Global archaeological evidence for proboscidean overkill

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One million years ago, proboscideans occupied most of Africa, Europe, Asia, and the Americas. Today, wild elephants are only found in portions of sub-Saharan Africa and South Asia. Although the causes of global Pleistocene extinctions in the order Proboscidea remain unresolved, the most common explanations involve climatic change and/or human hunting. In this report, we test the overkill and climate-change hypotheses by using global archaeological spatiotemporal patterning in proboscidean kill/scavenge sites. Spanning ≈1.8 million years, the archaeological record of human subsistence exploitation of proboscideans is preferentially located on the edges of the human geographic range. This finding is commensurate with global overkill, suggesting that prehistoric human range expansion resulted in localized extinction events. In the present and the past, proboscideans have survived in refugia that are largely inaccessible to human populations.

archaeology | Pleistocene extinctions | proboscideans

Proponents of the overkill hypothesis argue that the global rash of large mammal extinctions that occurred during the Quaternary can be explained by a single factor: the arrival of a novel and efficient predator to new regions, that predator being prehistoric humans armed with a Stone Age hunting technology (1–3). This hypothesis is a difficult one to test and one that has often hinged on the relative timing of two events: (*i*) the local arrival of *Homo* and (*ii*) the local extinction of Pleistocene fauna. But even in the New World, where for more than a half-century the near synchrony of these two events has been known, the causes of Pleistocene extinctions remain unresolved (1–8). Confounding simple explanation in the New World case is the similar timing of a third event, the onset of the Younger Dryas stadial, a sharp reversal to glacial climate that coincides with New World large mammal extinctions (9).

If mammalian Pleistocene extinctions resulted from human overkill as humans expanded their range across the globe, now extinct large mammals should have experienced complementary range contractions. As simple as this prediction is, it is far from simple to test, because it could require precisely dating the first appearance of humans and the last appearance of extinct mammals across the globe. Although the timing of Late Pleistocene extinctions is fairly well known for some species in some parts of Europe, Asia, Australia, and the Americas (5, 10–14), the timing of extinction events predating 40–50 ka (thousand years B.P.) (the effective temporal limit of ^{14}C dating) are less well known. However, we argue that by using only spatiotemporal patterning in archaeological sites demonstrating the spatiotemporal contemporaneity of humans and extinct fauna, it is possible to test the overkill and climate hypotheses without knowing the precise timing of extinction events.

The overkill and climate-change hypotheses can be expressed as two simple alternative scenarios to illustrate this point (Fig. 1). Consider a predator and prey in a confined space. In the case of overkill, the predator expands its range and, while doing so, hunts the prey to extinction, which is only possible if the predator has the ability to switch prey: something humans have the capacity to do. In the case of climate change, the predator

expands its range into that of the prey but does not drive it to extinction. Instead, the predator and prey spatially coexist until a later time when climate change causes the prey to suffer extinction. These two scenarios create dramatically different spatiotemporal patterning in the distribution of kill sites (Fig. 1). In the first case, predation events will occur only along the frontier of dispersal. In the second case, predation events will occur along the frontier and well behind it. In the case of a latitudinal migration, when sites are plotted with respect to age and latitude with climatic extinctions, a wedge-shaped distribution is expected; in the case of overkill, a linear or curvilinear distribution is expected (Fig. 1*b*). Therefore, it should be possible to distinguish between these two hypotheses by using only spatiotemporal patterning in archaeological sites showing overlap between hominid predators and now extinct prey.

In this simplified system, the contrasting predictions of the overkill and climatic hypotheses should be easily detectable archaeologically, assuming a sufficiently large sample of sites spread through the space-time of colonization. In actuality, global colonization by *Homo* was likely not so simple. It involved multiple species of hominids, whose ranges expanded and contracted in part due to glacioclimatic fluctuations and related ecological shifts, particularly along northern frontiers (15–18). Presumably, when hominid ranges contracted, prey ranges would have expanded complementarily. Therefore, we might expect kill sites to appear at multiple times in high latitude regions where hominid population densities fluctuated. Also, if relatively stable ecological/climatic boundaries to hominid range expansion existed, it is possible that prolonged periods of predator–prey interaction took place in regions situated at the interfaces of human and mammalian ranges. Finally, in the case of extremely rapid range expansion by humans, as in the case of New World colonization, the "frontier" may not take the form of simple linear front (19), and rapid colonization events are not expected to produce archaeologically detectable space- and time-transgressive evidence (20). Therefore, distinguishing between these two hypotheses archaeologically may not be as straightforward as in the ideal case outlined above. Nonetheless, this framework provides a starting point for distinguishing between the overkill and climate hypotheses by examining global spatiotemporal patterning in archaeological sites evidencing use of extinct mammals.

Extinctions in the order Proboscidea provide an excellent test case for examining the global overkill hypothesis for three reasons. First, relatively abundant evidence of human–proboscidean interactions is known archaeologically. Second, because of large body size, proboscideans are especially prone to extinction from predation pressure and other anthropogenic impacts (21, 22). Third, 1 million years ago, proboscidean taxa occupied most of Africa, Eurasia, and the Americas, with species eventually suffering extinction in all regions except portions of
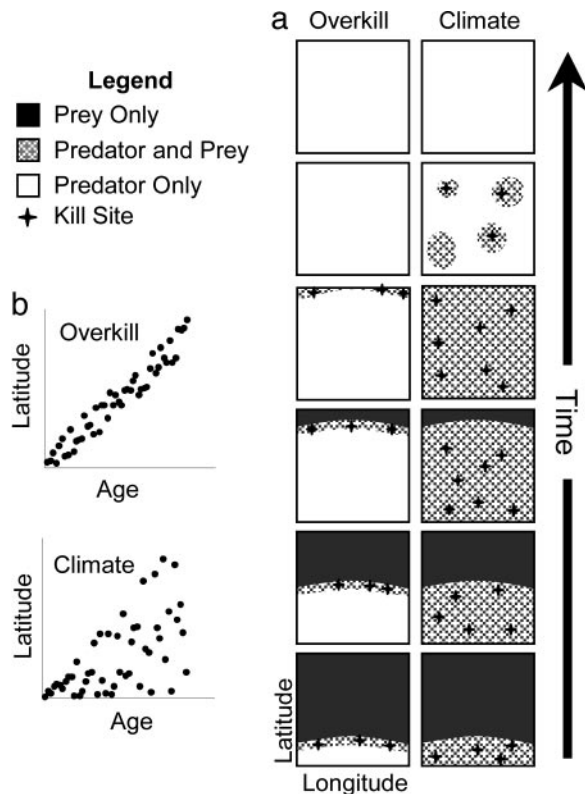
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Fig. 1. Schematic representation of spatiotemporal patterning in archaeological kill sites predicted by the overkill and climate-change hypotheses. (*a*) For overkill, a predator invades the range of prey and concomitantly hunts it to extinction. For climate change, the predator invades the range of the prey but does not hunt it to extinction. Instead, climate change results in extinction at a later time. (*b*) The predicted spatiotemporal distribution of kill sites plotted with respect to age and latitude for the overkill and climate-change hypotheses.

South Asia and sub-Saharan Africa. We are not proposing that evidence in support of extinction of proboscideans due to overkill or climate change can be extended to the total array of taxa that suffered extinction during the Pleistocene. Instead, we are only examining extinction within one mammalian order, and we agree with recent reports by researchers who suggest that Pleistocene extinction for all taxa may not have a common cause (4–6).

Identifying Spatiotemporal Overlap of *Homo* and *Proboscidea*

Critical to testing the climate change and overkill hypotheses in this framework is the identification of the spatial and temporal overlap of populations of proboscideans and *Homo*. Although proboscidean remains are common in Eurasian Paleolithic sites, establishing spatiotemporal contemporaneity is not a simple matter of presence or absence in faunal assemblages, because past humans used proboscidean bone for fuel, technological raw material (e.g., carved and flaked bone tools and ornaments), and architectural purposes (23), all of which can postdate local extinction. By contrast, a considerably stronger argument for spatiotemporal contemporaneity can be made through the identification of subsistence use (whether hunting or scavenging), which is most likely to occur shortly after the death of an animal. Unfortunately, identification of subsistence use of proboscideans is complicated, because death and butchery may not leave clear indications of human involvement (e.g., cut marks or impact fractures) (24). To overcome this problem, we rely on kill/scavenge sites, which typically contain small numbers of animals

(usually <10), often partially articulated and tightly associated with <10 to a few hundred artifacts (8).§

From Africa, Europe, Asia, and the Americas, we identified a total of 41 sites, localities, or components that provide strong evidence of spatiotemporal overlap of humans and proboscideans (Table 1 and Fig. 2). These sites range in age from ≈1.8 ma (million years B.P.) to 10 ka, with 12 dating to the Lower Paleolithic, 4 dating to the Middle Paleolithic, 7 dating to the Upper Paleolithic and Later Stone Age, and 18 dating to the New World Paleoindian period. All five continents are represented in the sample, but North America and Europe are somewhat overrepresented relative to land area.

Human Global Colonization and Proboscidean Exploitation

The biogeographic history of the genus *Homo* is characterized by range extensions into increasingly extreme environments. The earliest hominids of the genus *Homo* appear in the fossil record *circa* (*ca.*) 2.4 ma in Africa (27). Based on marked changes in behavior and cranial and postcranial morphology, the evolution of *Homo erectus* 1.9–1.8 ma is believed to mark a shift in human evolution from hominid species primarily dependent on plant foods to one in which carnivory greatly increased in importance (27). The first archaeological evidence of subsistence exploitation of proboscideans (*Deinotherium*) in Upper Bed I of Olduvai Gorge at *ca.* 1.8 ma is spatially and temporally coincident with the appearance of *H. erectus* in the fossil record (see Table 2, which is published as supporting information on the PNAS web site, for site-specific references). Additional evidence for use of proboscideans (*Elephas*) in the Early Pleistocene is restricted to sub-Saharan East Africa, where four additional localities are known.

Although *H. erectus* dispersed into Asia as early as 1.8 ma, hominid occupations of regions outside Africa during the Early Pleistocene appear to have been intermittent and limited to low latitude (<45° N) areas (15). Long-term resident populations were probably only established in western Asia between 1.0 and 0.8 ma (28). The earliest evidence of proboscidean (*Elephas*) exploitation outside Africa dates to the early Middle Pleistocene at Gesher Benot Ya'qov, in the Jordan Valley of Israel.

Initial hominid dispersal into Western Europe dates between *ca.* 1.0 and 0.78 ma (15, 29, 30). Occupation of both Northern and Southern Europe began by at least 500 ka, with a hominid presence extending up to *ca.* 52° N latitude in temperate Atlantic Europe (15). Continuous occupation of Europe during the Middle Pleistocene was likely restricted to low-latitude refugia, with hominid incursions into Northern Europe occurring during interglacials (17). Evidence of Lower Paleolithic exploitation of *Elephas* in the Middle Pleistocene is concentrated in the Mediterranean region, where five occurrences are known. A sixth, although poorly dated, site is located in southern Great Britain.

Cold-tolerant archaic *Homo sapiens* may have slightly extended its range northward during oxygen isotope stage (OIS) 5 (130–74 ka) (31, 32), but population densities at high latitudes likely decreased during OIS 4 (73–59 ka) as later seen for modern humans in Late Pleistocene, high-latitude Eurasia (Fig. 3) (16). Four occurrences of proboscidean (*Elephas* and *Mammuthus*) exploitation are known from the Middle Paleolithic dating to late OIS 6 and early OIS 5. Spatially, these sites are concentrated in Northwestern and North Central Europe.

Colonization of the high arctic and the New World by *Homo* postdates the evolution of behaviorally modern *H. sapiens* in Africa *ca.* 120 ka. Although anatomically modern *H. sapiens*

Table 1. The known global sample of proboscidean kill/scavenge sites

Site and locality	Country	Latitude	Longitude	Phase	Age	Taxon
FLK North Upper Bed I	Tanzania	3° S	35° E	LP	1.7–1.8 ma	*Elephas recki*
FLK North Lower Bed II	Tanzania	3° S	35° E	LP	1.2–1.7 ma	*Deinotherium sp.*
Barogali	Djibouti	11° N	42° E	LP	1.3–1.6 ma	*E. recki*
Olorgesaille Member I Site 15	Kenya	2° S	36° E	LP	.974–.992 ma	*E. recki*
Mwanganda's Village	Malawi	10° S	34° E	LP	0.6–1.2 ma (?)	*Elephas sp. (?)*
Gesher Benot Ya'aqov	Israel	33.0° N	35.6° E	LP	*ca.* 750 ka	*E. antiquus*
Notarchirico	Italy	41° N	16° E	LP	600–740 ka	*E. antiquus*
Aridos I	Spain	40.3° N	3.5° W	LP	300–500 ka (?)	*E. antiquus*
Aridos II	Spain	40.3° N	3.5° W	LP	300–500 ka (?)	*E. antiquus*
Ealing	U.K.	51.5° N	0.3° W	LP (?)	300–500 ka (?)	*Elephas sp.*
Ambrona	Spain	41° N	2.5° W	LP	200–400 ka (?)	*E. antiquus*
Torralba	Spain	41° N	2.5° W	LP	200–400 ka (?)	*E. antiquus*
La Cotte de St. Brelade Level 3	U.K.	49.2° N	2.3° W	MP	120–200 ka	*Mammuthus primigenius*
La Cotte de St. Brelade Level 6	U.K.	49.2° N	2.3° W	MP	120–200 ka	*M. primigenius*
Lehringen	Germany	52.8° N	9.5° E	MP	*ca.* 120 ka	*E. antiquus*
Gröbern	Germany	51.8° N	12.5° E	MP	*ca.* 120 ka	*E. antiquus*
Lake Nojiri	Japan	36.8° N	138.2° E	UP (?)	33–39 ka	*Elephas naumanni*
Nowa Huta	Poland	50° N	20° E	UP	35 ka (?)	*M. primigenius*
Skaratki	Poland	52.0° N	19.8° E	UP (?)	29–32 ka (?)	*M. primigenius*
Halich	Ukraine	49.1° N	24.7° E	UP	20–24 ka	*M. primigenius*
Shikaevka II	Russia	56.3° N	66.4° E	UP	18 ka	*M. primigenius*
Lugovskoye	Russia	61.0° N	68.5° E	UP	*ca.* 13.5 ka	*M. primigenius*
Hebior	U.S.A.	43° N	88° W	PI	12.5 ka	*M. primigenius*
Taima-Taima	Venezuela	11° N	70° W	PI	12.5 ka (?)	*Haplomastodon sp.*
Colby	U.S.A.	44.0° N	107.9° W	PI	11.2 ka	*Mammuthus columbi*
Domebo	U.S.A.	35.0° N	98.4° W	PI	11.1 ka	*Mammuthus imperator*
Lubbock Lake	U.S.A.	33.6° N	101.9° W	PI	*ca.* 11 ka	*M. columbi*
Blackwater Draw Mammoth Pit	U.S.A.	34.3° N	103.3° W	PI	*ca.* 11 ka	*M. columbi*
Blackwater Draw El Llano Dig No. 1	U.S.A.	34.3° N	103.3° W	PI	*ca.* 11 ka	*M. columbi*
Escapule	U.S.A.	31.6° N	110.2° W	PI	*ca.* 11 ka	*M. columbi*
Kimmswick	U.S.A.	38.4° N	90.4° W	PI	*ca.* 11 ka	*Mammut americanum*
Miami	U.S.A.	35.6° N	100.6° W	PI	*ca.* 11 ka	*M. columbi*
Naco	U.S.A.	31.4° N	109.9° W	PI	*ca.* 11 ka	*M. columbi*
Lehner	U.S.A.	31.3° N	110.1° W	PI	10.9 ka	*M. columbi*
Murray Springs	U.S.A.	31.6° N	110.2° W	PI	10.9 ka	*M. columbi*
Lange-Ferguson	U.S.A.	43° N	103° W	PI	10.8 ka	*Mammuthus sp.*
Dent	U.S.A.	40.3° N	104.8° W	PI	10.8 ka	*M. columbi*
Iztapan I	Mexico	19° N	99° W	PI	10–11 ka (?)	*M. imperator*
Iztapan II	Mexico	19° N	99° W	PI	10–11 ka (?)	*M. imperator*
Taguatagua-II	Chile	34.5° S	71.2° W	PI	10.3 ka	*Stegomastodon humboldti*
Zoo Park	Namibia	22.5° S	17.1° E	LSA	10 ka (?)	*Loxodonta sp. (?)*

Ages <40,000 years B.P. are presented in radiocarbon years B.P. LP, Lower Paleolithic; MP, Middle Paleolithic; UP, Upper Paleolithic; PI, Paleoindian; LSA, Later Stone Age; (?), uncertain phase, age, or taxon.

dispersal into southwest Asia occurred as early as 100 ka, behaviorally modern humans likely arrived during OIS 3 at ≈50–40 ka (35). Initial occupation of the high arctic (above 60° N) is dated to 37.4–36.6 ka at Mamontovaya Kurya (36) and at the Yana RHS site by *ca.* 28 ka (37), but radiocarbon-dated archaeological deposits from Siberia support the conclusion that sustained human presence in the high arctic coincided with increased human population densities early in the postglacial period <20 ka (Fig. 3). Before the Last Glacial Maximum (LGM), Upper Paleolithic evidence of *Mammuthus* exploitation in Europe is limited to three occurrences in continental Eastern Europe at ≈50° N latitude. Early Upper Paleolithic exploitation of proboscideans (*Elephas*) in Asia is seen only at Lake Nojiri in Japan. This site, dating to *ca.* 33 ka,

is situated at the relatively southerly latitude of ≈37° N, but, importantly, it likely corresponds with the earliest occupation of Japan by *Homo* (38).

Frequencies of radiocarbon-dated archaeological components from Siberia indicate human population expansion into high-latitude regions after the LGM (Fig. 3), and the colonization of the Americas (*ca.* 12.5 ka) was likely an extension of this event. Spatially and temporally associated with this major episode in human demic expansion are 20 occurrences of proboscidean (*Mammuthus*, *Mammut*, *Haplomastodon*, and *Stegomastodon*) exploitation stretching in space from Arctic Western Siberia to North and South America. Despite spanning a huge geographic range, these sites date within a very narrow time range between *ca.* 13.5 and 10.3 ka. Notably, the

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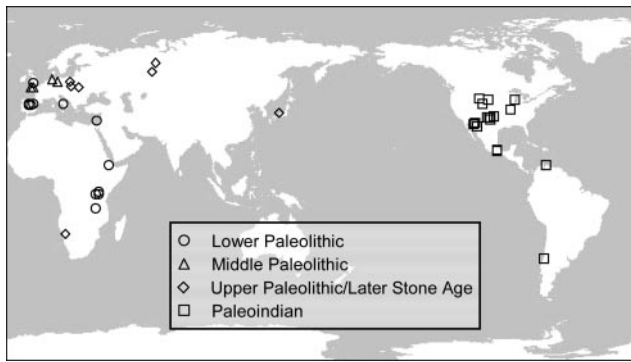
Fig. 2. The global spatiotemporal distribution of proboscidean kill/scavenge sites. The location of multicomponent and multilocality sites are shown slightly offset from actual positions to indicate spatially congruent occurrences.

youngest (although very poorly dated) site in our sample at 10 ka is located in southern Africa, attesting to the Holocene survival of *Loxodonta*.

Overkill or Climate Change?

Strong spatiotemporal patterning supporting only overkill is evident in the data set. In the Old World, a statistically significant (Pearson's $r^2 = 0.783$, $P < 0.001$) linear latitudinal trend is seen in the Paleolithic, with a mean rate of range expansion of 4×10^{-5} degrees of latitude per year (Fig. 4a). Importantly, during this time, sites cluster on the edge of the *Homo* range with no evidence of proboscidean exploitation significantly behind it. In the latest Pleistocene, this trend continues into the New World, where widespread evidence of proboscidean exploitation correlates only with the initial colonization event.

Additional statistical analysis indicates that these patterns cannot be explained by small sample size (Fig. 4b). The total archaeological sample was divided into five temporal groups: Early Lower Paleolithic (2–0.78 ma; $n = 5$), Late Lower Paleolithic (780–250 ka; $n = 7$), Middle Paleolithic (250–50 ka; $n = 4$), Upper Paleolithic (50–13 ka; $n = 6$), and Paleoindian/Later Stone Age (13–10 ka; $n = 19$). Based on the
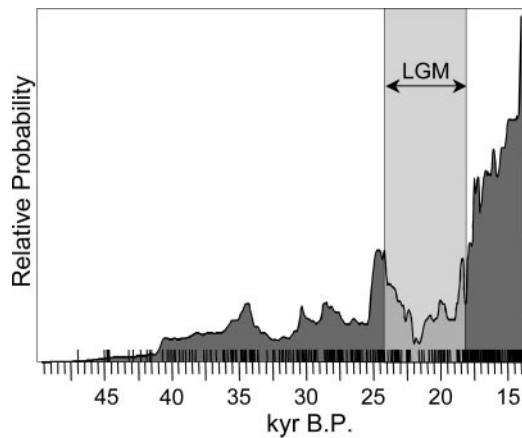
Fig. 3. Calibrated age probability distribution [created by using CALPAL software (33)] for Siberian archaeological ^{14}C bone and charcoal dates ($n = 369$; data from ref. 34) from Paleolithic Siberia. Relative probability serves as a proxy for occupation intensity, which is indirectly related to regional population size. Occupation intensities generally increase geometrically through time, with significant declines occurring during the LGM (23–18 ka). With northward population expansion after the LGM, proboscidean exploitation is seen in an area stretching from Arctic Siberia to the New World.
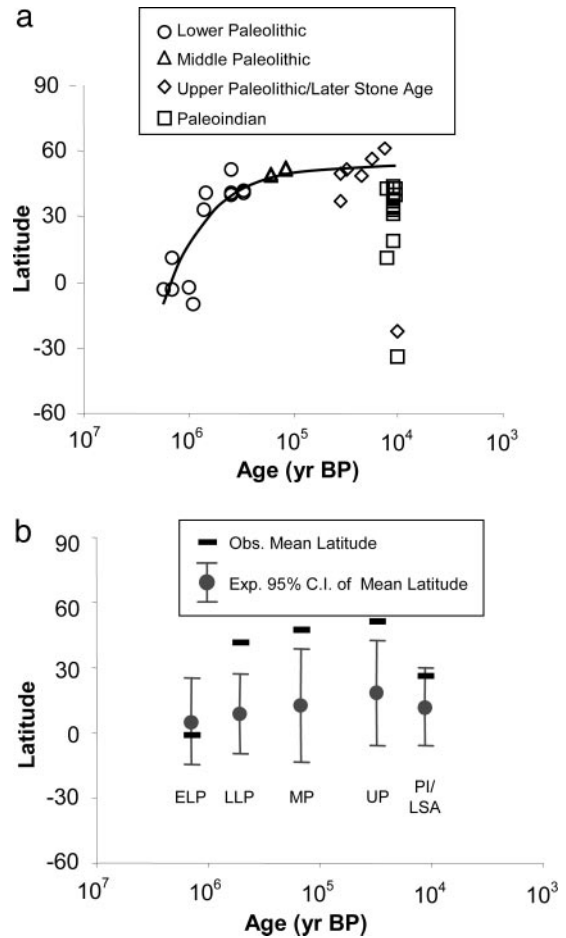
Fig. 4. Global archaeological spatiotemporal patterning in proboscidean kill/scavenge sites. (a) Age vs. latitude of archaeological sites showing subsistence use of proboscideans. The regression line (latitude = [age]4 $\times 10^{-5}$ + 53.5, $r^2 = 0.78$, $P \ll 0.001$) is calculated for Old World sites dating between 1.8 ma and 13.5 ka. (b) Mean latitude of proboscidean kill/scavenge sites vs. the 95% confidence interval of the expected mean latitude calculated by Monte Carlo methods for five time periods. ELP, Early Lower Paleolithic; LLP, Late Lower Paleolithic; MP, Middle Paleolithic; UP, Upper Paleolithic; PI/LSA, Paleoindian/Later Stone Age.

known latitudinal distribution of *Homo* for each archaeological period,[¶] by Monte Carlo methods, we calculated the expected 95% confidence interval of the mean latitudinal distribution of the observed n archaeological sites. During the Early Lower Paleolithic, proboscidean exploitation is seen at a mean latitude of 1.4° S, and there is no significant difference ($P = 0.73$) between the global latitudinal distribution of *Homo* and the distribution of archaeological sites showing use of proboscideans. By the Late Lower Paleolithic, however, a highly statistically significant ($P < 0.0001$) northward deviation is seen when proboscidean kill/scavenge sites occur at a mean latitude of 41.2° N. This pattern continues through the Middle and Upper Paleolithic, when the mean latitude of proboscidean exploitation climbs to 47.9° N ($P = 0.002$) and 50.9° N ($P = 0.004$), respectively. With New World coloniza-

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[¶]For this analysis, the following latitudinal ranges were assumed: Early Lower Paleolithic, 35° S to 45° N; Late Lower Paleolithic, 35° S to 52° N; Middle Paleolithic, 35° S to 60° N; Upper Paleolithic, 35° S to 72° N; Paleoindian/Later Stone Age, 56° S to 80° N. The Old World estimates are based on Dennell (15) and Hoffecker (32). For the Paleoindian/Late Stone Age estimate, we assume that humans occupied the entire latitudinal extent of North and South America during this time.

tion in the latest Pleistocene, proboscidean exploitation is seen across a wide range of latitudes but does not differ significantly from the latitudinal distribution of humans ($P = 0.055$). Importantly, during this time (13–10 ka), sites are limited to the New World and sub-Saharan Africa.

Although we have argued that to test the overkill and climate-change hypotheses the local timing of proboscidean extinction events is not critical, spatiotemporal patterning in proboscidean extinction relative to hominid arrival does show similar global trends. After the first archaeological evidence of exploitation of *Deinotherium* and *Elephas* in sub-Saharan Africa, both genera suffer extinction during the Middle Pleistocene (39). In the Levant, *Elephas* extinction likely occurred during the Middle Pleistocene as well (40). Extinction of *Elephas* in Europe occurred during the late Middle Paleolithic (120–40 ka) while *Mammuthus* persisted at high latitudes (10–12, 41). In Eurasia, the strongest evidence for extant mammoth populations during the late glacial (20–11 ka) is found from Northwest Europe to Northeast Asia (10, 11). By the latest Pleistocene (<11 ka), mammoths in Eurasia are found only in extreme high-latitude regions, with extinction occurring by the early Holocene in all areas except Wrangel Island (11), which, notably, was bypassed by humans. In the Americas, *Mammuthus*, *Mammut*, *Stegamastodon*, *and Haplomastodon* all suffered extinction by 10 ka, shortly after human arrival (1–9, 14).

Discussion

The global distribution of proboscidean kill/scavenge sites provides strong support for the overkill hypothesis. Beginning at least by the start of the Middle Pleistocene (780 ka), human northward range expansion resulted in local extinction and contraction of proboscidean ranges. In the latest Pleistocene (after 20 ka), rapid demic expansion of *Homo* into Arctic Eurasia and North and South America resulted in exploitation and, ultimately, extinction of proboscideans in areas in which humans had existed only intermittently, at very low population densities, or not at all. We suggest that the relatively slow northward range expansion of humans in Eurasia was likely mediated by the evolution of increasing behavioral and cultural phenotypic plasticity in the genus *Homo* over the course of the Pleistocene (42). During this time, Eurasian continental proboscidean populations remained viable in high-latitude refugia largely inaccessible to hominid populations. The lag between the arrival of modern humans into Eurasia and the final push into Arctic biomes was due to historical factors, specifically, that modern humans arrived as global climate drifted toward the LGM, making high Arctic areas largely unsuitable for human habitation (Fig. 3). With post-LGM climatic amelioration and the influx of modern humans into Arctic Eurasia, the primary factor limiting range expansion was human fertility. Compared with the previous 1 million years, the culturally flexible modern humans involved in the north-to-south New World colonization event faced few true ecological barriers to dispersal, allowing range expansion to occur at a brisk pace.

Critical to our argument is the assumption that Middle Pleistocene hominids hunted proboscideans at sufficient levels to cause local extinction. We have relied on kill/scavenge sites to demonstrate spatiotemporal overlap of *Homo* and proboscideans, but scavenging individuals that died of natural causes should not have affected prey populations. Although the question of hominid hunting and scavenging remains controversial, Middle Pleistocene hunting weaponry *ca.* 400 ka in age is known (43), and a wooden spear was recovered from the remains of an *Elephas antiquus* at the Middle Paleolithic site of Lehringen dating to *ca.* 120 ka (44), indicating that, at least by the end of the Middle Pleistocene, hominids were successfully killing proboscideans. There are theoretical reasons to suspect that early *Homo* would have hunted proboscideans. Successful coloniza-

tion of seasonal, temperate biomes by tropical hominids would not have been possible without a regular supply of cold-season foodstuffs, and hunting provides the most consistent means of regular access to calories when plant foods are not available (15). Furthermore, lacking bows, arrows, and spear throwers, the greatest obstacle to successful large mammal hunting for Middle Pleistocene hominids would have been gaining a close striking distance. Adult proboscideans have no natural predators and are therefore less predator-wary than other species, making it possible to spear these animals at pointblank range, a technique used by central African hunter-gatherers in modern times. Therefore, proboscideans might be expected to be among the prey that Middle Pleistocene hominids could most successfully stalk and kill, and we suspect that proboscideans may have been among the first large mammals to have been hunted by hominids.

Because of extreme body size in proboscideans, even minimal predation can cause extinction, as has been demonstrated by computer simulation (21). Large body size equates to delayed reproductive maturation and low population growth rates, and, because of high caloric requirements, proboscideans require very large contiguous ranges to maintain viable populations (22). It is well documented that extant elephant populations are highly susceptible to human impacts, with viable populations persisting only in contexts of explicit management and/or where human–elephant contact is minimal (22). Through active predation, removal as a form of agricultural pest control, range fragmentation, and habitat destruction, human populations have excluded proboscideans from historically occupied regions (22, 45–47). Clear negative correlations between human and elephant population densities demonstrate the incompatibility of elephant populations coexisting among human settlements (45–47). Although human predation ultimately caused local extinctions of proboscideans, the combined impacts of predation, range fragmentation, Allee effects, and demographic stochasticity would have hastened them.

The glaring anomaly to global overkill of proboscideans and other taxa has always been the survival of numerous large mammal taxa in sub-Saharan Africa, and elephants have survived in portions of South Asia, as well. *Homo* has likely inhabited both regions for >1 million years. The survival of *Loxodonta* and *Elephas* has traditionally been explained by long-term predator–prey coevolution, whereby elephants have had sufficient time to evolve effective defense mechanisms due to the relatively prolonged evolution of human predation abilities in these regions (1–3, 48). That elephants show aggressive behaviors toward humans in both regions (22) provides some support for this hypothesis, but we argue that historical and biogeographic factors provide additional reasons why elephants may have survived.

In both Africa and Asia, elephant populations remain most viable in tropical forests biomes where preagricultural humans may have never lived at high population densities. Human foraging populations are not able to occupy tropical forests at high densities because most of the biomass is inaccessible to human digestive tracts, and carbohydrates are limited (49, 50). That forests served as refugia for elephants is supported by disparities in genetic diversity among forest and savannah *Loxodonta*, a record that demonstrates that savannah elephants experienced a population bottleneck not experienced by their forest-dwelling counterparts (51, 52). Although humans likely initially evolved from a tropical forest ape, it may be our lack of tropical forest adaptations that ultimately led to the survival of *Loxonta* and *Elephas* in these regions. Swidden agriculture, logging, and mining in tropical forests today present serious threats to elephants in Africa and Asia (22, 45), but all of these factors have only begun to seriously impact elephant population survival in recent times. Most importantly, they can be seen as an extension of the global pattern that we have documented

archaeologically: Humans cause local extinction at the intersection of *Homo* and proboscidean geographic ranges.

Conclusions

Global spatiotemporal patterning in proboscidean exploitation and extinction cannot be explained by climate change unless one were to invoke serial climatic change that perfectly tracks human global colonization. Over 1 million years and on five continents, *Homo* has spatially excluded and driven proboscidean taxa to extinction. A repeated pattern is evident in the global archaeological and paleontological records. Humans disperse into new regions. They exploit proboscideans. Proboscideans suffer local extinction. In the present and past, elephants have survived in refugia unreached by humans or those where humans did not exist at sufficient population densities to cause local extinction.

This is not to say that climate change played no part in proboscidean extinctions, but it did not play a direct causal role. Human range expansion involved the interplay of human behavioral evolution and climate change. Climate change served to open new environments to humans at various stages of our evolutionary history, thereby providing access to proboscidean populations that were previously inaccessible. In this light, we see three events as critical to causing the near global demise of proboscideans: (*i*) the evolution of a technologically hunting hominid, (*ii*) the evolution of hominids behaviorally and culturally flexible enough to inhabit the total range of environments inhabited by proboscideans, and (*iii*) dispersal into proboscidean ranges. Notably, the final event continues to the present, and proboscidean populations continue to be negatively impacted as we expand our range into theirs.

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