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



Long-term biotic homogenization in the East African Rift System over the last 6 million years of hominin evolution

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Eastern Africa preserves the most complete record of human evolution anywhere in the world but we have little knowledge of how long-term biogeographic dynamics in the region influenced hominin diversity and distributions. Here, we use spatial beta diversity analyses of mammal fossil records from the East African Rift System to reveal long-term biotic homogenization (increasing compositional similarity of faunas) over the last 6 Myr. Late Miocene and Pliocene faunas (~6–3 million years ago (Ma)) were largely composed of endemic species, with the shift towards biotic homogenization after ~3 Ma being driven by the loss of endemic species across functional groups and a growing number of shared grazing species. This major biogeographic transition closely tracks the regional expansion of grass-dominated ecosystems. Although grazers exhibit low beta diversity in open environments of the Early Pleistocene, the high beta diversity of Mio-Pliocene browsers and frugivores occurred in the context of extensive woody vegetation. We identify other key aspects of the Late Cenozoic biogeographic development of eastern Africa, their likely drivers and place the hominin fossil record in this context. Because hominins were undoubtedly influenced by many of the same factors as other eastern African mammals, this provides a new perspective on the links between environmental and human evolutionary histories.

Late Cenozoic fossil sequences in the East African Rift System (EARS) provide the richest, longest and most continuous records of human evolution and its environmental context anywhere in the world. As such, the hominin and faunal records of eastern Africa have occupied a central role in understanding the factors that shaped human evolutionary history^{1,2}. Ever since Vrba's^{3–5} pioneering formulation of the turnover pulse hypothesis, which causally linked the tempo of macroevolution to that of environmental change, analysing patterns of temporal turnover (changes in species composition through time) in relation

to palaeoenvironmental records has been a long-standing focus of palaeoanthropological research^{6–9}. In contrast, we know comparatively little about spatial turnover patterns—biogeographic structure—in the EARS fossil record. Because many macroevolutionary processes have explicitly geographic components (for example, allopatric speciation and extinction), there has been growing recognition that the lack of a biogeographic context for human evolution in eastern Africa has constrained our understanding of the processes that shaped hominin species diversity and distribution patterns^{10–13}.

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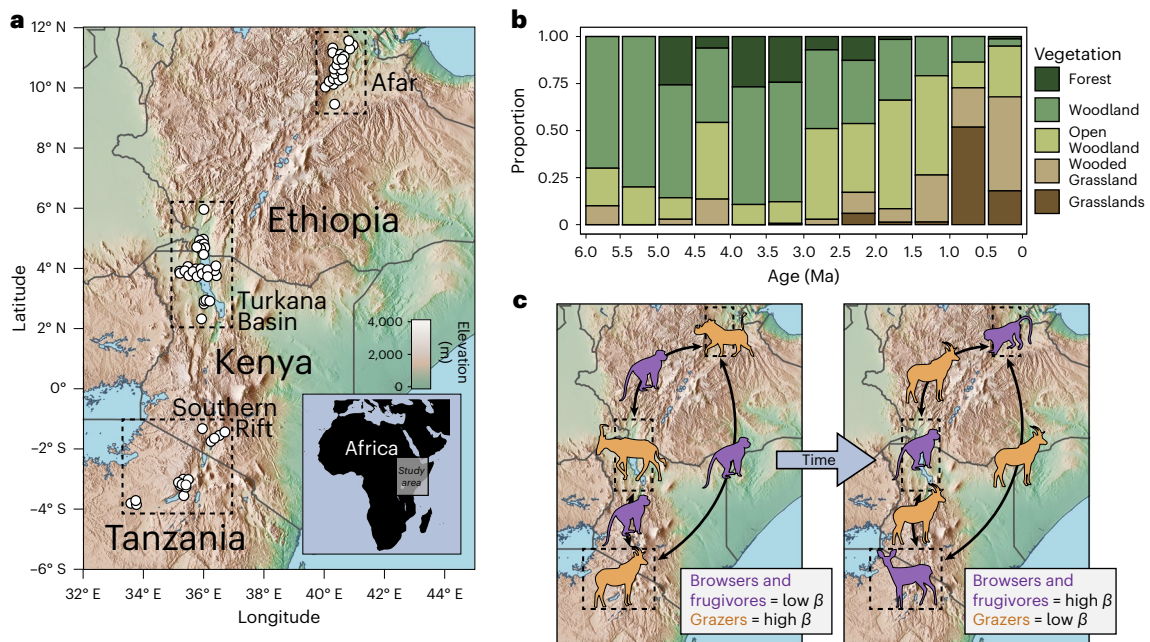


Fig. 1 | Fossil and paleoenvironmental data from the EARS and study predictions. **a**, Map of EARS fossil mammal assemblages used in this study, showing the three subregions of focus: the Afar of Ethiopia, the Turkana Basin of Ethiopia and Kenya and the Southern Rift subregion of Kenya and Tanzania. **b**, Stacked barplots showing changes in EARS vegetation structure over the last 6 Myr, converted from stable carbon isotopes ($\delta^{13}\text{C}$) of palaeosol carbonates into vegetation types based on ref. 78. The palaeosol data compilation comes from

ref. 86 and spans a spatial extent comparable to the mammal fossil assemblages analysed here. **c**, Biogeographic predictions in this study, with a shift from low to high beta diversity (β) in frugivores and browsers and high to low beta diversity in grazers over the last 6 Myr. Arrows show connections between the subregions, not hypothesized dispersal routes, which may have been constrained by rift topography (Discussion). Map generated using GMT v.6 (ref. 87).

With this in mind, we draw on the rich mammal fossil record from the EARS to provide a quantitative synthesis of biogeographic evolution in eastern Africa over the last 6 million years (Myr). Mammals comprise the bulk of the EARS fossil record and their taxonomic and ecological diversity provide a key comparative and contextual framework for understanding human evolution^{14,15}. We compiled a fossil mammal dataset from three EARS subregions: the Afar of north-eastern Ethiopia, the Turkana Basin of northern Kenya and southern Ethiopia and the Southern Rift of southern Kenya and northern Tanzania (Fig. 1a). We limit our analyses to these subregions because each contains multiple fossil-bearing formations that in aggregate span the last 6 Myr, whereas other important EARS subregions (for example, the Baringo Basin, Kenya) were excluded because of data limitations. However, we consider our analyses as broadly representative of EARS biogeographic dynamics because the Afar, Turkana Basin and Southern Rift have produced the majority of hominin and faunal records for eastern Africa, including its most prolific fossil sites (for example, Hadar, Koobi Fora and Olduvai) and span $>15^\circ$ latitude from equatorial Africa through the Horn, meaning that they enclose most other EARS subregions with Late Cenozoic fossil records.

We focused our analysis of EARS biogeographic dynamics on patterns of spatial beta diversity (hereafter, ‘beta diversity’) across the three subregions over the last 6 Myr. Beta diversity quantifies the compositional variation in two or more communities of species across space^{16–18}, such that changes in EARS beta diversity reflect shifts in the biogeographic structure (taxonomic similarity) of subregional mammal faunas through time. Beta diversity measures are typically bound between zero and one, with low values indicating greater similarity (more species shared), whereas higher values indicate greater dissimilarity (fewer species shared). A large body of literature has demonstrated how beta diversity patterns can be leveraged towards a greater understanding of the relationships between the environmental, evolutionary and biogeographic histories of biotas^{19–22}. In the EARS, for

example, environmental change could lead to the emergence of ecologically suitable dispersal corridors which facilitate species exchange among subregions, thus lowering beta diversity and driving biotic homogenization (increasing similarity of species compositions across subregions). On the other hand, ecological filters (for example, habitat fragmentation) or physical barriers (for example, tectonic uplift) can isolate subregions by preventing or constraining species exchange. If separated long enough, independent histories of speciation and extinction in each subregion would increase beta diversity and lead to provincialism (each of the subregions is largely composed of endemic species). In either scenario—biotic homogenization or provincialization—functional traits (for example, diet and body mass) are a key consideration because they mediate the interactions of organisms with their environments²³ and thus the patterns of species exchange, or lack thereof, among EARS subregions over the last 6 Myr.

One of the most important changes to eastern African environments over the last 6 Myr is the expansion of open ecosystems dominated by hot- and arid-adapted C_4 grasses²⁴, which has long been invoked as a driver of hominin and faunal evolution in the region^{2,14}. EARS terrestrial palaeovegetation records derived from pedogenic carbonates of ancient soils document a steady rise of ecosystems dominated by C_4 grasses (grasslands and wooded grasslands) over the last 3 Myr, replacing wooded ecosystems with abundant C_3 trees and shrubs (Fig. 1b). We used our beta diversity analyses to test two predictions for how the biogeographic structure of mammal faunas responded to this major shift in EARS environments (Fig. 1c). First, we predict that the fossil record of mammal taxa linked to forest and woodland habitats (browsers and frugivores) should exhibit low beta diversity early in time (>3 million years ago (Ma)) when forested corridors permitted species exchange among EARS subregions. Conversely, the fragmentation of woody habitats and continued rise of ecosystems dominated by C_4 grasses would have driven vicariance among forest and woodland taxa while facilitating range expansions for species favouring open habitats,

namely grazers. Thus, we expect that grazing taxa should show a trend towards lower beta diversity through time, whereas browsers and frugivores show trends towards higher beta diversity. In addition to diet, we also examined beta diversity patterns across body size classes, as body size is known to directly influence mammal range sizes and dispersal capabilities. Second, we predict that dispersal capability is greater in larger-bodied taxa, meaning that beta diversity should decline with increasing body size^{25,26}.

Results

We compiled a presence–absence matrix of large-bodied (>1 kg) terrestrial mammal species in the orders Artiodactyla, Carnivora, Hyracoidea, Perissodactyla, Primates, Proboscidea and Tubulidentata from Late Miocene to recent fossil assemblages ($n = 95$) in the Afar, Turkana and Southern Rift subregions (Supplementary Data). Each species was assigned a body size class (size 1, <18 kg; size 2, 18–80 kg; size 3, 80–350 kg; size 4, 350–1,000 kg; size 5, >1,000 kg) and dietary ecology (carnivore, omnivore, frugivore, browser, mixed feeder and grazer) following previous studies^{14,27}. To test our biogeographic predictions, we divided the last 6 Myr into 500 kyr time bins and constructed a species-by-subregion presence–absence matrix for each time bin. We quantified beta diversity across the three subregions for each time bin using the Simpson-based multisite dissimilarity index²⁸, β_{SIM} (equation (1) in Methods). The β_{SIM} values range from zero to one, where zero indicates identical species composition across subregions and one indicates completely distinct subregions. We then additively partitioned the eastern African β_{SIM} trend into its functional (diet and body size class) components (equation (4)) to determine how species with different functional traits contributed to regional biogeographic change. Finally, we isolated the endemic (restricted to one subregion) and shared (present in two or more subregions) species components of β_{SIM} (equations (2) and (3)) to see how each contributed to the overall β_{SIM} pattern through time; these two components were also additively partitioned by functional groups (equations (5) and (6)). Further information about our dataset and analyses is provided in Methods and Extended Data Fig. 1.

Patterns of biogeographic change

Our analyses reveal a long-term trend towards lower beta diversity in eastern African mammal faunas over the last 6 Myr (Fig. 2), with β_{SIM} values strongly correlated with the midpoint age of each time bin (ordinary least squares regression: $r^2 = 0.69$, $P < 0.001$). Beta diversity is high from 6 to 3.5 Ma (β_{SIM} values range 0.68–0.77) but declines markedly after this period, reaching its lowest level in the youngest time bin (0.5–0 Ma, $\beta_{\text{SIM}} = 0.25$). There are two excursions towards higher beta diversity at 3–2.5 Ma ($\beta_{\text{SIM}} = 0.66$) and 1–0.5 Ma ($\beta_{\text{SIM}} = 0.56$) but these are followed by steep drops in the subsequent time bins. As such, we focus on the overall 6 Myr trend in our β_{SIM} curve rather than over interpret results from individual time bins. When additively partitioning the regional β_{SIM} trend by diet (Fig. 3a), it becomes clear that grazers, mixed feeders and browsers and frugivores largely drive the overall regional beta diversity trend (Fig. 2) because of their greater observed diversities but the relative contribution of these groups varies by time bin. Partitioning by size classes (Fig. 3b) indicates that beta diversity changes for size 5 (>1,000 kg) taxa primarily drove the regional β_{SIM} trend (Fig. 2).

Processes underlying biogeographic change

The regional β_{SIM} decline could have been driven by the loss of endemic taxa, the dispersal of shared taxa or both. To better understand the processes underlying biogeographic change, we calculated proportions of endemic versus shared species by diet (Fig. 4a) and size class (Fig. 4b) which shed light on the underlying drivers of eastern African β_{SIM} patterns. Our calculated proportions follow the β_{SIM} mathematical framework (equations (5) and (6)). We find that endemic browsers and frugivores show a decline from the earliest Pliocene (–5 Ma) onwards,

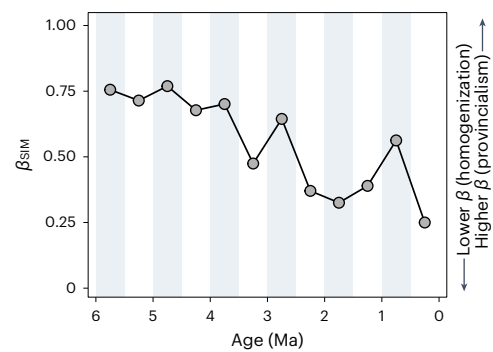


Fig. 2 | Temporal trend in multisite Simpson dissimilarity (β_{SIM}) for eastern African mammal species over the last 6 Myr. Higher β_{SIM} values indicate stronger provincialism, meaning that the faunas from EARS subregions were mainly composed of endemic species, whereas the long-term trend towards lower β_{SIM} values indicates biotic homogenization (increasing similarity of taxonomic compositions across EARS subregions).

whereas endemic grazers and mixed feeders show more abrupt losses from 5 to 4 and 3 to 2 Ma, respectively. With respect to shared species, the only noticeable change among diet groups is an increase in the number of shared grazers from –3 Ma onwards. For size classes, there is a steep decline in endemic species within the largest size class (size 5, >1,000 kg) and, to a lesser extent, size 3 (80–350 kg) taxa through time. Gains in shared medium-sized species (size 2 and size 3, collectively 18–350 kg) begin after 4 Ma.

Discussion

Eastern Africa is a global hotspot of biodiversity²⁹ and hosts one of the richest assemblages of large mammals anywhere in the world today³⁰. For nearly a century, it has been recognized that past environmental change played a key role in the diversification and biogeographic history of the rich mammalian fauna of eastern Africa. Early appreciation of this derived from comparisons of present-day species distributions and centres of endemism with proposed Pleistocene refugia^{31–33}, later expanded upon by phylogeographic data (genetic population structuring and the spatial patterning of lineage divergence) across mammal clades³⁴. Although it now appears that the recent biogeographic evolution of eastern Africa was primarily governed by the recurrent expansion and contraction of forested versus grassy habitats tracking orbitally forced wet–dry climate cycles^{35–37}, we know comparatively little about long-term (10⁶ years) biogeographic dynamics in the region and their drivers. Here, we have drawn on the rich mammal fossil record of the EARS to provide a quantitative synthesis of past beta diversity patterns and a Late Cenozoic biogeographic framework for eastern Africa that sheds light on the long-term development of this global biodiversity hotspot and our own evolutionary history.

Over the last 6 Myr, the biogeography of mammal faunas in the EARS was characterized by a lowering of beta diversity through time, leading to biotic homogenization (increasing compositional similarity of the subregional faunas). Growing interest in the processes underlying biotic homogenization in the context of ongoing anthropogenic change³⁸ has highlighted the importance of the twin forces of species introduction and extinction in driving beta diversity patterns^{39,40}. In other words, increasing compositional similarity of faunas could have been driven by the exchange of species among subregions and/or the loss of local endemics, such that shared taxa comprise a greater proportion of the regional pool. We found that both processes were important for shaping biogeographic evolution in the EARS over the last 6 Myr (Fig. 4). Our first prediction was only partially supported—though we found that grazers exhibit very low beta diversity in grass-dominated Early Pleistocene environments, high beta diversity and strong

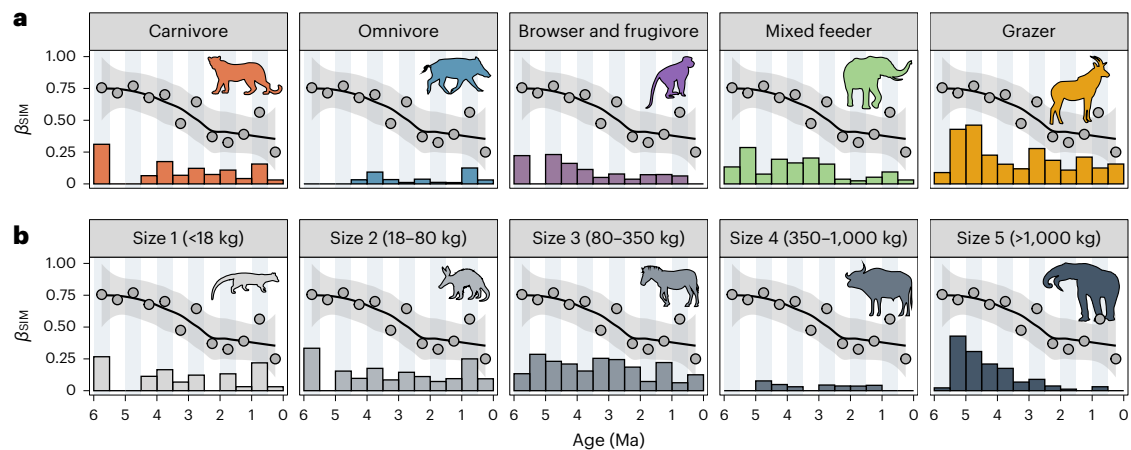


Fig. 3 | Biogeographic evolution of eastern African mammal faunas over the last 6 Myr. The temporal trend in multisite Simpson dissimilarity (β_{SIM}) for all eastern African mammals (same as in Fig. 2) is shown again in each panel with grey points and a locally estimated scatterplot smoothing (LOESS) curve (span = 0.75) and 95% confidence interval (grey shading) to highlight the overall β_{SIM} trend.

a, b, Barplots show the eastern African β_{SIM} trend additively partitioned into its dietary (a) and body size class (b) constituents. Summing β_{SIM} patterns across categories within a functional group (for example, diet) returns the overall β_{SIM} trend. The biogeographic interpretations of β_{SIM} values are the same as described for Fig. 2.

provincialism in Late Miocene to Pliocene browsers and frugivores occurred in the context of extensive woody vegetation. The second prediction of our study was not supported—we found that the largest mammals (size class 5, taxa >1,000 kg) showed the greatest proportion of endemic species, whereas smaller taxa either showed little change or gains in shared species through time. Overall, biogeographic changes were driven by the gradual loss of endemic species across many functional groups before ~2 Ma, followed by strong gains in shared grazers (most of which are size 2 and 3 taxa, such as bovids and suids) after this time in parallel with the steady rise of ecosystems dominated by C_4 grasses through time (Fig. 1b).

Expansion of C_4 -dominated ecosystems and grazer diversity

The coupled expansion of C_4 -dominated ecosystems and shift to faunal communities largely comprised by grazing mammals by ~2 Ma is one of the most robust palaeoecological patterns in the eastern African fossil record^{2,14,41,42} and has figured prominently in narratives of human evolution for decades^{3,43}. Our analyses provide new information on this important biotic transition by revealing that Pleistocene increases in regional grazer species richness occurred in parallel with lowering beta diversity in the eastern African grazing guild. This pattern stands in contrast to predictions from macroevolutionary theory that cladogenesis in large-bodied vertebrate taxa most often occurs via geographic isolation of populations and allopatric speciation⁴⁴, wherein one would expect regional beta diversity and regional species richness to be positively correlated through time¹⁹. One explanation for the eastern African pattern is that increasing regional richness and decreasing beta diversity of grazers can be accounted for by dramatic increases in mean within-subregion richness (increasing gamma diversity and decreasing beta diversity implies large increases in mean alpha diversity). Such large increases in the carrying capacity of grazers would be expected given the dramatic expansion of grassy biomass across each of the three EARS subregions (Fig. 1b) and a previous study demonstrating fossil assemblages hosted a larger number of grazers between 2 and 1 Ma than is observed today or in other periods of the Late Cenozoic¹⁴. In addition, the evolution of greater niche differentiation among Pleistocene grazers could help explain their high regional species richness but low beta diversity. Field studies in eastern Africa have long highlighted how body size and forage selectivity can mitigate competitive exclusion and promote co-existence and/or facilitation among sympatric herbivores^{45,46}. A recent study⁴⁷ demonstrated that body

size partitioning among grazing bovids from Bed II of Olduvai Gorge, Tanzania (~1.7–1.4 Ma) was similar to that of the present-day Serengeti ecosystem, suggesting that niche differentiation was well-developed by the Early Pleistocene and permitted the co-existence of a speciose and ecologically diverse grazing guild.

Implications for hominin evolution and biogeography

We found that the Late Miocene and most of the Pliocene (6–3 Ma) was a period of relatively high provincialism among eastern African mammal faunas when woody habitats dominated EARS vegetation (Fig. 1b). While it would be expected for herbivore diet groups dependent on C_4 vegetation (grazers and mixed feeders) to show high endemism at this time, we found that the regional pool of browsers and frugivores was also largely comprised of endemic species. This might suggest that suitable woody habitat corridors between the EARS subregions were not as widespread and/or stable enough to facilitate dispersal or that browsing and frugivorous taxa faced stronger dispersal constraints overall, which is consistent with observations from contemporary primate communities^{48,49}. Mio-Pliocene hominins were medium-sized (30–50 kg (ref. 50) dietary generalists, probably feeding on fruit, leaves and limited amounts of animal tissue⁵¹. Palaeoenvironmental reconstructions of EARS hominin-bearing sites place basal hominins (*Orrorin* and *Ardipithecus*) in forested to woodland contexts⁵², whereas early australopiths (*Australopithecus* and *Kenyanthropus*) occupied both wooded and slightly more open environments⁵³. In addition, both basal hominins and australopiths possess postcranial morphology indicating a reliance on arboreal behaviours^{52,54}. Because many of the omnivores in our fossil mammal dataset are terrestrial taxa (for example, hyenas, civets and bushpigs) without strong preferences for woody habitats, we view the biogeographic patterns for browsing and frugivorous taxa—which include several arboreal and semi-arboreal non-hominin primates—as a more ecologically relevant point of comparison for understanding early hominin distribution patterns.

The fossil evidence for a diversity of penecontemporaneous early hominin taxa in eastern Africa has been highly debated. A growing number of fossils have been used to argue for elevated species diversity during the Mid-Pliocene, ~3.5–3 Ma (refs. 55,56). These include *Kenyanthropus platyops* from West Turkana⁵⁷ and *Australopithecus deyremeda*⁵⁸ and the morphologically primitive Burtele Foot⁵⁹ from Woranso-Mille in the Afar. None of these taxa has been clearly recovered from the same fossil localities as the more widely distributed

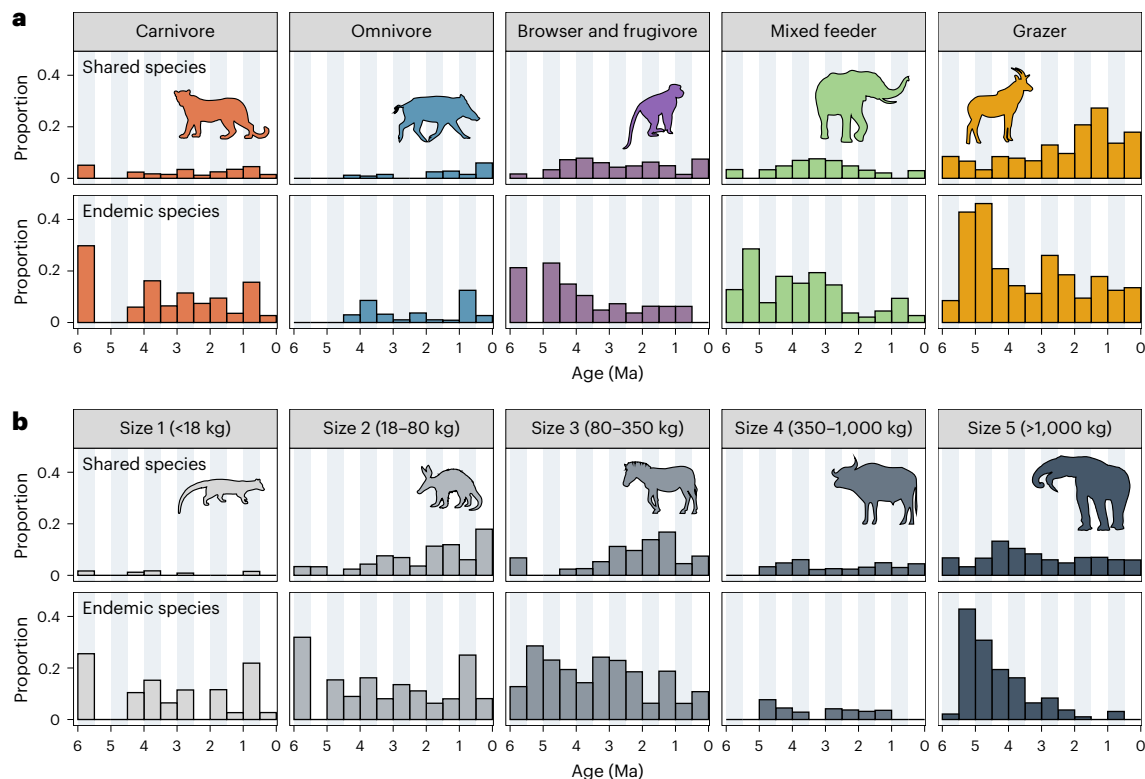


Fig. 4 | The contribution of shared versus endemic species in driving the biogeographic evolution of eastern African mammal faunas over the last 6 Myr. a, Barplots showing temporal trends in the proportion of shared

(top row) and endemic (bottom row) species within diet groups over the last 6 Myr. **b,** Barplots showing temporal trends in the proportion of shared (top row) and endemic (bottom row) species within body size classes over the last 6 Myr.

Au. anamensis–*Au. afarensis* lineage, which is found at several fossil sites throughout much of the EARS from -4.2 to 2.95 Ma. At Worsano-Mille, fossils of *Au. afarensis* and *Au. deyiremeda* come from different collection areas, which has been used to suggest that, even within the Afar subregion, they never occurred in sympatry⁶⁰. While the validity of species-level distinctions of Mid-Pliocene *Au. deyiremeda* and *K. platyops* from *Au. afarensis* is controversial⁵⁵ and perhaps doubtful^{61,62}, it would not be surprising for eastern Africa to have supported a diversity of largely allopatric hominin species at this time from the perspective of mammal biogeography. Indeed, given that spatially adjacent and temporally overlapping fossil sequences in the Afar–Hadar and Woranso-Mille–have potentially produced remains of different hominin taxa⁵⁸, the strong provincialism documented for EARS mammals might have occurred within each of the subregions (Afar, Turkana and Southern Rift) we analysed as aggregates here.

Although we still have much to learn about the factors that shaped hominin species diversity and distributions^{11–13}, we can synthesize our biogeographic findings with palaeoenvironmental records to provide a preliminary discussion of possible drivers. Fossil and molecular data suggest that by the Late Miocene, -7–6 Ma, the human–chimpanzee divergence had occurred⁶³. A study of ichthyofaunas demonstrated similarities among the Late Miocene sites of Toros-Menalla (Chad), Semliki (eastern Congo) and Lothagam (Turkana Basin), suggesting the presence of a permanent trans-African hydrological network at this time. In the EARS, Pliocene faunas in the Afar and Turkana Basin shared a single, large-bodied hippopotamid species between -4.2 and 2.95 Ma (ref. 64) but hosted endemic hippo assemblages from 2.95 Ma onwards. This pattern has been suggested to reflect the disruption of the hydrological networks of Africa by the Late Pliocene, during which regional aridification and/or local tectonism forced the isolation of the basin drainages of each rift and thus promoted endemism among aquatic taxa. We found the opposite pattern for EARS terrestrial

mammals, which were largely endemic from -6 to 3 Ma. These patterns are complementary, as large water bodies present dispersal barriers to many terrestrial mammals, especially primates⁶⁵ but facilitate the dispersal of aquatic taxa. Furthermore, river barriers have long been proposed as drivers of genetic structuring, speciation and allopatry in extant African apes^{66,67}, which are often viewed as important referential models for early hominin evolution. Thus, despite the existence of ecologically suitable woody habitat corridors, it could be that the presence of perennial water bodies throughout the floor of the EARS acted to constrain the dispersal of many species of terrestrial mammals, including early hominins, among the Afar, Turkana Basin and Southern Rift until the break-up of major hydrological networks after 3 Ma (ref. 68). Although individual subregions experienced local tectonism that shifted topography through time (for example, ref. 69), broader reconstructions of EARS evolution via thermochronological, structural and tectonic modelling studies^{70–73} suggest that much of the Eastern Branch had obtained rift structure by the Mio-Pliocene boundary. Extension-driven footwall uplift along rift flanks followed the initiation of border fault systems throughout the EARS before the latest Miocene^{74,75}, indicating that steep topographic gradients were present for the last 6 Myr. Thus, while the modern EARS topography (Fig. 1a) is not fully representative of its Late Cenozoic evolution, its primarily north–south trending rift valley structure provides a useful analogue for thinking about topographic controls on biogeography.

By the Early Pleistocene -2 Ma, species of *Homo* were widely distributed among the EARS subregions. Previously proposed models linking larger geographic distributions of African early *Homo* with increased home range size or other important palaeobiological shifts as compared to earlier hominins^{76,77} should be interpreted cautiously, as these species occurred alongside an EARS-wide lowering of beta diversity across mammals. On the other hand, *Paranthropus boisei* presents an interesting case, given that this species was a dedicated

consumer of C_4 resources⁷⁸ and EARS biotic homogenization was mostly driven by increases in shared grazing species. Although well-documented from the Turkana Basin and Southern Rift⁷⁹, *P. boisei* is yet unknown from the Afar despite decades of field work. Whether this reflects a true distributional pattern or a sampling artefact is difficult to determine, although some have suggested that stable isotopic evidence for C_4 -dominated diets in *P. boisei* might reflect a reliance on wetland sedges^{80,81} and a narrow ecological niche associated with mesic habitats^{42,82}. In this case, the low hydrological connectivity among EARS subregions after 3 Ma could have imposed an important dispersal constraint. However, this is difficult to test at present and evidence for a C_3 -rich diet of *P. boisei* specimens from Malawi, much further south in the EARS⁸³, suggests that any biogeographic scenario linking the distribution of *P. boisei* to C_4 wetland resources is probably too simplistic. Instead, we use the examples above to demonstrate how a Late Cenozoic biogeographic context for the EARS greatly enhances our view of the hominin fossil record and promises to stimulate new approaches for understanding how environmental factors shaped human evolutionary history.

Conclusions

Because hominins were undoubtedly influenced by many of the same factors as other eastern African mammals, our synthesis of Late Cenozoic biogeographic dynamics in the EARS can be leveraged towards a greater understanding of the relationships of hominin species diversity and distributions with environmental change through time. Our beta diversity analyses revealed strong long-term biotic homogenization (greater compositional similarity of faunas) among EARS mammals over the last 6 Myr. Biotic homogenization was largely driven by losses of endemic browsers and frugivores and size 5 (>1,000 kg) taxa, alongside a rise in the number of shared grazers and medium-sized (size 2 and 3) species. This important biogeographic transition parallels the Plio-Pleistocene rise of C_4 -dominated ecosystems in the EARS and is probably causally linked to it given the functional ecological make-up of the particular groups. On the other hand, in contrast to the predictions of our study, wooded habitats of the Late Miocene and Pliocene did not correspond to a period of widely distributed browsing and frugivorous mammal species. Instead, all EARS mammal faunas at this time were strongly provincial (largely composed of endemic species), which we suggest may reflect extensive hydrological connections among rift basin areas that presented dispersal barriers to terrestrial taxa. Although species diversity of Pliocene hominins continues to be highly debated^{155,56,62}, from the perspective of EARS biogeography, it would not be unexpected for the region to have supported many largely allopatric hominin species at this time. By the Early Pleistocene, mammal species exchange among the Afar, Turkana Basin and Southern Rift was extensive, especially for grazers, following the dissolution of hydrological networks in the Late Pliocene and the continued expansion of grassy ecosystems. Although we still have much to learn about the long-term factors shaping eastern African biodiversity, including members of our own evolutionary lineage, our analyses identify several salient points of the Late Cenozoic biogeographic development of the region and provide a new perspective on the links between environmental and human evolutionary histories.

Methods

Fossil dataset

We compiled a dataset of 95 EARS large mammal fossil assemblages spanning the last 6 Myr from the literature and our own study of fossil collections from Ethiopia and Kenya. Here, 'large mammals' are members of Artiodactyla, Carnivora, Hyracoidea, Perissodactyla, Primates (including hominins), Proboscidea and Tubulidentata. For each fossil assemblage, we collected data on taxa present as well as the most recently published age estimate for the assemblage, relying mainly on absolute geochemical dates when available. On the

basis of geography (Fig. 1a) and geological data, we grouped each of these assemblages into one of our three subregional aggregates (Afar, Turkana Basin or Southern Rift) to generate subregional species pools in 500 kyr intervals (6–5.5, 5.5–5 Ma and so on). Shifting the bin start age by 100 kyr increments did not alter overall trends (Extended Data Fig. 2a). Functional trait data (diet and body size) were assigned to each species using published data following refs. 14,27 or, in few cases, extant relatives when palaeoecological data were not available (Supplementary Data).

For analysis, we treated open nomenclature as follows: taxa with 'cf' qualifiers were combined with their likely identification (for example, *Equus cf. quagga* to *Equus quagga*), 'sp' or 'indet' taxa were dropped (for example, *Equus sp.* or Equidae gen. et sp. indet.), while 'aff' taxa were retained as distinct species (for example, *Equus aff. quagga*). This system was used following common taxonomic practice that 'sp' and 'indet' taxa are those unidentifiable to species, those with 'cf' probably belong to a known taxon but lack diagnostic elements and those with 'aff' belong to a closely related but distinct taxon⁸⁴. Analyses using various treatments of open nomenclature produced qualitatively identical results (Supplementary Information and Extended Data Fig. 2b), therefore we only present the latter here but include four different versions of the presence-absence matrix in Supplementary Data.

Beta diversity analyses

We quantified beta diversity across the three subregions using the Simpson-based multisite dissimilarity metric (β_{SIM} ; refs. 16,28). Values for β_{SIM} range from zero to one, where zero indicates identical subregions in terms of taxonomic composition and one indicates completely distinct subregions. The β_{SIM} treats completely nested subregions as identical (for example, $\beta_{SIM} = 0$ when comparing a subregion with a lion, zebra and wildebeest; a second subregion with a zebra and a wildebeest; and a third with just a zebra). We view this β_{SIM} behaviour as a way to account for differential fossil preservation and sampling intensities across subregions. Three subregions may be compositionally identical in reality but become nested subsets when subregions with smaller observed diversities have lower degrees of fossil preservation and/or sampling. We demonstrate this by correlating preservation measures (for example, number of sites and number of species) with β_{SIM} values through time (Supplementary Information, Extended Data Figs. 3–5 and Supplementary Table 1).

The generalized β_{SIM} equation for two or more subregions, following the notation of ref. 16, is:

$$\beta_{SIM} = \frac{[\sum_{i < j} \min(b_{ij}, b_{ji})]}{[\sum_i S_i - S_T] + [\sum_{i < j} \min(b_{ij}, b_{ji})]}, \quad (1)$$

where b_{ij} is the number of species found in subregion i but not j , b_{ji} is the number of species found in subregion j but not i , S_i is the number of species found in subregion i and S_T is the total number of species found across all subregions. Within the β_{SIM} framework (equation (1)), one can view $[\sum_{i < j} \min(b_{ij}, b_{ji})]$ as a measure of number of endemic species and $[\sum_i S_i - S_T]$ as a measure of number of shared species¹⁶. However, because β_{SIM} is standardized to range from zero to one, the endemics and shared species components are not independent (for a given β_{SIM} value, if the number of endemics increases, the number of shared species must decrease and vice versa). To see how each component independently influences β_{SIM} on a scale of zero to one, we divided each by a different standardizing factor (this means that the two standardized components are not directly comparable). For the standardized endemics component, we calculated:

$$\beta_{SIM_END} = \frac{[\sum_{i < j} \min(b_{ij}, b_{ji})]}{[\sum_{i < j} \min(b_{ij}, b_{ji}) + a_{ij}]}, \quad (2)$$

where a_{ij} is the number of species shared by subregions i and j , following ref. 28 notation. For the standardized shared species component, we calculated:

$$\beta_{\text{SIM,SH}} = \frac{[\sum_i S_i - S_T]}{\sum_i S_i} \quad (3)$$

Because the numerators of β_{SIM} (equation (1)) and $\beta_{\text{SIM,END}}$ (equation (2)) are effectively counts of endemic species and the numerator of $\beta_{\text{SIM,SH}}$ (equation (3)) is effectively a count of shared species, we can additively partition these numbers by categories within a functional group (for example, grazers or browsers within diet) to see how each category influences the metric in question. Letting f index a functional category within a functional group, the functional category partition for β_{SIM} (equation (1)) is:

$$\beta_{\text{SIM}_f} = \frac{[\sum_{i<j} \min(b_{ij}, b_{ji})_f]}{[\sum_i S_i - S_T] + [\sum_{i<j} \min(b_{ij}, b_{ji})]}, \quad (4)$$

where $\min(b_{ij}, b_{ji})_f$ is the number of species in functional category f belonging to whichever group is smaller: the number of endemic species in subregion i or the number of endemics in subregion j . Likewise, the functional category partition for $\beta_{\text{SIM,END}}$ (equation (2)) is:

$$\beta_{\text{SIM,END}_f} = \frac{[\sum_{i<j} \min(b_{ij}, b_{ji})_f]}{[\sum_{i<j} \min(b_{ij}, b_{ji}) + a_{ij}]}. \quad (5)$$

The functional group partition for $\beta_{\text{SIM,SH}}$ (equation (3)) is:

$$\beta_{\text{SIM,SH}_f} = \frac{[\sum_i S_{if} - S_{Tf}]}{\sum_i S_i}, \quad (6)$$

where S_{if} is the number of species in subregion i belonging to functional category f and S_{Tf} is the total number of species across all subregions belonging to functional category f . Summing all partitions within a functional group returns the original metric, $\sum_f \beta_{\text{SIM}_f} = \beta_{\text{SIM}}$, $\sum_f \beta_{\text{SIM,END}_f} = \beta_{\text{SIM,END}}$ and $\sum_f \beta_{\text{SIM,SH}_f} = \beta_{\text{SIM,SH}}$.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data generated or analysed during this study are provided on Zenodo via <https://zenodo.org/records/11187857> (ref. 85).

Code availability

All code used for main text analyses is provided on Zenodo via <https://zenodo.org/records/11187857> (ref. 85).

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Author contributions

J.R. designed the research and compiled the data. J.R. and A.D. analysed the data. J.R., A.D., E.J.L., J.T.F., L.B., C.J.C., J.C.J, I.A.L., E.M.L., I.E.S, K.E.R. and J.M.K. contributed to the interpretation of results. J.R. wrote the manuscript with input from all authors. J.M.K. and K.E.R. secured the primary funding for this study with contributions from L.B.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-024-02462-0>.

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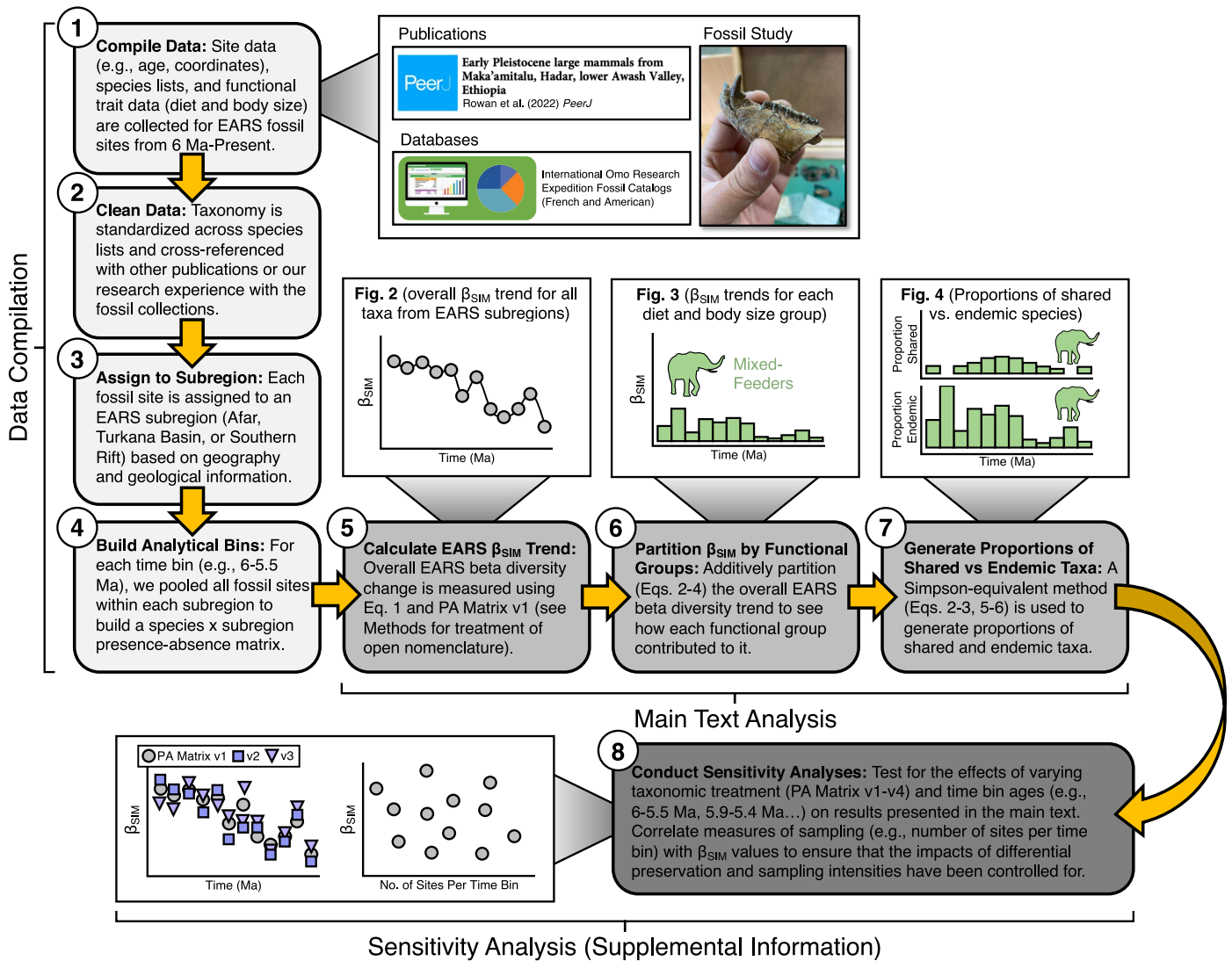
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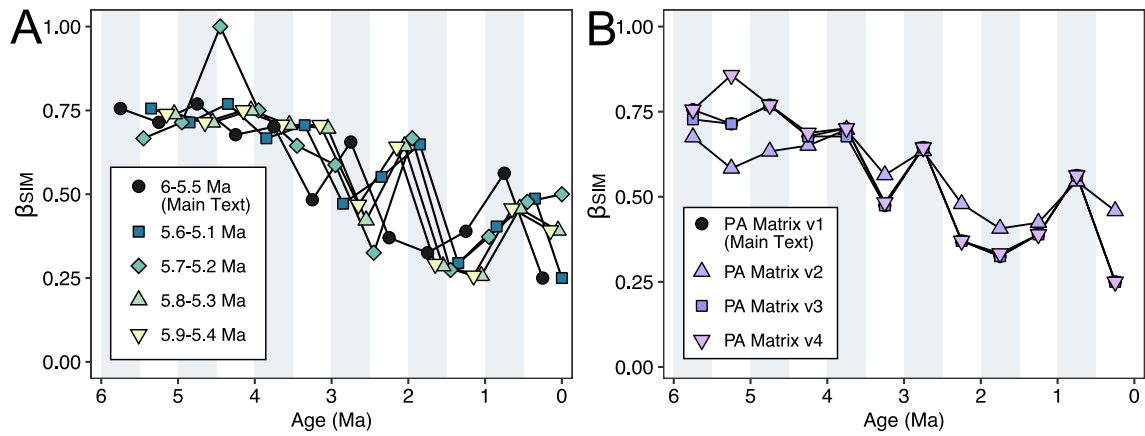
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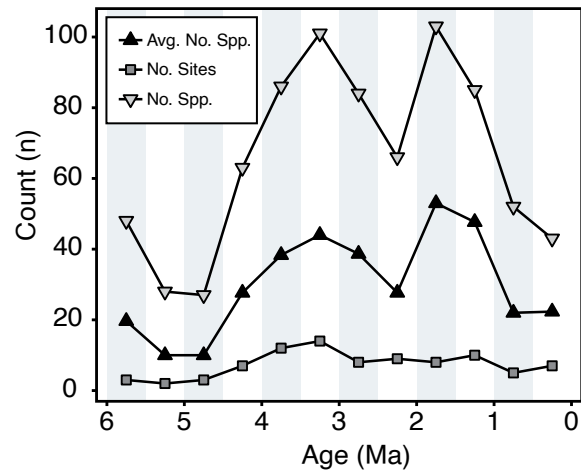
Extended Data Fig. 1 | Overview of analytical workflow used to generate main text results. Main text (Figs. 2–4 and generated values reported in Supplementary Dataset 1) and sensitivity analyses (results reported in Extended Data Figs. 2–5, Supplementary Table 1 and generated values reported in

Supplementary Dataset 1) are shown. Each step of the analysis is outlined, with schematic data plots illustrating examples of where the results of each analytical step are presented.

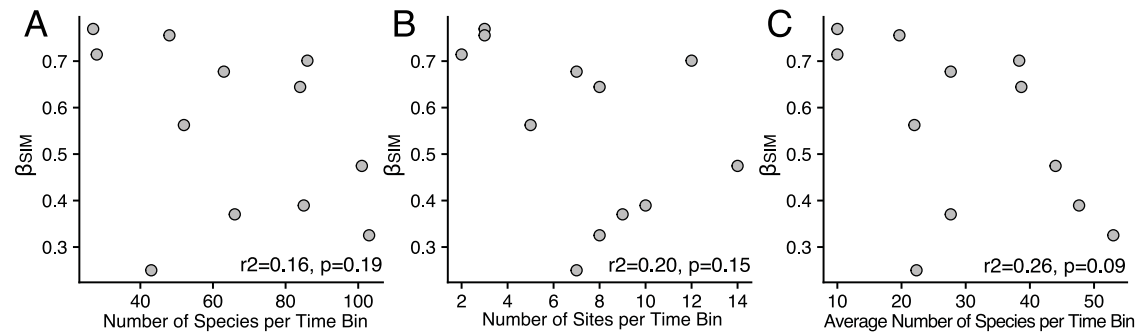


Extended Data Fig. 2 | Sensitivity analysis for time bin starting age. **a)** Our main text analyses of multisite Simpson dissimilarity (β_{SIM}) used 500-kyr time bins starting at 6 Ma (6-5.5 Ma, 5.5-5 Ma...), but shifting the bin start age by 100-kyr increments (6-5.5 Ma, 5.9-5.4 Ma, 5.8-5.3 Ma, 5.7-5.2 Ma, 5.6-5.1 Ma) does not change the overall pattern. **b)** Temporal trend in multisite Simpson

dissimilarity (β_{SIM}) for eastern African mammal species over the last 6 Myr using our main text dataset (PA Matrix v1) and alternate versions of the dataset that with different treatments of open nomenclature; all four presence-absence matrices are included in Supplementary Dataset 1.

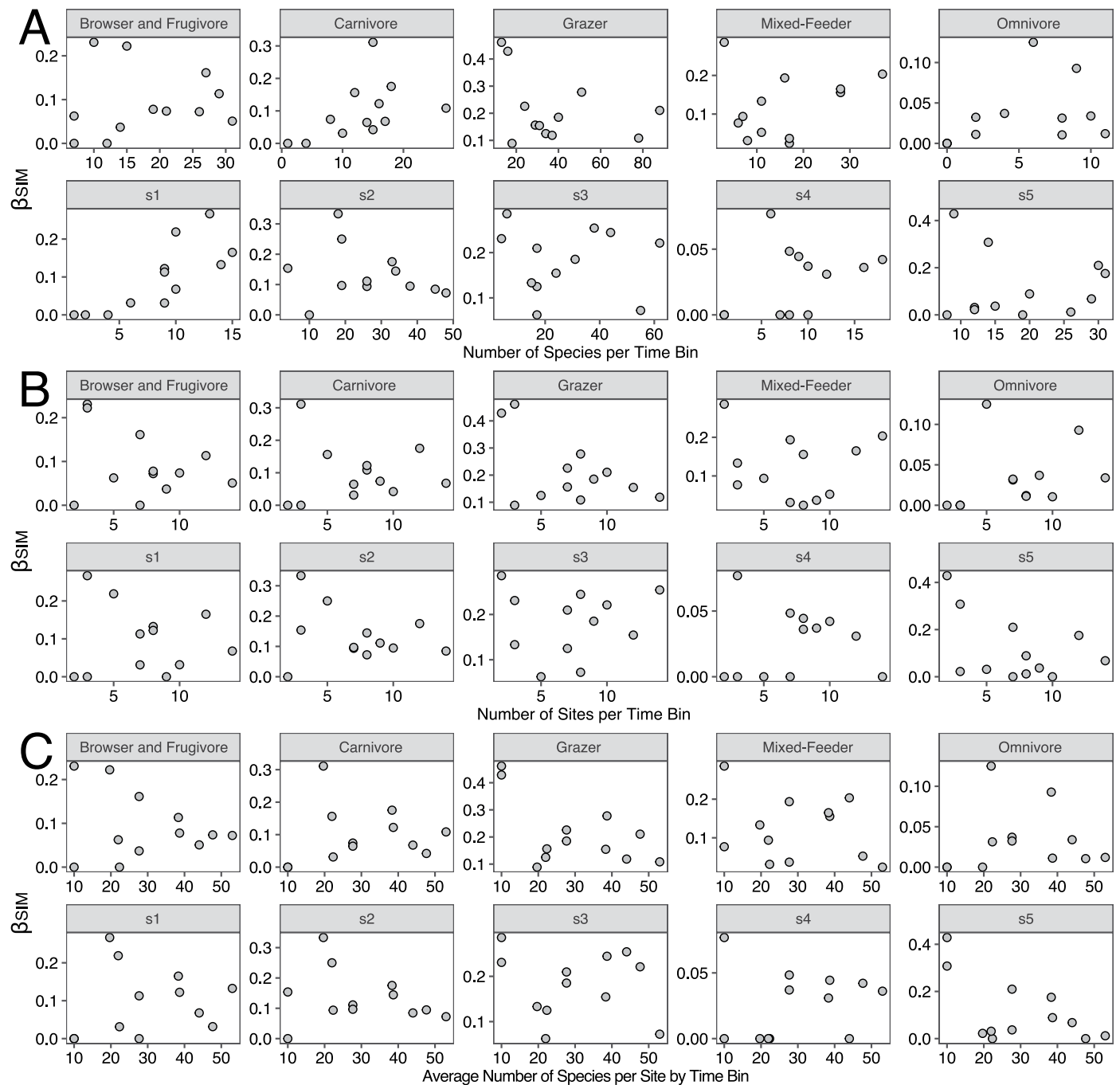


Extended Data Fig. 3 | Raw sampling of the East African Rift System fossil record based on PA Matrix v1. Measures include the number of sites per time bin, number of species per time bin and the average number of species per site by time bin.



Extended Data Fig. 4 | Multisite Simpson dissimilarity (β_{SIM}) in relation to sampling measures. Scatterplots of our multisite Simpson dissimilarity (β_{SIM}) for the overall East African Rift System trend by (a) number of species per time

bin, (b) number of sites per time bin and (c) the average number of species per site by time bin. Correlations were assessed with a linear model using the `lm()` function in R.



Extended Data Fig. 5 | Multisite Simpson dissimilarity (β_{SIM}) in relation to sampling measures by functional group. Scatterplots of our multisite Simpson dissimilarity (β_{SIM}) for each diet and body size class functional group by number of (a) species per time bin, (b) number of sites per time bin and (c) the average

number of species per site by time bin. All correlations, except for number of species for s1 taxa (see SI text) are weak and non-significant (see Supplementary Table 1).

Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

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<i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i> |
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| <input checked="" type="checkbox"/> | <input type="checkbox"/> For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
<i>Give P values as exact values whenever suitable.</i> |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated |

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

- | | |
|-----------------|---|
| Data collection | Custom code was written for some of the analyses and has been uploaded to Zenodo: https://zenodo.org/records/11187857 |
| Data analysis | All data analysis was performed using the R statistical computing language (R v4.3) and the following packages: betapart (v1.6), readxl (v1.4.2), reshape2 (v1.4.4), tidyverse (v2.0). The code and dataset have been uploaded to Zenodo: https://zenodo.org/records/11187857 |

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- A description of any restrictions on data availability
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All data generated or analyzed during this study (presence-absence matrix, functional traits, etc) are provided on Zenodo (<https://zenodo.org/records/11187857>)

Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender	N/A
Reporting on race, ethnicity, or other socially relevant groupings	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Our study made use of a new compilation of eastern African fossil mammal communities dating from 6 Ma to the present-day. We used the multi-site Simpson index to quantify compositional similarity across three major regions of eastern Africa through time, and then partitioned the overall trend by different functional groups (diet groups and body size groups).
Research sample	To our knowledge, our fossil compilation includes all eastern African fossil mammal sites in our three regions of interest (Afar, Turkana Basin, Southern Rift) over the last 6 Ma.
Sampling strategy	Exhaustive: Our fossil compilation includes all eastern African fossil mammal sites in our three regions of interest (Afar, Turkana Basin, Southern Rift) over the last 6 Ma.
Data collection	J. Rowan compiled all data for this project and has curated the dataset as new descriptions of fossil fauna or site ages have been published.
Timing and spatial scale	This dataset has been compiled by one of us (J. Rowan) over the last several years. It spans all fossil sites from three major three regions of interest (Afar, Turkana Basin, Southern Rift) in eastern Africa over the last 6 Ma.
Data exclusions	No data were excluded.
Reproducibility	The entire dataset (both raw and generated values) are provided as a multi-tab Excel file with the supplementary information. The code for all analyses is also included.
Randomization	N/A
Blinding	N/A

Did the study involve field work? Yes No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

- n/a | Involved in the study
- Antibodies
- Eukaryotic cell lines
- Palaeontology and archaeology
- Animals and other organisms
- Clinical data
- Dual use research of concern
- Plants

Methods

- n/a | Involved in the study
- ChIP-seq
- Flow cytometry
- MRI-based neuroimaging

Palaeontology and Archaeology

Specimen provenance

Our compilation of fossil mammal sites primarily comes from previously published reports, though we have studied many of the collections first-hand (they were collected by separate research teams operating under government-issued collection permits).

Specimen deposition

The fossil mammal species lists derive from specimens primarily deposited in the National Museum of Kenya (Nairobi), National Museum of Ethiopia (Addis Ababa), and the National Museum of Tanzania (Dar es Salaam).

Dating methods

No new dates are provided.

Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Ethics oversight

For museum studies in Kenya, NACOSTI (National Commission For Science, Technology & Innovation) and the National Museums of Kenya. For Ethiopia, the ARCCH (Agency for Research and Conservation of Cultural Heritage).

Note that full information on the approval of the study protocol must also be provided in the manuscript.