EXTINCTION

Body size downgrading of mammals over the late Quaternary

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Since the late Pleistocene, large-bodied mammals have been extirpated from much of Earth. Although all habitable continents once harbored giant mammals, the few remaining species are largely confined to Africa. This decline is coincident with the global expansion of hominins over the late Quaternary. Here, we quantify mammalian extinction selectivity, continental body size distributions, and taxonomic diversity over five time periods spanning the past 125,000 years and stretching approximately 200 years into the future. We demonstrate that size-selective extinction was already under way in the oldest interval and occurred on all continents, within all trophic modes, and across all time intervals. Moreover, the degree of selectivity was unprecedented in 65 million years of mammalian evolution. The distinctive selectivity signature implicates hominin activity as a primary driver of taxonomic losses and ecosystem homogenization. Because megafauna have a disproportionate influence on ecosystem structure and function, past and present body size downgrading is reshaping Earth's biosphere.

Wild mammals are in decline globally because of a lethal combination of human-mediated threats, including hunting, introduced predators, and habitat modification (1–5). Extinction risk is particularly acute for the largest mammals, which are more frequently in conflict with humans (1, 6). The ongoing extirpation of large-bodied mammals is a major conservation concern because their decline can lead to the loss of ecological function within communities (3, 5, 7). Megafauna have crucial direct and indirect impacts on vegetation structure, biogeochemical cycling, ecological interactions, and climate (7–10). Although the current extinction rate is higher than earlier in the Cenozoic (4), the ongoing biodiversity crisis may be an acceleration of a long-term trend over the late Quaternary. For example, a striking feature of the Pleistocene was the abundance and diversity of extremely large mammals such as the mammoth, giant ground sloth, wooly rhinoceros, and sabretooth tiger on all habitable continents. The debate about the causes of the terminal Pleistocene megafauna extinction has been long and acrimonious, with particular controversy surrounding the role of humans (11–13).

Multiple hominins—including at a minimum Neandertals, Denisovans, and archaic/modern humans—have been part of ecosystems throughout the late Pleistocene. Genetic analyses reveal a complicated history, with substantial admixture between populations (14). Anthropologists remain divided about the routes, exact timing, and number of early migrations from Africa (14–18), but several hominin species were probably widespread across Africa and Eurasia around 80 thousand to 60 thousand years (ka) ago (15–17). Further expansion followed, with modern *Homo sapiens* reaching Australia ~60 to 50 ka ago and crossing into the Americas ~15 to 13 ka ago (15). Migrations were likely driven or facilitated by climatic factors (17, 18) and were followed by rapid increases in population sizes (17, 19). For example, hominin populations in western Europe increased 10-fold by the Neandertal-to-Modern human transition ~40 ka ago (19). Middle to Upper Paleolithic hominins were hunters who lived in groups and used both tools and fire (20); thus, it is plausible that their activities and rapid population growth influenced mammal biodiversity well before the terminal Pleistocene.

We investigated the influence of these emerging and increasingly sophisticated hominin predators on continental and global mammalian biodiversity over the late Quaternary (21). Ongoing biodiversity loss is robustly linked to human activities (1–5); and previous work linked extinction risk over the Holocene, terminal Pleistocene, and end-Pleistocene to human activities (4, 6, 11–13, 22–25); but earlier influences remain poorly characterized. Although recent work on paleodemography exists for *H. sapiens* over the late Pleistocene and Holocene (17), a lack of data for other hominins precludes direct comparison of mammalian extinction risk over time against hominin population density. However, should we find significant differences between the pattern of late Quaternary extinction selectivity and the rest of the Cenozoic mammal record, this would strongly suggest a role of hominin activity (13, 24, 25).

We used two data sets to test the potential role of hominin activity on extinction selectivity, mammalian body size distributions, and patterns of biodiversity over time and into the future (21). First, we updated a spatially explicit global record of body size and trophic mode for nonvolant, terrestrial mammals for the late Quaternary (MOM). Second, we constructed a global data set of Ce-

nozoic mammals with associated stratigraphic duration, body mass, and trophic mode. We categorized late Quaternary extinctions into five temporal bins: late Pleistocene (125 to 70 ka ago), which corresponded with the initial waves of migration of hominins out of Africa; end Pleistocene (70 to 20 ka ago), which represented the continued expansion of hominins into Eurasia and the colonization of Australasia; terminal Pleistocene (20 to 10 ka ago), which encompassed the migration of humans into the Americas; Holocene (10 to 0 ka ago), which represented further expansion of humans throughout the globe; and future (~+0.2 ka), where we assumed that all currently threatened mammals become extinct (21). We binned the Cenozoic fossil data set into intervals of 1 million years (Ma) as a reference standard and computed temperature metrics for each bin (21). For each time interval, we characterized the size selectivity of extinction using logistic regression and examined overall body size distribution and trophic guild structure (tables S1 to S7) (21). For the late Quaternary, we also characterized size selectivity by continent and trophic level.

Our analyses demonstrated a striking and significantly size-biased pattern of mammalian extinction over the late Quaternary, distinct in the Cenozoic record (Figs. 1 to 3 and fig. S1). We found a mass difference of two to three orders of magnitude between victims and survivors of late Quaternary extinction intervals (Fig. 2A and table S1), reflecting a significant association between size and extinction probability (Fig. 2B and table S5). This size bias occurred on each continent (Fig. 2, C and D) and within each major trophic group (Fig. 2, E and F), with the magnitude of the size difference and the statistical measure of size selectivity decreasing between the Pleistocene and Holocene (Fig. 2, A to F). The reduced selectivity of the Holocene and future extinctions likely reflects changes in the nature of threats. Today, many smaller-bodied animals are vulnerable because of habitat alteration, introduced predators, or urbanization (5–7, 11, 26).

Comparison of extinctions across the entirety of the Cenozoic demonstrated that body mass was rarely significantly associated with the probability of extinction before the late Pleistocene (Figs. 1 and 3, E and F), and further, size differences between victims and survivors never approached those observed in the Pleistocene (tables S1 and S3). There was a preferential loss of small-bodied species in the Oligocene that is perhaps linked to expansion of grasslands and prairies (~29 Ma ago) (Fig. 3E), although this value had high uncertainty. However, no interval over the past 65 Ma was as selective as the late Quaternary. Moreover, climate change did not increase extinction risk for large-bodied mammals before the spread of hominins. We found no relationship between temperature change over the Cenozoic and size bias of extinction; neither small nor large mammals were more vulnerable to extinction during times of high climate variability (table S3 and fig. S4). The probability that the late Pleistocene and Cenozoic selectivity

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coefficients came from the same distribution was very low ($P < 0.001$), given either log likelihood or nonparametric tests (fig. S3). Moreover, grouped as a single extinction event (as they would appear to a future paleontologist), the Quaternary extinction pulse was by far the most selective episode of extinction in the Cenozoic (Fig. 1). Such pronounced size selectivity is highly unusual in other fossil records; larger-bodied vertebrates and mollusks did not experience increased extinction risk over the Cenozoic or during the five mass extinction events (27). Because a reported signature of human hunting is size selectivity (24, 25), our results are consistent with the hypothesis that hominin activities contributed to extinctions long before the terminal Pleistocene.

The late Quaternary biodiversity losses led to dramatic, time-transgressive shifts in both mean and maximum body mass on each continent (Fig. 3), which followed hominin dispersal patterns (15) and began much earlier than previously suspected. Because body size distributions are related to the size of the landmass (28), the largest average or maximum body mass would be expected on Eurasia, followed by Africa, then North and South America, and the smallest on Australia. This expectation was largely met in the late Pleistocene (Fig. 3), but Africa was a notable outlier, with a mean body mass ~50% less than that of Eurasia or the Americas before 125 ka ago (table S1). We hypothesize that the late Pleistocene size distribution in Africa reflects the long prehistory of hominin-mammal interactions (29). This finding suggests that the homogenization of natural ecosystems was a consequence of hominin behavior in general and not specific to *H. sapiens*. Over the following ~100 ka, mean body mass dropped dramatically—first by 50% in Eurasia, and then by an order of magnitude in Australia—while remaining largely unchanged in the Americas until the terminal Pleistocene. Thus, for most of the late Quaternary, mean and maximum body masses were larger in the Americas than elsewhere—a pattern largely exceptional in the mammalian fossil record (Fig. 3 and table S1) (28). By the terminal Pleistocene, other hominin species were extinct, and the remaining *H. sapiens* had developed efficient long-range weapons (11). The latter likely contributed to the severity of the extinction in the New World (Fig. 1), with 11.5 and 9.7% of nonvolant terrestrial species lost in North and South America, respectively (tables S1 and S2). The loss of biodiversity resulted in a greater than 10-fold drop in both mean and maximum body mass, which was a steeper decline than elsewhere (Fig. 3, B and D). For example, mean mass of nonvolant terrestrial mammals in North America fell from 98.0 to 7.6 kg (table S1).

Future extinctions will continue the pattern of biodiversity loss and body size downgrading (fig. S1). If all species currently at risk are eventually driven extinct, ~22.4 to 53.7% of mammals will be lost relative to 125 ka ago (table S2). This will further decrease mean body mass in North America from 7.7 to 4.9 kg (Fig. 3B and table S1); similar declines are predicted for other continents. Thus, the largest mammal on earth in a few hundred
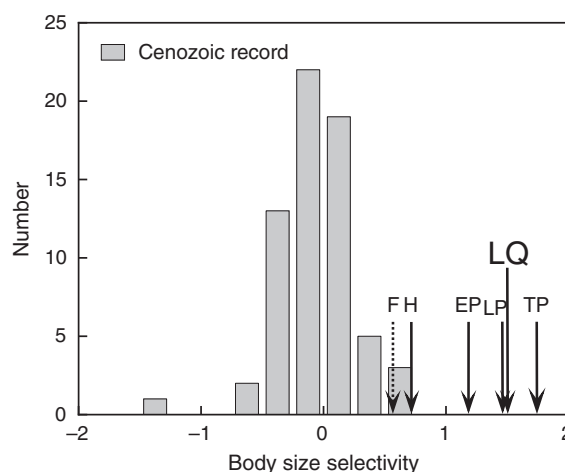

Fig. 1. Distribution of body size selectivity coefficients over the Cenozoic mammal record. All selectivity coefficients reflect change in the natural logarithm of the odds of extinction associated with a one-$\log_{10}$-unit change in body mass. Values of zero indicate no bias, positive values indicate bias against larger size, and negative values indicate bias against smaller size. LQ, average of all late Quaternary (LP to H) extinctions; LP, late Pleistocene; EP, end Pleistocene; TP, terminal Pleistocene; H, Holocene; and F, future extinctions.
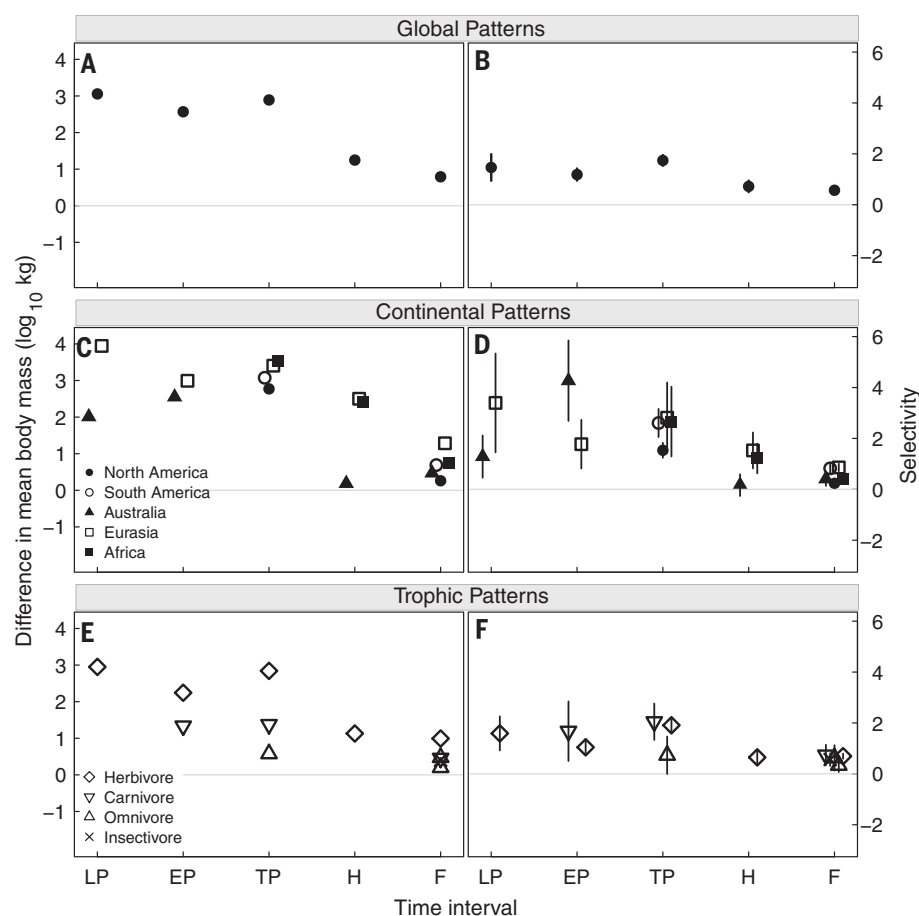

Fig. 2. Analyses of size bias in the mammalian fossil record. (**A** and **B**) Global patterns of extinction. (A) Difference in the mean of log-transformed sizes of victims versus survivors for intervals across the late Quaternary. (B) Selectivity coefficients measuring the association between body size and extinction probability derived from logistic regression of extinction status as a function of body mass. Multiple regressions controlling for the additive contributions of continental location and trophic guild yield even stronger associations between extinction status and body mass (table S5) (21). (**C** and **D**) Extinction patterns on each continent. (C) Size differences. (D) Size selectivity coefficients. (**E** and **F**) Influence of trophic guild on extinction risk. (E) Size differences. (F) Size selectivity coefficients. Bars indicate 95% confidence interval (CI).
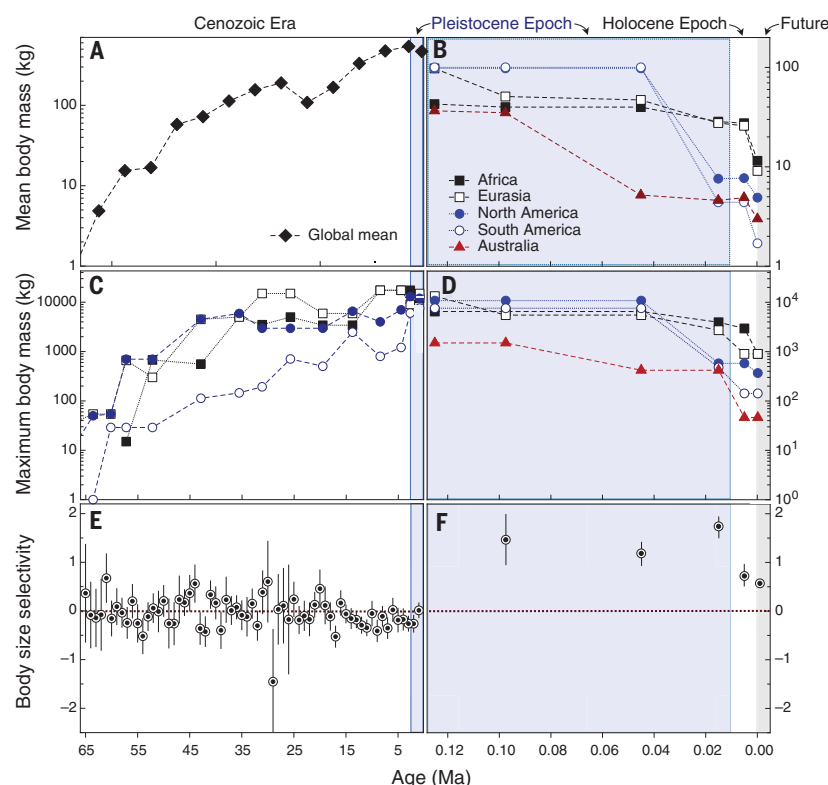
Fig. 3. Body size and its influence on extinction risk. (**A**) Global mean body size over the Cenozoic (65 to 1 Ma ago). (**B**) Mean body size by continent over the late Quaternary (past 125 ka). (**C**) Maximum body size across the Cenozoic by continent. (**D**) Maximum body size over the late Quaternary and into the future. (**E**) Size selectivity coefficients across the entire Cenozoic fossil record. (**F**) Size selectivity of late Quaternary extinctions. Bars indicate 95% CI. All masses are in kilograms. Light blue shading indicates late Pleistocene, white shading indicates Holocene, and gray shading indicates the future (+200 years). Ages here and elsewhere are plotted as midpoint of time interval.
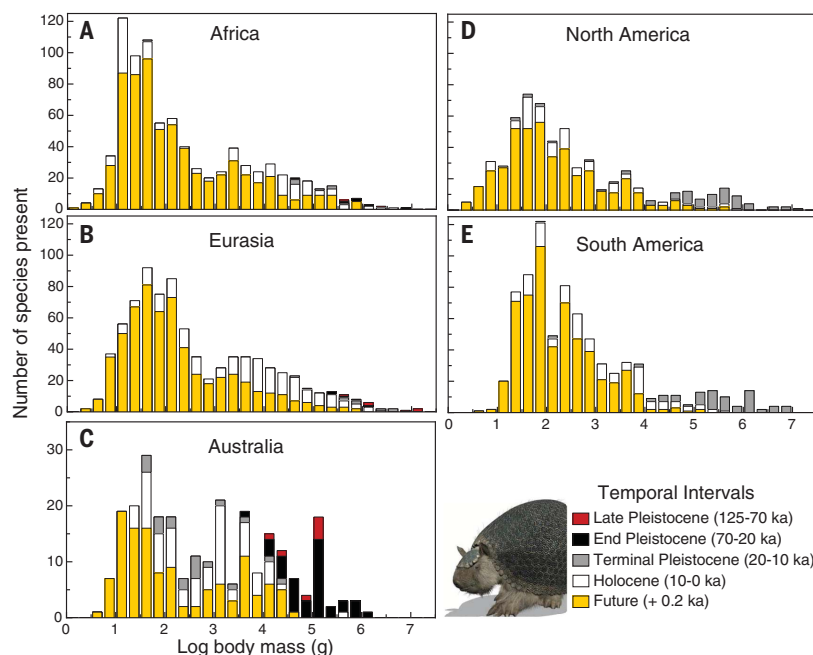

Fig. 4. The body size distribution of terrestrial, nonvolant mammals on each continent over the late Quaternary. (**A**) Africa. (**B**) Eurasia. (**C**) Australia. (**D**) North America. (**E**) South America. Body sizes for each temporal interval are plotted; distributions are overlaid from oldest to youngest. Yellow shading indicates the predicted distribution in the future, if vulnerable species go extinct.

years may well be a domestic cow (*Bos taurus*) at ~900 kg. Furthermore, the loss of currently endangered species would reduce terrestrial mammal body mass to the lowest values in the past 45 Ma (Fig. 3, A and C, as compared with Fig. 3, B and D). The last time the body size distribution of terrestrial vertebrates was similarly disrupted was ~66 Ma ago, during the end-Cretaceous mass extinction.

Because body size is strongly linked to most biological rates and processes (*30*), the extirpation of large mammals led to a fundamental restructuring of energy flow through mammal communities over the late Quaternary. The severe body size downgrading—a truncation of more than two orders of magnitude—resulted in substantial shifts from bimodal toward unimodal size distributions (Fig. 4 and fig. S1). Homogenization of distributions continued through the Holocene and is predicted to continue into the future (Fig. 4 and table S4). Extinctions also led to changes in the proportional representation of trophic guilds, especially herbivores (fig. S2). In the future, continental distributions will be severely skewed toward smaller mammals (Fig. 4)—in particular, rodents (fig. S2). Ecological principles suggest that changes in energy flow over the Pleistocene likely led to compensatory changes, potentially numerical responses by surviving smaller-bodied mammals to maintain ecosystem homeostasis (*31*). By the Holocene, however, humans were a strong influence on energy flow within ecosystems. Global expansion was accompanied by increased human densities (*17*) and animal domestication (*10*). By historical time, the terrestrial biosphere was transformed from one dominated by wild animals into one dominated by humans and their livestock, many provisioned with domesticated crops (*2, 5, 10*). Today, the biomass of the >4.5 billion domesticated animals on Earth exceeds estimates for wild mammals at the terminal Pleistocene (*10*).

Our study highlights the long and sustained influence of humans and other hominins on terrestrial ecosystems. As Neandertals, Denisovans, and humans spread across the globe over the late Quaternary, a highly size-biased extinction followed, a pattern distinct in the Cenozoic mammal record. The subsequent downgrading of body size was severe and differentially targeted herbivores. Thus, contemporary biodiversity loss is part of a trend spanning more than 125 ka, with expected future extinctions of greater magnitude, but reduced size selectivity, than in the past. The homogenization of ecosystems has dramatically influenced the past, present, and future role of wild mammals in the terrestrial biosphere.

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