Preindustrial Human Impacts on Global and Regional Environment

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Abstract

Humans have had an impact on regional and global environments even prior to the Industrial Revolution through anthropogenic fire, agriculture, and the extinction of the Pleistocene megafauna. The preindustrial impact of anthropogenic fire to modify ecosystems and affect climate may have been small because in regions where impacts were once thought to be large, such as in Australia, the evidence now suggests a smaller effect. Both the extinction of the megafauna, which evidence indicates to be at least partially caused by humans, and preindustrial agriculture may have affected climate, but the effects may have offset each other. For instance, climate simulations indicate that megafauna extinctions may have led to a slight global warming, but later, agriculture led to a slight global cooling. Prior to the industrial era, the largest ecological and climate anomaly may have been associated with forest expansion during the early and mid-Holocene when there were few megafauna and agriculturalists to reduce this expansion.

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ppm: parts per million

Anthropocene: an informal geologic chronological term that serves to mark the evidence and extent of human activities that have had a significant global impact on Earth's ecosystems

BP: before present

NPP: net primary production

INTRODUCTION

There is increasing evidence that humans are affecting Earth's climate by modifying the composition of the atmosphere and changing the land surface. Since about 1800 AD, the burning of fossil fuels to power the Industrial Revolution has increased atmospheric CO_2 concentrations from ~270 to ~400 ppm today. Projected future emissions (the A2 scenario of the Intergovernmental Panel on Climate Change) are expected to warm the planet over the next 100 years by 2.0–5.4°C (1). The evidence of human impact on the planet is so great that it has been suggested that Earth has entered a new geological era dominated by human activity, called the Anthropocene (2). However, as there is yet no set definition of the Anthropocene, there is also no official agreement as to its starting date.

The Anthropocene has many potential definitions. For geologists, its definition involves estimating when humans first began to globally influence the planet's sediments. The anthropogenic chemostratigraphic signal is dominated by the effects of CO_2, particularly via ocean acidification (3). However, in the future, other signals will likely emerge, such as a twofold increase in the amount of reactive nitrogen at Earth's surface and increased radionuclides associated with nuclear explosions (4). Most of the major changes to Earth's sediments are recent, but some have been hypothesized to be more ancient, such as an increase in lead deposition dating back to Roman times, which has been detected in ice cores and alluvial sediments (5). Humans now move an order of magnitude more sediment than natural processes do (6). This impact likely began ~3,000 years BP (before present) but accelerated ~1,000 years BP (7). The stratigraphic signal is negligible to date but may become geologically significant over longer timescales (4).

However, the Anthropocene can be defined in other ways. For instance, ecologists may define it as the period when humans began to dominate consumption of the global net primary production (NPP). An early paper estimated that humans currently appropriate ~40% of potential terrestrial NPP (8). This study has since been supported by more complex recent calculations that have revised this figure to 24%, and of this, 53% is the result of harvesting plants (9). Globally, much of Earth's land surface cover has been transformed by humans into 18 "anthropogenic biomes," which cover more than 75% of Earth's ice-free land, whereas wild areas compose just 11% of land for terrestrial NPP (10). Only in the past century has the majority of the terrestrial biosphere been transformed by such novel anthropogenic ecological processes (11).

A third potential definition of the Anthropocene is when humanity first began to affect global climate. Because climate change may be the most important global impact of humans on the planet, it may also be a good proxy for the start of the Anthropocene. This date most often corresponds with the start of the Industrial Revolution when extensive coal burning in Britain began to greatly change the composition of the atmosphere (2). However, humans have been potentially modifying the planet through land-use changes before that. It has been hypothesized that this process began nearly 8,000 years BP, near the dawn of agriculture, called the early Anthropocene hypothesis (12). Early farmers may have put sufficient additional CO_2 and methane into the atmosphere to have prevented the onset of the next ice age. This theory was originally published in 2003, and there have now been many studies over the past decade to evaluate it. There are other possibilities of when humans first began to affect global climate. For instance, humans could have affected climate through large-scale conversion of ecosystems through fire (13, 14). In addition, there is substantial evidence that humans played a role in the extinction of the Pleistocene megafauna. Large animals play an important role in shaping their ecosystems. Could their disappearance have affected global environment and climate (15)? In this review, I look at three aspects of preindustrial human impacts on global or regional environment: fire, Pleistocene megafauna extinctions, and preindustrial agriculture.

HOW DOES VEGETATION IMPACT GLOBAL CLIMATE?

Prior to the Industrial Revolution, the principal human mechanism of modifying the environment and climate was through land-use change, often through the conversion of forests to cropland. This conversion of forest to cropland does more than just release CO_2 to the atmosphere, it also modifies the surface energy balance, evapotranspiration, and surface roughness. Climate models and field studies have shown that in certain regions (e.g., tropical, temperate, boreal forest) modifying such biophysical parameters can impact climate more than the accompanying change in atmospheric composition (16–18). CO_2 is released into the atmosphere during the transition from forests to crops because a tree stand contains more carbon within its biomass than an equivalent area of grassland. Therefore, tropical, temperate, and boreal deforestation can add CO_2 to the atmosphere.

In the process of deforestation or afforestation, other biophysical processes are modified including surface albedo. Changing albedo has a larger local impact, whereas the impact of an increase in CO_2 is spread more uniformly over the globe. In regions of the world where snow or ice are present, changes in surface albedo from deforestation can have a larger impact on climate than the influences of changing atmospheric CO_2 concentrations. For instance, several modeling studies have found that afforestation in boreal regions has a net global warming effect as dark boreal trees overtopped surface snow, reducing winter albedo (17–20). All such simulations agree that mean global temperatures were more affected by surface albedo changes in boreal regions than by changing atmospheric CO_2 concentrations, and the world would cool if all trees were converted to grasses in boreal regions. However, afforestation in Siberia could still have a global warming mitigation potential because past land-use decisions resulted in the use of the most productive land with larger carbon stocks and less snow than average, and therefore, actual afforestation in Siberia may lead to stronger CO_2 effects versus albedo effects than had been previously demonstrated in idealized deforestation experiments (21).

Rates of evapotranspiration also change as forests are converted to crops, and these changes can have a significant global influence. In fact, a recent review found that tropical forests were beneficial for the mitigation of climate change principally resulting from their greater evapotranspiration relative to grasslands (16). Climate simulations show that increased evapotranspiration rates lead to evaporative cooling and potentially more clouds, increased albedo, and cooler temperatures. Changes in evapotranspiration can also have a large impact on global climate in boreal

Megafauna: animals with weights greater than 44 kg

Evapotranspiration: the sum of evaporation and plant transpiration from Earth's land surface to the atmosphere

Surface roughness: a measure of the texture of a surface, quantified by the vertical deviations of a real surface from its ideal form

Albedo: the diffuse reflectivity or reflecting power of a surface regions. For instance, a modeling study wherein grassland in boreal regions was replaced with broadleaf deciduous trees found that the top-of-atmosphere radiative imbalance from enhanced transpiration (associated with the expanded forest cover) was up to 1.5 times larger than albedo forcing (22), although other climate simulations have found a smaller role for evapotranspiration in boreal regions (17, 20).

The influence of surface roughness changes on climate are the least well known but may potentially be important for regional climate. Changing surface roughness does not modify global climate but can impact local temperatures, with rougher surfaces encouraging atmospheric mixing between atmospheric air and Earth's surface. Some model studies have shown that roughness may have a dominant effect on local land surface temperatures. For instance, decreasing surface roughness by decreasing canopy height can warm the land surface by reducing atmospheric mixing, and warmer temperatures increase rates of evapotranspiration, often increasing precipitation (23, 24). A field study in the southeastern United States separated out the albedo effect from the aerodynamic/ecophysiological effect and found similar results with a 2.18–2.98°C cooling during the transition from grass fields to tree plantations from only aerodynamic/ecophysiological effects (25). There has been less research on the impacts of prehistoric or historic changes in surface roughness on global climate than on carbon, albedo, or evapotranspiration.

PREINDUSTRIAL ANTHROPOGENIC FIRE

Humans have had a long relationship with fire. Even before modern humans evolved there is evidence that *Homo erectus* was already manipulating fire, with the earliest evidence found in a South African cave from one million years BP (26), and routine use of fire by hominins after leaving Africa likely by ~400,000 years ago (27). The spread of flammable C_4 grasslands in Africa before the origin of bipedalism in hominids likely contributed to our close early relationship and comfort with fire (28). Cooked food may have appeared as early as 1.9 million years BP according to physiological evidence such as smaller teeth (29). However, these are small-scale uses of fire, and it was probably only tens of thousands of years ago when hunter-gatherers may have begun to use fire to modify the environment over large scales (30).

Fire itself obviously has a much longer history in the Earth System, and fire activity was greater than at present prior to 50 million years BP but less than at present during most of that time (31). Global fire activity was on average greater during the Holocene than in the Pleistocene owing to the cooler, drier, and lower-biomass conditions of the Pleistocene (32, 33). The 20,000-year record shows an apparent global peak in fire activity ~2,000 years BP (33). The regional trends through time are correlated mainly with different climate controls, such as changing regional solar insolation patterns. However, predicting fire trends is complicated because similar changes in climate can impact fires differently depending on the state of the vegetation. For instance, increased rainfall reduces fires in most forests, but in areas where fuel is limited, rainfall increases plant growth and fires. Overall, the record does not distinguish between anthropogenic and natural fires, although certain regional trends are occasionally correlated with human activity.

Interestingly, the global trend in fire activity over the past 2,000 years has been downward, with the exception of a large peak between 1750 and 1870 (34). The more recent decrease since 1870 is attributed to the global expansion of intensive grazing, agriculture, and fire management. The long-term trend over the past two millennia has been attributed to a gradual cooling prior to the current warming, despite increases in global population. However, the charcoal record may underrepresent recent global fire activity because it does not reflect the large increase in fires in the western United States and in tropical forests over recent decades.

Did early human fire lead to large enough ecosystem shifts to modify global or regional climate? If large-scale shifts in ecosystems occurred, they might have been most common in Australia, the most fire-prone continent, and one with a very long interaction with humanity (∼50,000 years). Several early iconic sites, such as Lake George and the Darwin Crater, showed increased charcoal during the arrival of Aboriginals in Australia. It was therefore thought that early anthropogenic burning may have transformed the Australian landscape and affected its climate (13, 14). However, other studies began to question this assumption by using pollen and charcoal records that show that fire regimes did not appear to change when humans first arrived (35, 36). A larger recent review, based on 223 sedimentary charcoal records from Australasia, found no change in the fire regime following the arrival of humans in Australia 50,000 years BP and no correlation between archaeological evidence of increased human activity during the past 40,000 years BP and increased biomass burning (37). However, the authors do not rule out the possibility that their methods may have missed some of small-scale burning by the Aborigines.

Some authors claim that it is much harder to detect the impact of humans in Australia because natural fire is so prevalent there and because it is difficult to differentiate between natural and man-made fires. A way to test this would be to examine a region that had humans arrive at a time when there was no major climate change. Such was the case following the initial colonization of New Zealand by the Maori 800 years BP, when there was a rapid increase in fire and forest cover loss (38). Likewise, in Tasmania, when humans arrived, increased fires may have established open moorlands in regions that had been occupied by rain forest during previous interglacial periods (39). These two cases indicate that humans may have increased fire in these regions upon their arrival.

Fires in South America correlate with El Niño events but even more strongly with the solar insolation minima. They appear to have peaked between 800 and 1500 AD and became much scarcer within Amazonia following the population declines after European contact (40). Another study found isotopic evidence from methane trapped in ice-core bubbles that early Americans had been doing an unexpectedly large amount of biomass burning prior to being decimated by European diseases in the 1500s (41). However, there appears to be much regional diversity because another recent study showed fewer fires before 1492 AD in raised-field agriculture, and more fires following the arrival of Europeans (42). In Africa, charcoal data demonstrate that fire activity was greater between 19,000 and 4,000 years BP than after 4,000 years BP (33); this decrease in fires is attributed to the spread of agropastoralism, which reduced fuel loads through grazing and cultivation (43). In Europe, fire appears to have been controlled by climate during the early and middle Holocene and by humans during the late Holocene (44). A study of charcoal records from France also showed increased human influence on fire starting ∼3,000 years BP (45). Therefore, outside of Australia and potentially Africa, anthropogenic fire influence was greatest in the mid-to-late Holocene.

There appear to be certain conditions under which humans can affect burned areas. For instance, changes in ignition frequency seldom increase burned areas unless they are in highly fragmented landscapes (43). An analysis of 50 years of contrasting fire management styles showed little effect on the areas burned or fire-free intervals in Kruger National Park, South Africa (46). If tree cover is greater than 40% of the landscape, burned areas also decrease (43). For instance, tropical forests do not burn readily without the influence of humans (40). Therefore, anthropogenic fire may influence climate mainly in grass-forest mosaics by preventing forest encroachment into savannas.

Fires can impact climate in several ways. Foremost, the burning of vegetation releases CO_2 into the atmosphere. However, regrowth in burned areas often sequesters this carbon, leading to minimal longer-term climate trends. Therefore, an increase in fire activity without a corresponding shift in vegetation is unlikely to affect long-term climate. However, if fires lead to a shift from forest cover to grasslands or vice versa, then this leads to a shift in carbon storage, surface albedo, and evapotranspiration. Such vegetation shifts have been hypothesized to modify climate. For example, there have been theories that anthropogenic burning in Australia changed vegetation cover, which in turn affected global circulation patterns, thus increasing aridity in Australia (13, 14). However, recent evidence has questioned the quantity of anthropogenic burning in Australia (37), and modeling evidence indicates that such changes in vegetation were insufficient to cause increased aridity (47).

Fires may impact climate in other ways, such as through adding aerosols to the atmosphere. For instance, aerosols from tropical forest fires have been shown to inhibit rain cloud formation and lengthen the dry season by 15–30 days (48). This may have two effects. First, extending the dry season increases the likelihood of fires, thus creating a positive feedback, which leads to additional fires. Second, reducing cloud cover in tropical regions leads to warming because planetary albedo decreases with fewer high albedo rain clouds (16). Such changes could have had a significant early impact on climate, but charcoal records show a strong climatic, and not anthropogenic, control of fires in South America until 1750 (34). Therefore, it is unlikely that anthropogenic fires in South America caused a strong aerosol cloud climate feedback prior to the industrial era.

When did humanity enter the "pyric transition," the period when we began to shift the type and scale of our fire practices (30)? Current estimates of prehistoric anthropogenic fire impact on ecosystems range from "catastrophic to negligible" (49, p. 2223). Another recent review noted that, although human-caused fires may have had an important role in modifying ecology, especially in the past 1,000 years, only in the past two centuries have anthropogenic fires been dominant over natural fires (50). Therefore, more evidence is still necessary to fully quantify the role of human-induced fires on global ecology. As of yet, there have been few climate simulations estimating the impact of early man on climate through fire. However, because most larger charcoal studies do not find a substantial human influence on ecosystems through fire in the regions where we might most expect to see it, such as in Australia (37), and fire likely peaked ~2,000 years BP when human populations were much smaller (34), the very early anthropogenic effect on global climate from fire before the mid-Holocene is expected to be small.

Changes in vegetation cover have occurred in the past, but did these changes result from changing climate, changing fire activity, or the extinction of common herbivores in the system? It is difficult to distinguish between causes because fire generally acts in concert with herbivores. For instance, a recent study found that large ungulates prefer grazing in recently burned patches of grasslands and avoided feeding in patches that had not recently been burned (51). This means that herbivores can amplify the effect of fire on ecosystem structure and climate. It has also been hypothesized that the extinction of the large herbivores in Australia caused increased fuel buildup and thus subsequent changes to fire regimes (52). In the next section, I focus on how the extinction of many of the world's large herbivores may have impacted global environment and climate, but in practice, it may be difficult to separate the impacts of fire and herbivores on vegetation changes.

PLEISTOCENE MEGAFAUNA EXTINCTIONS

In the late Pleistocene (~50,000–10,000 years BP), 97 genera of large animals (megafauna >44 kg), concentrated in the Americas and Australia, went extinct (53). There is still much debate as to what caused the extinction of the megafauna. The classic debate was between whether human hunters caused the extinctions through overkill [a "blitzkrieg extinction event" (54, 55)], or whether climate change or a combination of climate change and hunting caused the extinctions (53, 56). Here, I briefly review new findings that provide insights into this debate, but my primary focus is on the environmental impact of the extinctions and not on what caused them. However, in the context of describing preindustrial influences of humans on the global environment, it is important to evaluate how likely it is that humans were responsible for the megafaunal extinctions.

There are many ways to examine the cause of the extinctions: geographically, temporally, or by animal type. For instance, a recent study focused exclusively on proboscideans (elephants, mammoths, mastodons, gomphotheres). This family is the largest terrestrial megafauna and has the most potential for transforming ecosystems (57). Therefore, their extinction may have had the largest impact on the environment and climate. In the late Pleistocene, proboscideans initially had an almost global range, which was drastically reduced in the Holocene. Prehistoric human range expansion corresponded in time with localized extinctions of proboscideans, and they survived only in refugia that were initially largely inaccessible to human populations (58). The Xenarthran suborder Phyllophaga (sloths) represent a numerous group that lost 22 of 24 genera, ranging in size from 4–3,000 kg during the Pleistocene extinctions. Radiocarbon data showed that their last appearance varied from ∼10,500 years BP in South America to only ∼4,400 years BP on Caribbean islands, which, in each case, closely tracked the first arrival of humans (59).

In addition, we can evaluate the extinctions geographically. In most cases, such as in South America and Southeast Asia, the final extinctions appear during periods when a climatic event, like the Younger Dryas in South America (60) or a change in sea level in Southeast Asia (61), corresponds in time with the additional pressure of human hunting. Another study found a long-term cyclical trend in population numbers of Siberian mammoths, which the authors described as "Milankovitch-like" (62, p. 2309). These investigators hypothesized that the extinction event came as expanding human pressure corresponded to a natural strong minima of their numbers at the very beginning of the Holocene (62). In Australia, the arrival of humans was probably the main factor causing the extinction of the megafauna, with the extinctions occurring well in advance of the most extreme climatic perturbations, but changes in climate and fire activity may have also been factors (63). These studies highlight the importance of multiple pressures, both human and climate, on causing the extinctions.

In addition, there is genetic evidence that climate also played an important role in determining total population numbers. For instance, genetic diversity in musk oxen was much higher during the Pleistocene than at present, and the arrival of humans did not affect this genetic diversity (64). Another study using ancient DNA, species distribution models, and the human fossil record found that climate has been a major driver of population change (65). The investigators also noted that each species responds differently to climatic shifts, habitat redistribution, and human encroachment (65). However, there is also increasing evidence that the extinction chronologies were rapid, such as that of North American Pleistocene mammals, which took place in a "geological instant" (12,000–10,000 radiocarbon years BP) (66).

Overall, the cause of the extinctions is not definitely known, but it is very likely that most early extinctions occurred under the dual stress of human hunting and some additional climate changes. The question for continuing research is how big was the human role? For instance, megafauna extinctions in New Zealand and Madagascar clearly followed the arrival of man during historical periods and occurred in the oceans as humans gained the ability to hunt large ocean-dwelling megafauna such as whales as a result of greater seagoing capabilities. Megafauna survived climate-driven stresses during previous interglacial periods, likely because there was not the additional stress of human hunting outside of Africa. Therefore, it seems clear that without the recent arrival of humans many megafauna extinctions would not have occurred, and I attribute the climate and environmental repercussions of the extinctions at least partially to humans.

A previous paper noted that the extinction of so many large herbivores may have changed plant communities, vegetation openness, species diversity, and fire regimes (67). Interactions with the now extinct herbivores have left some plant species with obsolete defenses and nonfunctional adaptations for seed dispersal (67). For instance, the extinction of the Pleistocene megafauna may have had a large effect on plant species distributions by reducing distributors of large-seeded fruits (68). A recent study has estimated that there are 103 fruit species in South America that were likely dispersed by megafauna out of 1,361 species tested (69). The small average size of present-day neotropical vertebrate frugivores, except for tapirs and introduced species, would limit dispersal of seeds >2.5 cm in diameter (70). Why would such large seeds evolve? Larger animals tend to have larger gut lengths and home ranges, and the extinct South American megafauna would have been ideal for wide dispersal of these fruits. For example, one study found elephants improve the probability of germination of *Balanites wilsoniana* seeds and play a vital role in their dispersal (71). Several studies have suggested that such selective pressure of megafauna on seed development may have occurred worldwide (71–73). On islands, the extinction of large birds and reptiles in the past two or three millennia has led to a reduction in fruit dispersal on the islands, similar to the reduction that was hypothesized to have taken place in the Americas (74). How have such species survived the extinction of their main dispersers? They likely now rely on secondary dispersal agents, such as generalist frugivores, gravity, water, scatter hoarding, or vegetative propagation (69). Pre-Colombian Native Americans may also have played a role in the dispersal of some of the larger or multiseeded fruits by widely planting fruit trees throughout the Amazon basin (75).

The Pleistocene megafauna extinctions may have led to extinctions and range restrictions not just in coevolved plant species, but also in insect species, such as dung beetles, that may have coevolved with the megafauna. It is more difficult to quantify extinctions in invertebrates, but several species of now extinct dung beetles were found in the La Brea tar pits in California near the remains of other Pleistocene megafauna (76). Removing temperate or tropical animals, and their dung, can disrupt the diversity and abundance of dung beetle communities (77) or force them to alternative feeding habits (78). These beetles provide many ecosystem services, such as nutrient cycling, plant growth enhancement, seed dispersal, and trophic regulation (79). Therefore, the extinctions of the Pleistocene megafauna may have led to a cascade of other extinctions of coevolved tree species and insect communities that had performed a wide range of ecosystem services. However, the impact of these extinctions on global ecology has not been widely explored.

Did the Extinctions Affect Climate?

There are two possible ways that the extinction of the megafauna could have affected global climate: through changing atmospheric concentrations of CO_2 or methane or by modifying land surface properties, such as albedo or evapotranspiration. As an example, we can focus on Siberia, where previous modeling studies of afforestation have demonstrated strong albedo (18) and evapotranspiration feedbacks on climate (22).

Megaherbivores can play a dominant role in the maintenance of grassland against the expansion of trees in savannas (80, 81). One of the most comprehensive studies to document this was a recent aircraft campaign that flew over two similar African savanna ecosystems. The only difference between the two was that in one all animals >5 kg were excluded, whereas in the other, they were included. Woody cover increased ~9% over ~36 years when megafauna were excluded from a large African savanna (57, 82). This study confirms that elephants are chiefly responsible for the tree falls and can uproot up to 1,500 trees per elephant each year (83).

The mammoth steppes were remarkably productive, and researchers have hypothesized that they may have functioned like current African grazing systems (84), with abundant herbivores maintaining productivity by enhancing the rate of nutrient cycling (85, 86). Mammoth diet may have been similar to the diet of African elephants as excavated guts of frozen mammoths contain grass and a variety of common Pleistocene tree species, such as willow, birch, larch, and alder (87). Indeed, archaeological and pollen evidence indicate human colonization, mammoth extinction, and rapid increases in tree cover all took place within a narrow (<1,000 years) period of time in Alaska, Yukon Territory (56).

In the past, it was difficult to determine whether the vegetation change took place before or after the Pleistocene megafauna went extinct. The problem was compounded because megafauna remains are rare, especially in the lakes that generally archive late Quaternary pollen records. However, recently, a technique has been developed using *Sporormiella* spores to determine which came first: changing vegetation or the extinctions. These spores are associated with dung and tend to follow the end of Pleistocene megafauna population decline: They are abundant in late-glacial sediments, rare through the Holocene, and increase in abundance with the historic introduction of domestic grazers (88). A recent study used these spores to show that vegetation change followed the extinction of the Pleistocene megafauna in North America rather than preceding it as had been previously thought (81). Another study using *Sporormiella* data found that human arrival was correlated with the extinctions of the Australian megafauna, which then caused a major change in vegetation through a combination of reduced herbivory and increased fire (89). This new technique seems to promise clear answers that have been previously lacking. Although such a study has not yet been performed in Siberia, there is other evidence of a similar Siberian transition. Plant and animal DNA data from an ice core stretching back 400,000 years show an herb-dominated Siberian landscape during the last interglacial period compared with mainly shrub cover, with similar snow masking properties such as trees, today (90, 91).

However, there are a few papers that have cautioned against over interpreting the *Sporormiella* data and have suggested that there are still critical taxonomic investigations necessary for the proper interpretation of the data (92). Another study tested the reliability of *Sporormiella* as a proxy for herbivores using records from the South Island of New Zealand where extinctions occurred independently of major climate change. The study shows that *Sporormiella* spores from dry soils are a good proxy for herbivores, but spores from wet sites showed fluctuations with changing hydrological conditions (93). Overall, this area of research seems promising once certain methodological issues have been resolved, and this technique may help clarify the chronology of vegetation and megafauna changes in other regions of the world.

Pollen data indicate that birch tree abundance increased rapidly as mammoths went extinct. For instance, in Beringia within 1,000 years of mammoth extinctions, birch increased from ∼1% of land surface cover to 20% (15, 56). This is an increase of ∼1.1% per decade, comparable to the ∼2.4% increase per decade in African megafauna exclusions (82). There are few concrete ways to determine if mammoths and elephants had similarly destructive behaviors. Yet, a recently discovered well-preserved mammoth reveals the existence of a small opening on the side of its face, theorized to be the outlet of the temporal gland, which in living elephants produces an oily liquid called temporin (87). This indicates that mammoths may have exhibited behavior similar to modern elephants called musth, which is when the bulls become aggressive and knock down trees. Other indications of shared behavior between elephants and mammoths are rubbing rocks, which African elephants use to rub off mud and parasites, and these rocks have been found in California and are hypothesized to have been used by mammoths (87).

Post-megafaunal extinction tree growth in Siberia decreased surface albedo and increased evapotranspiration. Climate model simulations indicate that globally averaged surface temperatures would increase by 0.005°C for each percent increase of high-latitude forest cover or

Table 1 Estimate of the sign (increase or decrease) of the impact of preindustrial anthropogenic fire, the extinction of the Pleistocene megafauna, and preindustrial agriculture on global CO_2 concentrations, methane concentrations, albedo, and nutrient distributions[a]

Historical event	CO_2 concentrations (reference)	Methane concentrations (reference)	Albedo (reference)	Nutrient distribution (reference)
Preindustrial anthropogenic fire	Increase, but uncertain (31)	Increase, but uncertain ~5+ Tg yr^{-1} CH_4 ~1,000 BP[b] (41)	Uncertain[c] (31)	Increase, but highly uncertain
Extinction of the Pleistocene megafauna	Decrease, but uncertain (81, 89), also see (94)	Decrease ~9.6 Tg yr^{-1} CH_4 (2.3 to 25.5 Tg yr^{-1}) ~12,000 years BP (96)	Decrease 0.175°C, resulting in global warming for mammoth extinction[d] (15, 94)	Decrease, but uncertain (104)
Preindustrial agriculture	Increase 5–6 ppm (130)	Increase 4–14 Tg yr^{-1} CH_4 ~2,000 BP (123)	Increase 0.13–0.25°C, resulting in global cooling (131)	Decrease, but highly uncertain

[a] If available, we cite an estimate, but in most cases, the global impact is still uncertain.

[b] Global pyrogenic CH_4 impact is 25 Tg yr^{-1} from 0–1000 AD. Approximately 5 Tg yr^{-1} is the drop (assumed anthropogenic) after 1000 AD. The direct anthropogenic influence is not included in this review.

[c] The global impact is difficult to estimate because black carbon and other fire-related aerosols can have a complicated effect on ice and atmosphere albedo.

[d] This is the maximum impact scenario. However, this may decrease if the effect of temperate and tropical regions is included.

by 0.28°C with a 60% increase in tree cover. Siberia warmed by more than the rest of the world, by 1.33°C when tree cover increased 60% (15). Using models that predict the impact of elephants on trees (83), it was estimated that the extinction of the mammoths increased tree cover in Siberia by an average of ~28%, and this would have warmed high-latitude regions by ~0.5°C. Locally, this could have increased temperatures by up to 3°C (15). Another study, using a different coupled climate model [the University of Victoria Earth System Climage Model (UVic ESCM) with the Top-down Representation of Interactive Foliage and Flora Including Dynamics (TRIFFID) vegetation model] found a larger impact of the mammoth extinction on climate with a total global warming of 0.175°C for the maximum impact scenario (**Table 1**) (94). The timing of the extinctions was also investigated (10,000 years BP versus 15,000 years BP), and a later extinction event had a slightly larger impact (~0.20°C global change) owing to fewer continental ice sheets and more room for vegetation expansion. This biogeophysical warming from additional forest cover leads to more feedbacks, such as reduced sea ice and reduced high-latitude ocean albedo, which have also been demonstrated in several other idealized deforestation climate simulations (17, 20, 22). Recent additions of megafauna to a large "Pleistocene Park" in Siberia have led to increased land surface albedo and cooler temperatures (86).

How did potential increases in tree cover affect climate in other regions? There are now data from North America (81) and Australia (89) showing increased tree cover following the megafauna extinctions. As forests expand, global atmospheric CO_2 concentrations tend to decrease because forests hold more carbon in their biomass than grasses. However, in regions of abundant snowfall, such as boreal forests, global biophysical effects of deforestation tend to outweigh the global CO_2 effects (16). In North American temperate regions, it is unclear whether any biophysical forcing would outweigh the impact of the change in atmospheric CO_2 (16), whereas in regions without snowfall, such as Australia or South America, changes in atmospheric CO_2 would likely dominate over any biophysical effect because there is no snow on the ground. Therefore, the net global effect of the megafauna extinctions on climate may be smaller than that calculated just for Siberia. However, future climate simulations are necessary to understand the net climate impact. More data from regions of the world like Siberia and South America would be useful to better parameterize such simulations.

Methane

The extinction of the megafauna could also affect global climate by changing global methane concentrations. A large source of current annual methane emissions (~20%) is from domestic livestock through cellulolytic microbial fermentation during digestion. The current biomass of livestock owned by humans (e.g., cows, pigs) is ~5–10 times greater than the total biomass of the extinct megafauna (95), and therefore, their extinction may have also played a role in changing global methane concentrations. A recent study examined this possibility by determining the relationship between animal size and methane release (96). Using this relationship, the researchers calculated that the extinctions of the American Pleistocene megafauna decreased annual methane flux by ~9.6 Tg yr^{-1} (2.3–25.5 Tg yr^{-1}, possibly toward the higher range if global megafauna extinctions are included) (**Table 1**). This drop corresponded in time with a drop in methane concentrations of >180 ppbv as measured by ice cores at the onset of the Younger Dryas 12,800 years ago. It was estimated that the extinction of the megafauna could explain 12.5 to 100% of this decrease, suggesting that if the drop in methane led to the drop of global temperatures during the Younger Dryas, then early humans (if they are partially responsible for the extinctions) may have indirectly impacted global climate (96).

Other authors have noted that the direct radiative forcing effect (~−0.05 W m^{-2} using a common parameterization of radiative forcing) of this decrease in methane concentrations would have been too small to have caused the cooling during the Younger Dryas period (97). These authors instead suggest that decreasing temperatures led to the reduced methane concentrations seen in the ice-core record. Changes of that magnitude in methane during the Younger Dryas are not particularly rare, and the Greenland ice-core record has shown similar drops that were not contemporary with the megafauna extinctions and are instead closely associated with abrupt temperature changes (97). The extinction of the megafauna would have decreased atmospheric methane concentrations, but the exact quantity and its corresponding effect on climate is still unclear.

W m^{-2}: watts per meter squared

Metabolic scaling theory: the metabolic rate of organisms is the fundamental biological rate that governs most observed patterns in ecology

Did the Extinctions Affect Nutrient Distributions?

Could the extinctions of the megafauna have affected global environment and climate by disrupting nutrient cycling? Nutrients in Siberia have been hypothesized to have become less labile following the extinction of the megafauna (85, 86). Animals distribute nutrients through their bodies and feces. Larger animals may be disproportionally important in the spread of nutrients because they travel further distances and have longer food passage times than smaller animals (98, 99). If so, the extinction of the Pleistocene megafauna could have had a large impact on the distribution of global nutrients.

Researchers have long noted the ability of animals, such as seabirds, to concentrate nutrients, e.g., phosphorus (P) (100). More recently, there has been a growing body of literature documenting animal-mediated translocation of nutrients across gradients, thus providing fertility to nutrient-limited ecosystems (101–103). This process was demonstrated in Amazonia, where large quantities of P (similar in quantity to that arriving from atmospheric deposition) were transported by monkeys in seed biomass to lower-P regions (102).

A recent study used metabolic scaling theory to make predictions about the megafauna nutrient-spreading capacity and hypothesized that the extinction of the Amazonian megafauna led to a >98% reduction in the lateral transfer flux of the limiting nutrient P in Amazonia (104, 105). The investigators hypothesize that the Pleistocene megafauna extinctions resulted in major and ongoing disruptions to terrestrial biogeochemical cycling at continental scales, which led to increased nutrient heterogeneity globally (104). If there were large global changes to nutrient cycling, how would this affect the environment and climate? Nutrients are one of the strongest determinants of productivity and growth in ecosystems (106). It is an interesting and as yet unexplored question how such changes in nutrient distributions would have affected forest growth and net global carbon uptake.

Megafauna Extinctions and Agriculture

The extinction of the Pleistocene megafauna led to an increase in tree and shrub growth (81, 89), and the spread of agriculture often led to the replacement of forests with grasses (crops). It is unclear to what extent the climate impacts of the extinctions were offset by the development of agriculture (**Figures 1** and **2**).

The total large-body mammal biomass in the terrestrial biosphere decreased substantially following the extinctions of the Pleistocene megafauna (95) and only recovered to levels of the Pleistocene ∼1800 AD, with the expansion of the human population and domesticates, such as cattle. Over the past 200 years, total animal biomass has increased ∼sevenfold, vastly exceeding the preextinction Pleistocene steady-state total animal biomass. It has been hypothesized that fossil-fuel energy subsidies that began at around the start of the Industrial Revolution may have provided the additional energy needed to exceed the previous steady-state total animal biomass. This dearth of large-animal biomass during the early Holocene has interesting implications. For instance, following the extinctions, fewer herbivores led to suppressed global herbivory, and therefore, more NPP was available (estimated

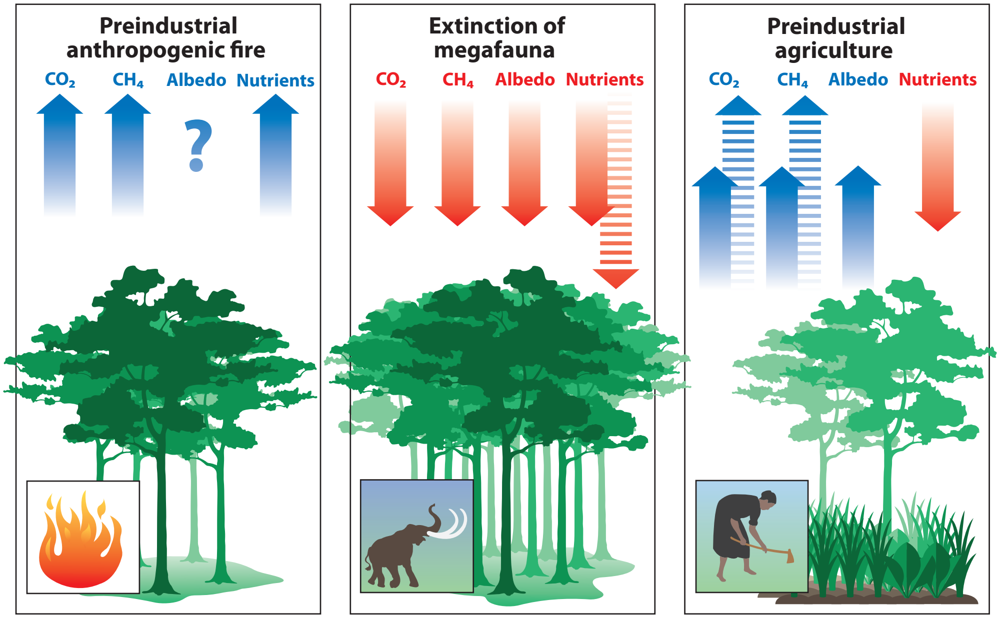

Figure 1

The estimated sign of the impact on climate and the environment of preindustrial anthropogenic fire (*left*), megafauna extinction (*middle*), and preindustrial agriculture (*right*). Red arrows indicate an estimated decrease, and blue arrows indicate an estimated increase. The larger striped arrows indicate a potential, but still uncertain, larger impact.

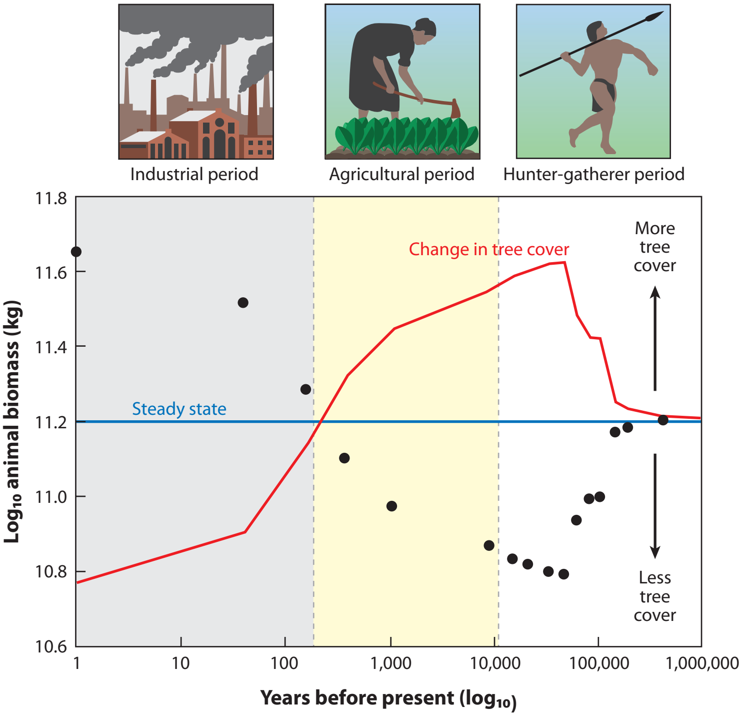

Figure 2

Change in the sum of human and nonhuman megafaunal biomass through time (*black circles*) [see Barnosky for methods (95)]. Qualitative estimate of the potential change in nonclimate-related tree and shrub growth (*red line*) assuming a negative linear relationship between woody plant cover and megafauna biomass; this does not include the climate-driven changes in increased tree growth between the Pleistocene and the Holocene (81, 89). The gray shaded area represents the industrial period, the yellow shaded area represents the agricultural period, and the white area represents the hunter-gatherer period.

using metabolic scaling to be ∼2.5% of global terrestrial NPP, ∼1.4 Pg C yr^{-1} of 56 Pg C yr^{-1}) (107). By 1850, this "liberated" NPP had been largely consumed through human agriculture, but NPP was still available in the western United States, South America, and Australia.

Agriculture developed independently in several continents ∼10,000 years BP near the onset of the Holocene (i.e., North America 10,000 years BP, South America ∼10,000 years BP, Near East ∼10,500 years BP, China ∼8,000 years BP) (108), which also roughly coincided with the extinctions of the Pleistocene megafauna. There are reasons to believe that agriculture developed more quickly in the absence of the megafauna because NPP became available for human utilization; the domestication of wild crop types was more feasible in the absence of megaherbivore competition; and hunting societies became more sedentary as their prey went extinct, the first step toward agriculture. The extinction of so many keystone herbivores may have accelerated the development of agriculture, specifically in the Americas where the largest number of extinctions took place, with humans essentially filling some of the empty herbivore niches (109).

GLOBAL CHANGE WITH PREINDUSTRIAL AGRICULTURE

It has been hypothesized that humans began to affect global climate through the development of agriculture thousands of years prior to the industrial era (12). Ice-core records show the current interglacial period had a methane peak ~11,000 years BP, which was followed by a steady decline in methane concentrations, similar to previous interglacial periods. However, in contrast to previous interglacial periods, methane concentrations begin to rise ~5,000 years BP, which had been attributed to the onset of rice farming in Asia, a potent producer of methane. Likewise, atmospheric CO_2 concentrations were declining 11,000 years BP, but then began to rise ~8,000 years BP. This is in contrast to previous interglacial periods in which atmospheric CO_2 concentrations continued to decline. The onset of farming may have released significant quantities of CO_2 and methane into the atmosphere, which may have caused these anomalous increases, and these increases may have warmed Earth sufficiently to avert a new ice age (12). The previous few interglacial periods lasted on average ~10,000 years. In the modern-day Holocene, roughly 12,000 years have passed since the previous ice age.

The ice age cycles are controlled by changes in Earth's orbital parameters (110). Did orbital parameters signify that we should have headed toward an ice age several thousand years ago? One study comparing current orbital parameters to those from previous interglacial periods showed that Earth's current orbital parameters (low eccentricity and weak precessional forcing) are most similar to an interglacial period called marine isotope state (MIS) 11, which took place ~430,000 years BP (111). Because this interglacial period lasted 28,000 years and our current interglacial period has lasted ~12,000 years, the investigators estimate that our current interglacial will last another ~16,000 years. This has been followed by modeling results showing that even with a declining trend in atmospheric CO_2, glacial inception did not occur (112).

Ice age cycles can be predicted either through a comparison with previous interglacial periods or through numerical simulations of orbital parameters. Most comparisons are with MIS 11 (111, 113), but other studies question whether this comparison is justified (114, 115). Rohling et al. (114) showed that, although MIS 11 did last >20,000 years, it was prolonged by weak insolation changes, and the actual peak in its ice-volume minimum/sea-level height maximum lasted ~10,000 years, similar to other major interglacial periods. The researchers suggest that all interglacial periods last ~10,000 years and that, therefore, the Holocene may have been expected to end 2,000–2,500 years BP. It is difficult to predict the onset of the next ice age with the past because no perfect insolation analog for the Holocene exists, and therefore, detailed numerical simulations are also used. Experiments with various numerical models of glacial cycles show that the next glacial inception may still be delayed by several tens of thousands of years, even with the assumption of a decline in greenhouse gas concentrations during the Holocene (116). A more recent study hypothesizes that the minimum age of a glacial inception is constrained by the onset of bipolar-seesaw climate variability and suggests that the end of the current interglacial would occur within the next 1,500 years if atmospheric CO_2 concentrations do not exceed 240 ppmv (117). In summary, predicting ice age cycles is not yet an exact science, and there remains a possibility that small disturbances may, at strategic times, delay glacial events by several thousands of years, which could support the early Anthropocene hypothesis (116).

Methane and Carbon Dioxide Anomalies

Was there a methane anomaly caused by the anthropogenic production of rice? Two mechanisms have been proposed to explain the increase in methane concentrations ~5,000 years BP, an increase in early rice cultivation or an increase in methane from either tropical (118) or boreal wetlands (119). Recent speleothem data show a gradual decrease in Northern Hemisphere monsoon intensity and a gradual increase in Southern Hemisphere monsoon intensity in the Holocene. This led to predicted decreases in Northern Hemisphere methane emissions and increases in Southern Hemisphere emissions (120). It had been hypothesized that, although Amazonian source emissions were likely increasing, northern emissions may have overwhelmed those from the Amazon (115). This was tested using an Earth System modeling approach, which showed changing orbital parameters in the mid-Holocene led to increased emissions of methane mainly owing to wetlands in the Southern Hemisphere tropics (121). Crucially, this model accurately predicted decreased global methane concentrations during the previous interglacial period. The researchers therefore conclude that no early agricultural sources are required to explain the early methane record (121). The theory is still contentious, and data from 311 archaeological sites in rice-growing regions of China show an almost tenfold increase in rice production compared with previous millennia, which supports a larger early methane emission from human activities (122, 123).

What caused the rise in CO_2 ~8,000 years BP (~40 ppm anomaly) that was not seen in previous interglacial periods? This rise was initially hypothesized to be caused by the regrowth of forests into formerly glaciated areas, followed by a readjustment of ocean chemistry. Forest regrowth following glacial retreat initially would have both reduced atmospheric CO_2 and increased the carbonate ion content of the ocean, which increased the calcite accumulated in the ocean's sediments. This drawdown would have caused the sediment transition zone to shoal with a time constant of ~5,000 years. This then decreased ocean carbonate ion concentrations, leading to a rise in ocean CO_2 content, which released a burst of CO_2 to the atmosphere (113, 124). A second hypothesis was that coral reef formation accelerated ~7,000 years BP after oceans stabilized at peak interglacial sea levels. Building such reefs removed carbonate ions from the ocean, which left the ocean richer in CO_2, and thus more CO_2 was transferred to the atmosphere (125). Finally, the increase in CO_2 could have been the result of increased deforestation following an acceleration of farming (12).

However, there have been several criticisms of this last anthropogenic hypothesis. First, it was noted that the amount of deforestation necessary to cause such a change in atmospheric CO_2 concentrations (a 40-ppm anomaly) is enormous because the oceans would absorb a substantial portion of the released CO_2. Next, if the increase in atmospheric CO_2 was from deforestation, we would expect a change in the ratio of two common carbon isotopes, ^{13}C and ^{12}C. For instance, stable isotope data from an Antarctic ice core showed a small average decrease in $\delta^{13}C$ of ~0.05‰, which would limit the estimated net emission of terrestrial carbon to 50 gigatons (Gt), ~a seventh of the necessary amount. This group then concluded that most of the Holocene CO_2 increase came not from deforestation but from emissions of inorganic carbon from the oceans (126).

Even at earlier periods, there was a large amount of deforestation because per capita land use has decreased as farming has become more intensive through time. There are estimates that owing to less intensive land use than in the past, total land clearing could have released ~340 Gt C because of land-use change (127, 128). Another recent study found a cumulative net uptake of 272 Gt C in peatlands during the early Holocene (11,000–7,000 years BP) (129). Peat carbon has a $\delta^{13}C$ isotopic value of −27 (versus −25 for terrestrial C_3 vegetation) and therefore, a burial of 270 Gt C peat plus a release of 330 Gt C from the removal of forests could also explain the −0.05‰ isotopic signature. This estimate of 330 Gt C is close to that of the 340 Gt C because of less intensive land use in the distant past (127). Therefore, the researchers estimate that of the 40 ppm anomaly, 23–24 ppm could be the result of deforestation, 9 ppm could be from ocean solubility feedback, and the remaining could be from the Southern Ocean (115).

Although there is still much debate on the validity of the early Anthropocene hypothesis, climate simulations clearly show that land-use change over time has impacted global climate.

Transient model simulations show anthropogenic deforestation increased atmospheric CO_2 by 5–6 ppm by 1850 (**Table 1**) (130). A compilation of six Earth System models of intermediate complexity estimated a decrease in global mean annual temperature in the range of 0.13 to 0.25°C in response to the forcing, mainly associated with albedo changes, of historical (since 1000 AD) deforestation (**Table 1**) (131). Therefore, humans began affecting climate through land-use change prior to the industrial era, but whether the effect was small or large enough to have prevented an ice age is still debatable.

Changes in Atmospheric Carbon Dioxide Caused by Global Pandemics

Finally, it has hypothesized that fluctuations in atmospheric CO_2, such as during the "Little Ice Age," may have been caused by large-scale disturbances to human populations, e.g., the bubonic plague (12). The Little Ice Age was first hypothesized as a 1.2–1.4°C decrease in temperature in England between 1200 and 1600 AD (132). Modern simulations estimate that Northern Hemisphere temperatures cooled by ~0.15°C (133) to ~0.25°C (134) relative to average temperatures during this period.

What caused this Little Ice Age? One possibility is that global pandemics impact global climate because as humans die, farmland is converted to forest, decreasing atmospheric CO_2 concentrations (12). The bubonic plague, which struck Europe from 1347–1352 AD, may have been the largest pandemic in history, causing the death of an estimated 40–50% of the population. The large decrease in population led to abandoned farmland, which was eventually replaced by forest. This increase in forest cover corresponds in time to an anomalous decrease in atmospheric CO_2 concentrations (12). Forest cover reached a maximum in ~1400 AD following substantial abandonment of farmlands in Europe (135). However, other studies have found that decreased temperatures during the Little Ice Age were mainly caused by solar activity (75%) and volcanic activity (25%) (136).

Were there any human catastrophes, either warfare or pandemics, that had a big enough impact on land surface cover to affect global climate? It is a difficult question to answer, but there have been several studies that have looked into this possibility. Other authors specifically looked for a climate impact of the conquest of the Americas (~1500 to ~1750 AD) (137), and they estimate that there was enough forest regeneration during this period to reduce atmospheric CO_2 levels. This study, as well as Ruddiman (12), used similar methodologies, whereby first, land use per person was determined, then, based on estimated population decreases, abandoned agricultural area was determined. This abandoned agricultural area was converted to carbon by multiplying by a fixed estimate of regional carbon density per unit area of forest. Then, this carbon either all remained in the atmosphere or some equilibrated with the oceans.

However, another paper with a more complex methodology found that no major perturbations, such the Mongol invasion (~1200 to ~1380 AD), the Black Death (~1347 to ~1400 AD), the conquest of the Americas (~1519 to ~1700 AD), or the fall of the Ming Dynasty (~1600 to ~1650 AD), had any significant impact on global atmospheric CO_2 concentrations (atmospheric CO_2 impact <1 ppm) (138). This study showed that, because forests need 50–100 years to regrow following deforestation, abandonment does not lead to an instantaneous gain of all vegetation carbon previously lost. Deforestation transfers living biomass to soil carbon pools, where it will increase heterotrophic respiration rates. During shorter perturbations, such as during the Black Death and the fall of the Ming dynasty, heterotrophic respiration rates remained high enough to offset the carbon uptake in regrowth. The other two events were long enough to have a net decrease in atmospheric CO_2, but the effect was small because much carbon equilibrates with the ocean and the land surface, and other sources and sinks of CO_2 continue in the rest of the world, which may swamp out any signal from a local event. Therefore, neither was big enough to be resolved within the ice-core signal (>1 ppm), and the authors conclude that anthropogenic perturbations were not of sufficient magnitude to cause the observed changes of CO_2 in the ice-core records.

These studies focused on the atmospheric signal, but, as we have seen previously, biophysical impacts could have been as important as the carbon impact. Biophysical effects with deforestation tend to cause cooling, whereas the carbon effects tend to lead to warming. For instance, biophysical cooling from deforestation has been hypothesized to have caused the long-term cooling over the past 1,000 years (139), although other studies calculate a smaller effect (140). All studies, however, agree that there was the potential for major regional changes in the surface energy balance of up to -2.0 W m^{-2} as a result of major epidemics and warfare (140). The net effect of preindustrial agriculture from several studies was compiled, and the global average was found to range between -0.04 and -0.06 W m^{-2} (131, 140, 141).

CONCLUSION

Did humans affect global climate and the environment before the industrial era? The potential earliest human effect on climate is due to fire because humans used fire prior to the existence of modern *Homo sapiens*. However, the question in this review is not whether humans used fire, but whether its effect on the environment was globally significant. To have more than a transitory effect on climate, fire must change the ecosystem structure. Many early studies focused on Australia, which is the continent most susceptible to burning and with a long history of human presence. Early evidence and climate theories predicted that human-induced fires may have changed ecosystem structures, which modified climate and increased aridity (13, 14). Evidence now suggests that early human influence from using fire in Australia may have been small (37) and that such changes in vegetation were unlikely to have a large effect on climate (47). Also, fire incidence likely peaked ~2,000 years BP when human populations were much smaller, but climatic conditions were better for fire (34), suggesting broadly that climate has a greater impact than humans on fire to modify ecosystems and change climate.

The extinction of the megafauna and early agriculture both impacted preindustrial climate (**Table 1**). However, instead of viewing the climate impacts of these two events separately, we can instead view them as one event. Proboscideans and other megafauna have the capabilities of transforming ecosystems (57, 81), but they were largely extinct by the start of the Holocene (58). Agriculture also began independently in several continents around the time of the extinctions, although it was initially concentrated in small patches (108). Therefore, for much of the early to mid-Holocene, there were both few agriculturists and few megafauna (95) to control forest expansion, so forests may have expanded and impacted climate (**Figure 2**). For instance, one study estimated the megafauna extinctions could have warmed the planet by as much as ~0.175°C (94), whereas land-use change from agriculture may have cooled the planet by a similar amount (0.13–0.25°C) (**Table 1**) (131). Likewise, methane concentrations decreased by ~10 Tg yr^{-1} following the megafauna extinctions (96), but they increased by approximately that much because of agriculture ~2,000 years BP (**Table 1**) (123). The Pleistocene megafauna extinctions may have led to forest expansion and a slight planetary warming, but as preindustrial human populations expanded, forest cover was reduced, and there was a slight planetary cooling.

Preindustrial anthropogenic impacts also could have caused major climate changes. There is still great uncertainty in the prediction of glacial and interglacial cycles, and there remains a possibility that small disturbances may, at strategic times, delay glacial events by several thousand years (116). It was initially proposed by Ruddiman (12) that preindustrial agriculture caused a delay in the next ice age by increasing atmospheric concentrations of methane and CO_2 (12). The evidence is still clearly mixed regarding the role early agriculture played in preventing an ice age, but it has not yet been disproven. Likewise, could the extinction of the high-latitude megafauna have disrupted glacial inception? There is preliminary evidence that high-latitude regions, such as Siberia, remained grasslands during previous interglacial periods (91). In some ways, this is more plausible than the agriculture hypothesis because the major climatic influence from the extinctions would have potentially taken place in high-latitude regions where glaciers would have begun to form (94). However, at this time, there is no evidence to support such a hypothesis, but if future evidence is found to support either hypothesis more fully, then either scenario would clearly constitute a preindustrial start to the Anthropocene.

More data and climate simulations are now needed to test these predictions, especially in the case of the megafauna theories, which are supported by less data. There exist several potential ways of testing these theories by making use of exclosure experiments (57) or by experimentally adding large herbivores to ecosystems (86, 142). More useful data could also come from a comparison of nutrient cycling and forest structure in South America, with the largest impacts from megafauna extinctions, and Africa, with the fewest impacts.

This review suggests that current evidence indicates a smaller role for anthropogenic fires on preindustrial climate (34, 37, 47). The climate impact of the extinction of the megafauna and early agriculturists ranges from small to large (12, 94, 130). If future evidence supports a large role, then the Anthropocene began during the preindustrial era. This review also highlights the interesting correlations of the climate impacts of megafauna and early agriculturalists (**Figures 1** and **2**). As total large-animal biomass (95) and total NPP consumption (107) recovered through the Holocene, forest cover was reduced and methane emissions increased. Therefore, prior to the industrial era, the largest ecological and climate anomaly may have been associated with forest expansion during the early and mid-Holocene owing to the dearth of large animals following the extinctions but before a sufficient number of agriculturalists could expand to fill that role.

SUMMARY POINTS

1. Humans may have affected early climate through preindustrial anthropogenic fire, agriculture, and the extinction of the Pleistocene megafauna.
2. Prior to the industrial era, humans affected the climate mainly through changing the land surface, which affects atmospheric CO_2 concentrations, albedo, evapotranspiration, and surface roughness.
3. The impact of anthropogenic fire on climate may have been small because where impacts were once thought to be large, such as in Australia, the evidence now suggests a smaller effect. Also, fire likely peaked ~2,000 years BP when human populations were much smaller, but climatic conditions were better for fire, meaning broadly that climate had a greater impact than humans on fire.
4. Both preindustrial agriculture and the extinction of the megafauna may have affected climate, but the effects may have been offsetting. For instance, climate simulations indicate that megafaunal extinctions may have led to a slight global warming, but later, agriculture led to a slight global cooling.
5. Prior to the industrial era, the real ecological and climate anomaly may have been during the early and mid-Holocene when there were few megafauna and agriculturalists to reduce forest expansion.

FUTURE ISSUES

1. It is important to further resolve which came first: changing vegetation or megafaunal extinction in several regions of the world, especially in Siberia and South America, possibly using *Sporormiella* data.
2. The creation of global maps of estimated preindustrial anthropogenic burned areas can be used in general circulation models to better estimate the global climate impact of preindustrial anthropogenic fire.
3. Likewise, the creation of a global map of the estimated impact on forest cover of megafaunal extinctions can be used in general circulation models to better estimate the global climate impact of the megafaunal extinctions.
4. It is important to better quantify the impact of preindustrial agriculture and fire on global nutrient distributions.
5. It is important to get more data on the impact of megafauna on ecosystems using experimental approaches, such as exclosure experiments (57), or by experimentally adding large herbivores to ecosystems (142).
6. Finally, it is important to better understand what drives the transition between interglacial and glacial periods.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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