the extinct Australasian megafauna had gone by about 46 ka (e.g. Roberts *et al.*, 2001), which is much earlier than

in other regions. In Australia, as in North America, there is much lively, even fierce, debate between the proponents of 'overkill' (e.g. Miller *et al.*, 1999, 2005; Roberts *et al.*, 2001; Burney and Flannery, 2005; Johnson, 2005, 2006, 2009; Brook *et al.*, 2007; Turney *et al.*, 2008; Roberts and Brook, 2010; Rule *et al.*, 2012) and the advocates of climate change (e.g. Field and Fullager, 2001; Wroe and Field, 2006; Wroe *et al.*, 2006, 2013a, b; Field *et al.*, 2008; Webb, 2008, 2009; Price *et al.*, 2011; Field and Wroe, 2012). Proponents of the 'overkill' hypothesis discern a close correspondence in time between the arrival of humans and the demise of the megafauna and infer that the key factors in their extinction were predation and habitat modification (especially burning of vegetation) by humans. Rule *et al.* (2012) concluded from the high-resolution 130 000-year environmental record at Lynch's Crater, Queensland, that human arrival rather than climate caused megafaunal extinction. They interpret the replacement of mixed rainforest by sclerophyll vegetation as due to a combination of relaxed herbivore pressure and increased fire in the landscape (micro-charcoal), following on from megafaunal extinction, not climatic change. The dung fungus *Sporormiella* shows a sharp decline *ca.* 40 ka, interpreted as due to megafaunal loss, although three later peaks are attributed to surviving kangaroos and/or ratites. However, others argue that there is no good evidence for a correlation between human arrival and megafaunal loss and that extinctions were staggered over a much longer time frame and resulted from progressively increasing aridity (Wroe and Field, 2006; Wroe *et al.*, 2013a, b). This hypothesis receives some support from the record of wind-blown dust derived from interior South-eastern Australia in sediment cores from the Tasman Sea. Dust levels increased markedly at *ca.* 350 ka and were high in subsequent glacial periods (Hesse, 1994).

Wroe *et al.* (2013a, b) interpreted the rather patchy fossil record from Australia and New Guinea (Sahul) as indicating that most losses occurred long before human arrival. 'Mounting evidence points to the loss of most species before the peopling of Sahul (*circa* 50–45 ka)' (Wroe *et al.*, 2013a, p. 8781) and 'A paucity of empirical data; shortfalls in radiometric dating; and, until recently, a limited appreciation of the paleoenvironmental record have placed considerable constraints on the ability to resolve "who or what" was responsible for these extinctions' (Wroe *et al.*, 2013a, p. 8777). Moreover, Trueman *et al.* (2005), Field *et al.* (2008) and others claim that several sites have associated megafauna and archaeology, which if correct would rule out any sudden extinction event concomitant with human arrival. Cuddie Springs in New South Wales has provided probably the best case for the coexistence of extinct megafauna and humans in this continent. At this site, sediments

dated to 36 to 30 ka contain the remains of extinct megafauna and stone tools. The evidence has been much disputed, however (e.g. Brook *et al.*, 2013), as it has been suggested that material of various ages is mixed together, and ESR and Uranium Series dating by Grün *et al.* (2010) of tooth enamel from the site suggests a minimum age for the megafaunal remains of around 45 ka. Brook *et al.* (2013, p. E3368) take the view that 'The arguments of Wroe *et al.* for an extended overlap between late-persisting megafauna and humans after 40,000 y ago rest largely on secondary dating of sediments and charcoal from Cuddie Springs. However, they ignore recent direct dating of primary material (megafaunal remains) from this contentious site, which show the fossils to be more than 50,000 y old. Claims for late survival of megafauna at other sites, including Nombe and Seton Rockshelters, are also based on contested radiocarbon dates'.

One extinct species, the large flightless goose *Genyornis newtoni* ('mihirung'), was the subject of an extensive study by Miller *et al.* (1999) in which they dated 700 eggshell fragments by amino acid racemization and optically stimulated luminescence (OSL) dating of the enclosing sediment. The youngest dates obtained were about 50 ka, the inferred time of extinction. In marked contrast, a series of dates on *Dromaius novaehollandiae* (emu) shell fragments from the same sites continued through to the present day. Miller *et al.* (1999) suggest that the extinction of *Genyornis* and other Australian megafauna resulted from habitat modification resulting from the burning of vegetation by humans, although not surprisingly, this interpretation is disputed by Wroe and Field (2006).

As elsewhere, the debate hinges very largely on the timing of extinctions, but the quality of the available data appears to be wholly insufficient to construct a robust chronology; certainly not one that all can agree on. Price *et al.* (2011, p. 912) very reasonably conclude that 'It is increasingly clear that the "megafauna" did not act as a single biological unit as it has been traditionally applied, but rather, they responded independently to former changes in the environment. The results presented here highlight the extreme importance of constructing a robust spatially-constrained chronology for each individual megafaunal species that suffered extinction during the Pleistocene. Until those data become available, it will be difficult to constrain the timing and specific agent(s) involved in the continental extinction of Pleistocene megafauna'.

6.1. Survivors

The only surviving species (Fig. 6) that qualify as megafauna (i.e. greater than 45 kg weight) are *Macropus rufus* (red kangaroo) at 85 kg, the rather smaller *Macropus fuliginosus* and *Macropus giganteus* (western and eastern grey kangaroos), the flightless ratite *Dromaius novaehollandiae* (emu), which

averages only about 36 kg although some individuals reach 50 kg, and the somewhat larger *Casuarius casuarius* (southern cassowary) which can reach 58 kg (females). A large and formidable reptilian survivor is the saltwater or Indo-Pacific crocodile (*Crocodylus porosus*), of South-east Asia and northern Australasia. At 400–1000 kg male body weight, this is the largest extant species of reptile in the world. Although at home in both marine and freshwater habitats, it has a place amongst the megafauna as today it is an important predator on large terrestrial animals and presumably was also in the Pleistocene.

There have been several recent extinctions among the smaller marsupials (Webb, 2008, table 2), and the inexcusable fate of *Thylacinus cynocephalus* (Tasmanian wolf or Tasmanian tiger) is well known. Bounty hunters were actually paid by the Tasmanian government for dead 'tigers'. The last wild specimen is recorded as having been shot in 1932, and the last captive animal died in 1936 (Turvey, 2009b).

7. AFRICA (AFRO-TROPIC ECOREGION)

Here I consider just sub-Saharan Africa. North Africa is generally regarded as part of the Palearctic ecozone, although transitional between the two as it has shares some sub-Saharan elements. This is an important distinction, as taking the two regions together considerably inflates the number of extinct taxa, which for sub-Saharan Africa alone is very modest (Fig. 7). It is striking that in this region most of the exceptionally rich Late Pleistocene megafauna, including all of the largest species (e.g. elephants, rhinos, hippos, buffalo), survive to the present day.

Following on from Klein (1984, 1994), Steele (2007) and Faith (2014) have provided up-to-date information on estimated last occurrences for several extinct species in the Late Pleistocene or Holocene. Faith (2014, table 2) gives a useful table of associated dates (including records from North Africa). However, most of these dates have wide ranges, and none were made directly on megafaunal remains, so the existing dating evidence must be seen as unsatisfactory. Moreover, several of the taxa are known from only a few fragmentary finds, so it is not possible to construct a meaningful extinction chronology for the region. Given the uneven geographical coverage and the relative lack of research on Late Quaternary sites in Africa, it is very probable that more extinct taxa will be discovered in the future. However, even substantial new data are most unlikely to change the view that the impact of extinctions in sub-Saharan Africa was small compared with most other ecoregions.

Extinct species include *Syncerus antiquus* (giant long-horned buffalo), *Megalotragus priscus* (giant wildebeest/hartebeest),

Hippotragus leucophaeus (blue antelope) and *Equus capensis* (cape zebra). *Megalotragus priscus* may have persisted into the Holocene and *Equus capensis* to the Late Pleistocene (Faith, 2014), while *Hippotragus leucophaeus* disappeared as recently as 1800 AD (Klein, 1984). *Syncerus antiquus* is recorded from several Late Pleistocene sites in sub-Saharan Africa and from Holocene archaeological sites in North Africa (Klein, 1984; Steele, 2007; Faith, 2014).

7.1. Survivors

Surviving megafaunal species include (Fig. 7) *Loxodonta africana* (bush elephant), *Loxodonta cyclotis* (forest elephant), *Diceros bicornis* (black rhinoceros), *Ceratotherium simum* (white rhinoceros), *Hippopotamus amphibius* (hippopotamus), *Choeropsis liberiensis* (pigmy hippopotamus), *Giraffa camelopardalis* (giraffe), *Okapia johnstoni* (okapi), *Syncerus caffer* (cape buffalo), *Hylochoerus meinertzhageni* (giant forest hog), *Phacochoerus africanus* (common warthog), *Tragelaphus durbianus* (giant eland), *Alcelaphus buselaphus* (hartebeest), *Tragelaphus strepciseros* (greater kudu), *Tragelaphus angasi* (nyala), *Hippotragus equines* (roan antelope), *Connochaetes taurinus* (common wildebeest), *Equus grevyi* (Grevy's zebra), *Equus quagga* (plains zebra), *Gorilla gorilla* (western lowland gorilla), *Pan troglodytes* (chimpanzee), *Pan paniscus* (bonobo), *Panthera leo* (lion), *Panthera pardus* (leopard), *Crocota crocuta* (spotted hyaena), *Orycteropus afer* (aardvark), *Struthio camelus* (ostrich) and *Crocodylus niloticus* (Nile crocodile). Of these, the IUCN Red List categorizes black rhinoceros and western lowland gorilla as 'critically endangered' and pigmy hippopotamus, okapi, Grevy's zebra, chimpanzee and bonobo as 'endangered'.

8. SOUTHERN ASIA (INDO-MALAY ECOREGION)

This geographically very complex and varied region includes the Indian Subcontinent, southern China, South-east Asia and the numerous islands of Indonesia (as far east as Wallace's Line) and the Philippines. Although there are abundant records of Pleistocene megafauna from across this region, stratigraphical control is generally very poor so that with rare exceptions it is not clear when many species became extinct (see Louys *et al.*, 2007). Although needing confirmation by secure stratigraphical association or direct radiocarbon dates, species that probably went extinct in the Late Pleistocene of southern China include *Stegodon orientalis* (a large proboscidean), *Palaeoloxodon namadicus* (extinct elephant), *Ailuropoda baconi* (a giant panda), *Megatapirus augustus* (a large tapir) and *Crocota [crocuta] ultima* (a hyaena) (Turvey *et al.*, 2013). *Stegodon orientalis* and *Ailuropoda baconi* are also recorded from Vietnam and

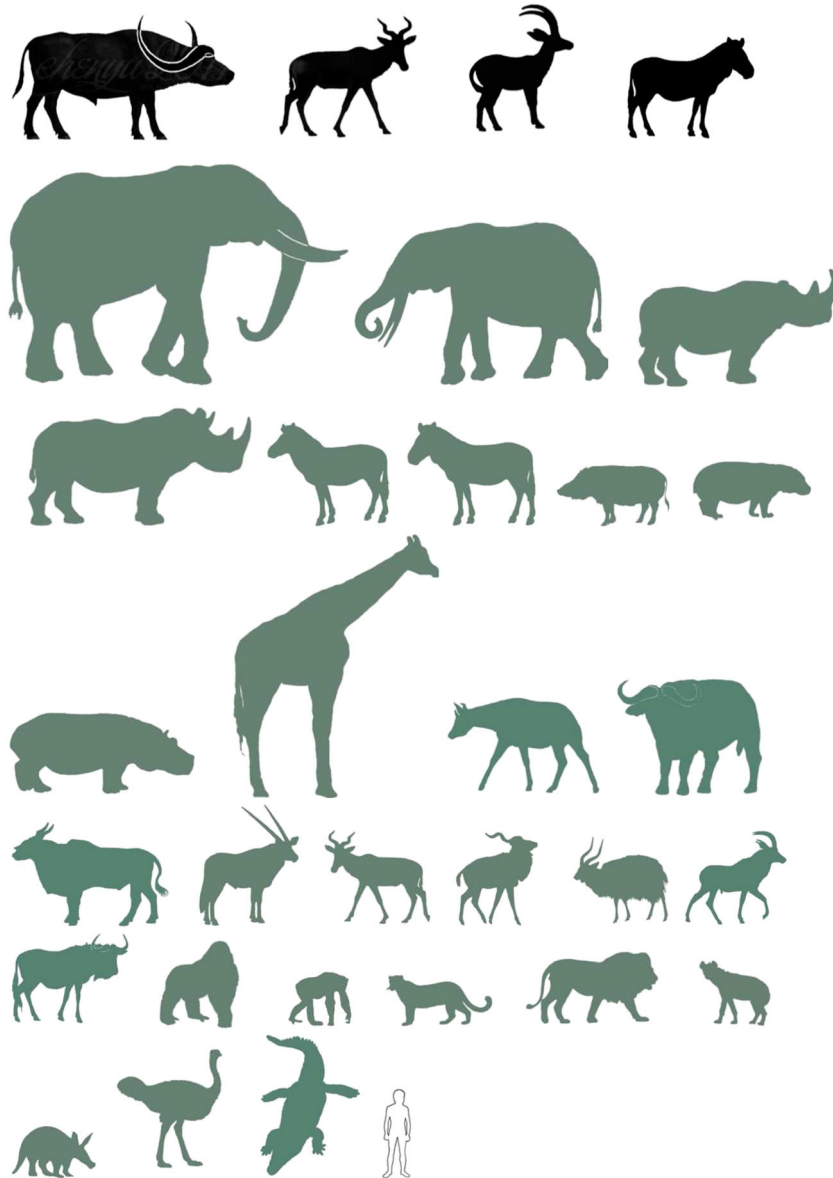


Figure 7. Sub-Saharan Africa (Afro-Tropic Ecoregion). Selected extinct species (black): *Syncerus antiquus*, *Megalotragus priscus*, *Hippotragus leucophaeus*, *Equus capensis*. Selected living species: *Loxodonta africana*, *Loxodonta cyclotis*, *Diceros bicornis*, *Ceratotherium simum*, *Equus grevyi*, *Equus quagga*, *Hylochoerus meinertzhageni*, *Choeropsis liberiensis*, *Hippopotamus amphibius*, *Giraffa camelopardalis*, *Okapia johnstoni*, *Syncerus caffer*, *Tragelaphus durbianus*, *Oryx gazella*, *Alcelaphus buselaphus*, *Tragelaphus strepciseros*, *Tragelaphus angasi*, *Hippotragus equinus*, *Connochaetes taurinus*, *Gorilla gorilla*, *Pan troglodytes*, *Panthera pardus*, *Panthera leo*, *Crocuta crocuta*, *Orycteropus afer*, *Struthio camelus*, *Crocodylus niloticus*. Outline *Homo sapiens* gives approximate scale. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

Java (Louys *et al.*, 2007) (Fig. 8). Claimed Holocene records of *Palaeoloxodon* sp. from China are based on misidentification of remains and artistic representations of extant *Elephas maximus* (Asian elephant) (see Stuart and Lister, 2012; Turvey *et al.*, 2013). Other notable megafaunal taxa such as *Gigantopithecus* (a giant ape) probably went extinct in the Middle Pleistocene.

There are claims that several megafaunal species survived into the Holocene in China, but a critical reassessment of the

evidence by Turvey *et al.* (2013) failed to confirm this except in the case of *Bubalus mephistopheles* (short-horned water buffalo). Although no direct radiometric dates are available, *B. mephistopheles* is present in a series of Early–Middle Holocene (Neolithic–Bronze Age) zooarchaeological deposits across southern, central and eastern China in association with representatives of the modern Chinese large mammal fauna. Ancient DNA analysis demonstrates that it is phylogenetically distinct from domesticated water buffalo *Bubalus bubalis*.

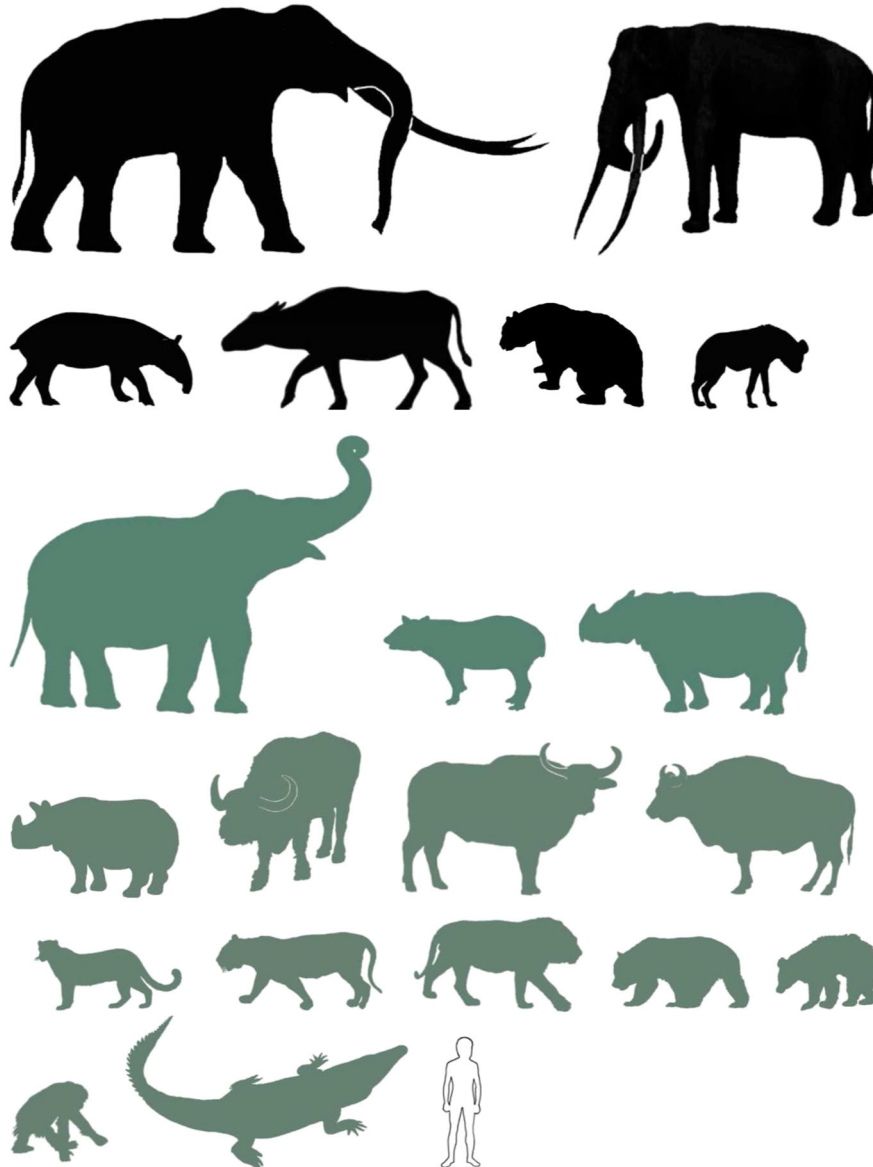


Figure 8. Southern Asia (Indo-Malay Ecoregion). Selected extinct species (black): *Stegodon orientalis*, *Palaeoloxodon namadicus*, *Megatapirus augustus*, *Bubalus mephistopheles*, *Ailuropoda baconi*, *Crocota (crocota) ultima*. Selected living species: *Elephas maximus*, *Rhinoceros unicornis*, *Rhinoceros sondaicus*, *Tapirus indicus*, *Bubalus arnee*, *Bos javanicus*, *Bos gaurus*, *Panthera pardus*, *Panthera tigris*, *Panthera leo*, *Ailuropoda melanoleuca*, *Melursus ursinus*, *Pongo pygmaeus*, *Crocodylus porosus*. Outline *Homo sapiens* gives approximate scale. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

8.1. Survivors

Surviving megafaunal species include (Fig. 8) *Elephas maximus* (Asian elephant), *Rhinoceros unicornis* (Indian rhinoceros), *Rhinoceros sondaicus* (Javan rhinoceros), *Dicerorhinus sumatrensis* (Sumatran rhinoceros), *Tapirus indicus* (Malayan tapir), *Bubalus arnee* (Indian water buffalo), *Bos javanicus* (banteng), *Bos gaurus* (gaur), *Pongo pygmaeus* (Bornean orangutan), *Pongo abelii* (Sumatran orangutan), *Panthera pardus* (leopard), *Panthera tigris* (tiger), *Panthera leo* (lion), *Ailuropoda melanoleuca* (giant panda), *Melursus*

ursinus (sloth bear), *Crocodylus porosus* (saltwater crocodile) and *Python reticulatus* (reticulated python). Of these, the IUCN Red List categorizes Javan rhino, Sumatran rhino and Sumatran orangutan as 'critically endangered' and Asian elephant, Indian water buffalo, banteng, Malayan tapir, Bornean orangutan, tiger and giant panda as 'endangered'. The Asiatic lion, subspecies *Panthera leo persica* survives today only as a small population in a reserve in the Gir Forest of north-west India but within the past 200 years ranged from North Africa through Iraq and Turkey to Iran, Pakistan and north-west India (Bartosiewicz, 2009).

9. CONCLUSIONS

Claims by some authors that the problem of cause has been solved, one way or another (e.g. compare Grayson and Meltzer, 2002, 2003, 2004, with Fiedel and Haynes, 2004, and Sandom *et al.*, 2014) are definitely premature. In my view, we require far more high-quality data, not more debate based on imperfect evidence. There is an overwhelming need to focus on obtaining a large body of reliable radiocarbon dates made directly on securely identified megafaunal remains for each region. However, where extinctions occurred beyond radiocarbon range, notably in Australasia, other dating methods are necessary.

Without a detailed chronology for the faunal histories and extinctions of a wide range of species for comparison with the climatic and archaeological records, I strongly believe that it will not be possible to pin down definitively the cause or causes of the Late Quaternary extinctions. We need to know first and foremost when each species became extinct both in time and geographically.

At present, as described above, much of northern Eurasia and Alaska/Yukon have by far the best coverage in terms of radiocarbon dates. However, there is still much work to be done in both of these regions. Ideally, the geographical coverage of radiocarbon dating in northern Eurasia should be extended to include the rest of the Palaearctic, namely North Africa, and South-west and Central Asia. On the face of it, there is a relatively large number of radiocarbon dates available for North America south of 60° latitude, but many of these were made on associated material, were done before subsequent improvements in dating techniques and/or have very large standard errors. A substantial programme of direct dating would undoubtedly yield important and exciting results. Although there is a growing interest in megafaunal extinctions for South America, the number of available dates for this region is insufficient at present, and again a major programme of direct dating would be highly desirable. There is a particular problem with Australia and New Guinea as most of the extinctions there evidently occurred beyond the range of radiocarbon dating, so that other, less precise dating methods have to be used. Future refinements in these dating methods are likely to provide the key to understanding the causes of the extinctions on that continent (e.g. Price *et al.*, 2013). At present, sub-Saharan Africa and Southern Asia, which have the lowest numbers of extinct megafauna, remain far behind in terms of research on Late Quaternary faunas and especially dating. Clearly, there is enormous potential for reconstructing the chronologies of both extinct and extant species in both of these regions. As a final observation, probably we should not expect to discover a 'one size fits all' explanation for Late Quaternary megafaunal extinctions, but instead a more complex picture in which

the relative contributions of environmental changes and 'overkill' were different for each region.

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