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Late Cenozoic Faunal and Ecological Change in Africa

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environmental change, evolution, hominin evolution, mammals, paleoecology

Abstract

Africa's fossil record of late Cenozoic mammals documents considerable ecological and evolutionary changes through time. Here, we synthesize those changes in the context of the mechanisms proposed to account for them, including bottom-up (e.g., climate change) and top-down (e.g., hominin impacts) processes. In doing so, we (*a*) examine how the incompleteness of the fossil record and the varied spatiotemporal scales of the evidence complicate efforts to establish cause-effect relationships; (*b*) evaluate hypothesized drivers of long-term ecological and evolutionary change, highlighting key unknowns; and (*c*) synthesize major taxonomic and functional trends through time (e.g., downsizing of faunal communities) considering the proposed drivers. Throughout our review, we point to unresolved questions and highlight research avenues that have potential to inform on the processes that have shaped the history of what are today the most diverse remaining large mammal communities on Earth.

- The study of late Cenozoic African mammal communities is intertwined with questions about the context, causes, and consequences of hominin evolution.
- The fossil record documents major functional (e.g., loss of megaherbivores) and taxonomic (e.g., rise of the Bovidae) changes over the past ~7 Myr.

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- Complexities inherent to the fossil record have made it difficult to identify the processes that drove ecological and evolutionary changes.
- Unanswered questions about the drivers of faunal change and the functioning of past ecosystems represent promising future research directions.

INTRODUCTION

The late Cenozoic fossil record of African mammals documents dramatic ecological and evolutionary changes over time. Bovids radiated and became the dominant large mammal taxon, grazers replaced browsers and mixed feeders as the core component of many savanna communities, and body size distributions shifted as the diversity of megaherbivores declined and many of the largest carnivorans became extinct. These and other changes have inspired a vast literature about the mechanisms that may have driven them. Because the insights provided by this research inform on our own evolutionary history, the study of Africa's fossil faunas is deeply intertwined with questions about the ecological context, causes, and consequences of hominin[1] evolution—e.g., How have African ecosystems changed through time? What role did climate forcing play in driving speciation and extinction events? Did top-down impacts by ancient hominins shape the history of Africa's flora and fauna? Though a considerable body of work has explored such questions (e.g., Faith et al. 2018, Reed 1997, Vrba 1995), the challenges involved in establishing robust cause-effect relationships using fossil evidence have precluded consensus (Behrensmeyer 2006, Faith et al. 2021). Indeed, the abundance of case studies, conducted on different taxonomic groups, encompassing a diversity of spatiotemporal scales, and with variable effort to contend with the complexities of the fossil record, has produced a dizzying number of interpretations about the drivers of long-term shifts in African faunal communities and hominin evolution.

With this in mind, we synthesize the fossil evidence of late Cenozoic African mammals in the context of the proposed drivers of ecological and evolutionary change. This includes research concerned with the forces that have shaped the taxonomic and functional composition of mammal communities, as well as the pattern and timing of macroevolutionary change (i.e., speciation and extinction). In doing so, we (*a*) briefly review features of the fossil record that complicate efforts to establish cause-effect relationships; (*b*) examine proposed drivers of African faunal and hominin evolution, highlighting unresolved questions that warrant further attention; and (*c*) synthesize major taxonomic and functional trends documented in the late Cenozoic fossil record. Though our review extends to fossil evidence from across continental Africa, much of our synthesis focuses on the eastern African large mammal record over the past 7 Myr. This record has received the vast majority of research attention because it encompasses the known temporal extent of hominin evolution based on the ~10–7 Ma divergence between the chimpanzee and human lineages (Langergraber et al. 2012). In addition, eastern Africa preserves the richest, most continuous, and best-dated late Cenozoic fossil sequence on the continent (Werdelin 2010).

THE FOSSIL EVIDENCE

Despite the enormous size of Africa (~30.4 million km^2), its late Cenozoic fossil record is primarily derived from a few small windows in the northern, southern, and eastern parts of the continent (**Figure 1*a***). The kinds of fossil records preserved within these regions vary. The northern African

[1]Hominins (tribe Hominini) include modern humans and the extinct species more closely related to *Homo sapiens* (e.g., species of *Homo*, *Australopithecus*, and *Paranthropus*) than to chimpanzees and bonobos (*Pan* spp.).

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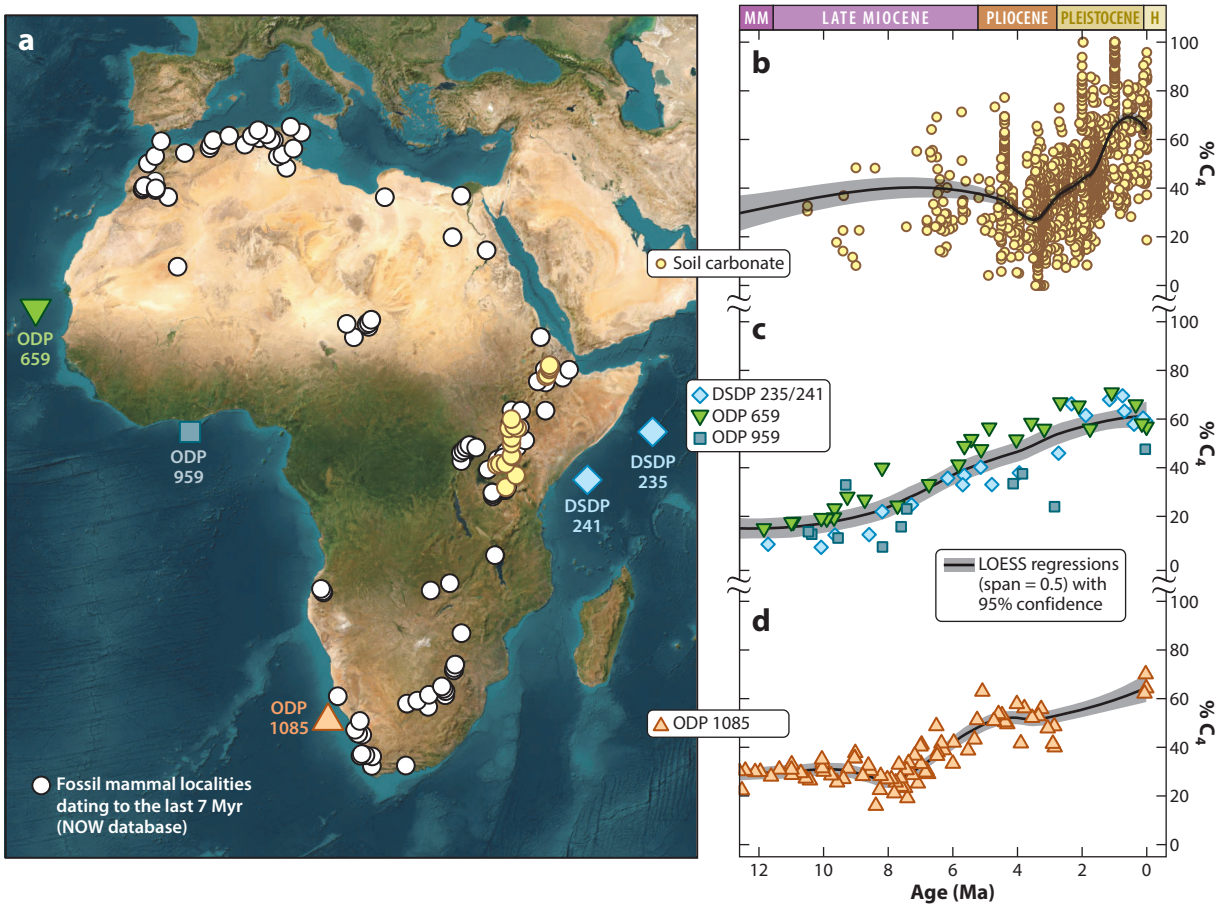

Figure 1

Africa's late Cenozoic fossil sites and select records documenting the late Cenozoic C_4 expansion. (*a*) Map showing the locations of select terrestrial (fossil and soil carbonate) and marine paleoarchives. (*b*) Percentage of C_4 biomass inferred from terrestrial record of soil carbonate $\delta^{13}C$ from eastern Africa (from Levin 2015). These data derive from localities that have provided most of the fossil evidence from the region. (*c*) Percentage of C_4 biomass inferred from marine records of plant-wax (*n*-C_{31}) $\delta^{13}C$ from northwestern and eastern Africa: ODP Site 659, ODP Site 959, and DSDP Sites 235/241 (from Polissar et al. 2019). (*d*) Percentage of C_4 biomass inferred from marine record of plant-wax (*n*-C_{31}) $\delta^{13}C$ from southern Africa (ODP Site 1085) (from Dupont et al. 2013). $\delta^{13}C$ values from Levin (2015) and Dupont et al. (2013) were converted to percent C_4 biomass following Faith et al. (2018) and Polissar et al. (2019). Fossil locations from the NOW Database of Fossil Mammals (**https://nowdatabase.org/**) by the NOW Community/CC BY 4.0. Abbreviations: DSDP, Deep Sea Drilling Project; H, Holocene; LOESS, locally estimated scatterplot smoothing; MM, middle Miocene; NOW, New and Old Worlds; ODP, Ocean Drilling Program.

record represents a combination of open-air sites and caves, the southern African record is best known from cave systems, and the eastern African record is derived primarily from sedimentary basins formed within the East African Rift System. The fossil records within these regions are unevenly sampled through time, with northern and southern Africa being richest over the past 1 Myr, and eastern Africa providing a more detailed and more precisely dated record from ~7 to 1 Ma (Werdelin 2010). This uneven sampling reflects variation in the ages of the sediments that are exposed and differential fossil preservation, as well as variable research effort. It follows that any discussion of the African record is necessarily an unevenly sampled spatiotemporal aggregate derived from a few small windows that more often than not sample different intervals in time.

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Attempts to use these records to evaluate the drivers of ecological and evolutionary change in hominins and faunal communities are complicated by two aspects of the fossil data: the challenges imposed by an incomplete fossil record and the role of spatiotemporal scale in structuring the empirical patterns and the drivers that shaped them. Because these are important to understanding the various and seemingly conflicting results produced by previous analyses, as well as our own efforts to synthesize the fossil evidence, we provide a brief overview below.

An Incomplete Fossil Record

The fossil record is incomplete in two important ways. Uneven preservation of fossil-bearing deposits coupled with variable research effort means that the observed record is characterized by gaps through time and space. This applies to the continental-scale record from Africa (noted above), and it is also true for individual regions, sedimentary basins, and sites. The fossil record is also incomplete in the sense that sampled faunal assemblages do not include all the species that were once present in an ancient community. This stems from insufficient sampling together with taphonomic processes that can preclude preservation, recovery, or identification of a taxon (Faith & Lyman 2019). One of the consequences of the incomplete record is that the empirically observed stratigraphic ranges of fossil taxa are systematically underestimated, resulting in first appearances that are too young and last appearances that are too old. Another is that the observed geographic distributions of fossil taxa are smaller than their true geographic ranges.

This incompleteness complicates efforts to examine rates of extinction and speciation (e.g., Vrba 1995), evaluate spatiotemporal patterns in taxonomic diversity (e.g., Du & Alemseged 2018), and reconstruct paleoenvironments (e.g., Faith & Lyman 2019)—all things of interest to researchers working on the late Cenozoic African record. The good news is that the challenges presented by an incomplete fossil record are reasonably well understood, and analytical techniques have been developed to contend with them (e.g., Close et al. 2018, Faith & Lyman 2019, Liow & Nichols 2010, Marshall 2010). The unfortunate news, however, is that such techniques have been inconsistently applied despite the clear need for them. For example, researchers have both accounted for uncertainty surrounding the stratigraphic ranges of fossil taxa (e.g., Cohen et al. 2022, Du et al. 2020) and assumed that observed first and last appearances are equivalent to speciation and extinction events (e.g., Potts & Faith 2015, Vrba 1995). Likewise, temporal trends in taxonomic diversity, particularly for fossil hominins, have been analyzed with and without addressing sampling effort, at times leading to very different interpretations (e.g., Maxwell et al. 2018, Shultz & Maslin 2013). As we outline later, variable effort to contend with the complexities of the fossil record is a major source of uncertainty in evaluating the drivers of late Cenozoic faunal change in Africa.

Spatiotemporal Scale

Deciphering the mechanisms responsible for patterns evident in the fossil record requires consideration of the spatiotemporal scales of the data. This is because ecological and evolutionary patterns and the processes that generate them are scale dependent (e.g., Blois & Hadly 2009, Du & Behrensmeyer 2018, Faith et al. 2021, Rapacciuolo & Blois 2019). With respect to the late Cenozoic African fossil record, the spatial scales of analysis typically range from individual localities (e.g., Bibi et al. 2017) up to geological formations (e.g., Bobe et al. 2002), sedimentary basins (e.g., Behrensmeyer et al. 1997), regions (e.g., Faith et al. 2019), and the continent (e.g., Vrba 1995). Temporal scale typically increases with spatial scale (Blois & Hadly 2009, Faith & Lyman 2019), and most analyses of faunal change (e.g., speciation and extinction events, changes in community structure) encompass time periods on the order of 10^3–10^6 years (Behrensmeyer et al. 2007).

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Being cognizant of spatiotemporal scale is important because the mechanisms that drive first-order changes evident in the fossil record depend on the scales of observation. For example, consider a stratified faunal sequence excavated from a few square meters that samples an ancient floodplain grassland adjacent to a riparian woodland over 10^3–10^4 years. Temporal change in the composition of the recovered faunas can be strongly influenced by the meandering of the watercourse through time, which alters the spatial distribution of grassland and woodland habitats (e.g., Behrensmeyer et al. 2007). Scaling upward, the faunas recovered from a sedimentary basin over 10^5–10^6 years might be influenced primarily by tectonic and volcanic forces that alter basin paleogeography and hydrology, with regional climate dynamics playing a secondary role (e.g., Levin 2015, O'Brien et al. 2020). Finally, a pan-African faunal record spanning 10^6 years averages out variation caused by local and regional processes, and it can instead record changes driven by continental- to global-scale climate processes (e.g., Vrba 1995). Though the drivers of faunal change differ in all three of these scenarios, the patterns evident in the fossil record may be broadly similar. Across these spatiotemporal scales, species will appear or disappear due to geographic range shifts, speciation, or extinction (e.g., Behrensmeyer et al. 1997, Faith & Behrensmeyer 2013), and community composition can change in conjunction with the vegetation (e.g., Faith 2013, Reed 2008). There may also be evidence for morphological change (e.g., Harris & White 1979, Klein & Cruz-Uribe 1996) or dietary shifts within lineages (e.g., Bibi et al. 2013, Cerling et al. 2015, Faith 2011) across both short (10^3–10^4 years) and long (10^5–10^6 years) timescales.

With respect to this review, two consequences of spatiotemporal scale are worth keeping in mind. First, the spatiotemporal scales of the data should be aligned with those of the processes of interest. This is because, for example, a faunal record that is highly sensitive to local- or basin-scale processes may not be well suited for exploring questions about the consequences of global-scale climate change (e.g., Faith et al. 2021, Levin 2015). Second, because analyses of the African faunal record have been conducted over a range of spatiotemporal scales (e.g., from collection locality to continent), this means that a diversity of scale-dependent drivers have shaped the empirical observations. It follows that seemingly incompatible observations—e.g., that Early Pleistocene mammal assemblages from eastern Africa are tracking lake-level dynamics at the local scale (O'Brien et al. 2020) or instead the expansion of C_4 biomass at the regional scale (Faith et al. 2019)—can both be valid at their respective scales of observation. Conversely, seemingly concordant observations—e.g., a temporal correlation between changes in local faunal community composition and regional environmental records (Bobe 2011)—do not require that both records are responding to the same thing (Levin 2015). Thus, if the question is "What are the drivers of late Cenozoic faunal change in Africa?" the answer will always depend in part on the scale(s) of observation.

PROPOSED DRIVERS

There are many interrelated ideas about the drivers of late Cenozoic faunal change in Africa. These hypotheses, and the data underpinning them, have been reviewed before, so we refer our readers elsewhere for more comprehensive treatments (deMenocal 2004, Faith et al. 2020, Kingston 2007, Maslin et al. 2015, Potts 2013). Here we outline essential details, focusing on some of the uncertainties that warrant future research attention.

Expansion of Grassy Ecosystems

The expansion of C_4-dominated ecosystems during the late Cenozoic is among the most significant environmental changes observed in Africa (e.g., Levin 2015) and beyond (Strömberg 2011). Though the timing and pattern of the expansion varied across Africa (**Figure 1**), parts of eastern Africa document locally abundant C_4 grasses in the Early Miocene (~21–16 Ma) (Peppe

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et al. 2023), with terrestrial and marine paleoenvironmental records subsequently indicating a long-term increase in grassy cover within the past 10 Myr (Dupont et al. 2013, Hoetzel et al. 2015, Polissar et al. 2019, Uno et al. 2016). This is thought to have had a profound effect on African mammals, as isotopic evidence documents elevated C_4 consumption among eastern African herbivore lineages beginning in the early Late Miocene (~10 Ma) (Cerling et al. 1997b; Uno et al. 2011, 2016). The continued expansion of grassy ecosystems through the Pliocene (5.33–2.58 Ma) and Pleistocene (2.58–0.012 Ma) has been linked by researchers to pulses of faunal turnover (deMenocal 2004; Vrba 1988, 1995), long-term changes in community composition (Bobe & Behrensmeyer 2004, Faith et al. 2019, Reed 1997), and morphological changes within lineages (Harris & Cerling 2002, Lister 2013).

Studies of the African fossil record have often emphasized the primacy of aridity in driving both C_4 expansion and associated faunal change. This can be traced to Vrba's (1988, 1995) influential formulation of the turnover-pulse hypothesis (detailed below), in which she linked global cooling evident in marine $\delta^{18}O$ records at ~2.5 Ma to aridification in Africa and the subsequent expansion of open environments and associated faunas. Many others followed suit in linking aridity with C_4 expansion and faunal change (e.g., Bobe 2006, Bobe & Behrensmeyer 2004, deMenocal 2004, Reed 1997), such that aridity-driven expansion of grassy ecosystems eventually became viewed as a driving force in the evolution of Africa's faunas and perhaps also members of the hominin clade (reviewed in Potts 2013).

Though global climate has become more arid since the Late Miocene (e.g., Herbert et al. 2016), there is limited terrestrial evidence from Africa indicating that long-term increases in C_4 vegetation—and associated faunal changes—temporally coincided with increased aridity (e.g., Blumenthal et al. 2017, Levin 2015; for marine records, see Polissar et al. 2019). Thus, the proximate driver is unresolved, paralleling a broader debate among geoscientists about the mechanisms underpinning late Cenozoic C_4 expansion across much of the globe. Because the expansion occurred at different times in different places, it is generally accepted that some combination of global forcing mechanisms together with smaller-scale processes were at play (Steinthorsdottir et al. 2021). Among the likely candidates are declining atmospheric CO_2 concentrations (e.g., Polissar et al. 2019) and increased aridity and seasonality (e.g., Hoetzel et al. 2015, Osborne 2008), though synergies with fire (e.g., Karp et al. 2021, Keeley & Rundel 2005) and herbivory (e.g., Staver et al. 2021) may have also played a role in promoting and sustaining grassy vegetation in some contexts.

If the goal is to determine how late Cenozoic C_4 grass expansion influenced Africa's faunas, then a key challenge will be to confront the varied spatiotemporal scales of the evidence more directly. For example, researchers have emphasized that the expansion of C_4 environments observed in (regional- to subcontinental-scale) marine records at ~10 Ma (**Figure 1**) is roughly coincident with early evidence of C_4 consumption documented in (basin-scale) fossil records from eastern Africa (e.g., Polissar et al. 2019; Uno et al. 2011, 2016). While this apparent synchrony may be indicative of a cause-effect relationship, the potential pitfalls of scale-jumping (e.g., linking regional- to subcontinental-scale environmental changes to basin-scale faunal records) are exemplified by the recent evidence for locally abundant C_4 grasses from multiple 21–16 Ma sites in eastern Africa, reinforcing how the pattern of C_4 expansion varies depending on the spatiotemporal scale of observation (Peppe et al. 2023). This variation arises in part because larger-scale forcing mechanisms (e.g., global expansion of grassy ecosystems) can be overprinted by smaller-scale processes (e.g., tectonism, volcanism, or paleogeographic change) (Levin 2015), leading to differences between records and across scales. It follows that building stronger inferences about how grassy ecosystem expansion impacted faunal communities will require that the spatiotemporal scales of the environmental and fossil evidence be aligned (Faith et al. 2021). Because the evolutionary and ecological

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responses of faunas to environmental change will also vary across scales (Blois & Hadly 2009, Rapacciuolo & Blois 2019), there is intriguing potential for a more scale-aligned research agenda to reveal the many different consequences of C_4 expansion on the history of Africa's late Cenozoic mammals.

Turnover-Pulse Hypothesis

Elisabeth Vrba's (1985b, 1992, 1993) turnover-pulse hypothesis outlines in broad strokes how paleoenvironmental change can drive macroevolution. It is based on the premise that all species are habitat specific, with particular tolerances to abiotic and biotic environmental conditions, such as substrate, vegetation structure, or the distribution of food and water. When the environment changes over time, the distribution of habitats suitable for some species can shift, resulting in dispersals as species track them. The habitats tolerated by some species may also become geographically discontinuous, resulting in populations that are geographically and genetically isolated (i.e., vicariance) and leading to a phase of allopatry that can promote extinction and speciation. Because paleoenvironmental change influences multiple different species, the turnover-pulse hypothesis predicts that turnover (encompassing dispersal, speciation, and extinction) will occur as synchronous pulses across disparate clades in conjunction with dramatic paleoenvironmental changes. Vrba (1987) also predicted that turnover rates would be higher in specialists (taxa with narrow niche breadths) than in generalists (taxa with wide niche breadths), as environmental changes would be more likely to exceed the ecological tolerances of the former. In her view, climate has been the dominant driver of large-scale paleoenvironmental change through Earth's history, such that it represents a central force in macroevolution.

Among paleontologists and paleoanthropologists working in Africa, Vrba's (1985a, 1988, 1995) efforts to test the turnover-pulse hypothesis are perhaps better known than its theoretical underpinnings. Vrba pointed to global cooling between ~2.8 and 2.5 Ma as a driver of grassland expansion in Africa, leading to a turnover pulse among antelope species (Bovidae), as well as the emergence of the hominin genera *Homo* and *Paranthropus*. This observation was based on an apparent cluster in the temporal distribution of first and last appearances of fossil bovids, which Vrba assumed were reflecting speciation and extinction events. Because expansion of grassy ecosystems was the central environmental shift, and many of the bovid species making their first appearances at this time belonged to open-habitat lineages (e.g., tribes Alcelaphini and Antilopini), the turnover-pulse hypothesis has become closely linked to ideas about the importance of C_4 grass expansion in the evolution of African faunas (deMenocal 2004).

The turnover-pulse hypothesis has inspired debate about the role of climate as a driver of macroevolutionary change (e.g., Barnosky 2001, Faith & Behrensmeyer 2013), as well as numerous case studies seeking to test and refine Vrba's proposed 2.8 to 2.5 Ma turnover pulse in Africa (Behrensmeyer et al. 1997, Bibi & Kiessling 2015, Bobe & Behrensmeyer 2004, Frost 2007, McKee 2001, Werdelin & Lewis 2005). These case studies have produced varied outcomes (**Table 1**), as exemplified by analyses of the eastern African record: Behrensmeyer et al. (1997) found no evidence for a turnover pulse between 2.8 and 2.5 Ma among large mammals in the Turkana Basin but instead documented a prolonged phase of elevated turnover from 2.5 to 1.8 Ma; Bobe & Behrensmeyer (2004) later reported multiple episodes of higher-than-average turnover among Turkana Basin large mammals from 3.4 to 3.2 Ma, 2.8 to 2.6 Ma, 2.4 to 2.2 Ma, and 2.0 to 1.8 Ma; Bibi & Kiessling (2015) provided tentative evidence for a turnover pulse among eastern African bovids at ~2.0 to 1.75 Ma but otherwise concluded that turnover has been continuous over the past ~7 Myr; and more recently, Cohen et al. (2022) documented steady turnover among ungulates from eastern Africa and the Turkana Basin, except for a prominent pulse in extinctions between 0.75 and 0.5 Ma. It is difficult to reconcile these seemingly contradictory results because there

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Table 1 A selection of efforts to quantify mammalian turnover through the late Cenozoic of Africa, oftentimes in the context of Vrba's turnover-pulse hypothesis

Reference	Where	Range (Ma)	Taxon	Turnover metric	Key observation(s)
Vrba 1995	Africa	7–0	Bovidae	Accumulation of FADs through time	Major turnover pulse from 2.8 to 2.5 Ma
Behrensmeyer et al. 1997	Turkana Basin	4.4–0	Mammals	(FADs + LADs)/ richness	Prolonged turnover from 2.8 to 1.5 Ma
McKee 2001	Eastern Africa	4.4–0.4	Large mammals	Number of FADs	Fossil record insufficient to distinguish continuous from pulsed turnover
Bobe & Behrensmeyer 2004	Turkana Basin	4.0–1.0	Mammals	Number of FADs, LADs	Multiple intervals of above average turnover: 3.4–3.2, 2.8–2.6, 2.4–2.2, and 2.0–1.8 Ma
Werdelin & Lewis 2005	Eastern Africa	4.2–0.9	Carnivora	Foote rates	LAD pulse 1.8–1.2 Ma; elevated FADs > 3 Ma and < 2.4 Ma
Frost 2007	Turkana Basin	4.2–1.0	Cercopithecidae	Number of FADs, LADs	High turnover from 4.0 to 3.5 Ma; stratigraphic gaps and sampling effects contribute
	Afar	4.4–0.3			
	Eastern Africa	4.4–0			Continuous turnover; variation in turnover linked to sampling
	Sub-Saharan Africa				Continuous turnover; apparent pulse at 3.0 Ma linked to sampling
Faith & Behrensmeyer 2013	Cape Floristic Region	0.02–0	Ungulates	Number of FADs, LADs	Climate drives turnover via vicariance and habitat change; role in speciation is unclear
Bibi & Kiessling 2015	Eastern Africa	3.75–1.25	Bovidae	Foote rates	Continuous turnover; possible FAD pulse 2.0–1.75 Ma
	Turkana Basin		Large mammals		
Cohen et al. 2022	Eastern Africa	3.75–0	Ungulates	Probability of extinction and speciation	Continuous turnover; extinction pulse at 0.75–0.50 Ma
	Turkana Basin	4.25–1.0			Continuous turnover; speciation pulse at 3.75–3.50 Ma; extinction pulse at 1.5–1.25 Ma

Abbreviations: FAD, first appearance datum; LAD, last appearance datum.

are differences in the spatial scales of observation (e.g., Turkana Basin versus eastern Africa), the temporal resolution of the fossil data, the approaches used to control for the incompleteness of the fossil record, and the criteria used to define a turnover pulse.

Further uncertainty arises from concerns about the quality of the fossil record and the analytical choices made for identifying turnover pulses. For example, McKee (2001) produced simulations showing that the eastern African record (at the time) was not sufficiently resolved to distinguish between turnover that was continuous or pulsed. More recently, Barr (2017) showed that analyses of faunal turnover are highly prone to false positives, with observed outcomes strongly influenced by analytical decisions (length of time bins) and how turnover pulses are defined. Likewise, Rowan et al. (2022) showed that apparent turnover pulses in the lower Awash Valley (Ethiopia) were largely a consequence of temporal discontinuities in the fossil record (see also Frost 2007). Taking

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all these complications into account (see also Hill 1987), a cautious assessment of the current state of knowledge is that the temporal pattern of faunal turnover across many different spatiotemporal scales within Africa is unclear and that deviations from continuous turnover over 10^4–10^5-year timescales remain to be convincingly demonstrated. Perhaps the only consistent pattern to emerge is that few studies have replicated Vrba's (1985a, 1988, 1995) observation of a major turnover pulse at ~2.8 to 2.5 Ma (**Table 1**). Progress will require future research efforts that more effectively account for the sampling biases inherent to the fossil record.

Environmental Variability

Developed over a series of papers by Potts (e.g., Potts 1998, 2013; Potts & Faith 2015), the variability selection hypothesis was initially formulated to account for adaptive changes in the hominin clade, such as the emergence of bipedality, encephalization, or enhanced sociality. It departs from earlier ideas linking key milestones in hominin evolution to directional environmental changes by emphasizing the role of environmental instability in selecting for greater adaptive versatility through morphological, ecological, and behavioral changes. Though the variability selection hypothesis has focused on hominin evolution, the initial ideas developed in part from observations of mid-Pleistocene mammals from the southern Kenya rift. Potts (1998) pointed to evidence from Olorgesailie and Lainyamok (~1 Ma to 350 ka) that documented the extinction of herbivores whose large body size and specialized craniodental morphology implied a reliance on low-quality grassy forage (e.g., *Elephas recki*, *Theropithecus oswaldi*, and *Metridiochoerus* spp.). These losses took place in the context of rapid environmental fluctuations (Potts et al. 2020), during which the ecologically specialized extinct forms were replaced by closely related extant taxa that were smaller in size and perhaps more flexible in their dietary ecology (e.g., *Loxodonta africana*, *Papio anubis*, and *Phacochoerus* spp.). According to the variability selection hypothesis, intervals of high-amplitude environmental variability can lead to preferential loss of lineages with habitat-specific adaptations (i.e., ecological specialists) in favor of those that are more ecologically flexible (i.e., ecological generalists) (see also Vrba 1987, 1992).

More recent work has emphasized the role of environmental variability as a driver of speciation and extinction (Potts 2013, Potts & Faith 2015). These ideas also focus on eastern Africa, where the interaction of orbital cycles (eccentricity and precession) led to alternating phases of high and low precipitation variability through the late Cenozoic. Potts (2013) observed that the first appearance dates of three hominin genera—*Australopithecus*, *Paranthropus*, and *Homo*—correspond with prolonged phases (~300 kyr duration) of heightened climate variability in eastern Africa, characterized by rapid shifts over precessional timescales (~20 kyr) between wet and dry conditions. Following some of the ideas underpinning Vrba's (1985b, 1992, 1993) turnover-pulse hypothesis, these phases of elevated variability are proposed to have promoted habitat fragmentation and reorganization, leading to vicariance, allopatry, and elevated rates of extinction and speciation (Potts & Faith 2015). A complementary set of ideas emphasize the role of eccentricity-modulated precession in the rapid (and repeated) appearance and disappearance of deep lakes in the East African Rift Valley at 2.7–2.5 Ma, 1.9–1.7 Ma, and 1.1–0.9 Ma (Maslin et al. 2014, Trauth et al. 2007), which is proposed to have led to biogeographic changes (species dispersal and population fragmentation) that could set the stage for extinction and speciation (Maslin et al. 2015, Trauth et al. 2010).

Although much has been written about environmental variability as a potential driver of macroevolutionary change with respect to the hominin clade, its role in the evolutionary history of African mammal communities is largely unknown. The hypothesis that phases of heightened environmental variability will lead to preferential loss of specialists relative to generalists (Potts

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1998) remains to be rigorously evaluated [e.g., high rates of vicariance in specialist clades could alternatively promote diversification (see Vrba 1987, 1992)]. Likewise, efforts to link increased environmental variability to extinction and speciation in hominin evolution have focused on the timing of first and last appearances of fossil hominins, without accounting for uncertainty in their stratigraphic ranges (Maslin & Trauth 2009, Potts 2013, Potts & Faith 2015). The exception is recent work by Cohen et al. (2022), who examined records of Plio-Pleistocene environmental variability in relation to large mammal turnover rates across eastern Africa and in the Turkana Basin. They found that the data were insufficient to infer a relationship between the environmental and faunal records, at least when the fossil data were binned across relatively coarse (250 kyr) intervals. Cohen et al. (2022) acknowledged that it remains possible for higher-frequency variability (e.g., precession scale) to have played a role in macroevolutionary change, touching on a broader uncertainty that remains to be resolved—environmental variability can be measured across varied timescales (e.g., from seasonal to orbital), and it is not clear which are most relevant to the evolutionary and ecological history of African mammals. Resolving this and other uncertainties about the influence of environmental variability on Africa's faunas will require further study and, once again, more deliberate efforts to control for the incompleteness of the fossil record.

Top-Down Processes and Hominin Impacts

The previous hypotheses view late Cenozoic faunal change as a consequence of bottom-up ecological processes, whereby climate and its effects on vegetation have cascading impacts on herbivores and the carnivores that prey upon them. Far less attention has been directed at top-down processes, in which ecosystems are regulated by species at high trophic levels, despite a growing appreciation of the importance of top-down effects, including those related to human impacts, in present-day ecosystems (Estes et al. 2011). However, building on broader debates concerned with the antiquity and consequences of human impacts on the natural world, especially the extinction of Earth's megafauna within the past ~50,000 years (Koch & Barnosky 2006), there is a growing body of literature addressing the history of hominin impacts on ancient African ecosystems. It was long thought that African megafaunal extinctions were relatively limited, perhaps due to long-term coevolution between hominins and their prey (see Faith 2014), but recent work has focused attention on large mammal losses throughout the past several million years and the potential role that increasingly carnivorous hominins may have played in their demise (reviewed in Faith et al. 2020). When did hominins begin to exert top-down control on African ecosystems, and what were the consequences?

Two related groups of hypotheses contend that hominin populations had been driving African mammal extinctions long before the appearance of *Homo sapiens* at ~300 ka. The first proposes that diversity decline in Africa's megaherbivores (animals greater than 1,000 kg), which formerly included an incredible variety of proboscideans, hippopotamids, and giraffids, among others, was a consequence of hominin predation potentially extending back to the Early Pleistocene (e.g., Lyons et al. 2004, Surovell et al. 2005). The second proposes that increasing carnivory since the appearance of early *Homo* (if not earlier) led to intensified competition within the large carnivore guild, with the outcome including extinctions across multiple carnivoran lineages (Faurby et al. 2020, Lewis & Werdelin 2007, Werdelin & Lewis 2013). Because megaherbivores and large carnivorans play an important role in ecosystem processes (Owen-Smith 1988; Ripple et al. 2014, 2015), the possibility of hominin involvement in their demise implies that top-down impacts may have played a key role in shaping the evolutionary history of African ecosystems.

Though it is tempting to envision a long history of hominin impacts, especially in light of present-day biodiversity loss (Johnson et al. 2017, Malhi et al. 2016), the arguments for

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anthropogenic extinctions before the latest Pleistocene and Holocene are disputed (for a critical review, see Faith et al. 2020). Both the diversity and abundance of megaherbivores in eastern African fossil communities have been in steady decline for the past ~4–5 Myr (Faith et al. 2018, Bibi & Cantalapiedra 2023), long before the appearance of hominin species realistically capable of exerting top-down control on large mammal communities. Many of the extinct megaherbivores were C_3 browsers and C_3-C_4 mixed feeders, suggesting that the expansion of grassy ecosystems contributed to their demise (Faith et al. 2018), with a corresponding decline in primary productivity further driving preferential losses of larger-bodied species (Bibi & Cantalapiedra 2023). Likewise, the largest carnivorans (>100 kg) have been in decline since the mid-Pliocene (Faith et al. 2019, 2020), prior to the appearance of any major hominin competitors. The C_4 expansion has also been linked to their decline (Faith et al. 2019, 2020), through declining availability of megaherbivore prey, loss of woody cover required by ambush predators, and the competitive disadvantage of species lacking cursorial body plans in open habitats (see Van Valkenburgh et al. 2016). Reductions in primary productivity may also be important (Bibi & Cantalapiedra 2023), by diminishing the prey base required to support viable populations of the largest carnivorans. And lastly, although increased carnivory and the appearance of *Homo erectus* ~2 Ma are often linked to extinctions (Lewis & Werdelin 2007, Lyons et al. 2004, Werdelin & Lewis 2013), the archaeological evidence supporting this—an apparent increase in anthropogenic butchery sites—seems to be tracking sampling effort rather than any meaningful dietary shift (Barr et al. 2022).

Arguments that African ecosystems were shaped by a long history of ancient anthropogenic extinctions are intriguing because they recognize that top-down processes, including but not limited to human impacts, can be important drivers of paleoecological change. Key ideas and debates about how and when hominins impacted African ecosystems are only beginning to take shape, lagging behind the vast literature concerned with megafaunal extinctions and anthropogenic ecosystem disruption in other parts of the world. However, as the African fossil record encompasses the entirety of hominin evolution, it is perhaps the ideal place to ask questions about when our lineage began to rival climate change and other bottom-up processes as a force of change. Exploring such questions promises to be an increasingly important research focus in the near future.

TEMPORAL TRENDS IN AFRICAN FAUNAL COMMUNITIES

The hypotheses outlined above are typically invoked to explain ecological and evolutionary changes that played out across spatial scales ranging from regional to continental. Because of the uneven spatial sampling of the African fossil record, the best datasets for examining such large-scale changes through the late Cenozoic are derived from eastern Africa (Cohen et al. 2022, Faith et al. 2019); even analyses that are focused on continental-scale phenomena are heavily biased toward eastern Africa (e.g., Bibi & Cantalapiedra 2023, Vrba 1995). With this in mind, we focus on synthesizing the fossil record from eastern Africa over the past ~7 Myr (see Datasets S1–S3 in the **Supplemental Material**), providing complementary evidence derived from elsewhere when possible.

Supplemental Material >

An Early Cenozoic Prologue

Before turning our attention to temporal trends in the late Cenozoic record, it is worth briefly considering the longer-term development of the continent's mammalian fauna (**Figure 2**). For much of the past 66 Myr, Afro-Arabia (the combined African and Arabian landmasses) was an island continent with few, or very short-lived, connections to surrounding regions (McLoughlin 2001), setting the stage for the development of a highly endemic mammalian fauna (Seiffert 2012). Paleontological collections from the Fayum region (Egypt) had established the distinctive composition

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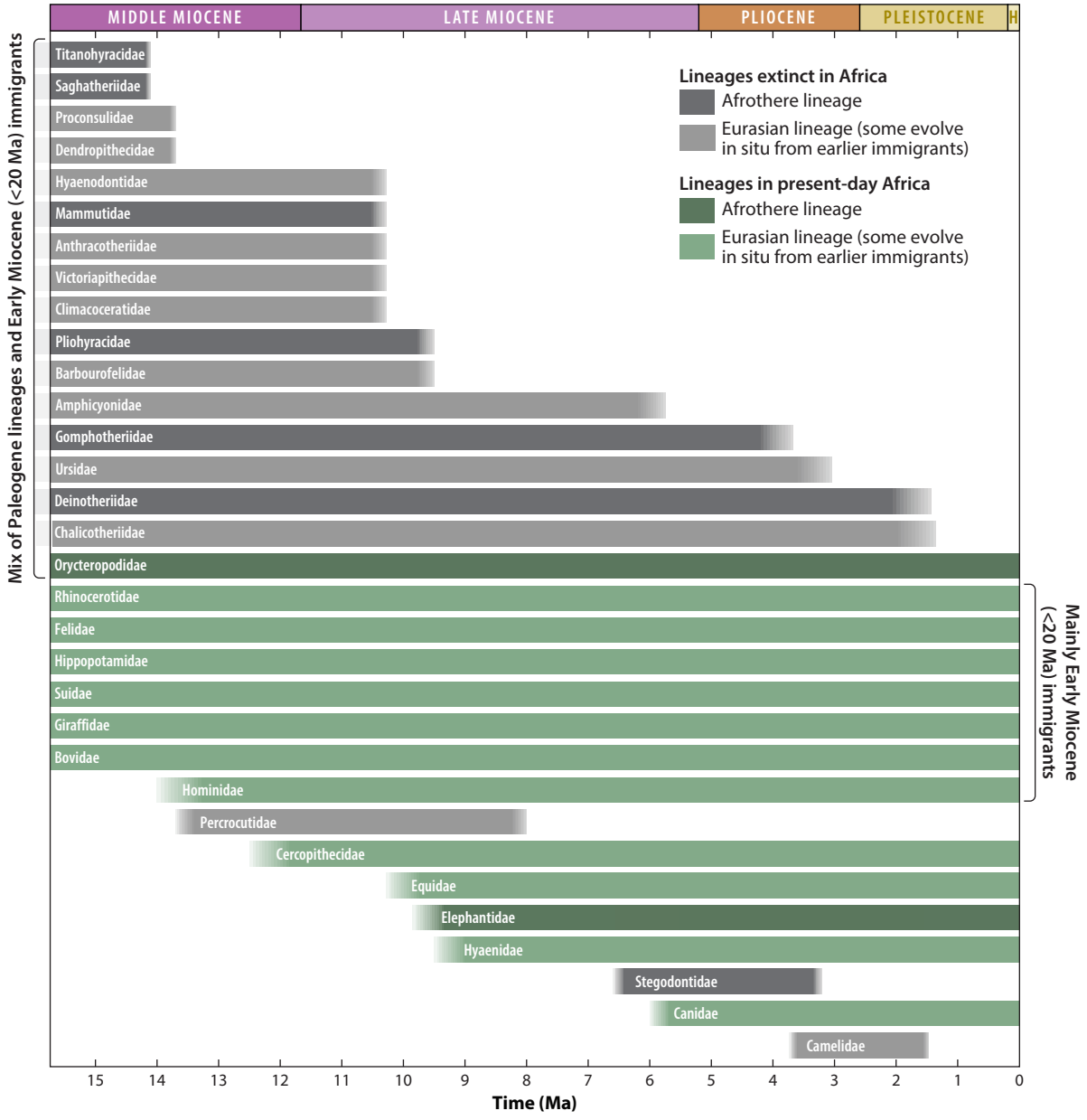

Figure 2

Temporal change in the composition of large mammal families found in eastern Africa over the past ~15 Myr. Afrothere lineages that dominated the continent's Paleogene faunas were largely replaced by Eurasian immigrant lineages that make up the bulk of present-day faunas. Many immigrant families show up just after ~20 Ma following formation of the Gomphotherium Landbridge and the final closure of the Tethyan Seaway. The protracted extinction of archaic mammal families occurred throughout the late Middle and Late Miocene but was essentially complete by the Early Pleistocene. Abbreviation: H, Holocene.

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of Afro-Arabia's Paleogene faunas by the early 1900s (Andrews 1906), which included a striking diversity of hyraxes (Hyracoidea), early elephant relatives (Proboscidea), and sirenians (Sirenia). The significance of this Paleogene menagerie would only be fully appreciated nearly a century later following the recognition of Afrotheria as molecular phylogenetics overturned widely held views on the relationships of placental mammal orders (e.g., Madsen et al. 2001, Murphy et al. 2001). Afrotheria is one of the four superordinal clades of placental mammals that have been recognized largely based on molecular data accumulated over the past three decades (Springer 2022). Living afrothere lineages include the hyraxes, proboscideans, and sirenians abundant in the Fayum fossil record, along with golden moles and tenrecs (Afrosoricida), sengis (Macroscelidea), and aardvarks (Tubulidentata). In addition to the Fayum, fossil records from elsewhere support the view that the Afro-Arabia's Paleogene faunas were dominated by afrotheres (e.g., Gheerbrant et al. 2018). A handful of Eurasian immigrants (taxa from the superorders Laurasiatheria and Euarchontoglires) had arrived via chance over water dispersal during the early Cenozoic and coexisted alongside afrothere endemics (Seiffert 2012). These include primates (Primates), hyaenodonts (Hyaenodonta), and anthracothere artiodactyls (Anthracotheriidae), which reached Afro-Arabia during the Paleocene and Eocene (Holroyd et al. 2010, Seiffert 2012, Sole et al. 2009).

Despite evidence for faunal turnover at the Eocene–Oligocene boundary (de Vries et al. 2021, Seiffert 2007), the ordinal composition of Afro-Arabian mammal communities remained relatively stable until the onset of the Miocene. Late Oligocene fossil assemblages from eastern Africa (e.g., Kappelman et al. 2003, Stevens et al. 2008) attest to the continued dominance of afrotheres but reveal that a small number of Eurasian immigrants arrived near the Oligo–Miocene boundary. For example, Friscia et al. (2020) described the carnivore fauna from ~24–21.5 Ma sites in the Turkana Basin (Losodok and Nakwai), showing that some immigrant carnivoran families (Barbourofelidae, Herpestidae, and Viverridae) were present by this time. In addition, at lower taxonomic levels, non-afrothere lineages that had arrived in Afro-Arabia earlier in the Paleogene show important evolutionary changes toward the end of the Oligocene. For example, crown catarrhine primates appeared in Afro-Arabia by ~29 Ma (Zalmout et al. 2010) with the divergence of stem apes (Hominoidea) and Old World monkeys (Cercopithecoidea) occurring by ~25 Ma (Stevens et al. 2013).

By the Early Miocene, mammalian faunas of Afro-Arabia more closely resembled their modern counterparts in taxonomic composition at the family level. Bovids (Gentry 2010), giraffids (Harris et al. 2010), suids (Bishop 2010), rhinocerotids (Geraads 2010), felids (Werdelin 2011), and other important components of present-day African mammal faunas made their first appearance on the continent just after ~20 Ma. The vast majority of these taxa are Eurasian immigrants that entered Afro-Arabia following the formation of the Gomphotherium Landbridge or the later collision of the Arabian plate with Eurasia, driving the final closure of the Tethyan Seaway (Bosworth et al. 2005). The earliest hippopotamids, such as *Morotochoerus* and *Kulutherium* (Orliac et al. 2010), also emerged during this time, having originated from advanced bothriodontine anthracotheres of the Oligocene (e.g., Lihoreau et al. 2015). With respect to paleoecology, the Early to Middle Miocene faunas of eastern Africa were almost exclusively composed of C_3 browsers (e.g., Cerling et al. 1997a).

The latest Miocene (~10–6 Ma) was a period of significant taxonomic and ecological turnover that set the stage for the evolution of Africa's Plio-Pleistocene mammal faunas and the development of its modern biota (**Figure 2**). Among the bovids, which comprise the bulk of Africa's herbivore faunas today, tragelaphins (kudu and relatives), alcelaphins (wildebeest and relatives), hippotragins (oryx, sable, and relatives), and impala all make their first appearance close to ~7 Ma (Geraads 2019). Reduncins (waterbucks, kobs, and relatives) may have emerged slightly earlier based on fossil remains from the Ngorora Formation of Kenya (Bibi et al. 2009). At the same

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time, archaic mammalian lineages, such as kubanochoere suids and amphicyonid carnivorans, went extinct on the continent as a handful of immigrant taxa, notably equids, dispersed inward from Eurasia. Stable isotope data show that from ~10 Ma onward, mammalian herbivores readily adopted C_4 grazing diets as environments dominated by C_4 biomass spread across eastern Africa (Uno et al. 2011).

These paleoecological shifts coincide with an important time for hominin evolution, as molecular clocks estimate the divergence of humans and chimpanzees occurred ~10–7 Ma (Langergraber et al. 2012). The relationships of Miocene African hominoids remain obscure, but it seems clear that some are members of the African ape-human clade (Homininae), such as *Nakalipithecus*, whereas others are far more distantly related (Pugh 2022). The period ~7–5 Ma has produced remains of probable early hominin taxa—*Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus kadabba*—but each of these is known from a small number of mostly nonoverlapping elements, preventing extensive comparisons to be made (Wood & Boyle 2016).

Functional Trends

To illustrate the major temporal changes documented in the late Cenozoic fossil record, we first consider the distribution of functional ecological traits such as diet, body size, and locomotor strategy. Such traits are known to be robust indicators of ecological function and change over time (Faith & Lyman 2019, Reed 1998), and they contextualize the associated taxonomic shifts that we address below. Beginning with Africa's herbivore communities, perhaps the best-documented temporal patterns involve the representation of browsers, mixed feeders, and grazers through time. There is ample evidence that grazers have increased in taxonomic richness and abundance since the Pliocene (**Figure 3**), a trend that is observed across a variety of spatial scales: in the Shungura Formation of Ethiopia (Bibi et al. 2013, Negash et al. 2020), throughout the Turkana Basin (Cerling et al. 2015), across eastern Africa (Faith et al. 2019), and in both eastern and southern Africa (Reed 1997). We caution that some patterns illustrated in **Figure 3** (e.g., changes in the proportions of taxa across dietary classes) are not immune to sampling problems (Faith & Lyman 2019, pp. 129–33), such that more rigorous analyses are worthy of future attention. Nonetheless, the ubiquity of the grazer increase enhances confidence that it captures meaningful ecological changes. This pattern is typically interpreted as a response to (or cited as evidence for) the expansion of C_4 biomass across Africa's ecosystems during the late Cenozoic. The parallel loss of mixed feeders and browsers (Cerling et al. 2015, Faith et al. 2019) (**Figure 3**), and especially frugivorous and arboreal taxa (Reed 1997)—functional groups that are dependent on woody cover—strengthens the argument that functional reorganization is underpinned by increasingly open vegetation. The different patterns observed between fossil localities (e.g., Robinson et al. 2017) and across different spatial scales (**Figure 3**) illustrate the importance of smaller-scale processes (e.g., basin-scale changes) in mediating the pattern and timing of the broader expansion of C_4 vegetation across Africa.

The reversal of long-term dietary trends ~1 Ma has posed an interpretive challenge. Especially in eastern Africa, despite terrestrial evidence for continued expansion of C_4 biomass through the Pleistocene (Levin 2015), grazers show a marked decline in diversity (Faith et al. 2019) (**Figure 3**). Many of the extinct grazers were hindgut fermenters (e.g., suids and equids), with ruminants, especially bovids, rising to prominence (Faith et al. 2019). We previously suggested that these changes were incompatible with C_4 expansion alone and proposed that intervals of aridity following the establishment of high-amplitude glacial-interglacial cycles during the mid-Pleistocene transition drove the loss of nonruminant grazers (Faith et al. 2019). Because of their less efficient digestive physiology, nonruminants are at a competitive disadvantage when resources are limited, as expected when aridity increases (Faith et al. 2019) and productivity declines (Bibi & Cantalapiedra 2023). Whatever the explanation, the loss of nonruminant grazers over the past 1 Ma represents

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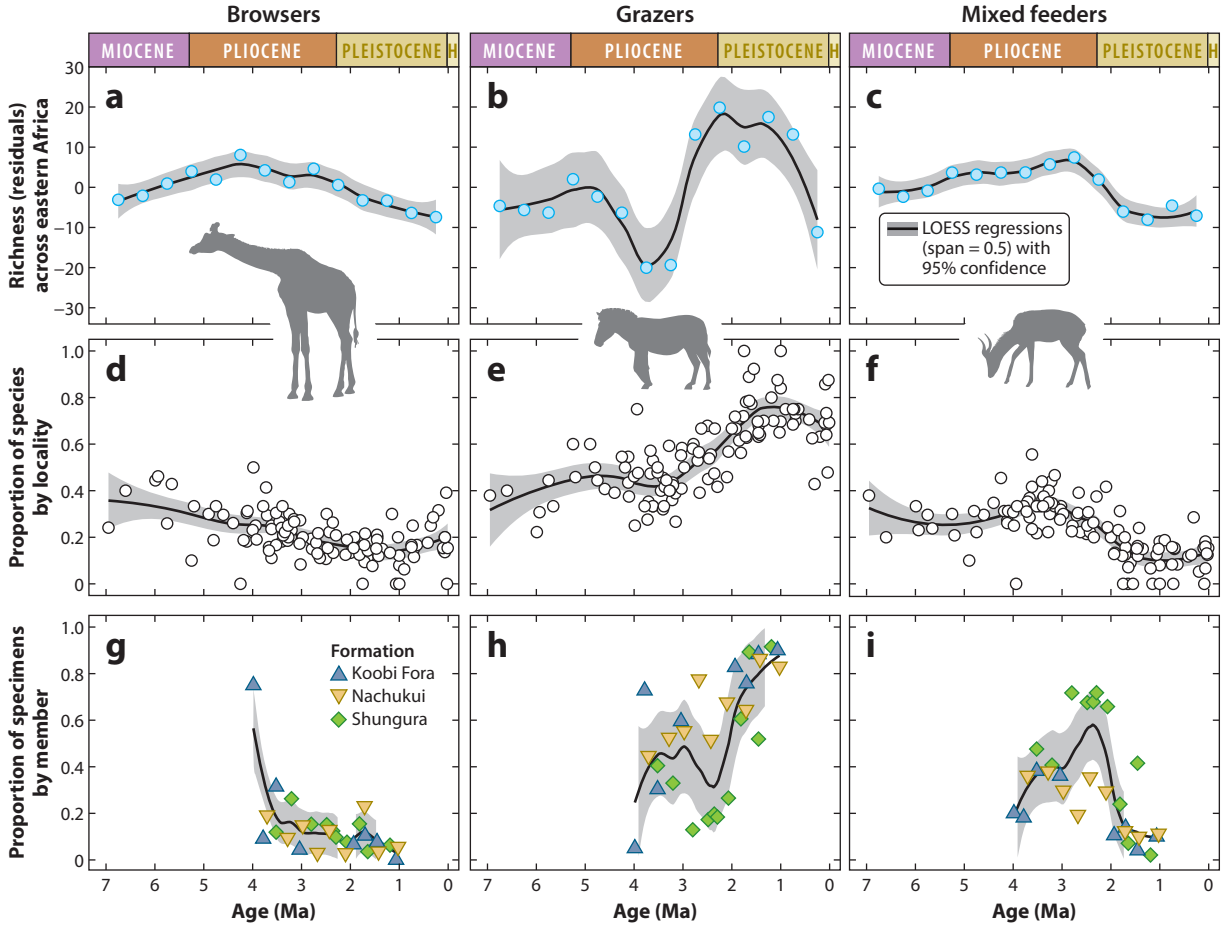

Figure 3

Temporal change in the representation of ungulate browsers, grazers, and mixed feeders through the late Cenozoic in eastern Africa. (*a–c*) The richness (number of species) of browsers, grazers, and mixed feeders known from eastern Africa across 0.5 Ma bins. To control for sampling effects arising from variation in the number of sites through time, these values are residuals derived from a linear regression of richness as a function of the number of sites within each bin (see **Supplemental Figure 1**). (*d–f*) The proportion of browsers, grazers, and mixed feeder species within eastern African fossil assemblages (each point represents a single locality). (*g–i*) The relative abundance (i.e., proportion of specimens) of browsers, grazers, and mixed feeders from different formations (Koobi Fora, Nachukui, and Shungura) within the Omo-Turkana Basin (each point represents a geological member) (abundance data are from Du & Alemseged 2018; dietary data are from Faith et al. 2019). Silhouettes are from PhyloPic. See the **Supplemental Material** for the data plotted in this figure. Abbreviations: H, Holocene; LOESS, locally estimated scatterplot smoothing.

an important step toward the ecological modernization of faunal communities in eastern Africa (Faith et al. 2019).

Supplemental Material >

Coinciding with long-term dietary shifts is dramatic downsizing of African herbivore communities. In eastern Africa, the steady decline of the largest-bodied species (megaherbivores greater than 1,000 kg) over the past 7 Myr is a dominant functional shift (Faith et al. 2018, 2019) (**Figure 4**). To put the magnitude of their decline into context, we note that present-day African mammal communities typically include up to 5 sympatric megaherbivores, yet fossil assemblages dating to the latest Miocene and Pliocene frequently included anywhere from 8 to 12 (Faith et al. 2018, 2019). Though comparable assemblage-level functional trends are unavailable from

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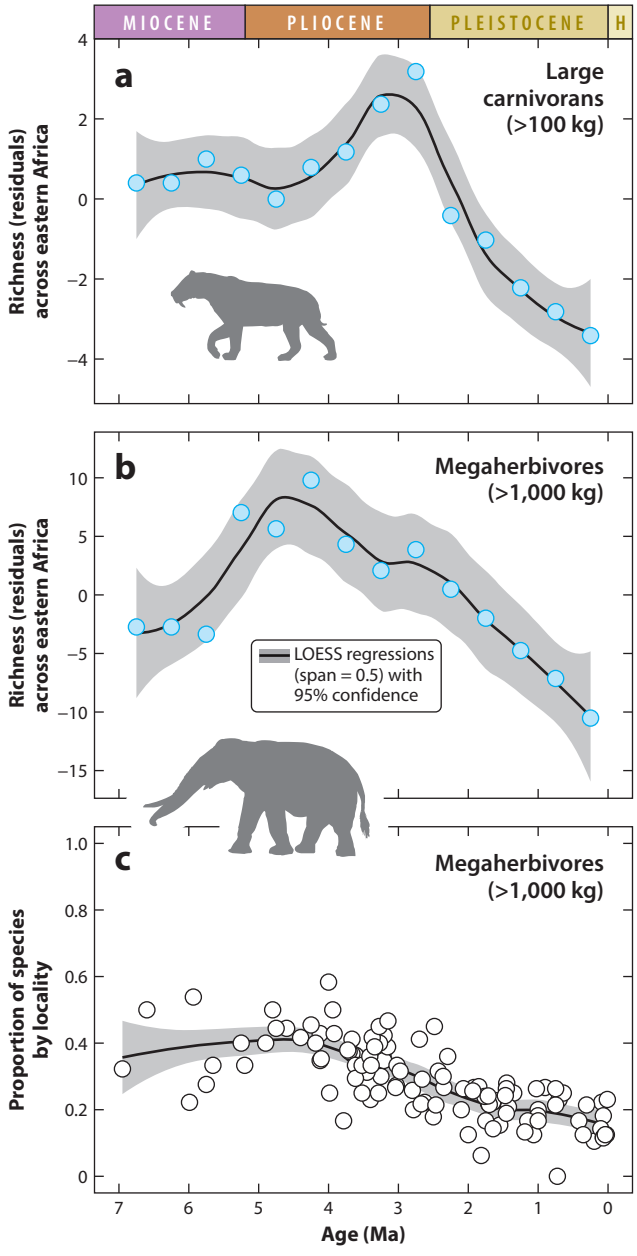

Figure 4

The fossil evidence for downsizing of eastern Africa's large mammal communities. (*a*) The richness (number of species) of the largest carnivorans (>100 kg) known from eastern Africa across 0.5 Ma bins. (*b*) The richness (number of species) of megaherbivores (>1,000 kg) known from eastern Africa across 0.5 Ma bins. Richness values in panels *a* and *b* are residuals calculated as in **Figure 3** (see **Supplemental Figure 1**). (*c*) The proportion of megaherbivores within eastern African fossil assemblages (each point represents a single locality). Silhouettes are from PhyloPic (M. Martyniuk). See the **Supplemental Material** for the data plotted in this figure. Abbreviations: H, Holocene; LOESS, locally estimated scatterplot smoothing.

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elsewhere, the high diversity of some megaherbivore lineages particularly proboscideans (Sanders et al. 2010), hippopotamids (Weston & Boisserie 2010), and giraffids (Harris et al. 2010) prior to ~1 Ma across Africa suggests that the megaherbivore decline is potentially a continental-scale phenomenon. Many of the extinct megaherbivores were browsers and mixed feeders, so their loss is likely intertwined with vegetation change (Faith et al. 2018). The ecological implications of the megaherbivore demise were likely significant (Faith et al. 2019) but remain to be fully explored (see the section titled Emerging Problems: Implications of Nonanalog Communities).

Major functional changes are also observed within the carnivore guild (**Figure 4**). Most notably, and paralleling functional changes in the herbivore guild, the richness of the largest carnivorans (>100 kg) has been in steady decline since the mid-Pliocene (Faith et al. 2019, Lewis & Werdelin 2007). Only a single carnivoran greater than 100 kg is found in Africa today (*Panthera leo*), whereas Pliocene eastern Africa was home to upward of half a dozen species. The decline in large-bodied species is accompanied by a loss in functional diversity, driven by the extinction of all large (>21.5 kg) hypocarnivores—e.g., bears, otters, and viverrids with omnivorous diets—since the Early Pleistocene (Werdelin & Lewis 2013). As noted previously, it is debated whether these trends are the result of top-down impacts by increasingly carnivorous hominins (Faurby et al. 2020, Lewis & Werdelin 2007, Werdelin & Lewis 2013) or instead a consequence of the diminished megaherbivore prey base, loss of wooded habitats required by ambush predators, and the disadvantage of species lacking cursorial body plans as open environments expanded (Faith et al. 2020). The early onset of the large carnivoran decline (**Figure 4**), at a time when members of the hominin clade were functionally equivalent to bipedal apes, would seem to rule out a hominin role in the decline (Faith et al. 2020), but not all agree (Faurby et al. 2020). It is unclear whether the temporal pattern of change observed in eastern Africa was replicated elsewhere on the continent, although it is apparent from observations in southern (O'Regan & Reynolds 2009) and northern Africa (Geraads 2008) that Plio-Pleistocene carnivore communities were richer in species exceeding 100 kg in body mass.

Taxonomic Trends

The functional ecological changes observed through the late Cenozoic were associated with major shifts in the taxonomic composition of faunal communities. Outside of hominins, primates are mainly represented by cercopithecid monkeys, but preservation, and thus observed species diversity, varies considerably across sites. The genus *Theropithecus* is widespread and often abundant in eastern African sites from ~4 Ma until ~400 ka, probably due to its large body size (later members of the genus from the Middle Pleistocene likely weighed more than 100 kg) and reliance on grazing lawns adjacent to water bodies (Fannin et al. 2021). Its sole living species, *Theropithecus gelada*, is a montane-dwelling relict of what was formerly a taxonomically diverse and widespread radiation of species that played an important role in the eastern African grazing guild.

Among the Artiodactyla, Perissodactyla, and Proboscidea, taxonomic diversity at the family level has declined considerably since the latest Miocene due to the extinction of most proboscidean lineages, including deinotheres (Deinotheriidae), gomphotheres (Gomphotheriidae), mammoths (Mammutidae), and stegodons (Stegodontidae), in addition to the demise of chalicotheres (Chalicotheriidae) and camelids (Camelidae) (**Figure 2**). Their loss drives the decline of megaherbivores (**Figure 4**), which is offset in part by a long-term increase in bovid (Bovidae) diversity (**Figure 5**). Suids (Suidae) show a modest increase from the Late Miocene through the Early Pleistocene (**Figure 5**), with some Pliocene and Early Pleistocene fossil assemblages including more than 5 co-occurring species (compared to typically 1–2 in present-day communities) (Harris & White 1979). Many of the Plio-Pleistocene grazing suids (e.g., *Notochoerus* spp.

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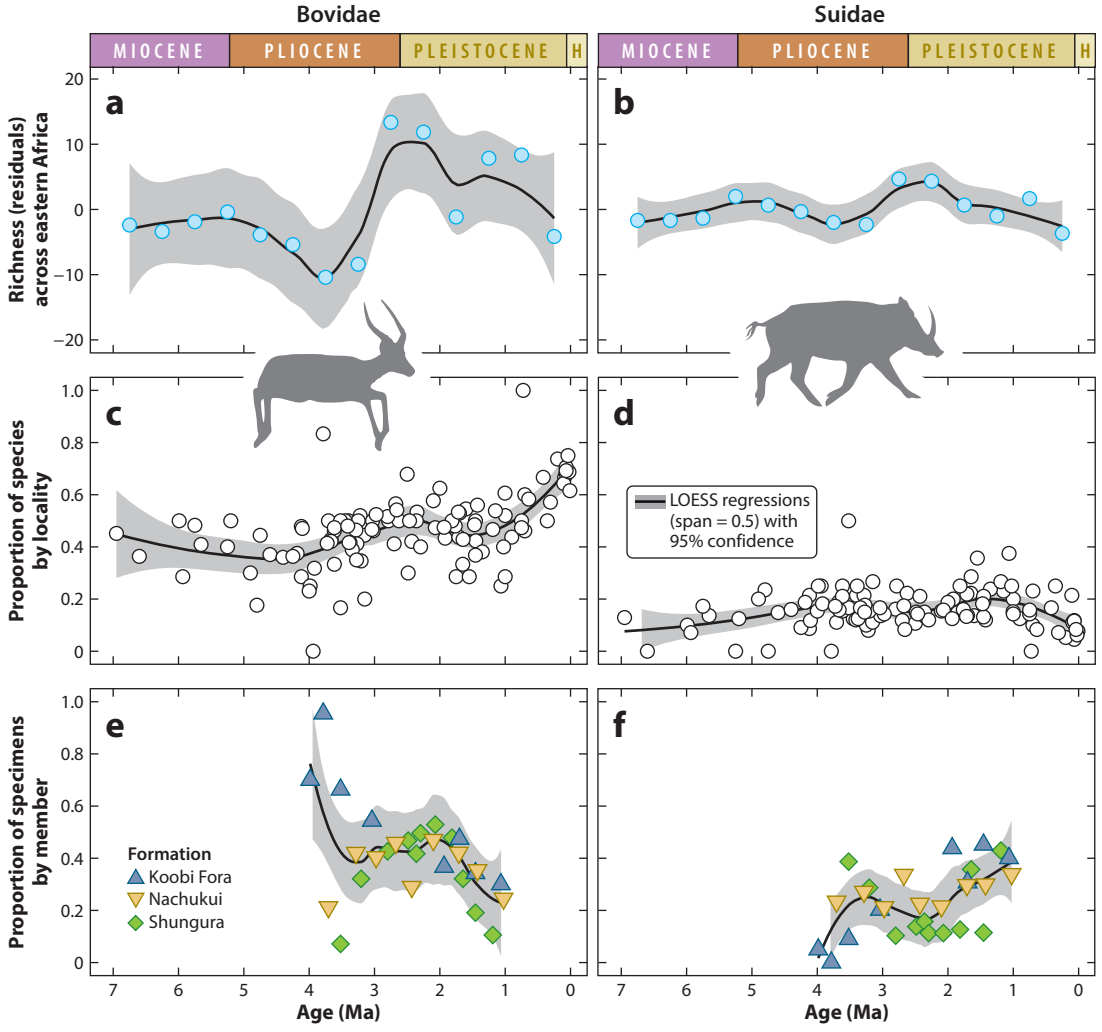

Figure 5

Temporal change in the representation of bovids (Bovidae) and suids (Suidae) through the late Cenozoic in eastern Africa. (*a*,*b*) The richness (number of species) of bovids and suids known from eastern Africa across 0.5 Ma bins. Richness values in panels *a* and *b* are residuals calculated as in **Figure 3** (see **Supplemental Figure 1**). (*c*,*d*) The proportion of bovid and suid species (relative to all ungulates) within eastern African fossil assemblages (each point represents a single locality). (*e*,*f*) The relative abundance (i.e., proportion of specimens) of bovids and suids (relative to all ungulates) from different formations (Koobi Fora, Nachukui, and Shungura) within the Omo-Turkana Basin (each point represents a geological member) (abundance data are from Du & Alemseged 2018; dietary data are from Faith et al. 2019). Solid black lines in all panels are LOESS regressions (span = 0.5) with shaded gray areas indicating 95% confidence intervals. Silhouettes are from PhyloPic (R. Wilhelmsen). See the **Supplemental Material** for the data plotted in this figure. Abbreviations: H, Holocene; LOESS, locally estimated scatterplot smoothing.

Supplemental Material >

and *Metridiochoerus* spp.) were considerably larger than their present-day counterparts, implying considerably greater ecological diversity within this clade. However, suid diversity declines over the past 1 Myr following the extinction of formerly widespread taxa, including several species of both *Metridiochoerus* and *Kolpochoerus* between ~1 and 0.5 Ma (Faith 2022).

Ecologically important changes are also well documented within bovids, a group that both is abundant in the fossil record and encompasses considerable taxonomic and ecological diversity. A

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well-documented pattern is the increasing abundance of the Alcelaphini (wildebeest and allies) and Antilopini (gazelles and allies) (Bobe 2006, 2011; Bobe & Behrensmeyer 2004), lineages that are today associated with relatively open and grassy environments. Work by Bobe and colleagues in the Omo-Turkana Basin has shown that their abundance relative to other bovids has increased through the Plio-Pleistocene (see review in Bobe 2011). A comparable trend is observed throughout eastern Africa (Bibi & Kiessling 2015), where there is a substantial increase in the proportion of alcelaphins in particular (**Figure 6**). Given their C_4-dominated diets (Cerling et al. 2015) and environmental associations, the increased dominance of alcelaphins is viewed as a consequence of the expansion of grassy ecosystems (e.g., Bobe & Behrensmeyer 2004). Whether aridity can also be implicated in these trends, as researchers have long suggested (e.g., Bobe 2006, deMenocal 2004, Vrba 1995), is less clear. Levin (2015) notes that Reduncini (waterbuck and allies), which today are C_4 grazers locally associated with well-watered environments, remain abundant through the Omo-Turkana Basin sequence, in contrast to expectations of aridity. Expanding on her arguments, we caution that inferences about regional climate shifts based on habitat preferences of reduncins, alcelaphins, or any other bovid tribe are tenuous because their relative abundances can be highly sensitive to local-scale environments.

The downsizing of Africa's carnivoran communities (**Figure 4**) reflects extinctions of very large-bodied species (>100 kg) across multiple taxonomic groups. These include the large ursine bear (Ursidae) *Agriotherium*, several massive otters (Mustelidae; *Enhydriodon dikikae*, *E. omoensis*, *E. afman*) (e.g., Grohe et al. 2022), and two of the largest known hyaenids (*Crocuta eturono* and *Pachycrocuta brevirostris*) (Werdelin 1999, Werdelin & Lewis 2008). The rarity of carnivorans in the fossil record makes it particularly hard to constrain the timing of these extinctions, but these taxa are all well documented in the Pliocene and appear to have disappeared just before or during the Early Pleistocene. Additional losses occurred with the more recent extinction (~1.5–1 Ma) of sabertooth felids (Machairodontinae), including *Homotherium*, *Dinofelis*, and the smaller-bodied (~50 kg) *Megantereon* (Werdelin & Lewis 2005). Peak diversity of the largest carnivorans (>100 kg) is observed during the mid-Pliocene (Faith et al. 2019, Lewis & Werdelin 2007) (**Figure 4**) when at least nine species are documented across eastern Africa (see Dataset S4 in the **Supplemental Material**), with increasing extinction rates through the Plio-Pleistocene (Faurby et al. 2020) leaving *Panthera leo* as the sole survivor.

Supplemental Material >

SYNTHESIS: EVALUATING THE DRIVERS

It is abundantly clear that there have been major changes in the functional and taxonomic composition of African faunal communities throughout the late Cenozoic. But how well can we link them to the proposed drivers? We begin with the expansion of grassy ecosystems. The fact that many different faunal records provide complementary trends indicating increasingly open environments suggests that a large-scale process such as the expansion of C_4 vegetation played a key role in shaping the history of Africa's faunas. However, caution is needed before assigning causality to the changes revealed by individual records or using those records to infer the larger-scale drivers of C_4 expansion because they are sensitive to different scale-dependent processes that may not reflect broader ecological changes across Africa (e.g., Levin 2015). For example, although faunal (**Figure 3**) and regional terrestrial vegetation records (**Figure 1**) across eastern Africa suggest a dramatic increase in grassy ecosystems beginning ~3–4 Ma, this is much later than what is seen in paleoecological archives that record larger spatial scales (**Figure 1**). In particular, marine records thought to document vegetation change across broad swaths of eastern and northwestern Africa suggest that the major C_4 expansion began ~10 Ma, with relative stasis through the Pliocene and Pleistocene (Polissar et al. 2019; for the early onset of C_4 expansion in southern Africa, see also Dupont et al. 2013) (**Figure 1**).

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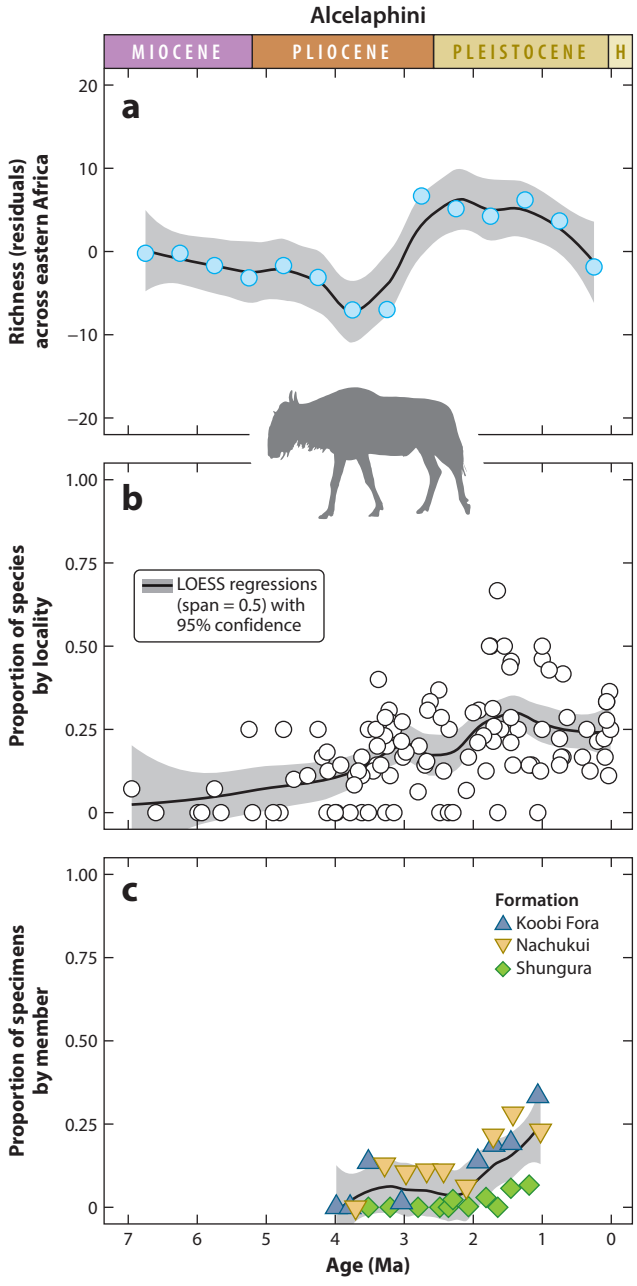
Figure 6

Temporal change in the representation of Alcelaphini through the late Cenozoic in eastern Africa. (*a*) The richness (number of species) of alcelaphins known from eastern Africa across 0.5 Ma bins. (*b*) The proportion of alcelaphin species (relative to all Bovidae) within eastern African fossil assemblages (each point represents a single locality). Richness values in panels *a* and *b* are residuals calculated as in **Figure 3** (see **Supplemental Figure 1**). (*c*) The relative abundance (i.e., proportion of specimens) of alcelaphins (relative to all Bovidae) from different formations (Koobi Fora, Nachukui, and Shungura) within the Omo-Turkana Basin (each point represents a geological member) (abundance data are from Du & Alemseged 2018; dietary data are from Faith et al. 2019). Solid black lines in all panels are LOESS regressions (span = 0.5) with shaded gray areas indicating 95% confidence intervals. Silhouette is from PhyloPic (Lukasiniho). See **Supplemental Material** for the data plotted in this figure. Abbreviations: H, Holocene; LOESS, locally estimated scatterplot smoothing.



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We suspect that apparent mismatches like this are a consequence of viewing Africa at different spatial scales. The marine records reflect larger-scale and likely climate-driven processes, whereas the terrestrial record from eastern Africa documents a history that has also been overprinted by regional processes specific to the depositional basins that provide most of the fossil evidence. More broadly, differences in the pattern and timing of change between different faunal records and across varied spatial scales, from local to regional, illustrate the importance of spatial heterogeneity and the role of different scale-dependent processes (e.g., herbivory, fire regimes, tectonics, climate) in driving ecosystem change. Rather than assuming that all faunal records are tracking the continental-scale C_4 expansion across Africa, future progress in identifying the forces that shaped the history of African mammal communities would benefit from efforts to understand the effects of different scale-dependent drivers on individual records and how those drivers vary as the scale of observation shifts from local to continental.

Things become much more uncertain when we turn our attention to the other proposed drivers. This is perhaps best exemplified by decades of literature that has set out to test Vrba's turnover-pulse hypothesis (**Table 1**), which has arguably revealed as much about the challenges involved in working with fossil data as it has about the pace of macroevolutionary change. Because Vrba's original work did not account for uncertainty in the stratigraphic ranges of fossil taxa, and the more rigorous attempts to do so have suggested primarily continuous turnover (Bibi & Kiessling 2015, Cohen et al. 2022), we see little reason to point to ∼2.8 Ma as marking significant turnover in African faunas. Likewise, whether environmental variability played any role in the evolutionary history of African faunas is uncertain for a different reason—there have been too few efforts to test it (but see Cohen et al. 2022). This uncertainty provides a prime opportunity for future research. Given the steadily growing number of fossil and paleoenvironmental records, coupled with the need for and availability of analytical tools for contending with an incomplete fossil record, the discipline is well prepared to make progress in the near future (Faith et al. 2021).

What about the role of fossil hominins in shaping the history of African ecosystems? Although the antiquity of hominin impacts is debated, it is true that at some point in the past our lineage began to rival climate and other bottom-up processes as a force of change. We suspect that this point in time is quite recent. Even African large mammal extinctions within the past ∼100 ka are consistent with paleoecological trends that were underway long before the appearance of *Homo sapiens* [e.g., long-term decline of grazers (Faith 2014, Faith et al. 2019)], the one hominin species unequivocally capable of major top-down impacts on terrestrial ecosystems. Whether or not our suspicion about the recency of hominin impacts is correct, resolving when hominin effects on African ecosystems became important, and identifying the consequences, will require considerable attention in the coming years. In addition, keeping in mind that hominins are not the only force capable of top-down impacts would also open the door to what is presently a largely untapped field of paleoecological research in Africa. We provide an example below.

EMERGING PROBLEMS: IMPLICATIONS OF NONANALOG COMMUNITIES

African faunal communities from the latest Miocene through the Early Pleistocene are unique compared to the present day in their exceptional diversity of megaherbivores (>1,000 kg) and very large carnivorans (>100 kg). For example, the Pliocene faunas from Aramis (4.4 Ma) in Ethiopia and Kanapoi (4.2 Ma) in Kenya both include at least 5 potentially sympatric proboscideans, in addition to an assortment of rhinos and giraffes (Sanders 2020, White et al. 2009). Many fossil assemblages from the same time also included several carnivorans greater than 100 kg (e.g., Werdelin & Lewis 2020, White et al. 2009). Such fossil communities are said to be functionally

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nonanalog in the sense that the distribution of taxa across functional ecological categories (e.g., diet, body size, digestive physiology) is unlike that of large mammal communities today or in the more recent geological record (Faith et al. 2019, Fillion et al. 2022).

As we outlined above, the decline of megaherbivores and the largest carnivorans has inspired a growing debate about the possibility of ancient anthropogenic extinctions. It should also inspire research seeking to understand the ecological consequences of their extinction. For example, megaherbivores are ecosystem engineers (Owen-Smith 1988)—how did the loss of megaherbivore diversity influence fire regimes, nutrient cycling, and biotic communities (Faith et al. 2019)? Likewise, carnivorans are top-down regulators of small to mid-sized (<150 kg) herbivore populations in the present day (Ripple et al. 2014, Sinclair et al. 2003)—did their demise lead to ecological release of herbivore populations, and what were the resulting trophic cascades (Fortelius et al. 2016)? These kinds of ecological processes are generally understood over short timescales, so teasing things apart in time-averaged paleo records, and distinguishing the effects of top-down (e.g., loss of carnivorans) and bottom-up processes (e.g., climate change), will likely require novel analytical approaches [e.g., simulations that bridge ecological and paleoecological timescales (Braun et al. 2021, Faith et al. 2021)].

Assuming that the co-occurring megaherbivores and large-bodied carnivorans were sympatric, the presence of nonanalog communities also raises intriguing questions about how ancient African ecosystems functioned. In present-day Africa, the largest megaherbivore, the bush elephant (*Loxodonta africana*), represents a relatively small proportion of herbivore populations, yet it accounts for most of the overall biomass (Hempson et al. 2015). Given that contemporary megaherbivore populations are thought to be largely regulated by forage availability (Sinclair et al. 2003), how is it that Late Miocene to Early Pleistocene ecosystems were able to sustain viable populations of diverse megaherbivores? Was carrying capacity considerably higher, or was megaherbivore biomass finely partitioned across multiple species? Furthermore, the allocation of relatively more biomass to megaherbivores (Bibi & Cantalapiedra 2023) also poses a challenge to the carnivores at higher trophic levels because the slow life history of megaherbivores (e.g., low birth and mortality rates) is incompatible with frequent predation (e.g., high mortality would lead to a population crash). So, how are these ancient faunal communities also able to support so many large predators? One potential solution to these problems is exceptionally high primary productivity (Bibi & Cantalapiedra 2023), perhaps facilitated by higher atmospheric CO_2 concentrations (Steinthorsdottir et al. 2021) or positive feedbacks between herbivory and plant biomass (Ritchie & Penner 2020), with greater production supporting massive populations of both megaherbivores and mesoherbivores, as well as the carnivores that consumed them. Alternatively, or perhaps in conjunction with these factors, high herbivore densities may have suppressed fire, such that relatively more plant biomass would have been available for herbivore consumption (see Staver et al. 2021). There are, of course, other potential explanations for the unusual composition of fossil communities (e.g., they may be partially a consequence of time-averaging). Whatever the answer may be, it is clear that there is much to learn about these ancient faunas.

FINAL REMARKS

The late Cenozoic record of African mammals has inspired many ideas about the forces that shaped the ecological and evolutionary history of what are today the most diverse large mammal communities on Earth. At the same time, the ever-growing body of fossil evidence attests to dramatic changes that demand explanation. Nevertheless, much work remains to be done before we can confidently assign causality to particular drivers of change (e.g., climate). Fortunately for paleoecologists, many of the factors that have made it difficult to establish cause-effect relationships,

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including the incompleteness of the fossil record and the challenges of working across vastly different spatiotemporal scales, are well understood (e.g., Behrensmeyer 2006, Bobe & Wood 2022, Faith et al. 2021, Kingston 2007). Just as important, the tools required to contend with these challenges are increasingly available (Braun et al. 2021, Wang & Marshall 2016). Faced with an ample supply of interesting questions (see the next section), an expanding body of empirical data, and the right analytical approaches, there is exciting potential to decipher the factors that shaped the evolutionary history of African mammals, including our hominin predecessors.

FUTURE ISSUES

1. Terrestrial faunal and vegetation records from eastern Africa document significant ecological changes resulting from C_4 expansion after the mid-Pliocene, long after the major continental-scale vegetation changes revealed in marine core records (**Figure 1**). How have local- to regional-scale processes overprinted the continental-scale trend? What processes are involved?
2. It is increasingly clear that our understanding of the pace of faunal turnover through time has been obscured by the incompleteness of the fossil record. Does climate change drive faunal turnover in the manner predicted by the turnover-pulse hypothesis? How have turnover rates varied through time and in relation to environmental change?
3. The role of environmental variability in shaping the evolutionary history of African mammal communities is poorly understood. Over what timescales (e.g., from seasonal to orbital) does environmental variability drive ecological and macroevolutionary change? Does environmental variability drive selective extinction (or diversification) of ecological specialists?
4. At some point in the past, members of the hominin clade began to rival bottom-up processes as a force of ecological and evolutionary change. When did this happen, and what were the consequences? How have other top-down processes shaped the history of Africa's faunas?
5. The long-term downsizing of the herbivore and carnivore guild means that ancient faunal communities are functionally distinct from any today. How did these ecosystems function with so many large-bodied species? What were the ecological consequences of their demise?

DISCLOSURE STATEMENT

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