What happened to **all the large** animals?

Illustration: "ArctodusSimusReconstruct" by Dantheman9758 via Wikimedia Commons

The limited diversity of large mammals in the fauna of Europe, America and Asia is due to humans. A detailed analysis of the published data on late Quaternary large mammal distribution and extinction clearly shows that their disappearance is closely linked to the spread of modern man across the world.

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When we want to see many species of large animals today, we really only have the choice between a trip to the zoo and a safari in Africa. However, if we had lived 130,000 years ago during the last interglacial period, we would only have had to go for a walk in the woods. Safari tourists often talk about wanting to see 'the big five' in Africa: the lion, leopard, African elephant, black rhino and African buffalo. In northern Europe, similar lists would have comprised close relatives such as the cave lion, leopard, straight-tusked elephant, Merck's rhinoceros and auroch, which could all potentially have lived in Denmark today from a climatic point of view. If we had gone to Australia instead, we might have seen relatives of wombats weighing several tons, land-dwelling crocodiles and six-metre long monitors. And if we had gone to South America, we might have seen elephant relatives with spiral-shaped tusks, along with armadillos weighing several tons, giant ground sloths and strange, large hoofed mammals with no close relatives among today's species. By comparison, the African fauna at that time was almost identical to what it is today, with the addition of an extra elephant, a huge, long-horned buffalo, and a few other species.

The main hypotheses

Over geological time, it is perfectly natural that some species die out, and over a period of 130,000 years, we would expect a few species to disappear. However, the mass extinction of large animals that has taken place in the last 130,000 years is strange, not just because of the number of extinct animals, where a total of 30% of all mammal species in excess of 10 kg disappeared within a relatively short period, but also because mainly large animals were affected. Europe, for example, which is probably the continent where the fauna is best understood, has lost 19 mammals weighing more than 10 kg along with a single mouse as the only small mammal. This extreme rate of extinction among large animals has been debated for a long time, and many different theories have been proposed. If we disregard religious theories such as the biblical flood, a number of more or less unlikely academic theories have been proposed such as a mysterious disease that would have been able to infect large marsupials in Aus-

Mapping of extinct animals

Our work began with the gathering of the latest knowledge about the large continental species of mammals for which we have evidence dating back less than 130,000 years (that is, covering last Ice Age and the last and current interglacial periods).

We thoroughly searched existing literature for fossil finds and noted evidence of the different species in all countries on a map. There were a number of gaps in the distribution, which must be due to a lack of fossil finds, and we therefore also added all other states/countries situated between the states where fossil finds had been made. Finally, we calculated the proportion of extinct species for all countries. We excluded isolated islands and countries that were completely or almost completely covered by ice caps during the last Ice Age (these countries are shown in black on the map). Islands were excluded because there is no doubt that the massive fauna collapses that occurred here were caused by humans. Ice-covered areas were excluded because the ice caps destroyed relevant deposits from the period, for which reason the fauna is not well known either.

The map shows the distribution of the North-American short-faced bear *Arctodus simus,* which is one of the 177 species that became extinct either globally or on a particular continent during the period. The short-faced bear was a giant species, standing up to 3.5 metres tall on its hind legs and weiging approximately 800 kg. Contrary to all of today's living bears, except for the polar bear, it was almost entirely carnivorous. Its closest living relative is the small and almost entirely vegetarian spectacled bear, which lives in the Andes. A green colour indicates that the species has been found in the states in question, while blue indicates 'gaps' without fossil finds, but where the species must have been present judging by its general distribution.

tralia and elephants in northern Eurasia and America, but apparently not in Africa and never small mammals; volcanic eruptions affecting Australia, Europe and America but not Africa or South-East Asia; or the impact of meteors, despite the fact that the extinction takes place at very different timeperiods around the world. In practice, there are only two realistic explanations: climate change or modern man, *Homo sapiens.*

Climate change as an explanation

The last 130,000 years have been characterised by huge changes in the climate, from the warm previous interglacial period and the cold temperatures of the last Ice Age to the present interglacial period. These dramatic changes in the climate present a seemingly likely explanation for the mass extinction of the large animals. Climate plays a major role in the distribution of many species. The large animals might have been under great pressure from climate-driven changes to their habitats and food resources. However, climate change as an explanation model presents a number of problems. First of all, the climate changes that have occurred in the last 130,000 years are not unique. During the last couple of million years, the climate has varied between ice ages and interglacial periods with a total of more than ten ice ages. However, it is only during the latest period that we see a large, selective loss of large animals. Neither should climate change affect large animals in particular, as their ecological requirements are typically quite generalized. In fact, during earlier periods of climate change, for example in connection with the first Pleistocene ice ages, the extinction that took place affected plants and small animals to the same or an even greater extent.

Fascinatingly enough, there is also considerable variation in the climatic factors proposed as the main cause of this mass extinction. An incomplete list of the reasons why different species have become extinct includes cold, heat, drought and increased precipitation. However, the problem with such analyses is that, if the climate varies more or less all the time, then extinctions can always be matched to a change in climate. The significance of such apparent correlations can be very difficult to assess. In addition, it is important to keep in mind that the distribution of virtually all species changes when the climate changes. During the most recent Ice Age, reindeer, musk ox and Arctic fox thus lived in South and Central Europe – disappearing from the region when the climate subsequently warmed up. A correlation between population changes in populations and in climate therefore does not necessarily tell us anything about why the species ended up going extinct. The climate hypothesis nevertheless provides a very clear, general geographical prediction: the rate of extinction should have been higher in the areas most affected by climate change. If the climate is mostly to blame for the loss of large animals, there should therefore be a clear connection between the loss of species and the degree of climate change.

Sabre-toothed cats such as the scimitar cat shown here were formerly common throughout Africa, all of Eurasia and America. They disappeared from Africa and most of Eurasia earlier than 130,000 years ago, with only a single more recent find (from as little as 30,000 years ago in the North Sea, which at that time was dry land), whereas they continued to be common in both North and South America until around 10,000 years ago. Their early disappearance in large parts of the Old World may be due to competition with primitive humans. The sabre-toothed cats were the size of today's lions and, like them, they were likely social animals. They were designed to hunt very large prey such as giant deer or juvenile elephants.

Illustration: Scanpix Denmark

Different species of elephants (including close relatives such as mastodonts and gomphotheres) existed in the recent past on all the continents on Earth, except Australia and the Antarctic, and even on many small islands. One of the many extinct species of elephants is the South and Central American *Cuvieronius hyodon* with spiral-shaped tusks. This species is extremely relevant for our study, as recent research has found archaeological evidence that some of the earliest Amerindians (the Clovis culture) hunted this species.

Illustration: "Cuvieronius" by Sergiodlarosa, Wikimedia Commons

South America was isolated from around 40 million years ago, when the continent separated from the Antarctic and Australia, until around 3 million years ago, when it collided with North America. During this extensive period, a number of unusual animal groups developed, several of which also colonised North America after the isolation of South America ended. One of these were the ground sloths (weighing up to 6.3 tons). Contrary to their sleepy relatives of today, they did not climb trees but wandered around on the ground. Different species of ground sloths were distributed from Argentina to Alaska.

Illustration: Scanpix Denmark

The overkill hypothesis

The other potential cause of the extinctions is modern man, *Homo sapiens.* It has been well documented that humans have been able to wipe out large animals in historic times, so why not also in pre-historic times? This is called the *overkill* hypothesis. Many archaeological sites show that pre-historic man was highly capable of hunting large animals, even as large as elephants. The first widely distributed culture in North America was one of large game hunters who favoured hunting mammoths and mastodons, and this culture actually disappeared at approximately the same time as the large animals in America. The hypothesis is that the impact of humans depends on the fauna's early contact with them. Our species developed in Africa south of the Sahara, and the fauna in Africa has therefore had a long time to adapt to human hunting, while our ancestors gradually became skilled hunters. This may explain why limited extinction has occurred there.

The fauna in Australia and America, on the other hand, had never met human before modern man arrived and would therefore have been vulnerable to humans with advanced hunting skills, which may explain the massive extinction that took place in these areas. Eurasia is somewhere between these as extremes, and the animals here have had at least some contact with primitive humans before modern man spread from Africa. The rate of extinction in this area is also halfway between the rates in Africa and Australia/America.

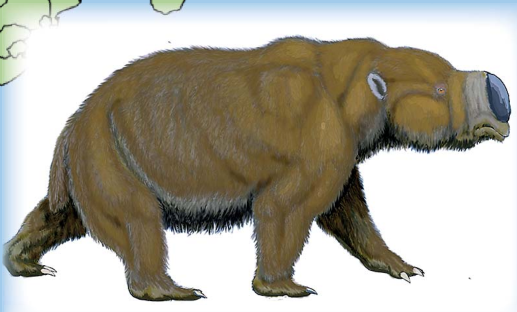
There are many examples showing that species on islands without prior contact with predators have no

In addition to the well-known woolly rhinoceros, three other species of cold-adapted rhinoceros disappeared from Eurasia. One of them was a giant rhinoceros, which despite its name *Elasmotherium sibiricum* lived on the central Eurasian steppes rather than in the northernmost regions. This giant with an estimated weight of 4 tons (the same weight as a modern African elephant) is described by Johannes V. Jensen in his book Bræen (The Glacier), where he called it Enhjørningen (the Unicorn). It has in fact been suggested that this rhinoceros with its single giant horn could have inspired some of the unicorn legends.

Illustration: Scanpix Denmark

Not all extinctions were global – some were only continental. The Przewalski horse, which lives on the steppes in Central Asia, is the last surviving original wild horse, which was previously much more widely distributed. Fossils of horses of the same species as the current living species are known from all land areas between Argentina and Morocco. The horse is thus the only mammal whose natural distribution covers five continents, and it is perhaps the mammal with the widest natural distribution.

Photo: "Takhi Hustai" by Chinneeb, Wikimedia Commons



Australia is known today for its very strange mammals, which are a result of the continent's long-term isolation. The current species are small or medium-sized, but this has not always been the case. When the first humans arrived in Australia around 50,000 years ago, they were able to experience the fascinating plant-eating *Diprotodon optatum*, which weighed more than 2 tons and measured almost 4 metres from head to tail – the largest marsupial that has ever lived. Another impressive creature was *Thylacoleo carnifex* (the Marsupial lion), which is the largest known carnivorous marsupial, weighing in excess of 100 kg. A surprising detail is that these two extinct giants were quite closely related, and that the nearest living relative to them both is the relatively small wombats (several extant species).

Illustration: Dmitry Bogdanov, Wikimedia Commons and Illustration pouch lion: Scanpix Denmark

fear. The best example is perhaps Darwin's fox, which lived on a small, isolated island off the coast of South America. Darwin killed his specimen by walking up to it and knocking it on the head with a geology hammer. It is unlikely that the fauna in mainland America was quite as naive, as the animals were used to being hunted by predators such as American lions, sabre-toothed cats and direwolves. However, none of these species had the same intelligence and ability to cooperate as humans do, and none of them were able to attack from afar like a hunter throwing a spear.

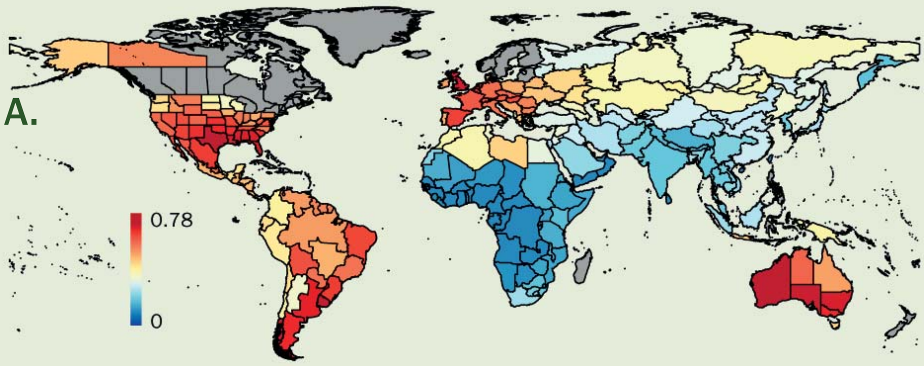
Advocates of the theory that humans were the cause of the loss of megafauna have often referred to the chronological overlap. Humans arrived in America approximately 10,000–15,000 years ago and in Australia approximately 50,000 years ago. The megafauna disappeared from America just over 10,000 years ago and from Australia approximately 40,000–50,000 years ago (somewhat later in Tasmania, where humans also arrived later). However, exact dating has proved difficult and, there has been much debate about whether the large animals disappeared shortly before or shortly after the arrival of *Homo sapiens*.

The suspicion falls on *Homo sapiens*

Both the climate and the *overkill* hypotheses provide clear predictions of the geographical variation in the extinction of the large mammals, but the predictions have so far only been tested using coarse, incomplete data. To remedy this situation we scrutinised the scientific literature to collect

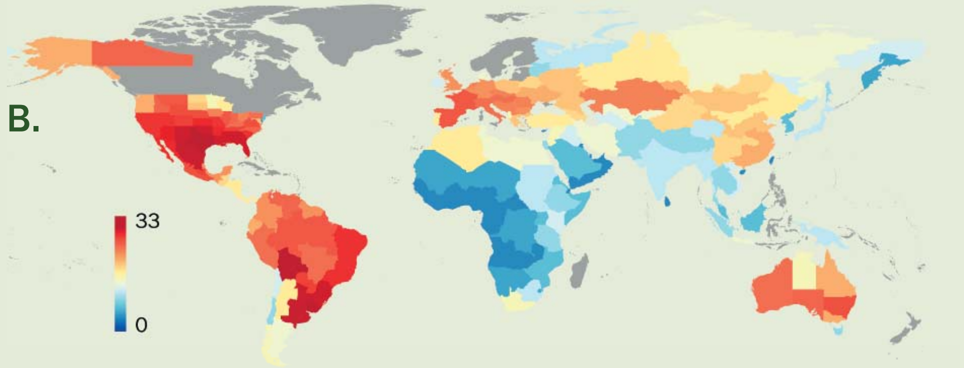
A) The frequency of large extinct species

Figure A shows the percentage of all large mammals weighing 10 kg or more known to have lived in a given country within the last 130,000 years (including present-day species) that have since become extinct on the continent in question or globally. In this and all other figures, the countries excluded from the analysis are shown in grey.



B) The number of large extinct mammal species

The total number of known species from each country that have become extinct.

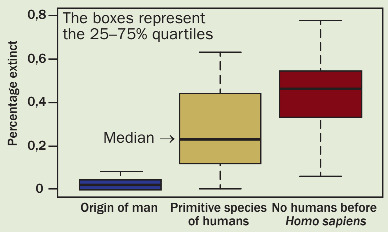


C) Historical contact with humans

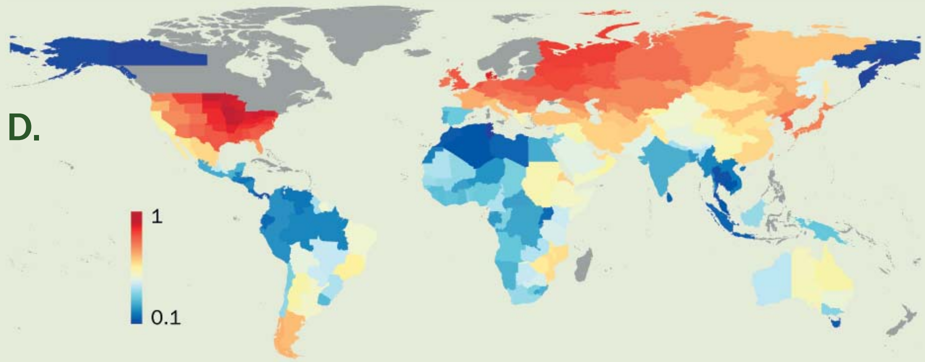
Historical biogeography of humans. Under the overkill hypothesis, large-animal extinctions should be lowest in areas where both ancient and modern humans (*Homo sapiens*) gradually evolved (shown in blue), while the most severe extinctions should occur where the fauna had no previous contact with primitive humans before the arrival of modern man (shown in red). The yellow areas are an intermediate zone outside the core area of human evolution, which were colonised by primitive pre-sapiens human species.

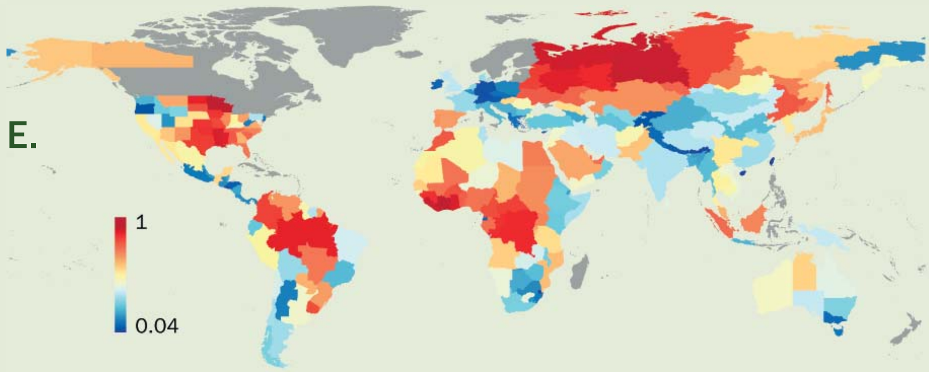
D) and E) Differences in temperature and precipitation

Figures D and E show the change in climate in terms of temperature and precipitation between the peak of the last Ice Age and today. Shades of red indicate that the climate was very different during the Ice Age compared with today, whereas countries with small climatic changes are shown in shades of blue.



The proportion of large mammals in each country that have become extinct in areas with three different histories of human occupation..





By comparing the different figures, it becomes obvious that the rate of extinction is much greater in the red areas in figure C than in the areas shown in blue.

A comparison of figures D or E with A, on the other hand, does not suggets a clear relation, but a statistical analysis showed that there was a weak trend towards greater extinction in areas with larger climatic variation, albeit only in Eurasia.

detailed data on the distribution of the large animal species that became extinct between 130,000 and 1,000 years ago (we ignored more recent cases of extinction, as it is obvious that they are all due to hunting and habitat destruction). We then proceeded to map the total distribution of the species throughout the period by country, with large countries such as the USA, Australia and Brazil being divided into states/regions. This enabled us to create the most complete mapping of extinct megafauna to date. Against this background, we were able to test the predicted relations between the loss of megafauna and climate fluctuations during the period – as predicted by the climate hypothesis – and between the loss of megafauna and the historical distribution of humans (i.e. the extinction was most widespread when *Homo sapiens* was the first human in the area, and the least widespread in areas where human development occurred over an extended period of time).

Our results were very clear and showed a strong relation between the historical distribution of humans and the extinction of the large mammals, in clear accordance with the *overkill* hypothesis. Conversely, we could only find a weak correlation with climate change. There can therefore be no reasonable doubt that modern man has played a major role in the global loss of large mammals. However, it is doubtful whether the climate has also played a role. Our data indicate a weak effect at the most, and this potential correlation only exists in Eurasia. Real climate effects should be just as strong in areas without previous human contact (America and Australia). It is furthermore remarkable that our mapping demonstrates a considerable loss of species in regions with a relatively stable climate, such as California, which served as effective refuges for many small animals and plants.

Several mechanisms at play

Although our results strongly indicate that *Homo sapiens* is the main cause of the loss of large animals, our analyses do not show exactly how this occurred, and it is far from certain that the cause is the same for all species. Some species were likely exterminated as a direct result of hunting, which was probably the case with the more than ten species of elephants and their near relatives that disappeared from the Americas and Eurasia, as they were obviously highly prized prey. In addition, these species have a low reproductive rate and are very sensitive to hunting.

Predators such as the sabre-toothed cats, which went extinct globally, the spotted hyena or the leopard, both of which became extirpated throughout continental Europe, are more likely to have disappeared because their food resources vanished. Yet other species may have disappeared due to changes in their habitats, for example due to the loss of elephants and other very large animals – which may have been of great importance to the ecosystems as a result of their impact on the vegetation – or due to environmental changes caused by human use of fire in connection with hunting.

Large animals and nature conservation

The immediate scientific consequence of our study is to provide an answer to what is akin to a scientific detective story, where we can now clearly see that modern man was by far the main cause of the massive loss of megafauna. The study therefore also indicates that, if it had not been for the hunting and habitat changes caused by humans, we could now have had similarly rich megafaunas all over the world as those found in Africa today, with large animals such as elephants, rhinos and lions. Unfortunately, the loss of large animals continues to this very day in large parts of the world, as seen by the current wave of poaching of elephants and rhinos.

Our results are relevant for nature conservation. As we now know that humans are responsible for the low diversity of large animals in many parts of the world, why should we not try to reintroduce them wherever possible? In fact, this is now happening to some extent in Denmark by reintroducing beavers and the European bison (although the latter remains in fenced areas), despite the fact that both species have been absent from the country for a millennium or more. As our results indicate that animals such as the spotted hyena, leopard, lion and elephant (the latter two only in the form of near relatives to existing species) can also be native to northern Europe and are only absent due to past hunting, then why not consider reintroducing these species as well wherever possible? This is particularly relevant, as there is growing evidence that the large animals could play very important roles in our ecosystems and promote a high species diversity through their grazing, rooting and predation.

The same considerations are relevant on a global level. One example is the management of wild horses in the New World. Wild horses used to live in a more or less continuous belt from Argentina via Alaska and Siberia to Morocco. However, they have been absent in America for the past 10,000 years, from the time they became extinct in that area along with many other large animals towards the end of the last Ice Age until a new population became established from domesticated horses that escaped from European immigrants in the course of the last 500 years. Today, the wild horses in America are often managed as an invasive, non-native species that by definition is a problem. From an historical point of view, we should instead look at it as a re-introduction of an extinct, native species. These wild horse populations should therefore be managed – and promoted – as a natural part of the fauna instead of being controlled. ■

Further reading:
Global late Quaternary megafauna extinctions linked to humans, not climate change doi: 10.1098/rspb.2013.3254.

Species-specific responses of Late Quaternary megafauna to climate and humans doi:10.1038/nature10574.

Assessing the Causes of Late Pleistocene Extinctions on the Continents doi:10.1126/science.1101476.

Martin P. S (1973) The discovery of America. Science 179: 969–974.

High herbivore density associated with vegetation diversity in interglacial ecosystems doi:10.1073/pnas.1311014111.

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