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The uncertain case for human-driven extinctions prior to *Homo sapiens*

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Abstract

A growing body of literature proposes that our ancestors contributed to large mammal extinctions in Africa long before the appearance of *Homo sapiens*, with some arguing that premodern hominins (e.g., *Homo erectus*) triggered the demise of Africa's largest herbivores and the loss of carnivoran diversity. Though such arguments have been around for decades, they are now increasingly accepted by those concerned with biodiversity decline in the present-day, despite the near complete absence of critical discussion or debate. To facilitate that process, here we review ancient anthropogenic extinction hypotheses and critically examine the data underpinning them. Broadly speaking, we show that arguments made in favor of ancient anthropogenic extinctions are based on problematic data analysis and interpretation, and are substantially weakened when extinctions are considered in the context of long-term evolutionary, ecological, and environmental changes. Thus, at present, there is no compelling empirical evidence supporting a deep history of hominin impacts on Africa's faunal diversity.

Keywords: Africa; carnivoran; extinction; *Homo*; human impacts; megafauna; overkill; proboscidean

INTRODUCTION

The decline of Earth's large-bodied mammals (megafauna) over the last few hundred years ranks among humankind's most widespread impacts on the natural world. In addition to triggering a biodiversity crisis that may be comparable to previous mass extinction events (Barnosky et al., 2011), anthropogenic impacts on the diversity, distribution, and biomass of megafauna have fundamentally changed ecosystem function on a global scale (Dirzo et al., 2014; Estes et al., 2011; Ripple et al., 2015). Though the magnitude of these impacts has increased dramatically in historical times, and in tandem with our growing population, human-driven ecosystem disruption is not a new phenomenon. It is now abundantly clear that anthropogenic impacts on the natural world extend deep in time (Boivin et al., 2016; Braje and Erlandson, 2013; Grayson, 2001; Smith et al., 2019). Just how deep in time and how severe the consequences, however, is a matter of debate.

Many Quaternary scientists argue that the extinction of Earth's megafauna over the last ~50,000 years signals a key tipping point in the history of human-environment interactions (reviewed in Barnosky et al., 2004; Koch and Barnosky, 2006). Though still the focus of ongoing debate, it is often suggested that the diaspora of modern humans (*Homo sapiens*) played a decisive role—either alone or synergistically with climate change—in megafaunal extinctions that occurred across most of the world during the Late Pleistocene and earliest Holocene (e.g., Koch and Barnosky, 2006; Sandom et al., 2014; Smith et al., 2018; Smith et al., 2019; but see Grayson, 2001; Meltzer, 2015; Wroe et al., 2013). However, a growing body of literature places the temporal depth of human impacts much earlier, proposing that our hominin ancestors contributed to large mammal extinctions in Africa throughout the Pleistocene (Fig. 1). Some contend that top-down impacts on mammal communities by tool-using and increasingly carnivorous hominins led to the demise of large-bodied herbivores long before *H. sapiens* (Lyons et al., 2004; Smith et al., 2018; Surovell et al., 2005). Others propose that encroachment of early *Homo* into the carnivore guild, and the attendant increase in kleptoparasitism and competition for herbivore prey, drove the

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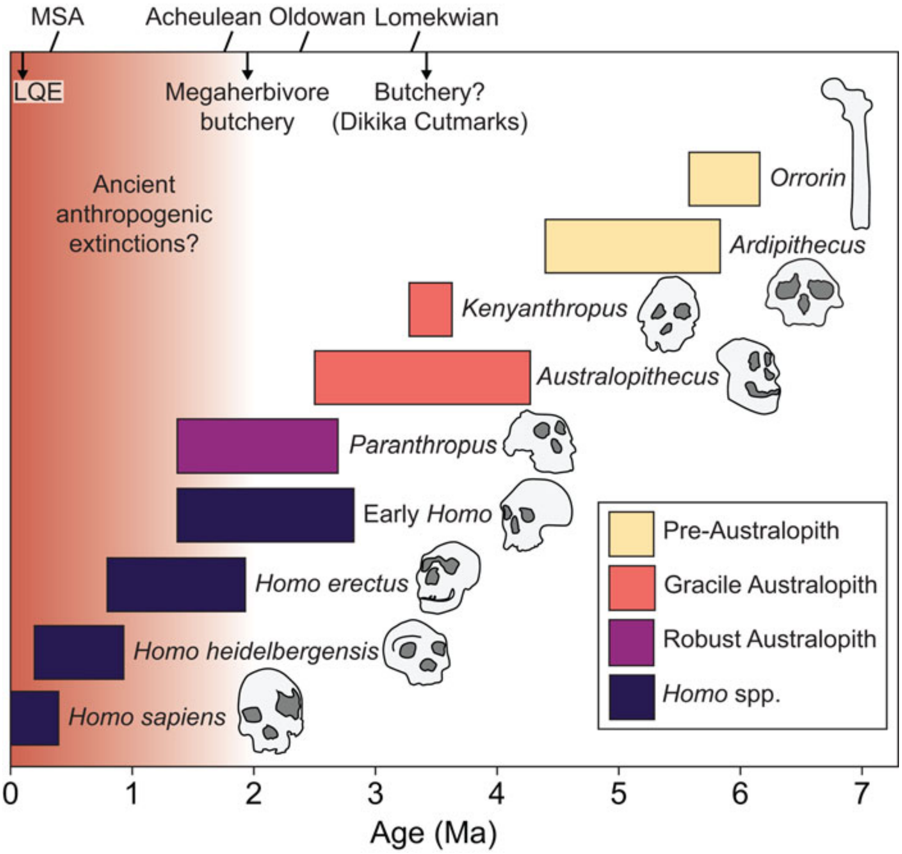

Figure 1. (color online) The timeline of late Quaternary extinctions (LQE) in the last ∼100,000 years and hypothesized ancient anthropogenic extinctions (after ∼2 Ma) relative to milestones in hominin evolution. These include the temporal ranges of eastern African hominin taxa and the appearances of novel technologies and behaviors. The boxes illustrating taxon temporal ranges are color-coded into four informal groups figured in the legend, which unite species sharing similar adaptations. MSA = Middle Stone Age.

extinction of several carnivoran lineages (Faurby et al., 2020; Lewis and Werdelin, 2007; Werdelin and Lewis, 2013b), with the ensuing trophic cascade leading to widespread environmental changes (Fortelius et al., 2016). Such ideas have been around for decades (Clark, 1959; Martin, 1966), but in recent years they have become increasingly cited in the ecological and conservation biology literature (e.g., Hoag and Svenning, 2017; Johnson et al., 2017; Malhi et al., 2016; Turvey and Crees, 2019). Surprisingly—especially in light of the massive and contentious literature surrounding the late Quaternary extinctions (Barnosky et al., 2004; Koch and Barnosky, 2006)—this has happened almost entirely in the absence of discussion or debate (but see Faith et al., 2018; Faurby et al., 2020).

We believe that such discussion and debate is overdue. If ancient anthropogenic extinction hypotheses are correct, it follows that our ancestors played a role in shaping past ecosystems long before the appearance of *H. sapiens*, effectively extending the temporal depth of anthropogenic impacts on biodiversity back hundreds of thousands if not millions of years (Fig. 1). And because data bearing on the history of our influence on the natural world are important to discussions about what it means to be human (e.g., Boivin et al., 2016) and the resilience of ecosystems to human impacts (e.g., Barnosky et al., 2017; Johnson et al., 2017), it is critical that the ancient anthropogenic extinction hypotheses be subject to careful scrutiny. In order to facilitate that process, here we provide an overview of ancient anthropogenic extinction hypotheses and a critical examination of the data and analyses underpinning them.

ANCIENT ANTHROPOGENIC EXTINCTION HYPOTHESES

The hominins involved

We use “ancient anthropogenic extinctions” to refer to hominin-driven extinctions prior to the emergence of *Homo sapiens* between ∼300-200 ka (Hublin et al., 2017; McDougall et al., 2005). The hominin species most often implicated in such extinctions is *H. erectus* (*sensu lato*, including specimens identified as *H. ergaster*), whose fossil occurrences in Africa range between ∼2.0 and 0.9 Ma (Antón, 2012; Herries et al., 2020), and its successor that is variably referred to as *H. heidelbergensis*, *H. rhodesiensis*, or “archaic” *H. sapiens* (Bräuer, 2008; Stringer, 2012); we use *H. heidelbergensis* here. *Homo erectus* is associated with a suite of adaptive shifts that have made it a prime candidate for ancient anthropogenic extinction hypotheses. It is the first hominin whose paleobiology (e.g., body size, obligate terrestrially, and life history) appears to bear strong similarities to later representatives of our genus (Wood and Collard, 1999) and whose diet likely included a substantial component of animal tissues (Aiello and Wheeler, 1995; Antón et al., 2014). Although evidence of hominin meat-eating dates back to at least ∼2.6 Ma (Domínguez-Rodrigo et al., 2005), if not earlier (>3.39 Ma) (McPherron et al., 2010), it is only after ∼2.0 Ma that we see repeated archaeological evidence for hominin carnivory (Braun et al., 2010; Ferraro et al., 2013; Pante et al., 2018; Thompson et al., 2019). This is followed by isotopic evidence for increased exploitation of C_4 resources among fossil *Homo* by ∼1.7 Ma (Cerling et al., 2013), likely reflecting increased consumption of grassland herbivores (Patterson et al., 2019). *Homo erectus* is also associated with technological change, namely the appearance of Acheulean stone tools ∼1.76 Ma (Lepre et al., 2011), and it is the first hominin to disperse out of Africa and across much of the Old World. To some, these changes set the stage for *Homo erectus* and its Middle Pleistocene successors to drive mammalian extinctions across Africa.

The early literature

To our knowledge, the earliest proposal of ancient hominin impacts in Africa can be traced to J. Desmond Clark's (1959) overview of southern African prehistory. Referring to a handful of large herbivores whose last appearances in southern Africa are now known to range in age from ∼1 Ma to the onset of the Holocene (Brink et al., 2012; Faith, 2014; Klein et al., 2007), including *Stylohipparion* (= *Eurygnathohippus cornelianus*), *Griquatherium* (= *Sivatherium maurusium*), and *Homoioceras* (= *Syncerus antiquus*), Clark (1959:57) suggested that "[t]heir final extinction may well have been due to man's improved methods of hunting these overspecialized and probably clumsy beasts." Clark did not specify which hominin species was to blame, but from the evidence available to him at the time, it was clear that at least some of these extinct taxa (e.g., *Stylohipparion* and *Griquatherium*) disappeared long before the Pleistocene-Holocene transition (Clark, 1959:54) and were associated with hominins that preceded the emergence of *H. sapiens*, including *H. heidelbergensis* (Drennan, 1953). However, other than to venture that control of fire may have enhanced hominin hunting abilities (Clark, 1959:134), Clark did not elaborate on his hypothesis, which was arguably little more than offhand speculation. Thus, this early explicit hypothesis of ancient anthropogenic extinctions had little influence on later developments.

A more concrete formulation of the ancient anthropogenic extinction hypothesis came nearly a decade later from Paul Martin (Martin, 1966), who was at the time strengthening the case for his influential end-Pleistocene overkill hypothesis (Martin, 1984; Martin and Steadman, 1999). With his first large-scale articulation of the overkill hypothesis in press (Martin, 1967b), Martin (1966) directed his attention to potential critics. Others had previously argued that if prehistoric hunters were capable of driving continental-scale extinctions, then there should not be such an impressive abundance and diversity of megafauna in present-day Africa, where large game had been hunted throughout human prehistory (Eiseley, 1943). According to Martin (1966), this viewpoint overlooked the considerable anthropogenic extinctions that occurred in the Pleistocene.

Using Cooke's (1963) review of Pleistocene African mammals as his data source, Martin (1966) compiled a list of extinct Pleistocene genera >50 kg body mass, focusing on those believed to have disappeared during the "late Middle Pleistocene," which he placed within the last 100,000 years. We provide his list in Table 1, which updates the taxonomic identities of the extinct taxa and their last appearances. Martin's list included 26 extinct genera derived primarily from eastern (e.g., Bed IV at Olduvai Gorge, Olorgesailie) and southern African Acheulean localities (e.g., Cornelia, Elandsfontein) now known to range in age from ∼1 Ma to ∼500 ka (e.g., Brink et al., 2012; Deino et al., 2018; Klein et al., 2007). Of course, this chronology was not accessible to Martin at the time. Believing the 26 extinct genera to have disappeared fairly late in the Pleistocene, perhaps by ∼50,000 years ago based on a problematic radiocarbon date associated with the final Acheulean at Kalambo Falls in Zambia (see Leakey, 1966), Martin (1966) argued that the magnitude of "late Middle Pleistocene" extinctions in Africa was substantially greater than losses earlier in time and comparable to those that occurred in North America at the end of the Pleistocene. Critically, the association of the extinct African mammals with Acheulean artifacts led him to argue that it was overkill, facilitated by technological development in premodern hominins, which played the decisive role in the extinctions.

The Acheulean overkill scenario envisioned by Martin (1966) inspired a brief debate with Louis Leakey (1966), who suggested that climate change was a more probable explanation for the megafaunal extinctions. Leakey's critique focused on data quality, reprimanding Martin for not making use of the taxonomic revisions provided in his recent volume on Olduvai Gorge (Leakey, 1965) and questioning whether some of the genera on Martin's (1966) list were indeed >50 kg body mass. His preoccupation with these issues, which Martin (1967a) later showed to have little influence on his initial analysis, overshadowed Leakey's (1966) other concerns, including the geological evidence suggesting that the Acheulean mammal faunas were far more ancient and temporally staggered than Martin (1966) supposed. Martin (1967a) never responded to this criticism, though we now know it is paramount. Rather than disappearing suddenly in the last 100,000 years, the extinct genera highlighted by Martin have last appearances spanning the last ∼1 Myr (Table 1). Indeed, in Martin's (1984) later work on the overkill hypothesis, he could not avoid the implications of emerging chronologies for African Pleistocene faunas (Maglio and Cooke, 1978), which made it abundantly clear that Africa's

Table 1. Martin's (1966) list of extinct "Middle Pleistocene" genera from Africa.

Extinct genus	Updated taxon	LAD	Reference
Simopithecus	*Theropithecus oswaldi*	549 - 509 ka	McBrearty and Jablonski, 2005
Machairodus	*Megantereon whitei*	1 Ma - 600 ka	Klein et al., 2007
Archidiskodon	*Elephas recki - E. jolensis*	90-75 ka	Sanders et al., 2010
Gomphotherium[1]	*Gomphotherium* sp.	13 Ma	Sanders et al., 2010
Stylohipparion	*Eurygnathohippus ethiopicum*	800 - 600 ka	Faith et al., 2019
Eurygnathohippus	*Eurygnathohippus cornelianus*	1.0 Ma	Brink et al., 2012
Potamochoeroides[2]	*Kolpochoerus majus*	100 ka	Souron et al., 2013
Mesochoerus	*Kolpochoerus olduvaiensis*	800 - 600 ka	Faith et al., 2019
Notochoerus	*Metridiochoerus hopwoodi*	800 - 600 ka	Faith et al., 2019
Tapinochoerus	*Metridiochoerus modestus* (Eastern Africa)	800 - 600 ka	Faith et al., 2019
	Kolpochoerus paiceae (Southern Africa)	1 Ma - 600 ka	Klein et al., 2007
Stylochoerus	*Metridiochoerus compactus*	800 - 600 ka	Faith et al., 2019
Orthostonyx	*Metridiochoerus compactus*	800 - 600 ka	Faith et al., 2019
Metridiochoerus	*Metridiochoerus andrewsi*	1 Ma - 800 ka	Faith et al., 2019
Kolpochoerus	*Kolpochoerus heseloni*	1.0 Ma	Brink et al., 2012
Camelus	*Camelus* sp.	19.9 ^{14}C ka BP	Faith, 2014
Megaceroides	*Megaceroides algericus*	7.5 ^{14}C ka BP	Fernandez et al., 2015
Libytherium	*Sivatherium maurusium*	800 - 600 ka	Faith et al., 2019
Homoioceras	*Syncerus antiquus*	5.4 ^{14}C ka BP	Faith, 2014
Bulcharus	*Pelorovis oldowayensis*	800 - 600 ka	Faith et al., 2019
Pelorovis	*Pelorovis oldowayensis*	800 - 600 ka	Faith et al., 2019
Lunatoceras	*Megalotragus priscus*	7.4 ^{14}C ka BP	Faith, 2014
Megalotragus	*Megalotragus eucornutus*	1.0 Ma	Brink et al., 2012
Gen. nov. 1	*?Parmularius* sp. nov.	1 Ma - 600 ka	Klein et al., 2007
Gen. nov. 2	Gen et. sp. nov. "spiral horn"	1 Ma - 600 ka	Klein et al., 2007
Makapania	*Makapania broomi*	780 - 578 ka	Lacruz et al., 2002
Phenacotragus	*Antidorcas recki*	800 - 600 ka	Faith et al., 2019

[1] The record of *Gomphotherium* from the Pleistocene Vaal River gravels in South Africa probably derives from much older deposits (Wells, 1964).
[2] *Potamochoeroides* is a synonym of *Metridiochoerus*. Cooke (1963) mistakenly listed *Potamochoeroides majus* (instead of *Potamochoerus majus*) from Olduvai Gorge, a species that is now assigned to the genus *Kolpochoerus*.

Pleistocene extinctions were not sudden and catastrophic. In opposition to his previous characterization of African Pleistocene extinctions, Martin (1984:382–383) remarked that "the outstanding feature of the African Pleistocene is the astonishing number of large animals which survived." According to his revised thinking, this reflected long-term coevolution between hominin hunters and their prey (see also Martin, 2005).

The recent literature

The early hypotheses of ancient anthropogenic extinctions in Africa had little influence on the development of the contemporary literature, and for good reason: Clark's (1959) speculation lacked detail and Martin's (1966) arguments became untenable as new chronological evidence came to light. After a hiatus of several decades, however, new versions of the ancient anthropogenic extinction hypothesis emerged. These have had a much greater impact in the sense that they are increasingly cited in the ecological and conservation biology literature as evidence for a deep history of hominin impacts on the natural world (e.g., Hoag and Svenning, 2017; Johnson et al., 2017; Malhi et al., 2016; Turvey and Crees, 2019).

The first set of these renewed ancient anthropogenic extinction hypotheses contends that hominin predation played a role in the demise of Africa's largest mammals. In a study of body size distributions of late Quaternary mammals across the Americas, Australia, and Africa, Lyons et al. (2004) called attention to the relative lack of megafaunal extinctions over the last ∼100,000 years in Africa. Attempting to explain this anomaly, they entertained two hypotheses. The first, consistent with previous suggestions (Martin, 1984), was that long-term co-evolution of African megafauna with our hominin ancestors led to the development of anti-predator behaviors that lessened the impacts of hominin predation. The second hypothesis, in contrast, proposed that the late Quaternary extinctions were limited because the majority of losses had already occurred much deeper in time as a result of ancient hominin impacts. Showing parallels with Martin's (1966) earlier work, Lyons et al. (2004:353) suggested "[i]t is also likely…that the entire Pleistocene fossil record for Africa would show corresponding 'pulses' of human-caused extinctions of large mammals as human culture and hunting technology developed." They provided some evidence for this scenario, noting a decline in proboscidean diversity from the Early Pleistocene to the Middle Pleistocene (from 12 species to two), which they linked to the appearance of *H. erectus*.

Others have since provided complementary ideas. Building an argument for global proboscidean overkill, Surovell et al. (2005) suggested that Middle Pleistocene hominins were capable of stalking and killing adult proboscideans, and they implicated hominins in the demise of *Deinotherium* and *Elephas* in Africa, noting an apparent chronological association between archaeological evidence of their exploitation and extinction. A more recent hypothesis is provided by Smith and colleagues (2018). In an exploration of mammalian body size trends throughout the Cenozoic, they observed that the average body mass of African mammals prior to the Late Pleistocene is smaller than on other continents. In their view, this reflects a long history of anthropogenic extinctions of Africa's large-bodied species, attesting to hominin impacts on natural ecosystems before the appearance of *H. sapiens*.

The second set of ancient anthropogenic extinction hypotheses contends that encroachment of Early Pleistocene *Homo* into the carnivore guild led to the demise of several carnivoran lineages (e.g., sabertooth felids). Focusing on the eastern African carnivoran fossil record, Lewis and Werdelin (2007) observed an increase in large carnivoran (>21.5 kg) extinction rates and a consequent decline in richness beginning ~1.8 Ma (see also Werdelin and Lewis, 2005) (Fig. 2). They recognized that environmental changes may have played a role in this pattern, but also suggested that confrontational scavenging (kleptoparasitism) by *H. erectus* may have been sufficient to drive extinctions among carnivorans. Werdelin and Lewis (2013b) later expanded on their hypothesis, documenting a decline in the functional ecological diversity of large carnivorans between 2.5-2.0 Ma and 2.0-1.5 Ma, and again between 2.0-1.5 Ma and the present (they did not examine fossil data <1.5 Ma). They noted that the earlier decline in functional diversity reflected the loss of omnivorous taxa (e.g., the giant otter *Enhydriodon*), with later extinctions occurring among hypercarnivores (e.g., hyaenids and felids). To them, this was further evidence of ancient hominin impacts, with the shift from initial diet breadth expansion (and increased carnivory) in early *Homo* to the more carnivorous niche of *H. erectus* translating to a staggered wave of anthropogenic extinctions across increasing trophic levels (i.e., from mesopredators to apex predators).

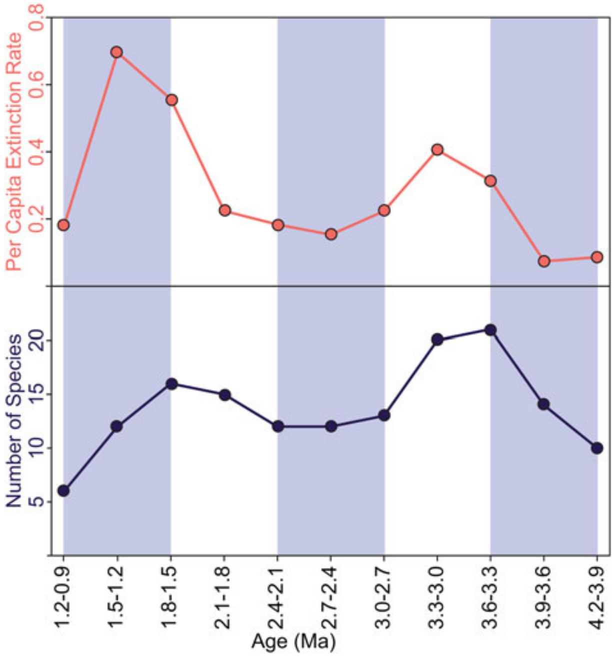

Figure 2. (color online) Per capita extinction rate and species richness of large-bodied (>21.5 kg) carnivorans from eastern Africa. Modified from Lewis and Werdelin (2007).

Fortelius et al. (2016) also relied on carnivoran turnover patterns to make an argument for ancient anthropogenic extinctions, though somewhat earlier in time than suggested by the studies above. In an analysis of late Cenozoic mammals from the Turkana Basin (Kenya), they observed a peak in carnivoran extinction rates between ~2.8-2.2 Ma that was unmatched by other lower trophic groups and out of sync with ecometric evidence (i.e., reconstructions of environmental parameters from herbivore dental traits) for climatic changes. They proposed this may indicate a biotic driver, namely a top-down trophic cascade driven by the appearance of a new apex guild member, tool-bearing hominins, leading to a collapse of carnivoran diversity. They further suggested that predator release could have led to an increase in herbivore populations, with the increased consumption of woody vegetation facilitating the expansion of C_4 grassland ecosystems. Fortelius et al. (2016) recognized that much more work was necessary to confirm this hypothesis, but if correct it implies that hominin impacts may account, at least in part, for the expansion of C_4 grasslands in Africa—one of the most significant environmental changes to have occurred over the last few million years (Levin, 2015).

The most recent argument for ancient anthropogenic extinctions is also based on extinction rates among eastern African carnivorans. Using a Bayesian framework for estimating extinction rates in the fossil record, Faurby et al. (2020) showed the extinction rate of large carnivorans (>21.5 kg) has increased steadily over the last 4 Myr, a trend that tracks increasing hominin brain size (e.g., Du et al., 2018) as well as environmental change, especially the expansion of grassland habitats (e.g., Levin, 2015). Based on an evaluation of environmental variables proposed to mediate carnivoran community composition across Africa today, they argue that environmental changes cannot account for the extinction of large-bodied carnivorans. Thus, Faurby et al. (2020) propose that the correlation between large carnivoran extinction rates and hominin brain size reflects a causal relationship, with larger brains associated with enhanced cognition, improved technology, higher population densities, and greater meat consumption. The outcome, according to Faurby et al. (2020), was increased extinction rates among large carnivorans, beginning long before the emergence of the genus *Homo*. Of course, the initial phase of increasing extinction rates begins well before we see archaeological evidence for hominin meat-eating or inferred predation on large mammalian prey, so they propose that early hominins drove the extinctions by stealing carcasses from large carnivorans. Later, as hunting became more prevalent among our hominin ancestors, Faurby et al. (2020) envision that prey availability was reduced to the point where many carnivoran species—faced with too much competition and too little food—became extinct.

Of these recent studies outlining ancient anthropogenic extinction hypotheses, the papers by Lewis and Werdelin (2005; Werdelin and Lewis, 2013b) and Faurby et al. (2020) are the only ones to provide lengthy consideration of the matter (see also the review in Lewis, 2017), helping to move the debate forward. The others offer only brief discussions, typically no more than a handful of sentences each—not much different from Clark's (1959) early speculation. We note this not as a point of criticism, but rather to highlight that the growing acceptance of ancient anthropogenic extinction hypotheses among ecologists and conservation biologists is based on a limited body of literature. Nonetheless, this literature has made an impact. For example, in their influential review of the consequences of megafaunal loss on ecosystem processes, Malhi et al. (2016:839) cite the reduction in proboscidean diversity previously noted by Lyons et al. (2004) as evidence for "abnormal rates of megafaunal loss" due to Early Pleistocene hominin impacts. Johnson et al. (2017) did the same in their overview of anthropogenic biodiversity loss, when they asserted that hominin impacts extend back to ∼2 Ma. These studies also accept and reiterate the argument that hominin carnivory led to extinction of carnivorans, as do many others (e.g., Hoag and Svenning, 2017; Miranda et al., 2019; Sandom et al., 2017). Reading this literature, which uncritically accepts ancient anthropogenic extinction scenarios, one might conclude that the underlying evidence is exceptionally robust. We turn to this issue next.

EVALUATING THE EVIDENCE

The extinction of megaherbivores

Since the initial observation by Lyons et al. (2004), the chronological association between the appearance of *H. erectus* and the reduction in proboscidean diversity is frequently cited as evidence for ancient anthropogenic extinctions (e.g., Hoag and Svenning, 2017; Johnson et al., 2017; Malhi et al., 2016). A deeper temporal perspective, however, casts doubt on the extent to which this association reflects a causal relationship. African proboscidean diversity has been in decline since peaking at ∼12 species (eight genera) near the Miocene-Pliocene boundary (Fig. 3) (Sanders et al., 2010; Todd, 2006). This decline occurs in the context of an increasingly well-sampled fossil record (e.g., Werdelin, 2010), meaning it cannot be accounted for by sampling artifacts.

In light of the current understanding of proboscidean evolution (Sanders et al., 2010), it is now clear that by the time *H. erectus* appeared at ∼2.0 Ma, only five species remained (*Deinotherium bozasi*, *Elephas recki*, *Mammuthus meridionalis*, *Loxodonta atlantica*, and *Loxodonta adaurora*)—far less than the dozen cited by Lyons et al. (2004; based on data in Coppens et al., 1978) as potential victims of anthropogenic extinctions. So, although it is true that proboscidean extinctions occurred after the emergence of *H. erectus*, there is little reason to infer that this species was the catalyst of their demise. Rather, these losses simply represent the more recent phase of an extinction process spanning millions of years that initiated not long after the emergence of the hominin clade at ∼7-6 Ma (Brunet et al., 2002; Haile-Selassie et al., 2004; Senut et al., 2001). To forge a causal link between hominin activities and the onset of the proboscidean decline, one would need to make the bold claim that candidates for the earliest hominins—i.e., *Sahelanthropus*, *Orrorin*, *Ardipithecus*—were capable of hunting elephant-sized animals. Yet in terms of their paleobiology, the earliest hominins were functionally equivalent to bipedal apes, being characterized by chimpanzee-sized brains and body sizes, predominantly frugivorous diets, and lacking flaked stone tools (e.g., White et al., 2009; White et al., 2015). Though it is reasonable to suppose that they may have occasionally preyed upon small-bodied vertebrates as do extant chimpanzees (Stanford, 1995, 1999, 2012), hunting proboscideans is far outside the realm of plausibility.

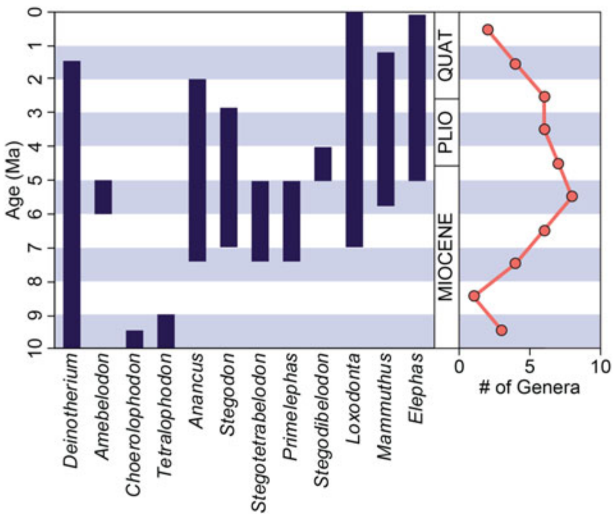

Figure 3. (color online) (Left) The currently known temporal durations of African proboscideans since the late Miocene. (Right) Changes in the number of proboscidean genera present in 1-Myr time bins. Data from Sanders et al. (2010). The last appearance of *Deinotherium* is earlier than in Sanders et al. (2010), given the revised understanding of the chronology of Kanjera (Ditchfield et al., 1999).

Given the decline of Africa's proboscideans over millions of years (Fig. 3), we question why archaeological evidence for hominin consumption of proboscideans need imply an anthropogenic role in their extinction, as suggested by Surovell et al. (2005). There are only a handful of Early-to-Middle Pleistocene archaeological sites that provide such evidence, including proboscidean skeletons associated with flaked stone artifacts (Chavaillon et al., 1987; Delagnes et al., 2006; Leakey, 1971; Potts et al., 1999) and a butchered elephant bone (Pante et al., 2018). In all cases it is unclear whether the proboscideans in question were hunted or scavenged, but even if they were hunted it is does not appear that this had much influence on their populations. Most evidence for hominin consumption of proboscideans involves *Elephas recki*, which is found in several single-carcass butchery sites ranging in age from ~1.6 Ma to ~0.7 Ma (Chavaillon et al., 1987; Delagnes et al., 2006; Potts et al., 1999). Yet despite consumption by hominins, its direct descendant *E. jolensis* persisted until the end of the Pleistocene (Manthi et al., 2019). This long-term persistence is incompatible with interpretation of the archaeological record as indicating intense, extinction-driving levels of predation by *H. erectus* and its successors.

The long-term decline of proboscideans undoubtedly led to a reduction in the mean body mass of African mammals. Smith et al. (2018) argued that the relatively low mean mass of African mammals prior to the Late Pleistocene (47 kg)—less than half that observed in Eurasia (98 kg), North America (98 kg), and South America (100 kg)—provided evidence for ancient hominin impacts (a similar pattern holds for median mass). Figure 4 shows the body mass distribution ($\log_{10}$-transformed grams) of late Quaternary African mammals relative to these other continents combined. These distributions are significantly different (Kolmogorov-Smirnov test: $p < 0.001$), with the most striking difference being the exceptional abundance of very small species (~10-20 g = 1-1.25 $\log_{10}$ mass) in Africa, most of which are shrews of the genus *Crocidura*. Importantly, these differences drive the anomaly noted by Smith et al. (2018). If we focus attention on species ≥ 1kg—i.e., those that are more likely to be included in the hominin diet—the difference in the size distribution between Africa and the other continents disappears (Kolmogorov-Smirnov test: $p = 0.101$). Likewise, a Mann-Whitney U-test shows the medians of species ≥ 1 kg (Africa = 11.5 kg; other continents = 11.0 kg) are statistically indistinguishable ($p = 0.498$). Thus, Africa is unique not because larger-bodied mammals are missing, but rather because it has high richness of the smallest taxa, namely shrews.

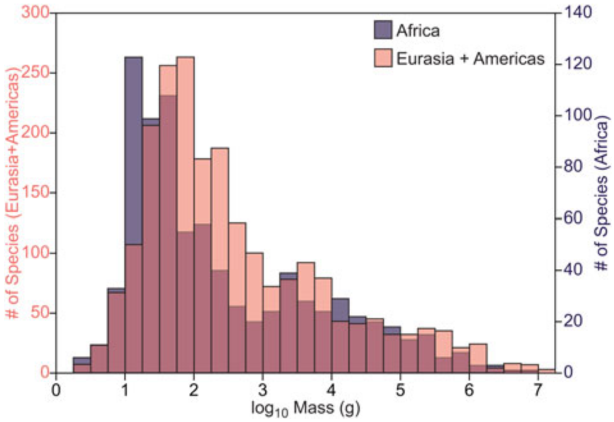

Figure 4. (color online) Body mass distributions ($\log_{10}$ transformed) of late Quaternary mammals from Africa compared to that from Eurasia and the Americas. Data from Smith et al. (2018: Table S6).

The case for environmental change

Recent analysis of eastern African fossil evidence reinforces the continental-scale patterns of proboscidean decline (Fig. 3), and provides insight into the mechanism underpinning it. Faith et al. (2018) examined the richness of megaherbivores (>1,000 kg) from eastern African fossil assemblages spanning the last 7 Myr (Fig. 5). They focused on megaherbivores, which include proboscideans, rhinos, hippos, and others, because the extinction of such large-bodied species is widely thought to be a hallmark of anthropogenic extinctions (Lyons et al., 2004; Smith et al., 2018, 2019). Their analysis showed that the number of megaherbivore taxa found in eastern African fossil assemblages has steadily declined since ~4.6 Ma, reflecting the extinction of more than two dozen taxa. Similar to the case of proboscideans across the continent (Fig. 3), the antiquity of this decline precludes hominin impacts as a plausible mechanism for setting it in motion, as it would have to involve hominin taxa (e.g., *Ardipithecus*, *Australopithecus*) that almost certainly could not hunt megaherbivore prey. The earliest archaeological evidence for hominin interaction with megaherbivores, which includes cut-marks on a rhinoceros rib from Koobi Fora (1.95 Ma; Braun et al., 2010) and an elephant metapodial from Olduvai Gorge (1.7 Ma; Pante et al., 2018), is considerably later, roughly corresponding to the appearance of *H. erectus*. There is ongoing debate about whether the faunas found in Early Pleistocene archaeological sites were acquired by hunting or scavenging (e.g., Domínguez-Rodrigo et al., 2014; Pante et al., 2015), and it is unknown whether these butchered megaherbivores indicate that *H. erectus* was capable of killing these animals. Though it is possible that *H. erectus* contributed to megaherbivore extinctions through overhunting, Faith et al. (2018) showed that its appearance is not associated with any acceleration in the rate of megaherbivore decline.

Instead of attributing the loss of eastern African megaherbivores to hominin impacts, a more likely candidate is the expansion of C_4 grasslands (Faith et al., 2018), one of the most substantial changes to eastern African ecosystems since the late Miocene (Levin, 2015). The decline in megaherbivore diversity closely tracks the expansion of grasslands inferred from the $\delta^{13}C$ of eastern African paleosol carbonates (Fig. 5), as well as a suite of other regional proxies for vegetation cover (Levin, 2015). A causal relationship between grassland expansion and megaherbivore decline is supported by paleodietary evidence, which indicates that most fossil megaherbivore taxa were browsers or mixed feeders that relied on C_3 plant foods, including trees, shrubs, or herbs (Fig. 5). Because megaherbivores tend to be strongly limited by forage availability (Owen-Smith, 1988), it is not surprising that the decline in megaherbivores tracks the loss of their food sources as C_4 grasslands expanded across eastern Africa (Fig. 5). At the same time, decreasing atmospheric CO_2 concentrations (Stap et al., 2016)—likely an important driver of the C_4 expansion (e.g., Cerling et al., 1997; Faith et al., 2018; Levin, 2015)—would have diminished the ecological advantage of massive body size, which allows megaherbivores to

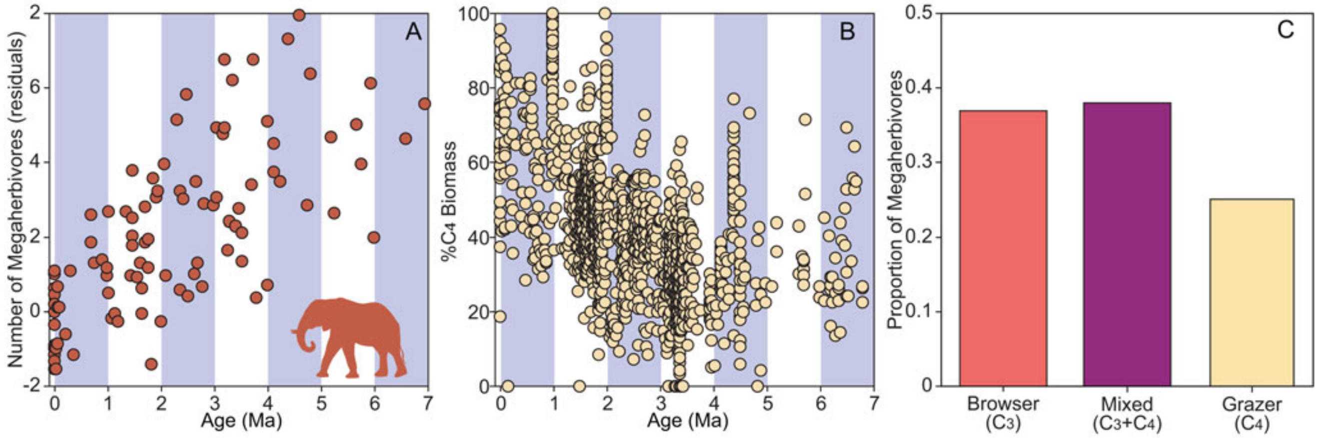

Figure 5. (color online) (A) The decline in megaherbivores from eastern African fossil sites. Data points represent residuals from the least-squares regression modelling the relationship between total ungulate community richness and megaherbivore richness in the present-day (see Faith et al. 2018). (B) Percentage of C_4 biomass inferred from $\delta^{13}C$ of eastern African paleosol carbonates. Percent C_4 data from Faith et al. (2018) using $\delta^{13}C$ data compiled by Levin (2015). (C) Dietary ecology of extant and fossil eastern African megaherbivore taxa inferred from various paleodietary proxies (data from Faith et al. 2018, 2019).

consume lower-quality forage than small-bodied species (Owen-Smith, 1988). This is because C_3 plants grown at lower CO_2 concentrations tend to have higher N content and fewer secondary compounds (e.g., Cotrufo et al., 1998; Owensby et al., 1996), expanding the range of the C_3 resources that would be palatable to smaller-bodied herbivores. Thus, not only did the availability of environments rich in C_3 foods diminish, but there is likely to have been greater competition for those that remained. The outcome of these environmental and ecological changes, according to Faith et al. (2018), was the loss of eastern Africa's megaherbivore diversity.

The extinction of carnivorans

Carnivoran extinction rates and diversity

Lewis and Werdelin (2007) demonstrated an increase in carnivoran extinction rates after ~1.8 Ma using Foote's (2000) per-capita extinction rate (q): $q = –\ln(N_{bt}/(N_{bt} + N_{bL}))/\Delta t$, where N_{bt} is the number of taxa whose temporal range crosses the bottom and top boundaries of a given time interval (i.e., taxa found in younger and older intervals), N_{bL} is the number of taxa that cross the bottom boundary of a given time interval (i.e., taxa found in older interval and whose last appearance occurs in the interval in question), and Δt is time interval length. Here we replicate their analysis using an updated eastern African fossil dataset of large carnivorans (>21.5 kg) spanning 7 to 1 Ma (Supplementary Table 1). Figure 6 shows the per-capita extinction rate across 0.5 Myr time bins, highlighting the increase in extinction rates around the same time that *H. erectus* appears (the 2.0-1.5 Ma bin). This increase in extinction rates also corresponds to a reduction in carnivoran richness (Fig. 6), consistent with the results obtained by Lewis and Werdelin (2007; compare to Figure 2).

Our concern with analyses like the one provided by Lewis and Werdelin (2007) and by us in Figure 6 is that sampling issues likely account for the empirical observations. Raw carnivoran richness is strongly correlated with the number of fossil sites across time bin ($r = 0.842$, $p = 0.001$), and the same is true of the per-capita extinction rates (correlation with number of sites: $r = 0.672$, $p = 0.033$; Figure 6). Thus, the trends in richness and extinction rates can be most parsimoniously interpreted as reflecting sampling intensity (i.e., the number of sites). The correlation between the number of sites and carnivoran richness is unsurprising given the well-documented relationships between sampling effort and richness (Grayson, 1984; Lyman, 2008). The likely mechanism underpinning the correlation with extinction rates is that these rates require that the last appearances of the taxa represented by N_{bL} be accurate reflections of their true extinction dates (Foote, 2000; Foote and Miller, 2007). However, it is well known that the temporal offset between last appearance and true extinction dates decreases as a function of more complete sampling (e.g., Signor and Lipps, 1982; Wang and Marshall, 2016; Du et al., 2020). And given that the fossil history of a taxon is typically characterized by a waxing and waning of occupancy, geographic range, and abundance through time (Žliobaitė et al., 2017), we expect that, on average, taxa that disappear within a given interval (N_{bL}) are likely to be numerically rarer than those that persist through the interval (N_{bT}). Thus, taxa that are on their way to extinction should be harder to sample than taxa that are not, meaning that increasing sampling effort (i.e., more sites) leads to a greater ratio of N_{bL} to N_{bT} and an apparent increase in per-capita extinction rates.

Given these observations on the influence of sampling, the extinction rates examined by Fortelius et al. (2016) also warrant further evaluation, especially considering that their analysis is based on a smaller subset (Turkana Basin) of the eastern African data examined by us in Figure 6. Figure 7 illustrates their per-capita extinction rates for carnivorans

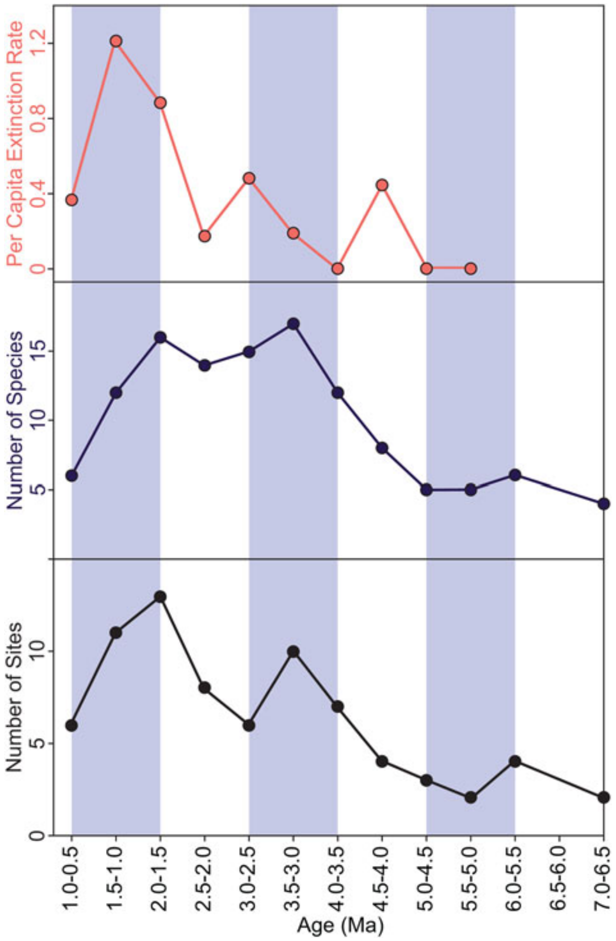

Figure 6. (color online) Per-capita extinction rate and species richness of large-bodied carnivorans (>21.5 kg) from eastern Africa relative to the number of fossil sites (data from Supplementary Tables 1-2).

and non-carnivorans. The early peak at 2.8-2.5 Ma, which Fortelius et al. (2016) attribute to hominin impacts because a corresponding peak is not observed among non-carnivorans, occurs in the context of a sparse fossil record that makes it exceedingly difficult to distinguish ecological signal from noise (the increasing extinction rates after 2.2 Ma correspond to increasing sample sizes). Their database includes only 41 carnivoran specimens assigned to genus or lower from 4.0 to 2.2 Ma, posing a problem for establishing reliable last appearances of extinct taxa—data that form the basis of per-capita extinction rates (Foote, 2000; Foote and Miller, 2007). Furthermore, there is only a single carnivoran specimen (identified only as Carnivora indet.) from the 2.5-2.2 Ma bin, leading Fortelius et al. (2016) to suggest that the temporal ranges of taxa that disappeared at 2.8-2.5 Ma could very well have extended into the stratigraphically higher 2.5-2.2 Ma bin. But if the two bins are merged, as this viewpoint implies, then interval length (Δt) doubles, the per-capita extinction rate is halved, and the extinction peak largely disappears (Fig. 7). Taken together, we see little evidence from the Turkana Basin carnivoran record for an anomalous collapse of the carnivore guild driven by the appearance of technologically advanced hominins.

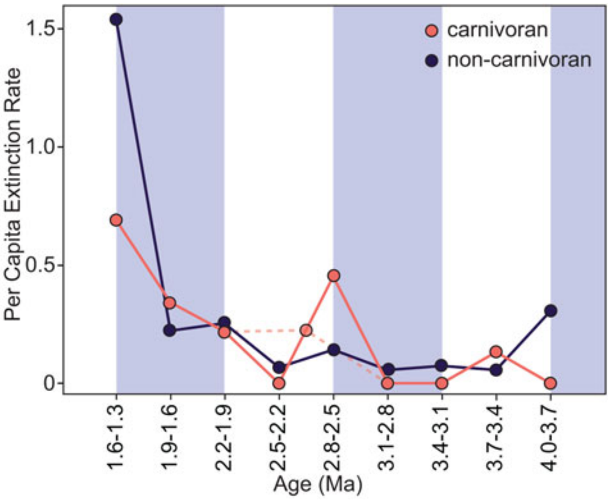

Figure 7. (color online) Per-capita extinction rate of carnivorans and non-carnivorans from the Turkana Basin (after Fortelius et al. 2016). The dashed line indicates the change in carnivoran extinction rates if the 2.8-2.5 and 2.5-2.2 Ma bins are combined.

Faurby et al. (2020) document a steady increase in large carnivoran (>21.5 kg) extinction rates over the last ∼4 Myr in eastern Africa using a Bayesian approach that explicitly takes sampling into account (Silvestro et al., 2014), so we accept their observation at face value. However, because the increase in large carnivoran extinction rates closely tracks environmental changes, especially the expansion of grassland ecosystems (Fig. 5B), their case for ancient anthropogenic extinctions required them to exclude these changes as a viable mechanism. To do so, they focused their attention on the proportion of large carnivorans relative to all carnivorans, the rationale being that the increase in large carnivore extinction rates together with stable small carnivoran (<21.5 kg) extinction rates should lead to changes in this proportion (implicitly assuming that origination rates are constant through time). Faurby et al. (2020) used regression techniques to model the proportion of large carnivorans as a function of various environmental variables (e.g., precipitation, temperature, forest cover) across Africa today, which they then used to predict temporal changes in the proportion of large carnivorans from independent paleoenvironmental proxies. Their predictions suggested that, in the absence of anthropogenic impacts, the proportion of large carnivorans should have remained unchanged through time. Yet they report “a drastic decline in the fraction of large carnivores” (p. 541), implying to them that hominin impacts had contributed to the loss of large-bodied carnivorans.

We have concerns with their approach to excluding environmental change as a driver of carnivore extinctions. First, their analysis showed that forest cover is a relatively unimportant predictor of the proportion of large carnivorans in Africa today. This may be so, but a reliance on modern carnivorans

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limits our ability to make inferences about the past, which included ecosystems that were fundamentally different (e.g., Faith et al., 2019). In particular, we note that as a result of past extinctions, present-day carnivoran communities are missing the large-bodied species that inhabited forested environments, including many sabertooth felids (Lewis, 1997; Marean, 1989). Thus, we question whether stasis in the proportion of large carnivorans through time is to be expected in the absence of anthropogenic impacts—the expansion of grasslands and loss of forest cover over the last several million years is likely to have been far more detrimental to large carnivorans than suggested by an analysis that relies on present-day relationships. Our second concern is that the decline in the proportion of large carnivorans is not statistically supported. In examining the proportion of large carnivorans through time (from 4 to 1 Ma), Faurby et al. (2020) account for chronological uncertainty (i.e., their range of values reflects a procedure that accounts for uncertainty in the temporal ranges of fossil occurrences), but they do not account for uncertainty in the target variable—the proportion of large carnivorans. We do so here in Figure 8, which illustrates the proportion of large carnivorans from 4-1 Ma with associated 95% confidence intervals. Our results are similar to those provided in Faurby et al. (2020), showing a decline in the proportion of large carnivorans after ~2.2 Ma, but the substantial overlap in 95% confidence intervals obscures any temporal trends over this interval. This combination of issues means (1) that we cannot be sure that stasis in the proportion of large carnivorans is to be expected in the absence of anthropogenic impacts, and (2) that we cannot provide a robust assessment of how this variable changed through time. Thus, it is premature to discount environmental changes as an important driver of carnivoran extinctions.

The viability of the anthropogenic extinction mechanism proposed by Faurby et al. (2020) is also questionable. Their scenario requires that pre-*erectus* hominins (e.g., australopiths and early *Homo*) were stealing prey from large carnivorans—on such a scale as to drive extinctions—long before we see archaeological or anatomical evidence suggesting that carnivory was important (Aiello and Wheeler, 1995; Antón et al., 2014; Braun et al., 2010; Ferraro et al., 2013; Pante et al., 2018; Thompson et al., 2019). It also implies that meat (rather than bone marrow) was central to early hominin animal exploitation, and that the benefits of its acquisition outweighed the risks involved in stealing it from large and dangerous carnivorans. Yet there is good reason to believe that the initial phase of large animal exploitation by early hominins was geared toward exploitation of within-bone nutrients like bone marrow, a resource that could be more safely acquired from carcasses abandoned by sabertooth felids and other flesh specialists (e.g., Blumenschine, 1987; Blumenschine and Madrigal, 1993; Marean, 1989; Thompson et al., 2019). These issues make it difficult to envision that australopiths or early *Homo* were actively involved in stealing prey from large predators, especially to the degree that could cause extinctions.

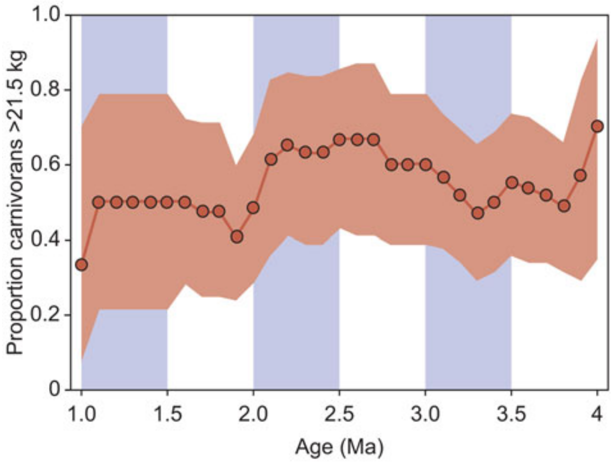

Figure 8. (color online) The proportion of carnivorans >21.5 kg (relative to all carnivorans) from 4 to 1 Ma across 100 kyr bins. Shading indicates 95% confidence intervals determined using an exact binomial test.

The pattern of large carnivoran diversity decline poses additional problems to ancient anthropogenic extinction hypotheses. Figure 9A illustrates temporal changes in the richness of size 3 carnivorans (21.5 to 100 kg) and size 4 carnivorans (>100 kg) from 4-1 Ma (size classes follow Lewis and Werdelin, 2007). The most substantial losses have been among size 4 carnivorans, which have been in steady decline since peaking (8 taxa) at ~3.6 Ma (see also Faith et al., 2019), with only a single species remaining today (*Panthera leo*). In contrast, the number of size 3 carnivorans is fairly stable at 7-10 species—not substantially higher than that presently found in eastern Africa (6 species; Lewis and Werdelin, 2007)—until after ~1.8 Ma. Similar patterns are observed when sampling is taken into account (Fig. 9B), with the decline in size 4 carnivorans occurring well before their size 3 counterparts. This offset timing is hard to reconcile with anthropogenic extinction hypotheses, which emphasize the detrimental effects of hominin competitors (Faurby et al., 2020; Lewis and Werdelin, 2007; Werdelin and Lewis, 2013b). Such a scenario would require that hominins be capable of competing with and ultimately driving to extinction the largest carnivorans (e.g., *Homothereium*, *Dinofelis*, and *Pachycrocuta*) since the Pliocene, while somehow sparing the smaller (and arguably less dangerous) carnivorans until ~1.5 Myr later. Under an anthropogenic extinction scenario, we would expect the opposite to occur, with hominin impacts initially restricted to the mesopredators and, as hominin carnivory increased, moving up trophic levels to include the apex predators (see also Werdelin and Lewis, 2013b). That the opposite has occurred strongly implies a non-anthropogenic mechanism.

Carnivoran functional diversity

An additional line of evidence used to support the ancient anthropogenic extinction of eastern Africa's carnivorans is derived from temporal changes in the functional morphospace among large-bodied (>21.5 kg) carnivorans (Werdelin

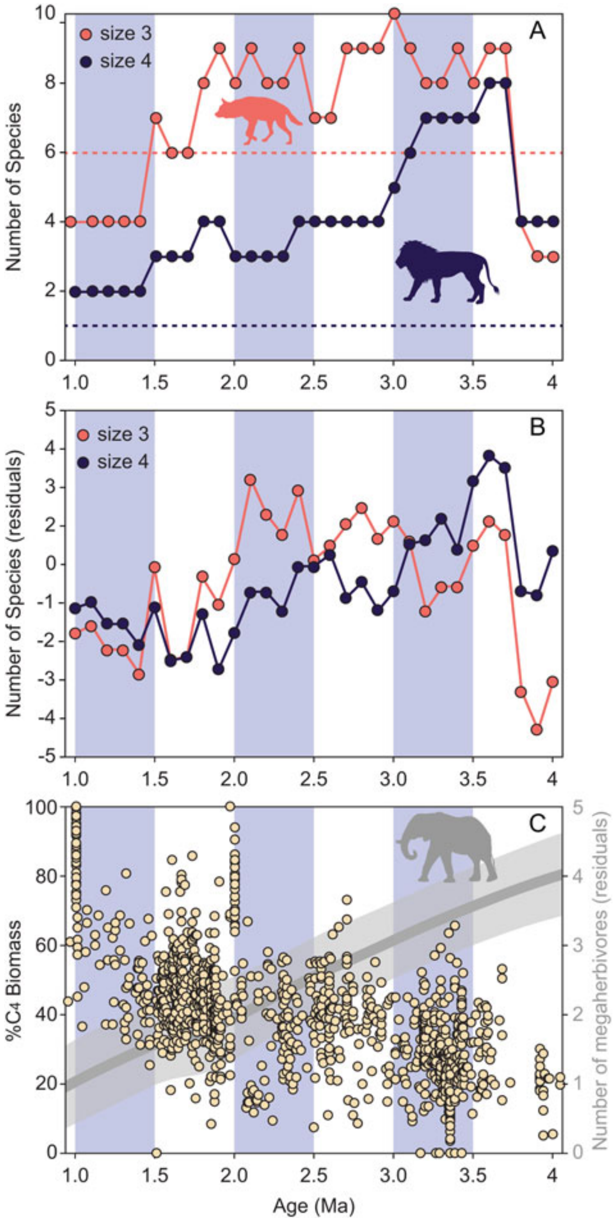

Figure 9. (color online) (A) Richness of size 3 (21.5 to 100 kg) and size 4 (>100 kg) carnivorans. Dashed lines indicate contemporary richness in eastern Africa. (B) Richness residuals of size 3 and size 4 carnivorans. Residuals are derived from ordinary least squares regressions modelling the relationship between the number of large (>21.5 kg) carnivoran fossil occurrences whose ages overlap with a given interval and the number of species in a given interval. For all analyses, the temporal range of a taxon is determined using the midpoint of its first and last appearances, and the taxon is assumed to be present in all intervening bins (range-through); richness is based on tallies of non-overlapping taxa (e.g., *Hyaena hyaena* and *Hyaena* sp. represent one species because the latter cannot be shown to represent a second species). Data from Faurby et al. (2020). (C) The decline of megaherbivores relative to the percentage of C_4 biomass inferred from $\delta^{13}C$ of eastern African paleosol carbonates (from Faith et al., 2018). Grey line is the LOESS regression (95% confidence interval in light grey) of the megaherbivore residuals shown in Figure 5A.

and Lewis, 2013b). This analysis was based on a correspondence analysis of a species by dental trait matrix for African carnivorans. Werdelin and Lewis (2013b) noted substantial declines in functional richness (convex hull area), between the 2.5-2.0 and 2.0-1.5 Ma time bins, and again between 2.0-1.5 Ma and the present (Fig. 10). This was accompanied by a loss of functional evenness, which they defined as the evenness of the taxon distribution in filled niche space and measured using multiple metrics (e.g., mean distance between taxa, variance of the distances between taxa).

We accept that there has been a change in African carnivoran functional diversity since the onset of the Pleistocene, but closer inspection of the data analyzed by Werdelin and Lewis (2013b) shows that the magnitude of the extinctions underpinning this trend is overstated—the trend is driven by the loss of a small number of functionally divergent species of uncertain relevance to hominins (Fig. 10). The earlier phase of functional richness decline (from 2.5-2.0 to 2.0-1.5 Ma) is driven by the extinction of the giant otter *Enhydriodon* (Fig. 10), and the later phase of decline (from 2.0-1.5 Ma to present) by the loss of two large-bodied viverrids (*Pseudocivetta ingens* and Viverridae sp. G) (Fig. 10). These extinctions also force the decline in Werdelin and Lewis' measures of functional evenness, as removal of these morphological outliers in the correspondence analysis translates to lower inter-point distances between taxa and reduced variance of those distances. Thus, the decline of functional diversity that provides the basis for Werdelin and Lewis' (2013b) ancient anthropogenic extinction argument boils down to the loss of three taxa, which occurs over a period of at least ~1 Myr: *Enhydriodon* and Viverridae sp. G make their last appearances at ~1.9 Ma (Werdelin and Lewis, 2005; Werdelin and Lewis, 2013a) (though the latest record of *Enhydriodon* is tentative and it may have disappeared prior to 2 Ma), and *P. ingens* persists until ~900 ka (Geraads et al., 2011; Geraads et al., 2004). In our view, the loss of three taxa over at least a million years is an insufficient ecological signal to warrant a unique anthropogenic extinction mechanism, especially considering the uncertain degree of competition between these taxa and ancient hominins. And though we hesitate to speculate about the loss of the two viverrids, Werdelin and Lewis (2005:130) argued "the extinction of *Enhydriodon* must surely be linked to the changes in the drainage patterns of the palaeolakes and palaeorivers in eastern Africa that occurred with the gradual aridification of the latest Pliocene and early Pleistocene." We agree that environmental change is a likely culprit for this extinction.

The case for environmental change

In the absence of robust evidence supporting ancient anthropogenic extinctions, a more viable explanation is that bottom-up forcing driven by environmental change played a

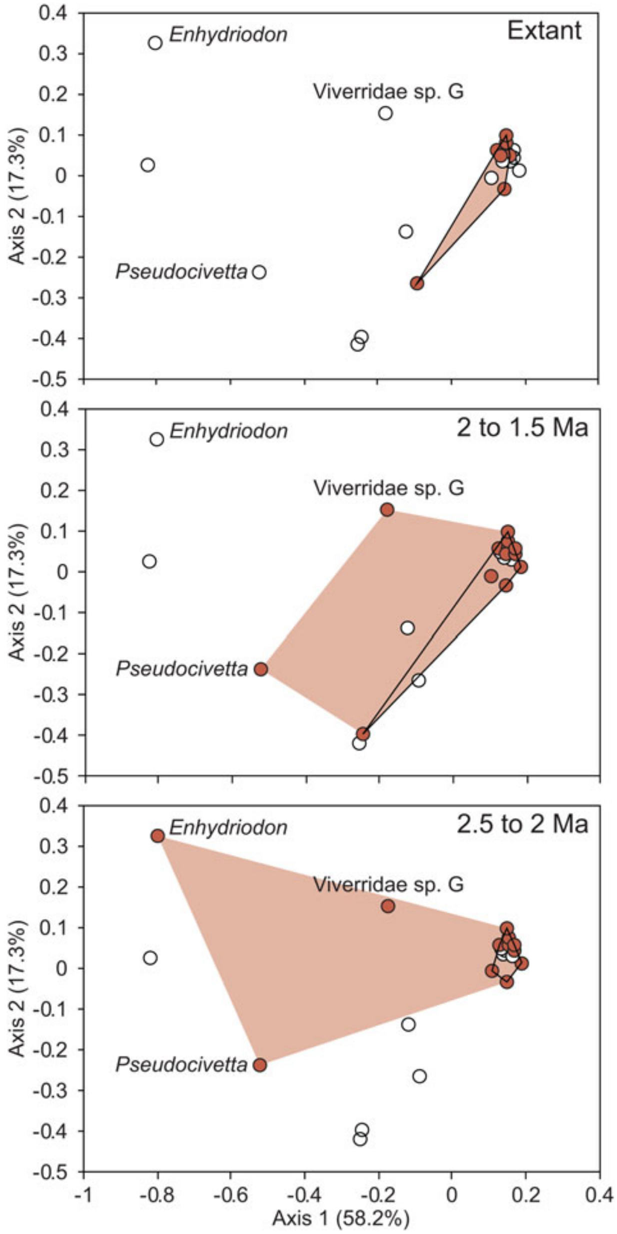

Figure 10. The first two axes of a correspondence analysis of large-bodied (>21.5 kg) carnivoran dental traits across 29 taxa found in eastern African fossil assemblages over the last 3.5 Myr (data from Werdelin and Lewis, 2013). The convex hulls represent functional richness of carnivoran taxa known from each time period with (solid fill) and without (black line) the inclusion of *Enhydriodon*, *Pseudocivetta ingens*, and Viverridae sp. G). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

central role in the loss of carnivoran diversity in eastern Africa (Faith et al., 2019; Faith et al., 2018; Marean, 1989). We note that the increase in large carnivoran extinction rates over the last 4 Myr (Faurby et al., 2020), which translated to considerable losses of species >100 kg (Fig. 9A), closely tracks the expansion of grassland across eastern Africa (Fig. 9C). The loss of tree and bush cover almost certainly played a role in the extinction of ambush predators associated with such habitats, including some of eastern Africa's sabertooth felids, such as *Dinofelis* and *Megantereon* (Lewis, 1997; Marean, 1989). Likewise, those species lacking cursorial body-plans that enable capture of prey in open environments, such as the giant hyaena *Pachycrocuta brevirostris* (Turner and Antón, 1996) or the extinct bear *Agriotherium* (Werdelin and Lewis, 2005), are also likely to have fared poorly as grasslands expanded.

In addition to loss of the habitats to which they were adapted, we suspect that extinction of the largest carnivorans (size 4: >100kg) was also facilitated by changes in the composition of herbivore communities. Work by Van Valkenburgh et al. (2016) demonstrates a strong association between the diversity of size 4 carnivorans and megaherbivores, leading them to propose that diverse communities of megaherbivores promote coexistence among large predators, probably because juvenile megaherbivores were important prey (see also Ripple and Van Valkenburgh, 2010). Their inference is supported by contemporary observations, evidence from fossil carnivoran den assemblages, as well as predator-prey size relationships, which indicate that many extinct size 4 carnivorans should have typical prey sizes that include juvenile megaherbivores. Given this association, Faith et al. (2018) suggested that the demise of megaherbivores could have facilitated the extinction of eastern Africa's largest carnivorans, including sabertooth cats (e.g., *Dinofelis* and *Homotherium*) and massive hyenas (e.g., *Crocuta eturono* and *P. brevirostris*). It is now clear that the demise of the largest carnivorans closely tracks the loss of megaherbivore prey (Fig. 9; see also Faith et al., 2019). Thus, we suggest that the combination of habitat loss and declining availability of megaherbivores were key mechanisms underpinning long-term changes in the eastern African carnivoran community.

The extent to which eastern African carnivorans preyed upon megaherbivores has been questioned by Faurby et al. (2020), who point to isotopic (Bocherens, 2015) and functional morphological evidence (Andersson et al., 2011) relevant to sabertooth dietary ecology. Bocherens (2015) shows that Late Pleistocene *Homotherium serum* from the mammoth steppe of Alaska and the Yukon did not specialize on *Mammuthus*, but it is not clear what this tells us about the feeding ecology of the Early Pleistocene *Homotherium* and other size 4 carnivorans from eastern Africa. Likewise, the functional morphological analysis provided by Andersson et al. (2011) shows that the elongated canines characteristic of sabertooths cannot be interpreted as an adaptation for taking very large prey. While this may be true, the juvenile megaherbivores thought to have been preyed upon by extinct carnivorans need not have been substantially larger than adults of other herbivore prey (Van Valkenburgh et al., 2016). There is still much more to learn about the ecology of eastern Africa's extinct carnivorans—providing data that would be useful for testing potential extinction scenarios—but presently there is little reason to disregard the hypothesis that juvenile megaherbivores were important prey items to the extinct carnivorans.

SUMMARY AND CONCLUSION

Ancient anthropogenic extinction hypotheses have been around for decades (Clark, 1959; Martin, 1966), and until recently had little influence on mainstream thinking with respect to the antiquity of human impacts on the natural world. In recent years, however, we have seen an increasing number of arguments supporting a long history of hominin impacts on Africa's biodiversity (e.g., Faurby et al., 2020; Fortelius et al., 2016; Lewis and Werdelin, 2007; Lyons et al., 2004; Smith et al., 2018), coupled with acceptance of those arguments by researchers concerned with biodiversity loss in the present-day (e.g., Johnson et al., 2017; Malhi et al., 2016; Sandom et al., 2017). The fact that ancient anthropogenic extinction scenarios are now presented as established fact in high-profile venues leaves little question that these ideas are now becoming mainstream. This has all happened quietly, with both tentative hypotheses and more detailed scenarios gaining traction with very little critical evaluation, discussion, or debate.

We have shown that the case for ancient anthropogenic extinctions is highly uncertain. The extent of the literature proposing ancient anthropogenic extinctions is limited, amounting to three detailed treatments (Faurby et al., 2020; Lewis and Werdelin, 2007; Werdelin and Lewis, 2013b) and a handful of brief preliminary hypotheses (Fortelius et al., 2016; Lyons et al., 2004; Smith et al., 2018; Surovell et al., 2005). More importantly, the data analysis supporting these hypotheses is problematic. With respect to the extinction of herbivores, the argument that the loss of Africa's formerly diverse proboscideans was related to predation by *H. erectus* or its successors (Lyons et al., 2004; Surovell et al., 2005) is weakened when viewed from a longer-term perspective (Figs. 3, 5), which highlights the importance of bottom-up ecological processes (Faith et al., 2019; Faith et al., 2018). Likewise, a closer look at the data shows that the body mass distribution of Africa's mammals is not unusual because premodern hominins eliminated the largest species (Smith et al., 2018), but rather because Africa has an impressive number of small-bodied ones (Fig. 4).

Concerning extinctions among eastern Africa's carnivorans, we have shown that the patterns used to support ancient anthropogenic extinction hypotheses are often confounded by sampling issues inherent to the fossil record. Many of the temporal trends in carnivoran richness and per-capita extinction rates cited as evidence for hominin impacts (Fortelius et al., 2016; Lewis and Werdelin, 2007) can be explained by variation in sampling effort (Fig. 6). And though there are exceptions (Faurby et al. 2020), the argument that ancient hominins are responsible for carnivoran extinctions does not adequately account for associated environmental changes or shifts in carnivoran diversity (Fig. 9). In addition, we have also shown that the massive reduction of carnivoran functional diversity considered to be the outcome of encroachment of *Homo* into the carnivore guild (Werdelin and Lewis, 2013b) resulted from the loss of only a handful of taxa over a vast period of time (Fig. 10). Even if it somehow could be shown that these extinctions were the result of hominin impacts, it hardly constitutes evidence for collapse of the carnivore guild. Instead of requiring an anthropogenic explanation, the timing and pattern of diversity decline (Fig. 9) is consistent with bottom-up forcing driven by grassland expansion (Faith et al., 2019; Faith et al., 2018; Marean, 1989), reducing access to suitable habitats and prey.

Despite the growing (and uncritical) acceptance of ancient anthropogenic extinction hypotheses, (e.g., Johnson et al., 2017; Malhi et al., 2016; Sandom et al., 2017), we have shown that there is no compelling empirical evidence supporting the notion that our hominin ancestors are responsible for African extinctions throughout the Pleistocene. The current lack of evidence does not preclude it from being produced in the future, though we are not optimistic that it will be. Looking to the last ∼100,000 years—a time interval encompassing massive demographic and technological change among human populations—it is clear that African megafaunal extinctions are readily explained by environmental changes (Faith, 2014). In particular, grassland herbivores disappeared following alterations in the structure, distribution, or productivity of their habitats (Faith, 2014), consistent with broader changes in herbivore community composition spanning the last 1 Myr (Faith et al., 2019). As Leakey (1966) noted decades ago, if populations of *Homo sapiens* armed with Middle or Later Stone Age technology had little obvious effect on Africa's faunal diversity, then it will be difficult to make the case that low-density populations of hominins relying upon relatively simple technology played a central role in much earlier extinctions. We conclude that in the search for prehistoric human impacts on Africa's ecosystems, we should focus attention on the much more recent record of human-environment interactions.

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SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at https://doi.org/10.1017/qua.2020.51

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