

## Plio-Pleistocene decline of African megaherbivores: no evidence for ancient hominin impacts

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**Abstract:** It has long been proposed that pre-modern hominin impacts drove extinctions and shaped the evolutionary history of Africa's exceptionally diverse large mammal communities, but this hypothesis has yet to be rigorously tested. Here, we analyze eastern African herbivore communities spanning the last 7 Myr—encompassing the entirety of hominin evolutionary history—to test the hypothesis that top-down impacts of tool-bearing, meat-eating hominins contributed to the demise of megaherbivores prior to the emergence of *Homo sapiens*. We document a steady, long-term decline of megaherbivores beginning ~4.6 Ma, long before the appearance of hominin species capable of exerting top-down control of large mammal communities and pre-dating evidence for hominin interactions with megaherbivore prey. Expansion of C<sub>4</sub> grasslands can account for the loss of megaherbivore diversity.

**One Sentence Summary:** Environmental change—not ancient hominin impacts—drove megaherbivore extinctions in eastern Africa over the last 4.6 million years.

**Main Text:** Africa is home to more species of large-bodied mammalian herbivores than anywhere else today (1). Because most of the world's large-bodied vertebrates became extinct towards the end of the Pleistocene (2), present-day African faunas serve as model systems for understanding the ecology of large mammal communities (3) and the impact of massive megaherbivores (>1,000 kg) on ecosystems (4). Such knowledge feeds directly into conservation biology on a global scale by highlighting the ecological consequences of ongoing large mammal diversity loss (1) and illustrating the potential consequences of their rewilding (5).

There is a perception that Africa's exceptional large herbivore diversity is due to the continent being spared the extinctions that occurred elsewhere (~50,000 to 10,000 years ago) as modern humans (*Homo sapiens*) dispersed across the world (2). This anomaly has been thought to reflect coevolution of hominin hunters and their prey (6) or perhaps a long history of extinctions precipitated by pre-modern hominins (7) in Africa. Indeed, for decades it has been suggested that hominins drove extinctions and shifts in the functional structure of large mammal communities throughout the Pleistocene (7-13). Many of these hypotheses posit that top-down control of mammal communities by tool-bearing, meat-eating hominins contributed to the demise of large-bodied herbivores (e.g., the formerly diverse Proboscidea) long before the emergence of *Homo sapiens* (7, 9, 11, 12). Other versions of the 'ancient impacts' hypothesis propose that encroachment of Early Pleistocene *Homo* into the carnivore guild led to the demise of several carnivore lineages (8, 10), perhaps leading to environmental changes through relaxed

predation pressure on large-bodied herbivores (10). Both scenarios imply that ancient hominins played a key role in shaping African ecosystems, and by extension the environmental settings that influenced our own evolutionary history.

Despite decades of literature asserting ancient hominin impacts on African faunas, there have been few attempts to test this scenario or to explore alternatives. Here, we test the hypothesis of top-down hominin impacts on mammal communities through the analysis of megaherbivore diversity over the last 7 Myr in eastern Africa. Our focus on this region reflects its rich and well-dated late Cenozoic fossil record coupled with the fact that the earliest members of the hominin clade are from here, meaning that eastern Africa provides the longest well-documented history of hominin-mammal community interactions in the world. Based on previous hypotheses (7-13), we expect declines in megaherbivore community richness to follow or temporally coincide with hominin expansion into carnivore niche space. Specifically, proponents of the ‘ancient impacts’ hypothesis typically place the onset of anthropogenic diversity decline between 2 and 1 Ma (7, 8, 10-12). This encompasses the earliest evidence for systematic hominin predation upon large-bodied mammals (~2 Ma) (14) and megaherbivores (~1.95 Ma) (15), as well as the appearance of *Homo erectus* (~1.9 Ma), the first hominin species whose paleobiology is similar to later representatives of our genus and that consumed large amounts of animal tissue (16). These evolutionary changes are thought to account for an unprecedented reduction of megaherbivore diversity coupled with collapse of the large carnivore guild (7, 8, 10-12).

We quantified long-term changes in the richness of eastern African megaherbivores using present-day and fossil herbivore community data (17). We used a dataset of more than 200 modern communities from protected areas across Africa to establish a baseline for present-day

variability in megaherbivore community richness (Fig. 1A, Table S1, Database S1). In addition, we compiled a fossil dataset that includes the presence of herbivore taxa in 101 eastern African fossil assemblages spanning the last ~7 Myr (Table S2, Database S2), a period that encompasses the earliest probable and definitive hominin species in eastern Africa. Our focus on individual fossil assemblages within a single region provides a pertinent spatiotemporal scale for our research question because it allows a more direct assessment of hominin impacts on ancient herbivore communities than is possible from analyses of species occurrences at continental scales (e.g., 9). Because hominin impacts need not be the only driver of change in the eastern African megaherbivore community, we also examine trends in megaherbivore community richness relative to independent records of climatic and environmental change. These include: global atmospheric  $p\text{CO}_2$  (18); the percentage of  $\text{C}_4$  biomass inferred from the stable carbon isotope ( $\delta^{13}\text{C}$ ) composition of soil carbonates in eastern Africa (19); estimates of paleo-aridity derived from the stable oxygen isotopes ( $\delta^{18}\text{O}$ ) of eastern African fossil herbivores (20); and the percentage of  $\text{C}_4$  grazers among ungulate taxa in eastern African fossil assemblages (20). The eastern African proxy data come from many of the same sites examined in our analysis of megaherbivore diversity.

Our compilation of the eastern African fossil record reveals substantial megaherbivore extinctions through time. Over the last 7 Myr, 28 megaherbivore lineages became extinct (Table S3), leading to present-day communities that are depauperate in megaherbivores. For example, modern African herbivore communities include only up to five sympatric megaherbivores (Database S1), including all of the extant species (*Giraffa camelopardalis*, *Hippopotamus amphibius*, *Ceratotherium simum*, *Diceros bicornis*, and *Loxodonta africana*). In contrast, the fossil record documents paleo-communities that were considerably richer in megaherbivores,

with some assemblages documenting the co-occurrence of up to 10 megaherbivore species (Database S2). Though time-averaging of fossil assemblages can produce associations of species that never spatiotemporally co-occurred, it cannot account for the exceptional richness of megaherbivores here (17; Fig. S1). Controlling for community richness, a variable that increases as a function of time-averaging and sampling effort, many fossil assemblages over the last ~7 Myr fall outside the modern range of variation because they include both a greater proportion and absolute number of megaherbivore species (Fig. 1B-C).

To illustrate temporal trends (Fig. 1C), we calculated residuals for fossil assemblages as deviations from expected megaherbivore richness modeled as a linear function of herbivore community richness based on our modern community data (Fig. S2). Residual analysis highlights the exceptional richness of fossil megaherbivore communities—many are well outside the modern range of variation—and documents a steady and long-term decline in richness beginning in the early Pliocene, with fossil assemblages consistently falling within the modern range of variation only after ~700 ka (Fig. 1C). Breakpoint analysis places the onset of the megaherbivore decline at ~4.6 Ma (95% confidence intervals: 3.3 to 5.9 Ma). After the ~4.6 Ma breakpoint, the rate of diversity decline through time does not change following the appearance of *Homo erectus* (1.9 Ma) or at either end of the hypothesized 2 to 1 Ma window of accelerated anthropogenic diversity decline (Table S4). Instead, the long-term decline in megaherbivore richness closely tracks global variation in atmospheric  $p\text{CO}_2$ , as well as the expansion of  $\text{C}_4$  grasslands and  $\text{C}_4$  grazers in eastern Africa, though there is no association with paleo-aridity (Fig. 2).

The loss of large-bodied mammals is thought to be a hallmark of anthropogenic extinctions (6, 7, 9), in part because large-bodied species are likely to have been preferentially targeted by hominin hunters and because their slower life history profiles (e.g., delayed

reproductive maturity, prolonged gestation, low population growth rates) render them more susceptible to extinction. Our analyses show that the diversity of megaherbivores in eastern African fossil assemblages has undergone a steady decline since ~4.6 Ma (Fig. 1), initiating long before the proposed timing of anthropogenic impacts (2 to 1 Ma) linked to encroachment of *Homo erectus* into the carnivore guild (Fig. 3). The antiquity of the megaherbivore decline effectively eliminates top-down hominin impacts as a plausible mechanism for setting it in motion, as it would have had to involve small-bodied australopiths or pre-australopiths (e.g., *Australopithecus*, *Ardipithecus*), which were functionally equivalent to bipedal apes. Like extant chimpanzees, these hominin taxa may have preyed upon vertebrate species smaller than themselves but they almost certainly did not hunt megaherbivore prey (21). Though we cannot rule out the possibility that the subsequent appearance of more derived hominin species, new stone-tool technologies, and increased carnivory may have incidentally contributed to the demise of megaherbivores, the steady decline of megaherbivores beginning ~4.6 Ma (Fig. 3, Table S4)—in contrast to proposed extinction pulses linked to major shifts in hominin evolution (7)—implies that the primary driver was decoupled from hominin evolution.

We propose that the expansion of C<sub>4</sub> grasslands (Fig. 2B) played a critical role in megaherbivore decline. Analysis of our fossil dataset indicates that the long-term decline of megaherbivores is primarily due to the loss of megaherbivore browsers and mixed feeders (i.e., consumers of C<sub>3</sub> plants) (Fig. S3). Unlike megaherbivore grazers, temporal declines in the richness of megaherbivore browsers and mixed feeders are in close agreement with the overall megaherbivore diversity loss (Fig. S3). Loss of C<sub>3</sub> consumers is also evident in a compilation of  $\delta^{13}\text{C}$  data from tooth enamel of eastern African megaherbivores (Database S3, Fig. S3). Their decline in fossil assemblages is likely related to the Plio-Pleistocene expansion of C<sub>4</sub> grassland

(Fig. 2B), which reduced the availability of  $C_3$  forage on the landscape. Because larger-bodied species are more strongly limited by forage availability than smaller-bodied species (4), a decline in megaherbivore species dependent on  $C_3$  forage is expected. At the same time, decreasing atmospheric  $CO_2$  concentrations (Fig. 2A) would have diminished the advantage of massive body size, which allows megaherbivores to consume lower-quality foods than their smaller-bodied counterparts (4). Especially among  $C_3$  plant species, plant tissue grown at lower  $CO_2$  concentrations provides higher-quality forage because they have higher N content (lower C:N ratios) and fewer secondary compounds (22). This would allow smaller-bodied species—which are restricted to high-quality forage (3)—to exploit a greater range of increasingly rare  $C_3$  resources, with the outcome being less food available to megaherbivore browsers and mixed feeders. Some or all of these mechanisms are likely to have played a role in driving large herbivore extinctions elsewhere. For example, although the timing of  $C_4$  expansion and the nature of its ecological consequences varied globally due to differences in climate and historical contingencies (23), the  $C_4$  expansion from ~8.5-6.0 Ma in the Siwalik Group (Pakistan) is associated with considerable losses among  $C_3$ -consumers and the last appearances of many massive herbivores, including five rhinos, a proboscidean, a chalicothere, and a sivathere (24).

There is a long history of debate concerning the mechanisms responsible for the expansion of  $C_4$  grasslands in eastern Africa (19). This phenomenon is often linked to increased aridity after the onset of Northern Hemisphere Glaciation ~2.8 Ma (25). However, dust flux records from marine sedimentary archives that reflect eastern African climate indicate significant long-term increases in aridity only after ~1.5 Ma (26), long after the onset of  $C_4$  expansion (Fig. 2B). In addition, recent analyses show that terrestrial proxies for aridity and vegetation in eastern Africa vary independently through the Plio-Pleistocene, implying that other abiotic or biotic

mechanisms likely underpin habitat change (20). Because C<sub>4</sub> grasses are favored at lower CO<sub>2</sub> concentrations (27), the Plio-Pleistocene CO<sub>2</sub> decline (Fig. 2A) is likely an important abiotic mechanism (19). For example, at high temperatures, such as those inferred from Turkana Basin paleosol carbonates (>30°C) (28), C<sub>4</sub> grasses (NAP-me subtype) are expected to expand when atmospheric CO<sub>2</sub> concentrations fall below ~450 ppm (27). The expansion of C<sub>4</sub> grassland and associated decline of megaherbivores are consistent with long-term decline of CO<sub>2</sub> (Fig. 2), likely facilitated by episodes of aridity (i.e., positive water deficit) that occur across the interval (Fig. 2C). The persistent expansion of C<sub>4</sub> grassland is remarkable in light of the decline of megaherbivore diversity. Megaherbivore browsers and mixed feeders, especially elephants (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*), promote grassland expansion through consumption of woody (C<sub>3</sub>) vegetation, toppling and ringbarking trees, and synergistic effects with fire (4, 29). With all other factors held constant, we would expect the considerable decline of such taxa—which implies a reduction in megaherbivore biomass (Fig. S4)—to drive an expansion of woody cover through the Plio-Pleistocene. That the exact opposite occurred (Fig. 2B) suggests a dominance of abiotic mechanisms in driving the C<sub>4</sub> expansion.

We note that the CO<sub>2</sub>-driven expansion of C<sub>4</sub> grasslands and the associated extinction of megaherbivores can account for other changes in eastern African mammal communities that have been attributed to ancient hominin impacts. As noted earlier, the loss of richness and functional diversity among eastern African carnivorans through the Pleistocene has been attributed to the encroachment of *Homo* into the large carnivore guild (8, 10-12). However, some extinct Pleistocene carnivorans lacking modern analogs (e.g., sabertooth felids) are known to have specialized on juvenile megaherbivores (30). Given the close association between large carnivore diversity and herbivore diversity (31), the loss of megaherbivore prey likely



contributed directly to the extinction of attendant carnivores. Thus, in the absence of detailed consideration of eastern African herbivores, it is premature to invoke hominin impacts as an important driver of carnivoran diversity loss and associated ecosystem change. Together with our observations indicating that bottom-up processes can account for the loss of megaherbivores, it follows that in the search for anthropogenic impacts on ancient African ecosystems, we must focus our attention on the one species known to be capable of causing them: *Homo sapiens* over the last 300,000 years.

**Supplementary Materials:**

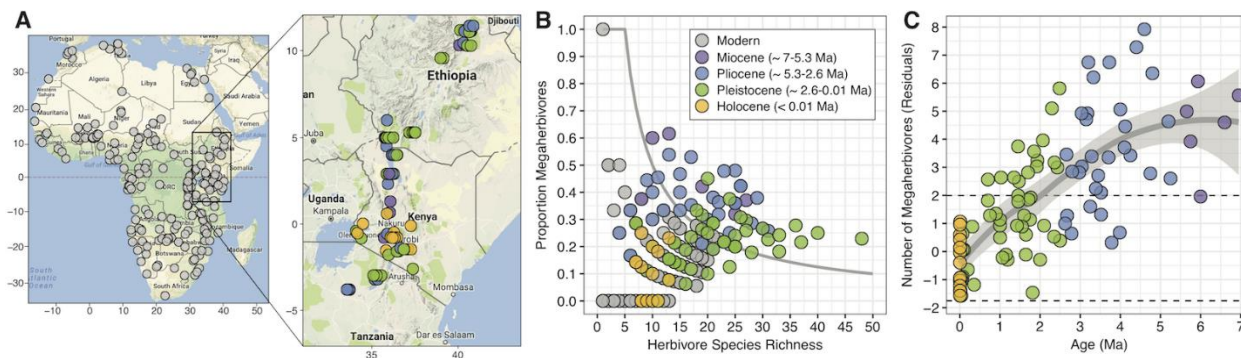
Materials and Methods

Figures S1-S4

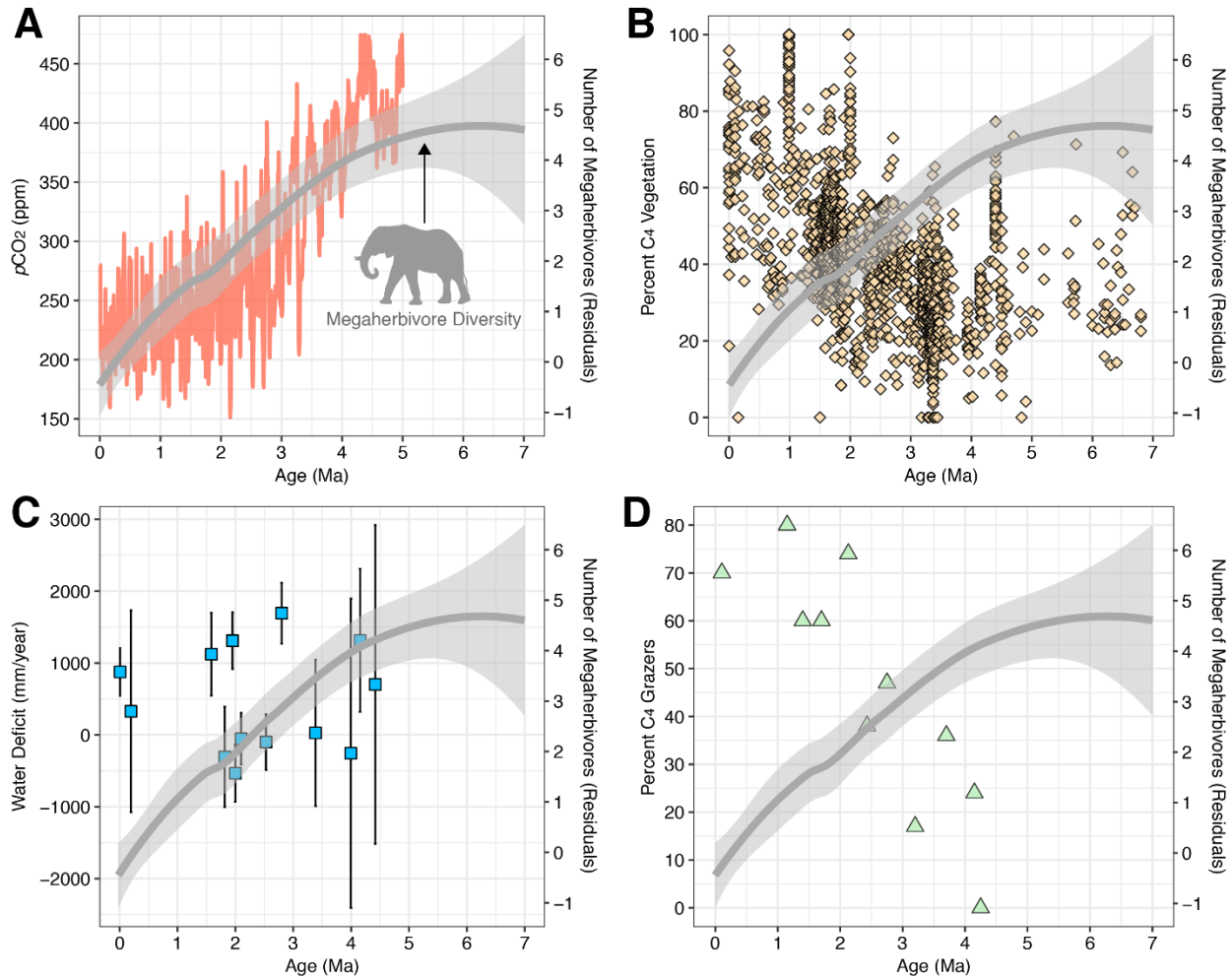
Tables S1-S4

Database S1-S3

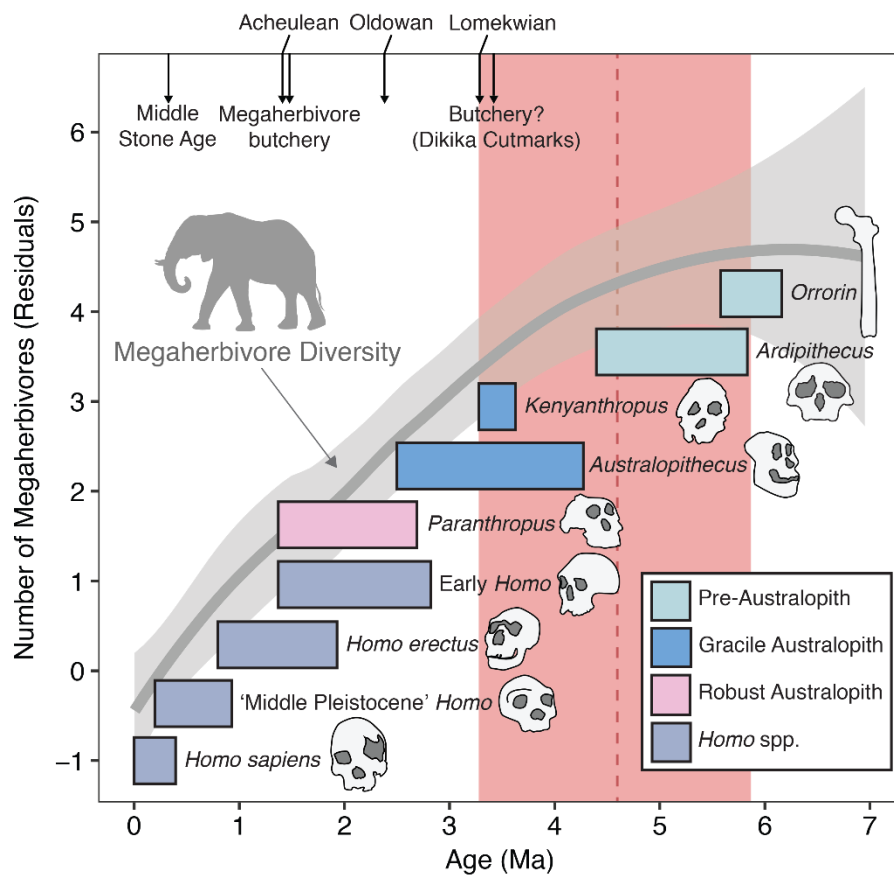
References (32 to 149)



**Fig. 1. Megaherbivore richness in modern and fossil communities.** (A) The geographic distribution of the 203 modern (continental map) and 101 fossil (inset map) herbivore communities. (B) The relationship between the total number of herbivore species and the proportion of megaherbivore species in modern African communities and eastern African fossil assemblages. The solid line represents the maximum proportion of megaherbivores that could coexist today based on the empirical observation of at most five sympatric megaherbivore species. Fossil assemblages falling above the line are non-analog because they include a greater proportion of megaherbivores than is observed today. (C) Megaherbivore richness residuals over the last 7 Myr, illustrating the long-term decline of megaherbivores starting ~4.6 Ma. Data points represent residuals from the least squares regression modelling the relationship of megaherbivore richness as a function of total community richness in the modern communities (Fig. S2). Solid gray line represents LOESS regression (smoothing factor = 0.35) with 95% confidence limits in light gray. Horizontal dashed lines encompass the middle 95% range of variation in the modern communities.



**Fig. 2. The decline of megaherbivore richness relative to climatic and environmental proxies.** (A) global  $p\text{CO}_2$ ; (B) % $\text{C}_4$  vegetation inferred from  $\delta^{13}\text{C}$  of eastern African paleosol carbonates; (C) estimates of water deficit (aridity) for eastern African fossil sites based on  $\delta^{18}\text{O}$  of herbivore tooth enamel; (D) the percentage of  $\text{C}_4$  grazers among herbivore taxa (Artiodactyla-Perissodactyla-Proboscoidea) from eastern African fossil sites, calculated as the percentage of taxa with mean enamel  $\delta^{13}\text{C}$  values  $>-1\%$ . The gray line in all panels represents the LOESS regression (95% confidence limits in light grey) for megaherbivore richness residuals (as in Fig. 1C).



**Fig. 3. The decline of megaherbivore richness relative to milestones in hominin evolution.**

These include the appearances of novel technologies and behaviors, as well as the observed temporal ranges of eastern African hominin taxa. Vertical dashed line indicates the breakpoint denoting onset of megaherbivore decline (4.6 Ma), with red shading representing the 95% confidence interval (3.3 to 5.9 Ma).

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