Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma

Thure E. Cerling[a,b,1], Samuel A. Andanje[c,2], Scott A. Blumenthal[d], Francis H. Brown[a], Kendra L. Chritz[b], John M. Harris[e], John A. Hart[f], Francis M. Kirera[g], Prince Kaleme[h,i], Louise N. Leakey[j,k], Meave G. Leakey[j,k], Naomi E. Levin[l], Fredrick Kyalo Manthi[m], Benjamin H. Passey[l], and Kevin T. Uno[n]

[a]Department of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112; [b]Department of Biology, University of Utah, Salt Lake City, UT 84112; [c]Kenya Wildlife Service, Nairobi, Kenya; [d]Department of Anthropology, City University of New York, New York, NY 10016; [e]Natural History Museum of Los Angeles County, Los Angeles, CA 90007; [f]Lukuru Foundation, Kinshasa, Democratic Republic of Congo; [g]School of Medicine, Ross University, Miramar, FL 33027; [h]Centre de Recherches en Sciences Naturelles, Lwiro, Bukavu, Democratic Republic of Congo; [i]Department of Zoology, University of Johannesburg, Johannesburg, South Africa; [j]Turkana Basin Institute, Nairobi, Kenya; [k]Department of Anthropology, Stony Brook University, Stony Brook, NY 11794; [l]Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD 21218; [m]Department of Earth Science, National Museums of Kenya, Nairobi, Kenya; and [n]Lamont Doherty Earth Observatory, Palisades, NY 10964

A large stable isotope dataset from East and Central Africa from *ca*. 30 regional collection sites that range from forest to grassland shows that most extant East and Central African large herbivore taxa have diets dominated by C_4 grazing or C_3 browsing. Comparison with the fossil record shows that faunal assemblages from *ca*. 4.1–2.35 Ma in the Turkana Basin had a greater diversity of C_3–C_4 mixed feeding taxa than is presently found in modern East and Central African environments. In contrast, the period from 2.35 to 1.0 Ma had more C_4-grazing taxa, especially nonruminant C_4-grazing taxa, than are found in modern environments in East and Central Africa. Many nonbovid C_4 grazers became extinct in Africa, notably the suid *Notochoerus*, the hipparion equid *Eurygnathohippus*, the giraffid *Sivatherium*, and the elephantid *Elephas*. Other important nonruminant C_4-grazing taxa switched to browsing, including suids in the lineage *Kolpochoerus-Hylochoerus* and the elephant *Loxodonta*. Many modern herbivore taxa in Africa have diets that differ significantly from their fossil relatives. Elephants and tragelaphin bovids are two groups often used for paleoecological insight, yet their fossil diets were very different from their modern closest relatives; therefore, their taxonomic presence in a fossil assemblage does not indicate they had a similar ecological function in the past as they do at present. Overall, we find ecological assemblages of C_3-browsing, C_3–C_4-mixed feeding, and C_4-grazing taxa in the Turkana Basin fossil record that are different from any modern ecosystem in East or Central Africa.

carbon isotopes | evolution | diet

The expansion of C_4 biomass beginning in the late Miocene marks a major vegetation change in the history of Earth. Today C_4 plants comprise *ca*. 50% of net primary productivity (NPP) in the tropics (1) yet contributed less than 1% of NPP only 10 million years ago. C_4 plants are primarily grasses and sedges, although C_4 photosynthesis is known to be used in ~20 plant families (2, 3). C_4 photosynthesis is an adaptation to low (*ca*. <500 ppm by volume) concentrations of CO_2 in Earth's atmosphere along with high growing-season temperatures (4). Although genetic evidence indicates an Oligocene origin of C_4 photosynthesis in the grasses (5, 6), macrofossil evidence for C_4 photosynthesis in grasses is extremely sparse (7, 8).

The expansion of C_4 biomass has been documented through stable isotopes in paleosols (9–12), grass phytoliths (13), herbivore tooth enamel (14–16), and biomarkers in deep-sea sediments (17, 18). At 10 Ma in Africa, Asia, and North America, the $\delta^{13}C$ values for equid tooth enamel indicate a diet dominated by C_3 vegetation; by *ca*. 7 Ma, equids in Africa have a diet dominated (>75%) by C_4 vegetation (14, 15). In East Africa today there is a distinct difference in diets of major herbivores, with most mammals either being predominantly browsing (>*ca*. 75% C_3)

or grazing (>*ca*. 75% C_4), and there are relatively few mixed feeders (Fig. 1).

A recent study of the early transition of C_3 to C_4 dietary change in the Turkana Basin from 10 Ma to *ca*. 4 Ma (15) showed that equids were the earliest mammals to fully exploit the C_4 dietary resource, attaining a predominantly C_4-grazing diet by 7 Ma. Other mammal groups (hippopotamids, elephantids, and bovids) changed to a C_4 diet later than did the equids. In this paper we document dietary changes in the major Artiodactyla-Perissodactyla-Proboscidea (APP) taxa in the Turkana Basin between *ca*. 4 Ma and 1 Ma and compare those to dietary preferences of extant APP taxa in East and Central Africa. The Turkana Basin has an excellent stratigraphy (19–22) with excellent preservation of fossils from 4 to 1 Ma; this study focuses on fossils recovered from the Koobi Fora, Kanapoi, and Nachukui Formations of northern Kenya.

We compare dietary changes within the major APP taxa through the past 4 Ma in the formations listed above using >900 individual fossils that represent the major taxa collected within the principal stratigraphic intervals of these formations. Fossil mammalian diets are compared with those of >1,900 extant mammal individuals sampled from >30 different regions and habitats in eastern and central Africa. We compare the ecosystem structure (C_3 browsers, C_3/C_4 mixed diets, and C_4 grazers) through the
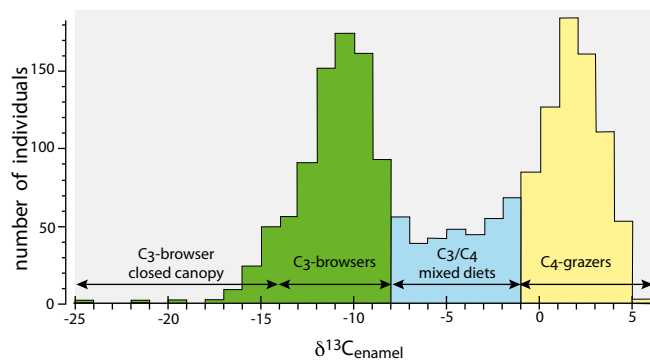
Fig. 1. $\delta^{13}C_{1750}$ values for tooth enamel (or equivalent) for >1,900 mammals from East and Central Africa (principal localities in *SI Appendix*, Table S1; data from Dataset S1).

Pliocene and Pleistocene and document changes in ungulate diets over time.

Results

The distinction between C_3 dicots and C_4 grasses makes stable isotopes a very useful tracer of diet in tropical ecosystems. Although C_4 dicots are known from Africa, they are uncommon in most biomes (23). Likewise, plants using the Crassulacean acid metabolism pathway (mostly succulents) are also uncommon in most African ecosystems and also often have chemical defenses that deter mammalian herbivory. In the discussion below, modern samples for plants and tooth enamel have their respective $\delta^{13}C$ values corrected for the anthropogenic CO_2 and are corrected to preindustrial values (see *SI Appendix, Detailed Methods*) and are reported as $\delta^{13}C_{1750}$. Using data reported in ref. 24, we find the $\delta^{13}C_{1750}$ values for C_3 plants from forest floor in closed canopy (Ituri Forest), mesic (Aberdares, Nairobi region), and xeric (Turkana, Samburu, Laikipia) biomes to be *ca.* −32.6, −26.6, and −25.6‰, respectively. Mesic (panicoids) and xeric (chloridoids and *Aristida*) grasses have $\delta^{13}C_{1750}$ values of −10.0 and −11.2‰, respectively. The isotopic distinction between mesic and xeric vegetation within C_3 and C_4 ecosystems has previously been noted for both C_3 plants (25) and C_4 plants (26, 27).

$\delta^{13}C$ Assignments for C_3 Browsing, Mixed C_3/C_4, and C_4 Grazing.
Diets of African mammals are frequently discussed in terms of C_3-dominated browsing, mixed feeding, and C_4-dominated grazing. In this discussion, a browsing diet is dominated by C_3 biomass (primarily dicots), whereas a grazing diet comprises primarily C_4 biomass (mainly grasses). *SI Appendix*, Table S1 gives geographic, climatic, and ecological information for 30 geographic localities with measured $\delta^{13}C$ on keratin, collagen, or enamel from APP mammals. In each collecting region we analyzed the different APP species to determine the characteristic $\delta^{13}C$ value for individuals in that particular region; thus, each taxon has a region-specific diet. Dataset S1 presents $\delta^{13}C_{1750}$ data for >1,900 individuals from East and Central Africa, distributed across >50 species of large mammals; *SI Appendix*, Table S2 summarizes data for individual species. For comparison between tissues, all values are reported as enamel values using isotope enrichments in *SI Appendix, Detailed Methods*. Analysis of these data using the Akaike Information Criterion indicates that there are multiple modes for these individual $\delta^{13}C_{1750}$ values: A three-component mixture analysis identifies C_3-browsing and C_4-grazing components with modal $\delta^{13}C_{1750}$ values of −10.9 ± 1.6 and 1.7 ± 1.6‰ for C_3-browsing and C_4-grazing taxa, respectively, with mixed feeders having intermediate values. Isotope enrichment values $\varepsilon^*_{enamel-diet}$ are between 13.3 and 14.6‰ for ungulate mammals (24, 28), with the higher values being associated with bovid ruminants; we use 14.1‰ for

all taxa in this paper (*SI Appendix, Detailed Methods*). Using these enrichment values and the xeric- and mesic-mixing lines for C_3 dicots and C_4 grasses, we have adopted a value of −8‰ as the boundary between C_3 browsers (<−8‰) and mixed C_3/C_4 diets (>−8‰ to <−1‰), and a value of −1‰ for the boundary between C_4 grazers (>−1‰) and mixed C_3/C_4 diets. Thus, defined isotopically, "mixed C_3/C_4 diets" have C_3/C_4 diet ratios between *ca.* 75/25 and *ca.* 25/75, given the uncertainties in the mixing lines (*SI Appendix*, Fig. S2).

Most samples used for stable isotope analysis of fossils are identified only to tribe for bovids and genus for other taxa; therefore, in the discussion below we evaluate taxonomic groups at the tribal level for bovids and at the generic level for other taxa using this diet classification (Table 1). We consider normalized proportions of C_4 grazers (G), mixed C_3–C_4 diet generalists (M), and C_3 browsers (B), referred to as G:M:B, using the isotope ranges described above and in *SI Appendix*. For comparison within a taxon in each time interval, we compare the fraction of individuals that are C_4 grazers, mixed C_3–C_4 diet generalists, or C_3 browsers. In contrast, for comparison of taxa with respect to all other taxa within a single ecosystem or a time slice, we use the average $\delta^{13}C$ value to define the predominant mode of feeding: C_4 grazer, mixed C_3–C_4 diet generalist, or C_3 browser.

Table 1. Modern East African large mammal taxon groups (tribe for Bovidae, genus for other taxa) used in this study

Taxon	n	%G	%M	%B
Artiodactyla				
Bovidae				
Aepycerotini	66	15	77	8
Alcelaphini	141	100	0	0
Antilopini	122	11	30	60
Bovini	167	84	13	4
Caprini	1	0	0	100
Cephalophini	63	0	2	98
Hippotragini	38	89	11	0
Neotragini	84	2	11	87
Reduncini	90	93	7	0
Tragelaphini	126	0	15	85
Giraffidae				
Giraffa	61	0	7	93
Okapia	2	0	0	100
Hippopotamidae				
Choeropsis	1	0	0	100
Hippopotamus	186	36	61	4
Suidae				
Hylochoerus	26	0	0	100
Phacochoerus	101	80	18	2
Potamochoerus	46	2	22	76
Tragulidae				
Hyemoschus	1	0	0	100
Perissodactyla				
Equidae				
Equus	157	91	8	1
Rhinocerotidae				
Ceratotherium	13	100	0	0
Diceros	145	0	6	94
Proboscidea				
Elephantidae				
Loxodonta	280	0	19	81

Classified by the percentage of individuals that are C_4 grazers (G), mixed C_3–C_4 feeders (M), or C_3 browsers (B) based on the isotope values ($\delta^{13}C_{1750}$ values >−1‰, >−1‰ and <−8‰, and <−8‰, respectively). See *SI Appendix* for complete data.

Dataset S2 presents $\delta^{13}C$ data for tooth enamel from >900 individual specimens from the Turkana Basin ranging in age from *ca.* 4–1 Ma. The same isotopic ranges are used to distinguish between C_3 browsing, mixed C_3–C_4 diets, and C_4 grazing for both fossil and modern mammals. We assume the $\delta^{13}C$ value of the atmosphere is constant for the Pleistocene and Pliocene and has the same value as the preindustrial atmosphere (see discussion in *SI Appendix, Detailed Methods*).

Diets of Mammalian Lineages in the Pliocene and Pleistocene. The mammalian lineages considered here derive from different members of the Kanapoi, Koobi Fora, and Nachukui Formations and are of comparable age to the Shungura Formation in the lower Omo Valley as shown in Fig. 2; K/Ar and $^{40}Ar/^{39}Ar$ dates from the sequence are derived from all four formations and many volcanic ashes are correlative between the formations. Time intervals used in this study are based on correlative marker horizons between the Koobi Fora and Nachukui Formations, and are as follows from oldest to youngest: >4 Ma, 4.0–3.6 Ma, 3.6–3.4 Ma, 3.4–3.0, 3.0–2.5 Ma, 2.5–2.35 Ma, 2.35–1.9 Ma, 1.9–1.5 Ma, 1.5–1.3 Ma, and 1.3–1.0 Ma.

The APP taxa for modern specimens is discussed using the normalized proportions of C_4 grazing, C_3–C_4 mixed, and C_3 browsing (G:M:B) for each taxon (*SI Appendix*). These results largely confirm previous isotope surveys (29, 30) for modern African bovids, hippos (31, 32), suids (33), and elephants (34) but expand the database severalfold. However, comparison of individual lineages of APP taxa show significant changes over time; a number of taxa had diets in the fossil record that are quite different from those of their modern representatives (e.g., Aepycerotini, Antilopini, Tragelaphini, and *Loxodonta*; *SI Appendix, Figs. S4 and S5*).
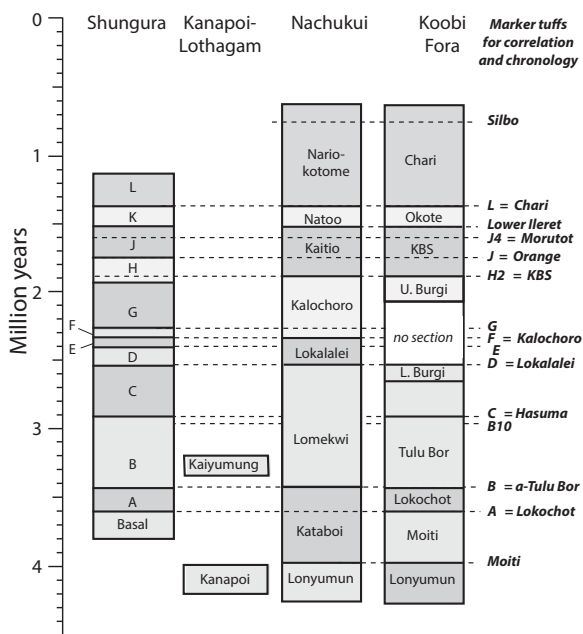

Fig. 2. Stratigraphic relationships in the Turkana Basin for major collecting geographic regions: Shungura, Nachukui, Koobi Fora, and Kanapoi Formations. Dashed lines show some important volcanic ash layers (tuffs) used for correlation between formations; tuff names are in bold. Stratigraphy and correlations based on earlier results (see *SI Appendix, Detailed Methods*).

Discussion

Ecosystem and Dietary Change Through the Past 4 Ma.

Dietary change through time for individual lineages. Many African taxa have diets that remained essentially the same (less than 2‰ change) for much of the past 4 million years (*SI Appendix*, Table S4 and Fig. S4). These include the taxa and lineages that are presently C_4 grazers, Alcelaphini, Bovini, Reduncini, *Ceratotherium* (=Rhino-G), *Metriochoerus-Phacochoerus*, and *Equus*, the C_3–C_4 mixed feeder *Hippopotamus* s. l., and the C_3 browsers Neotragini, *Giraffa*, *Diceros* (=Rhino B), and *Deinotherium*. Of these, it is notable that modern Alcelaphini have $\delta^{13}C_{1750}$ values that are consistently more positive relative to fossil Alcelaphini. Such differences could be due to several factors: a slight diagenetic exchange of ^{13}C resulting in the fossils $\delta^{13}C_{1750}$ values being slightly more negative relative to modern samples, a change in the atmospheric $\delta^{13}C$ value causing a shift in the $\delta^{13}C$ of plants and the derived dietary $\delta^{13}C$ of enamel, an increase in the isotope enrichment (tooth enamel relative to diet) of alcelaphins that occurred in the past million years, or a slight difference in diet whereby many modern alcelaphins are true hypergrazers and the fossil alcelaphins were not. Diagenesis is unlikely to more strongly affect alcelaphins than other taxa, so diagenesis does not explain such differences. Studies of North Atlantic benthic marine carbonates show relatively constant $\delta^{13}C$ values through the past *ca.* 6 Ma (see discussions in refs. 35 and 36), indicating that the $\delta^{13}C$ of the atmosphere was similar through the past 4 Ma. At present, we cannot distinguish between the last two possibilities—a change in the isotope enrichment specific to alcelaphins, or a more C_4-selective diet for alcelaphins than all other taxa—although we favor the latter.

Hippotragin bovids and suids of the *Nyanzachoerus-Notochoerus* lineage changed from a mixed feeding to a grazing diet during the interval represented by this stratigraphic sequence.

Aepycerotini, Antilopini, and Tragelaphini represent three bovid tribes whose diets have recently shifted to more negative $\delta^{13}C$ values, implying that the fossil representatives of these taxa had a higher C_4 component in their diet than their modern relatives (*SI Appendix*, Table S4 and Figs. S4 and S5). Fossil Aepycerotini in the Turkana Basin are enriched in ^{13}C by several per mil compared with modern *Aepyceros*; only specimens from the Mara and adjoining Serengeti have $\delta^{13}C$ values comparable to those of most of the fossil Aepycerotini. Fossil Antilopini in all except the lowest stratigraphic intervals have average $\delta^{13}C$ values between *ca.* −1 and −3‰, indicating a strong C_4 preference, which constrasts with modern antilopins that mostly prefer C_3 browsing. Only the modern antilopin *Eudorcas thomsonii* has values similar to the Turkana Basin fossil Antilopini (*SI Appendix*, Table S2). Thus, the Antilopini have shifted toward browsing since the early to middle Pleistocene. Tragelaphini also have shifted from *ca.* −5‰ in the fossil record to *ca.* −10 to −12‰ in extant tragelaphins. Our survey of 126 modern tragelaphin individuals includes only 7 (i.e., *ca.* 6%) with $\delta^{13}C$ values >−5‰, whereas 16 of 43 of fossil tragelaphins (i.e., *ca.* 37%) have $\delta^{13}C$ values >−5‰. Tragelaphins from the Shungura Formation (Members C–G; from *ca.* 3.0–2.0 Ma) also had high $\delta^{13}C$ values (37) similar to those measured on specimens from the Nachukui and Koobi Fora Formations in the equivalent time interval.

Loxodonta and *Kolpochoerus-Hylochoerus* are lineages that were primarily C_4 grazers from 4 to 1 Ma, but are now C_3 browsers (*SI Appendix*, Table S4 and Fig. S4). Both lineages have gone from average $\delta^{13}C$ values *ca.* −1‰ between 4 and 1 Ma to the modern average $\delta^{13}C_{1750}$ value of *ca.* −10 and −14‰, respectively. Such abrupt diet changes imply significant changes in the roles of these genera in the overall ecosystem, and perhaps a change in the ecosystems themselves.

Four C_4-grazer lineages become extinct in this interval: *Sivatherium*, *Notochoerus*, *Eurygnathohippus*, and *Elephas*

(*SI Appendix*, Table S4 and Fig. S4). *Sivatherium* was a browser at *ca*. 4 Ma and switched to grazing between 2 and 1 Ma, becoming extinct after adapting to a C$_4$-grazing diet. *Notochoerus* was a C$_4$-grazing suid; it became extinct in the basin by 1.6 Ma. *Eurygnathohippus* was a grazing three-toed equid related to hipparions that became extinct in the early Pleistocene. *Elephas*, a C$_4$-grazing elephant, was present in the basin from 4 to 1 Ma ago, but it became extinct in Africa in the middle to late Pleistocene.

Cephalophins, neotragins, *Giraffa*, and the browsing rhino lineage represented by *Diceros* have been dedicated browsers throughout their known history. *Deinotherium* was similarly adapted throughout the 4–1 Ma time interval but became extinct in Africa in the middle Pleistocene; it has the most negative δ^{13}C values of any taxon for all time intervals in the Turkana Basin for which we have analyses (Dataset S2).

Elephants and tragelaphin bovids are two groups often used for paleoecological interpretations, yet their respective fossil diets were very different from those of their modern closest relatives (*SI Appendix*, Table S4 and Figs. S4 and S5); therefore, the taxonomic presence of a lineage does not indicate that the earlier fossil representative of the lineage had an ecological function in the past similar to that of the modern representative. For example, *Loxodonta* is often considered to be a keystone species that strongly affects woody cover; although *Loxodonta* is now predominantly a C$_3$ browser (*SI Appendix*, Table S2), in the late Pliocene and early Pleistocene *Loxodonta* was primarily a C$_4$ grazer (*SI Appendix*, Table S4 and Figs. S4 and S5). Likewise, tragelaphins are commonly assumed to be indicators of forest or woodland (38, 39) because modern tragelaphins are browsers (e.g., see Table 1 and *SI Appendix*, Table S2); the strongly mixed C$_3$–C$_4$ diet of fossil tragelaphins suggests that they should not be considered as indicators of forest or woodland habitat for stratigraphic intervals in the Nachukui and Koobi Fora formations. Thus, the role of tragelephins in any fossil assemblage should be considered using the δ^{13}C of specimens specific to that assemblage.

Ecosystem change through time. This study demonstrates important changes in mammal diets and ecosystem structure through the past 4 million years. Three bovid tribes, the warthog lineage, *Equus*, and grazing rhinos have an essentially unchanged grazing regime through the Omo Group sequence; in contrast, the grazing giraffids, the grazing notochoere suids, grazing three-toed horses, and African representatives of grazing *Elephas* became extinct. The grazing gomphothere, *Anancus*, became extinct early in this record. Two bovid tribes, giraffes, and browsing rhinos remain dedicated browsers; browsing deinotheres became extinct. Three bovid tribes incorporate more C$_3$ browsing in the diets of extant versus early Pleistocene representatives, whereas the formerly C$_4$-grazing *Kolpochoerus* lineage culminates in the C$_3$-browsing *Hylochoerus* and the formerly grazing *Loxodonta* switched to a C$_3$ browsing-dominated diet. Hippos remain opportunistic feeders throughout.

Modern ecosystems in Africa are characterized by having a large mammal fauna with distinctly different mixtures of G:M:B than faunas in the fossil record. Many of the modern ecosystems sampled are considered to be mosaics, including riparian forest with nearby wooded grassland or grasslands. Forest ecosystems (closed canopy forests, coastal and montane forests, and Afro-alpine in *SI Appendix*, Table S1) are dominated by C$_3$ browsers and mixed C$_3$–C$_4$ feeders; pure grassland faunas have >80% C$_4$ grazers, and most of the modern mosaic ecosystems have subequal numbers of C$_4$ grazers and C$_3$ browsers, with a minor number of C$_3$–C$_4$ mixed feeders (Figs. 3A and 4B).

In this discussion we have assumed that C$_3$ grasses are insignificant in the isotopic contribution to the C$_3$ diet resources. If C$_3$ grasses play a role in this story, strong selectivity would have to be in play because some lineages are essentially C$_4$ grazers throughout the sequences (e.g., equids, Rhino-G, and alcelaphins). Although C$_3$
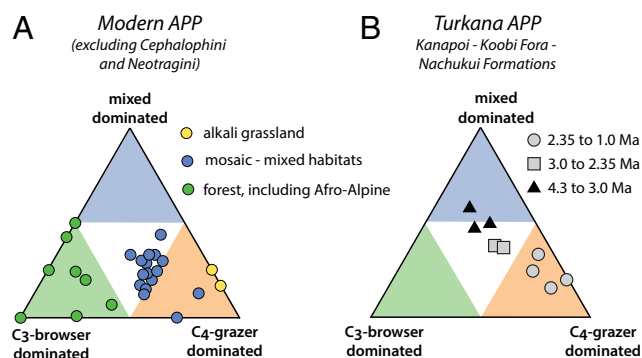

Fig. 3. Ternary diagram showing proportions of C$_3$ browsers, C$_3$–C$_4$ mixed feeders, and C$_4$ grazers from the orders Artiodactyla, Perrisodactyla, and Proboscidea (APP); each taxon in each locality or time interval is represented by the average δ^{13}C for that taxon. Each point in the figure represents the respective proportions of APP taxa that are C$_3$ browsers, C$_3$–C$_4$ mixed feeders, or C$_4$ grazers at one modern locality, or one fossil assemblage from the Turkana Basin of a specific age range. The green, blue, and orange triangles represent regions where >50% of the taxa are C$_3$ browsers, C$_3$–C$_4$ mixed feeders, or C$_4$ grazers, respectively. (A) Modern ecosystems as described in *SI Appendix*, Table S1, using data from Dataset S1; Neotragini and Cephalophini are excluded for comparison with fossil assemblages (see *SI Appendix*, Fig. S3 for comparison with, and without, inclusion of Neotragini and Cephalophini). (B) Fossil assemblages for age ranges discussed in this paper from the Kanapoi, Nachukui, and Koobi Fora Formations; data from Dataset S2.

grasses were possibly present, the selectivity for C$_4$ grasses by some species and for C$_3$ grasses by others must be invoked for such dietary differences.

Using this G:M:B ternary classification, the fossil record in the Turkana Basin shows distinctly different patterns for the early (4.3–3.0 Ma), middle (3.0–2.35 Ma), and later (2.35–1.0 Ma) time intervals compared with the modern ecosystems. Before *ca*. 2.35 Ma, the ecosystems had much higher percentages of C$_3$–C$_4$ mixed feeders than are found today in East and Central Africa, with all intervals having >40% C$_3$–C$_4$ mixed feeders. For comparison, only a few of the 30 modern ecosystems has such a high percentage of C$_3$–C$_4$ mixed feeders; those few are associated with forest or Afroalpine montane ecosystems with few large mammalian herbivores (e.g., Bale and Mt Kenya). Fig. 3B shows the G:M:B ternary for the individual stratigraphic collection intervals in each of the Kanapoi, Koobi Fora, and Nachukui formations. After *ca*. 2.2 Ma there was an abrupt change to many more grazing taxa and overall a higher fraction of grazers than are found most of the modern ecosystems studied for comparison (Figs. 3B and 4).

The number of nonruminant grazers after 2.35 Ma is particularly striking, with between five and nine C$_4$ grazers—in addition to grazing bovids—in these intervals. At the generic taxonomic level with which these comparisons are made, there are only three modern nonruminant C$_4$ grazers in East and Central Africa: *Phacochoerus*, *Equus*, and *Ceratotherium*, although *Hippopotamus* is locally a grazer in some regions (e.g., Turkana, Nakuru). Many of the nonbovid C$_4$-grazing fossil taxa are extinct (*Sivatherium*, *Notochoerus*, *Eurygnathohippus*, and *Elephas*) or have switched to browsing (the *Kolpochoerus-Hylochoerus* lineage and *Loxodonta*). The time interval from 2 to 1 Ma is noteworthy for the number of nonruminant grazers that are not part of the modern fauna.

Thus, there are several important ecological changes in the Turkana Basin over time: The earlier time interval (*ca*. 4.1–2.35 Ma) was dominated by C$_3$–C$_4$ mixed feeders, whereas the time interval from *ca*. 2.35–1.0 Ma was dominated by bovid and nonruminant C$_4$ grazers (Fig. 4A). The timing of this shift in herbivore diet is consistent with previous studies that rely on taxonomic and morphological indicators (38, 39); however, the previously presumed diets are not always consistent with the isotope
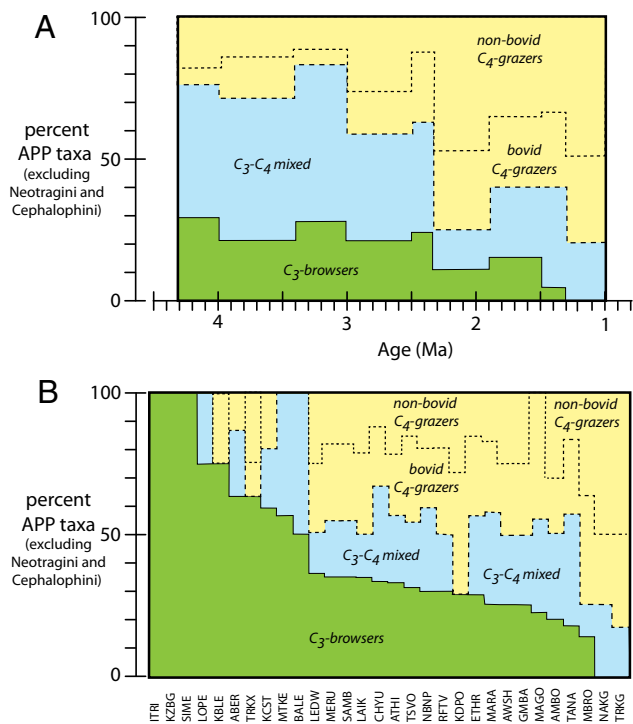
Fig. 4. Trends over time for percentages of C₃ browsers, C₃–C₄ mixed feeders, bovid C₄ grazers, and nonbovid C₄ grazers in the Kanapoi, Nachukui, and Koobi Fora Formations and modern ecosystems in East and Central Afria for APP taxa (excluding Neotragini and Cephalophini because of their rarity in the fossil assemblages). (*A*) Fossil assemblages from Kanapoi, Koobi Fora, and Nachukui Formations; time intervals as described in text (data from Dataset S2). (*B*) Modern ecosystems studied (see *SI Appendix*, Table S1; data from Dataset S1).

data. Modern analog collections from East and Central Africa do not represent ecosystems dominated by C₃–C₄ mixed feeders or nonruminant grazers (compare with Fig. 4*B*). After 1.0 Ma, there was a drastic transformation to the modern Africa dietary distribution, so that most nonruminant C₄ grazers either became extinct or changed their diets to browsing. The timing of the Pleistocene diet changes since 1.0 Ma is uncertain and will come into focus as samples are analyzed from this and other basins (40, 41).

The paleosol record in the Turkana Basin (11, 12, 42) shows a decrease in woody cover with an increase in C₄ biomass from 4 to 1 Ma, but changing from grassy woodland to wooded grasslands; no paleosols indicate open C₄ grasslands. Comparisons between the dietary categories and paleosol ecological reconstructions for the Shungura Formations and the Koobi Fora–Nachukui Formations will be illuminating: From 4 to 1 Ma the Shungura Formation was more wooded than the Koobi Fora and Nachukui formations.

Summary Statement. This study of the history of ecological change in the Kanapoi, Nachukui, and Koobi Fora Formations shows profound changes in ecosystem structure: For the period from 4.3 to 2.5 Ma, large mammal herbivorous taxa were dominated by C₃–C₄ mixed feeders. No modern dietary analog to this is found in East or Central Africa. From 2.5 to 1.0 Ma, grazing taxa, especially nonbovid grazers, became increasingly abundant; modern environments in East and Central Africa do not have such a high fraction of the nonbovid grazers. Many of the C₄ grazing nonbovid herbivores became extinct between 2 and 0 Ma; in addition, some taxa that previously were C₄ grazers or C₃–C₄ mixed feeders changed their diet to C₃ browsing. More APP taxa were present in the basin for many of the stratigraphic intervals than exist in any modern equivalent environment (e.g., compare totals for *SI Appendix,*

Tables S3 and S4); nowhere today in East or Central Africa is such taxonomic diversity found for the APP taxa as was found in the Turkana Basin from 4.3 to 1.0 Ma.

Interaction between the different large mammal herbivore taxa likely plays a role in diet change. In modern African ecosystems megaherbivores (>1,000 kg), particularly elephants and hippopotamus, maintain the structure and function of both wooded and grassy biomes (43, 44) and play a key role in determining the availability of food for mesoherbivores (4–450 kg; ref. 45). Therefore, changes in the diet of large herbivores throughout the 4–1 Ma time interval indicate significant alterations to mammalian dietary ecological structure and competitive interactions and may relate to shifts in vegetation structure. Ecological interactions with carnivores and primates, including hominins, may also be important for understanding the evolution of herbivore diets (46–48).

The interplay of grass expansion in the time period from 10 Ma to the present will be critical in understanding dietary changes that have occurred in the large mammal taxa in Africa. Although NPP of C₄ grasses in the tropics has gone from *ca.* 1% at 10 Ma to *ca.* 50% today, there are no known C₄-grass macrofossils (i.e., fossils exhibiting Kranz anatomy, fossil plants with $\delta^{13}C$ values indicating C₄ photosynthesis, or both) from Africa between 1 and 10 Ma. Which specific C₄ grasses were predominant, or even present, in the Pleistocene or Pliocene of Africa (or elsewhere) is not known; such information will be key toward understanding the development of tropical grasslands and in understanding how fauna used the C₄-grass dietary resources. Changes in digestibility, toxin level, palatability, nutrient distribution in space and in time, and relative abundances of the different C₄ grasses likely all played an important role in the evolution of the mammalian diet in Africa. These factors may be important in understanding how different APP herbivores competed for dietary resources. It is well known that C₄ photosynthesis is favored by low atmospheric CO_2 concentrations (i.e., less than 500 ppm by volume; refs. 4 and 14); the interval from 4 Ma to the present was continually below this CO_2 threshold (49–51). With each oscillation of CO_2 in the atmosphere, tropical ecosystems are subjected to stresses that could have cumulative effects on ecosystem structure with respect to the comparative success of C₃ and C₄ lineages. The role of climate change, including changes in atmospheric CO_2, will be better evaluated when details of extinctions and diet change are better known. These records are needed to evaluate the relationships between behavioral, morphological, and environmental change, which may not be synchronous (52).

This study of the dietary history of herbivores in the Turkana Basin shows that modern animals often have diets different from those of their closest fossil relatives. Likewise, for much of the past 4 million years, the large herbivorous fauna used dietary resources in different ways than do their modern analogs.

Methods

Modern samples of APP taxa from East and Central Africa, and fossil samples from the well-dated Turkana Basin in northern Kenya, were analyzed for $\delta^{13}C$ using standard methods (*SI Appendix, Detailed Methods*).

Ecological comparisons for modern taxa were made based on regional ecological grouping in restricted geographic areas, such as are presented in national parks or reserves (*SI Appendix*, Table S1). We used the classification of White (53) for discussion of African vegetation (*SI Appendix, Classification of African Vegetation*).

Fossil samples were grouped by stratigraphic age, using stratigraphic boundaries that are correlated between the Koobi Fora, Nachukui, Kanapoi, and Shungura Formations (Fig. 2).

1. Lloyd J, et al. (2008) Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: A quasi-global estimate. *Tree Physiol* 28(3):451–468.
2. Sage RF, Li M, Monson RK (1999) The taxonomic distribution of C_4 photosynthesis. *C_4 Plant Biology*, eds Sage RF, Monson RK (Academic, New York), pp 551–584.
3. Sage RF, Christin PA, Edwards EJ (2011) The C_4 plant lineages of planet Earth. *J Exp Bot* 62(9):3155–3169.
4. Ehleringer JR, Cerling TE, Helliker B (1997) C_4 photosynthesis, atmospheric CO_2, and climate. *Oecologia* 112:285–299.
5. Christin PA, et al. (2008) Oligocene CO_2 decline promoted C_4 photosynthesis in grasses. *Curr Biol* 18(1):37–43.
6. Vicentini A, Barber JC, Aliscioni SS, Giussani LM, Kellogg EA (2008) The age of the grasses and clusters of origins of C_4 photosynthesis. *Glob Change Biol* 14(12):2963–2977.
7. Tidwell WD, Nambudiri EMV (1989) *Tomlisonia thomassonii*, gen. et sp. nov., a permineralized grass from the upper Miocene Ricardo Formation, California. *Rev Palaeobot Palynol* 60(1):165–177.
8. Thomasson JR, Nelson ME, Zakrzewski RJ (1986) A fossil grass (gramineae: chloridoideae) from the miocene with kranz anatomy. *Science* 233(4766):876–878.
9. Quade J, Cerling TE, Bowman JR (1989) Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature* 342:163–166.
10. Fox DL, Koch PL (2003) Tertiary history of C_4 biomass in the Great Plains, USA. *Geology* 31(9):809–812.
11. Cerling TE (1992) Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeogr Palaeoclimatol Palaeoecol* 5:241–247.
12. Levin NE, Brown FH, Behrensmeyer AK, Bobe R, Cerling TE (2011) Paleosol carbonates from the Omo Group: Isotopic records of local and regional environmental change in East Africa. *Palaeogeogr Palaeoclimatol Palaeoecol* 307:75–89.
13. Strömberg CAE, McInerney FA (2011) The Neogene transition from C_3 to C_4 grasslands in North America: assemblage analysis of fossil phytoliths. *Paleobiology* 37:50–71.
14. Cerling TE, et al. (1997) Global change through the Miocene/Pliocene boundary. *Nature* 389:153–158.
15. Uno KT, et al. (2011) Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proc Natl Acad Sci USA* 108(16):6509–6514.
16. Kita ZA, Secord R, Boardman GS (2014) A new stable isotope record of Neogene paleoenvironments and mammalian paleoecologies in the western Great Plains during the expansion of C_4 grasslands. *Palaeogeogr Palaeoclimatol Palaeoecol* 399:160–172.
17. Feakins SJ, deMenocal PB, Eglinton TI (2005) Biomarker records of late Neogene changes in northeast African vegetation. *Geology* 33(12):977–980.
18. Feakins SJ, et al. (2013) Northeast African vegetation change over 12 my. *Geology* 41(3):295–298.
19. Cerling TE, Brown FH (1982) Tuffaceous marker horizons in the Koobi Fora region and the lower Omo Valley. *Nature* 299:216–221.
20. McDougall I, Brown FH (2006) Precise $^{40}Ar/^{39}Ar$ geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. *J Geol Soc London* 163:205–220.
21. McDougall I, Brown FH (2008) Geochronology of the pre-KBS Tuff sequence, Omo Group, Turkana Basin. *J Geol Soc London* 165:549–562.
22. McDougall I, et al. (2012) New single crystal $^{40}Ar/^{39}Ar$ ages improve timescale for deposition of the Omo Group, Omo-Turkana Basin, East Africa. *J Geol Soc London* 169:213–226.
23. Sage RF, Wedin DA, Li M (1999) The biogeography of C_4 photosynthesis: patterns and controlling factors. *C_4 Plant Biology*, eds Sage RF, Monson RK (Academic, New York), pp 313–373.
24. Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120:347–363.
25. Ehleringer JR, Cooper TA (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76:562–566.
26. Hattersley PW (1982) ^{13}C values of C_4 types in grasses. *Aust J Plant Physiol* 9:139–154.
27. Buchmann N, Brooks JR, Rapp KD, Ehleringer JR (1996) Carbon isotope composition of C_4 grasses is influenced by light and water supply. *Plant Cell Environ* 9:392–402.
28. Passey BH, et al. (2005) Carbon isotopic fractionation between diet, breath, and bioapatite in different mammals. *J Archaeol Sci* 32:1459–1470.
29. Cerling TE, Harris JM, Passey BH (2003) Dietary preferences of East African Bovidae based on stable isotope analysis. *J Mammal* 84:456–471.
30. Sponheimer M, et al. (2003) Diets of southern African Bovidae: Stable isotope evidence. *J Mammal* 84:471–479.
31. Boisserie JT, et al. (2005) Diets of modern and late Miocene hippopotamids: Evidence from carbon isotope composition and microwear of tooth enamel. *Palaeogeogr Palaeoclimatol Palaeoecol* 221:153–174.
32. Cerling TE, et al. (2008) Stable isotope ecology of modern *Hippopotamus amphibius* in East Africa. *J Zool (Lond)* 276:204–212.
33. Harris JM, Cerling TE (2002) Dietary adaptations of extant and Neogene African suids. *J Zool (Lond)* 256:45–54.
34. Cerling TE, Harris JM, Leakey MG (1999) Browsing and grazing in modern and fossil proboscideans. *Oecologia* 120:364–374.
35. Cerling TE, Harris JM, Leakey MG, Passey BH, Levin NE (2010) Stable carbon and oxygen isotopes in East African mammals: Modern and fossil. *Cenozoic Mammals of Africa*, eds Werdelin L, Sanders W (Univ of California Press, Oakland, CA), pp 949–960.
36. Tipple BJ, Meyers SR, Pagani M (2010) Carbon isotope ratio of Cenozoic CO_2: A comparative evaluation of available geochemical proxies. *Paleoceanography* 25.3, 10.1029/2009PA001851.
37. Bibi F, Souron A, Bocherens H, Uno K, Boisserie JR (2013) Ecological change in the lower Omo Valley around 2.8 Ma. *Biol Lett* 9(1):20120890.
38. Reed KE (1997) Early hominid evolution and ecological change through the African Plio-Pleistocene. *J Hum Evol* 32(2-3):289–322.
39. Bobe R, Behrensmeyer AK (2004) The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeogr Palaeoclimatol Palaeoecol* 207(3–4):399–420.
40. Chritz KL, Marshall F, Zagal ME, Kirera F, Cerling TE (2015) Environments and livestock disease risk of early herders in the later Holocene of the Lake Victoria Basin, Kenya. *Proc Natl Acad Sci USA* 112(12):3674–3679.
41. Garrett ND, et al. (2014) Stable isotope paleoecology of Late Pleistocene Middle Stone Age humans from the Lake Vicoria basin, Kenya. *J Hum Evol* 82:1–14.
42. Cerling TE, et al. (2011) Woody cover and hominin environments in the past 6 million years. *Nature* 476(7358):51–56.
43. Laws RM (1970) Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21:1–15.
44. Owen-Smith RN (1992) *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge Univ Press, Cambridge, UK).
45. Fritz H, Duncan P, Gordon IJ, Illius AW (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* 131:620–625.
46. Lewis ME (1997) Carnivoran paleoguilds of Africa: Implications for hominid food procurement strategies. *J Hum Evol* 32(2-3):257–288.
47. Cerling TE, et al. (2011) Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc Natl Acad Sci USA* 108(23):9337–9341.
48. Cerling TE, et al. (2013) Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proc Natl Acad Sci USA* 110(26):10501–10506.
49. Bartoli G, Hönisch B, Zeebe RE (2011) Atmospheric CO_2 decline during the Pliocene intensification of Northern Hemisphere glaciations. *Paleoceanography* 26(4), 10.1029/2010PA002055.
50. Zhang YG, Pagani M, Liu Z, Bohaty SM, Deconto R (2013) A 40-million-year history of atmospheric CO_2. *Philos Trans A Math Phys Eng Sci* 371(2001):20130096.
51. Martínez-Botí MA, et al. (2015) Plio-Pleistocene climate sensitivity evaluated using high-resolution CO_2 records. *Nature* 518(7537):49–54.
52. Lister AM (2013) The role of behaviour in adaptive morphological evolution of African proboscideans. *Nature* 500(7462):331–334.
53. White F (1983) *The Vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*. Natural Resources Research Report XX (UNESCO, Paris).

APPENDIX I. SUPPLEMENTARY INFORMATION.

Index:

1. Detail Methods. Modern herbivore mammal samples were collected from 30 national parks and reserves and other regions in Kenya, Ethiopia, Uganda, Gabon, and the Democratic Republic of Congo (Table S1); these modern samples were supplemented with museum collections (University of Addis Ababa, American Museum of National History, Lwiro-CRSN, Field Museum, National Museums of Kenya) and using published values. The habitat localities included a range of biomes from desert shrublands to closed forests (Table S1). We use the classification of White (53) for discussion of African vegetation (Appendix, Section 2).

Fossils from the Turkana Basin from 4.3 to 1.0 Ma in age were sampled from the collections of the National Museums of Kenya. Bovids were identified to tribe; most other samples were identifiable to genus. We note in Dataset II when our taxonomic or stratigraphic assignments differ from the NMK catalog (*ca*. 20 of >900 specimens). For discussion of diets through geological time, we use taxonomic classification to tribe for the Bovidae, and to genus for all other large mammal families. Groupings were made by time-intervals, using the established correlations, stratigraphic nomenclature, and geochronologies of the Koobi Fora Formation, the Nachukui Formation, Kanapoi, and Shungura Formations (2-16). See Figure 2 for stratigraphic relationships.

$^{13}C/^{12}C$ ratios of hair, collagen, and tooth enamel were analyzed using standard methods (i.e, combustion in O_2 for organic material; reaction with H_3PO_4 for tooth enamel). Stable carbon isotopes were measured on hair or collagen samples on an isotope ratio mass spectrometer operating in continuous-flow mode after combustion at 1,600 °C in an elemental analyzer. Most bioapatites were pretreated using standard methods (3%

H_2O_2 followed by 0.1 M buffered acetic acid) and then were reacted with 100% H_3PO_4 with the resulting CO_2 being analyzed on a dual-inlet isotope ratio mass spectrometer; ivory samples were treated as in (17). Some fossil samples were too small for pre-treatment due to sampling restrictions: such small samples were corrected by comparison with samples run with and without treatment: the correction was 0.4‰ or less for these samples (see discussion in SI). Results are reported in the standard per mil (‰) notation:

$$\delta^{13}C = (R_{sample}/R_{standard}-1) * 1000$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the sample and standard, respectively. The isotope standard is Vienna Pee Dee Belemnite (VPDB).

Bioapatite was assumed to be 11.1‰ enriched relative to hair, and 8.5‰ enriched relative to collagen as determined earlier (18, 19). $\delta^{13}C$ values of modern hair, collagen, and bioapatite were corrected to a common reference time near the beginning of the Industrial Revolution, considered to be 1750, using atmospheric $\delta^{13}C$ data for the change in isotopic ratio of atmosphere due to human activities (20, 21); the $\delta^{13}C_{1750}$ value for atmospheric CO_2 is taken to be -6.3‰. $\delta^{13}C$ of deep-sea carbonates shows that the $\delta^{13}C$ of the atmosphere, and therefore the end-members for C_3 and C_4 plants, is essentially constant back to *ca.* 6 Ma (35, 36). Plant data from Cerling and Harris (18) were used to estimate mixing lines for C_3- and C_4-plants, corrected to $\delta^{13}C_{1750}$. All analyses from a single individual for both fossils and modern mammals were averaged to give a single isotopic ratio for that individual.

Due to small sample size, some fossil samples were not treated prior to analysis. We compared the results for treated and untreated samples for >200 samples; the average difference was *ca.* 0.4‰ (see Figure S1). We corrected untreated samples using the relationship

$$\delta^{13}C_{corrected} = 1.13 \, \delta^{13}C_{untreated} + 0.64$$

Reported results are for the corrected $\delta^{13}C$ values.

2. Classification of African vegetation. Various schemes have been used to classify African vegetation (1, 22). Woody cover is readily quantified using a variety of methods, and so we adopt a vegetation classification system that is based primarily on woody cover (the United Nations Educational, Scientific, and Cultural Organization (UNESCO) classification of African vegetation; Ref 1). The principal vegetation types include forest, woodlands and grasslands, with some areas being mixed on the landscape scale (e.g., riparian woodlands associated with open woodlands or open grasslands). Forests have a continuous stand of trees at least 10-m tall with interlocking crowns; Woodland: an open-stand of trees at least 8-m tall with woody cover > 40% and a field layer dominated by grasses; Bushland: an open-stand of bushes usually between 3- and 8-m tall with woody cover > 40%; Thicket: a closed-stand of bushes and climbers usually between 3- and 8-m tall; Shrubland: an open- or closed-stand of shrubs up to 2-m tall; Wooded grassland: land covered with grasses and other herbs, with woody cover between 10 and 40%; Grassland: land covered with grasses and other herbs, with woody cover < 10%; Desert: Arid landscapes with a sparse cover dominated by sandy, stony or rocky substrate. This

classification does not define a boundary between forest and woodland in terms of woody cover, we will consider that "forest" has > 80% woody cover based on the requirement for "interlocking crown canopies". Within this structure, the scale at which fossil collections are made in both space (often 10s of km^2) and time (often 10^2 to 10^5 years) the mixing of habitats occurs: we consider mixed habitats as having elements both of forest (especially riparian forests or woodlands) with more open wooded grasslands or grasslands (i.e., savanna).

Woody cover in modern ecosystems can be quantified from ground observations and from satellite photography with results usually giving very close estimates (e.g., Ref 23). Here we make no distinction between woodland (woody cover > 8 m tall), bushland (woody cover 3 to 8 m tall) and shrubland (woody cover < 3 m tall) and use "woodland" synomously for all three vegetation structure classes. It is useful therefore, to further subdivide the classification above as follows: 0 to 10% woody cover: *grassland*; 10 to 20 percent woody cover: *open woody grassland*; 20 to 40 percent woody cover: *wooded grassland*; 40 to 60 percent woody cover: *open grassy woodland*; 60 to 80 percent woody cover: *woodland*; 80 to 100 % woody cover: *forest*.

In the text, we minimize use of the term "savanna", which suffers from colloquial misuse and, for that reason, is not recognized in the UNESCO classification. Still, a modern ecological definition of the term "savanna" is comprehensive and includes structural, functional and evolutionary aspects. Structurally, a savanna is a "mixed tree-grass systems characterized by a discontinuous tree canopy in a conspicuous grass layer" (24). This, and other common usage of the term would include at least "wooded grasslands" and "grasslands" in the UNESCO structural categories described above, although woody cover varies significantly within the savannas (25, 26). Rainfall is widely recognized as the primary determinant of woody cover along with tolerance to fire, herbivory, and soil fertility (26-28).

3. Principal biome collection areas for modern mammals. We collected the major large mammal extant taxa from 30 different regions in Eastern and Central Africa; collection regions, climate and ecological information is given in Table S1. Museum collections supplemented the collections we were able to make by visiting these localities. Collections were principally from National Parks (NP) and National Reserves (NR). Broader geographic regions were included as follows:

ABER Aberdares. Collections were from the park Headquarters (HQ) and local ranger stations; additional samples were collected by Kenya Wildlife Service (KWS) personnel. Museum samples included samples collected from forests north of Nairobi on the southern flanks of the Aberdares, but regions which are now outside the park boundaries.

AMBO Amboseli. Samples were from Koch (29) and Bocherens (30), with additional samples collected by KWS personnel.

ATHI Athi plains. Samples were from regions outside of the nearby Nairobi National Park. Samples were from game ranches and from museum collections.

AWSH Awash. Samples were from the Awash National Park HQ and samples collected within the park, with additional specimens from the larger Awash NP region from museum collections.

BALE Bale Mtns. Samples were from Bale NP and also from museum collections from nearby mountain regions of Ethiopia (south and east of Addis Ababa, elevation > 2500 m).

CHYU Chyulu Hills. Samples are from the Chyulu Hills NP; collections made by KWS personnel.

ETHR Ethiopian Rift lakes. Samples were from Rift Lake region of Ethiopia, including Nechisar NP.

GMBA Garamba. Samples are from Garamba NP in DR Congo.

ITRI Ituri Forest. Samples are from the Ituri NP in DR Congo.

KBLE Kibale National Park. Samples from Kibale NP; also includes data of Nelson (31).

KCST Kenya Coast. Samples are from the Boni NR and Arabuko-Sokoki NP, supplemented with museum samples collected from the coastal regions; also includes samples collected by KWS in the Tana delta region.

KDPO Kidepo. Samples from Kidepo NP.

KZBG Kuhuzi-Biega. Samples are from the mountain sector of Kahuzi-Biega NP and from forested mountains near Lake Kivu. "L" and "LP" samples are from the museum at CNRS-Lwiro.

LAIK Laikipia. Samples are from the Laikipia plateau region of Kenya.

LEDW Lake Edward. Samples are from Queen Elizabeth Park in Uganda, and the Ishango and Lulimbi regions of Virunga Park of DR Congo, all bordering Lake Edward.

LOPÉ. Samples were collected over 20 year period in Lopé National Park (data from Ref 32).

MAGO Omo / Mago. Samples are from the lower Omo Valley, principally from park headquarters region.

MARA Masai Mara. Samples are from the Serengeti plains, principally the Masai Mara region in Kenya with samples collected by KWS, but also including published samples in Tanzania (33, 34). Also includes museum specimens.

MBRO. Samples from Lake Mburo NP.

MERU. Samples from Meru NP, Bisandi NR, Kora NP and nearby regions.

MTKE Mt Kenya. Samples are from the Mt Kenya forests, including museum specimens.

NAKG Nakuru - shore. Samples are from the alkali grasslands in Nakuru NP.

NBNP Nairobi NP. Samples are from Nairobi National Park, including the grasslands, the woodland - grassland transition, and the riparian corridors.

RFTV Kenya Rift Valley. Samples are from the plains region from Lake Naivasha to Nakuru. This is principally wooded grasslands and grasslands; includes riparian woodlands and bushlands. Includes data from Ambrose and DeNiro (35).

SAMB Samburu NR. Samples were principally from Samburu and Buffalo Springs NRs, supplemented by museum samples collected before NR boundaries were established.

SIME Simien Mtns. Samples are from the Simien Mountains NP.

TANA lower Tana River. Samples are from the plains of the lower Tana River, between Garissa and Garsen; samples do not include the Tana River delta region, which are grouped in KCST.

TRKG Turkana - grassland. Samples were from the alkali grasslands on the eastern shore of Lake Turkana; from near Koobi Fora to Ileret. Includes data from (36).

TRKX Turkana - regional. Samples were from the inland parts of the Turkana region, principally on the east side of Lake Turkana, but not including the alkali grasslands immediately adjacent to the lake. Also includes a few specimens on the west side of Lake Turkana. Includes data from (36).

TSVO Tsavo NP. Samples were from both Tsavo East NP and Tsavo West NP and the greater region. Includes data from (37).

4. Mixing lines and $\delta^{13}C$ assignments for C_3-browsing, mixed C_3/C_4, and C_4-grazing.

Mixing lines for different estimating the fraction of C_3- and C_4-biomass contributions to herbivores are considered in the context of the range of $\delta^{13}C$ plants found in African ecosystems, and on the range of isotope enrichment factors which are likely related to digestive physiology (38). Figure S2 shows the mixing lines derived using $\delta^{13}C_{1750}$ values from modern African vegetation as discussed in the text, and the resulting mixing lines accounting for differences in isotope enrichment factors for enamel derived from diets of C_3 and C_4 biomass. The isotope mixing equation for biomass is:

$$\delta^{13}C_{i,mix} = f_{i,C3}\,\delta^{13}C_{i,C3}\ +\ f_{i,C4}\,\delta^{13}C_{i,C4}$$

Where $_{i,mix}$ is the mixture for xeric ($i = x$) ecosystems or mesic ($i = m$) ecosystems, respectively; $f_{i,C3}$ is the fractional contribution of C_3 biomass to the xeric ecosystem or mesic ecosystem, respectively; $f_{i,C4}$ is the fractional contribution of C_4 biomass to the xeric ecosystem or mesic ecosystem, respectively; $\delta^{13}C_{i,C3}$ is $\delta^{13}C_{1750}$ value of C_3 biomass end-member for the xeric ecosystem or mesic ecosystem, respectively; $\delta^{13}C_{i,C4}$ is $\delta^{13}C_{1750}$ value of C_4 biomass end-member for the xeric ecosystem or mesic ecosystem, respectively. End-member $\delta^{13}C_{1750}$ values for C_3 and C_4 plants are taken to be -25.6‰ and -11.2‰, respectively for xeric ecosystems; end-member $\delta^{13}C_{1750}$ values are -26.6‰ and -10.0‰, respectively, for mesic ecosystems (see text). The mixing line for tooth enamel is 13.3 to 14.6‰ enriched relative diet (38). Therefore, the thickness of the

mixing line for tooth enamel – and the projected fractions of C_3- and C_4-contributions to diet – results from the uncertainty in the end-member values for C_3- and C_4-dietary end-members and the isotope enrichment values.

To discuss dietary categories, it is necessary to define some terms. The isotope difference between C_3- and C_4-vegetation makes the grazing-browsing continuum easier to quantify. Because tropical grasses (below *ca*. 2500 m elevation) are almost exclusively C_4, we define C_4-grazers as having a predominantly C_4-diet. *Hypergrazers* have a diet indistinguishable from 100% C_4-diet; in Figure S2 this corresponds to tooth enamel values have $\delta^{13}C_{1750} > + 2‰$. C_3-dominated diets are considered to be browsers; note that this means that C_3 forbs contribute to the C_3-browse diet as well as do the C_3-woody plants. *Hyperbrowsers* have a diet indistinguishable from 100% C_3-diet; in Figure S2 this corresponds to a $\delta^{13}C_{1750}$ values $<-12‰$. In closed canopy forests, the understory can be very depleted in ^{13}C; a hyperbrowser with $\delta^{13}C_{1750} < -14‰$ is likely to be a *closed canopy C_3-browser*. The continuum of diets between the hypergrazers and hyperbrowsers is arbitrarily divided into C_3-browsers, mixed C_3-C_4 feeders, and C_4-browsers. For convenience we define *C_3-browsers* to have a C_3-dominated diet (> *ca*. 75% C_3) and *C_4-grazers* to have diets dominated by C_4 biomass (> *ca*. 75% C_4). Those with intermediate diets are called *C_3-C_4 mixed feeders*. For this paper, this gives the following ranges for the stable isotope dietary classification as derived from Figure S2:

$\delta^{13}C_{1750} > 2‰$: C_4-hypergrazers

$\delta^{13}C_{1750} > -1‰$: C_4-grazers

$\delta^{13}C_{1750} > -1‰$ and $< -8‰$: C_3-C_4 mixed feeders

$\delta^{13}C_{1750} < -8‰$: C_3-browsers

$\delta^{13}C_{1750} < -12‰$: C_3-hyperbrowsers

$\delta^{13}C_{1750} < -14‰$: C_3-closed canopy browsers

We note that the isotope enrichment factor may vary by $>1‰$ in the mammals considered in this paper, and that some minor differences in the $\delta^{13}C_{1750}$ values for enamel when comparing different taxa (e.g., suids to bovids) could arise from this difference. Evaluation of these enrichment factors could play a role in the future understanding the paleo-physiologies of digestion of the fossil mammal taxa. Given this uncertainty, we expect that the $\delta^{13}C_{1750}$ ranges used here may be changed in the future to recognize such physiological differences for certain taxa.

Table S2 shows the average $\delta^{13}C_{1750}$ values for the individual species analyzed in this study. Table S3 shows the distribution of C_4-grazers, mixed C_3-C_4 feeders, and C_3-browsers in each of the modern ecosystems considered in this study. Table S4 shows the average $\delta^{13}C$ values (tribe or genus) for modern and fossil time intervals for East and Central African large herbivore taxa (tribe/genus), summarized from Datasets I and II. Figures S4 and S5 show the trend over time for the diets of major lineages in the Turkana Basin for the normalized proportions of C_4-grazers, C_3-C_4 mixed, and C_3-browsers (G:M:B) with comparison to the modern diets of those lineages.

5. Diets of mammalian lineages in the Pliocene and Pleistocene. The mammalian lineages considered here derive from different members of the Kanapoi, Koobi Fora, and Nachukui formations and are of comparable age to the Shungura Formation in the lower Omo Valley as shown in Figure 2. Time intervals employed are as follows from oldest to youngest: > 4 Ma; 4.0 to 3.6 Ma, 3.6 to 3.4 Ma; 3.4 to 3.0; 3.0 to 2.5 Ma; 2.5 to 2.35 Ma; 2.35 to 1.9 Ma; 1.9 to 1.5 Ma; 1.5 to 1.3 Ma; 1.3 to 1.0 Ma.

Artiodactyla: Bovidae. The Bovidae comprise the most diverse large mammal family in Africa today, with dietary specialties ranging from closed-canopy C_3-hyperbrowsers to C_4-hypergrazers. Isotopic results on modern bovid specimens confirm previous observations (39, 40) for diets of East African and southern African bovids; however, as is shown below, many fossil bovids have a distinctly different diet than that of their modern counterparts.

Aepycerotini are today represented by the impala (*Aepyceros melampus*), which has a mixed diet throughout most of its modern range with an average $\delta^{13}C_{1750}$ value of -3.9 ± 2.6 (n = 66); the relative proportions of modern individuals with grazing:mixed:browsing (G:M:B) diets is 15:77:8 (Table 1 and Table S2). Aepycerotini from the > 4.0 Ma interval have a G:M:B diet of 25:50:25 (n =24), whereas those from all younger intervals together have a G:M:B diet of 53:47:0 (n = 43). Modern Aepycerotini have diets closer to their relatives 4.3 to 4.0 Ma in age, whereas from 4.0 to 1.0 Ma the Aepycerotini had a stronger grazing component to their diet than do their modern relatives

Alcelaphini consistently have the highest $\delta^{13}C$ of any bovid tribe or of any other APP taxa in East and Central Africa. All four genera of modern alcelaphins (*Alcelaphus, Beatragus, Connochaetes, Damaliscus*) have average $\delta^{13}C_{1750}$ values >2‰, indicating a pure or nearly pure-C_4 diet; few other modern APP taxa achieve such positive $\delta^{13}C_{1750}$ values. As previously noted (39, 40) such high values indicate either extreme selectivity in diets or that the isotope enrichment factor is especially high for alcelaphins compared to other mammals including other bovids.

Throughout the Pliocene and Pleistocene record in the Turkana Basin, alcelaphins have the highest, or second highest $\delta^{13}C$ value for any mammalian taxon within any time interval, with average values between -0.2 and 2.0‰ (G:W:B = 93:7:0; n = 129 individuals in the fossil record). Fossil specimens have slightly more negative $\delta^{13}C$ values than modern alcelaphins; thus, using the $^{13}C/^{12}C$ ratios defining hypergrazers discussed in this paper, none of the fossil alcelaphins are hypergrazers whereas most modern alcelaphins are hypergrazers.

Antilopini in our study include four extant genera—*Eudorcas* (Thomson's gazelle), *Litocranius* (gerenuk), *Nanger* (Grant's and Soemmering's gazelles), and *Oreotragus* (klipspringer). *Eudorcas* is primarily a grazer, *Litocranius* and *Oreotragus* are browsers, and *Nanger* is a mixed-feeder to browser (Table S2). Fossil Antilopini are difficult to distinguish from fossil Aepycerotini using only the dental material available for isotopic study; as a result, these fossil specimens are provisionally classified as Antilopini based on the judgment of the authors and generally agree with identifications in the Turkana Basin fossil catalog (41). Fossil Antilopini from the Turkana basin had diets with a much higher fraction of C_4-grass than those of modern Antilopini, especially the larger

members of the tribe. From *ca*. 4.3 to 2.35 the G:M:B proportion of antilopins is *ca*. 17:75:8 (n = 12), but from 2.35 to 1.0 Ma it is 54:46:0 (n = 26).

Bovini are today represented in Africa by the Cape buffalo (*Syncerus caffer*); domestic cattle are not reported here. The diet of the Cape buffalo ranges from pure-grazing in most open ecosystems to pure-browsing in closed forests. Fossil Bovini in the Turkana Basin were primarily C_4-grazers but with some C_3-C_4 mixed feeders (G:M:B = 76:24:0, n = 21). *Syncerus* are primarily C_4-grazers in most non-forested regions of East Africa.

Caprini are represented today in East and Central Africa by the Walia ibex (*Capra walie*), which has a C_3 diet (Table S2); it is restricted to high mountains in Ethiopia. Domestic caprins (sheep and goats) are present throughout East and Central Africa but are not reported here. Caprins are very rare in the Kanapoi, Nachukui or Koobi Fora Formations and none have been sampled for stable isotopes.

Cephalophini are represented in Africa today by the forest duikers (*Cephalophus* and *Philantomba*) and the bush duiker (*Sylvicapra*). All are C_3-browsers (Table S2). Cephalophini fossils are rare in the Kanapoi, Nachukui or Koobi Fora Formations; no fossil duikers have been sampled for stable isotopes from these formations.

Hippotragini are C_4-grazers today (G:M:B = 89:11:0; n =38) as were most fossil hippotragins younger than 2.5 Ma (G:M:B = 80:20:0; n =10). However, hippotragins from early stratigraphic intervals *ca*. 4 to 2.35 Ma in age, had a mixed C_3-C_4 diet (G:M:B = 29:71:0; n = 7) although the sample size is limited.

Neotragini today are mostly C_3-browsers with the exception of the oribi (*Ourebia ourebi*), which is a mixed C_3-C_4 feeder to C_4-grazer. Neotragin fossils are very rare in the Kanapoi, Nachukui, and Koobi Fora Formations.

Reduncini are today represented in 17 of the ecosystems we consider and are represented by four species: the waterbuck (*Kobus ellipsiprymnus*), the Ugandan kob (*Kobus kob*), Chanler's reedbuck (*Redunca fulvorufula*), and the Bohor reedbuck (*Redunca redunca*). The modern reduncins that we examined are primarily C_4-grazers (Table S2), with only a few mixed C_3-C_4 feeders that are generally associated with mountain habitats (e.g., Mt. Kenya, Bale Mountains; see Dataset I). Fossil reduncins in the Nachukui and Koobi Fora Formations are also primarily grazers (Dataset II and Figure S4).

Tragelaphini, the spiral-horned antelopes, today have diets strongly skewed towards browsing (Table 1 and Table S2). Although stable isotope data show the bongo and bushbuck to be hyper-browsers, all others are browsers. The eland, lesser kudu, and greater kudu have $\delta^{13}C_{1750}$ values averaging between *ca*. -8.5‰ and -10‰ and some individuals have a mixed C_3-C_4 diet (i.e., average $\delta^{13}C_{1750}$ between -1‰ and -8‰). However, the average $\delta^{13}C$ for fossil tragelaphins from all stratigraphic intervals is > -8‰ indicating that, on average, tragelaphins had a mixed C_3-C_4 diet for the period from 4 to 1 Ma. The extant tragelaphin with the most positive $\delta^{13}C_{1750}$ value is the eland (*Taurotragus oryx*, $\delta^{13}C_{1750}$ = -8.5 ± 2.1, n = 35; G:M:B = 0:31:69); its $\delta^{13}C$ values are significantly different (P = 0.0002) than the average of all fossil specimens of tragelaphins ($\delta^{13}C$ = -5.9 ± 2.9, n = 43; G:M:B = 7:67:26). Thus, fossil tragelaphins in

the Nachukui and Koobi Fora regions record a diet different than that of any extant tragelaphin species in East and Central Africa: fossil tragelaphins were predominantly mixed C_3-C_4 feeders, but extant tragelaphins are browsers or hyperbrowsers. Studies of tragelaphini in the Shungura Formation, in the lower Omo Valley, have previously noted $\delta^{13}C$ values that are more enriched in ^{13}C than extant tragelephins (42).

Artiodactyla: Giraffidae. The Giraffidae were represented in Africa from 4.3 Ma to the present Ma by 3 genera: *Giraffa*, *Okapia*, and *Sivatherium*. Extant giraffes live in open woodland habitats and the okapi is a forest-dweller. *Sivatherium* became extinct by *ca*. 1 Ma.

Extant giraffes are primarily browsers with only a small fraction being mixed feeders based on carbon isotope data ($\delta^{13}C_{1750}$= -10.6 ± 1.6 (n=61); G:M:B = 0:7:93). Fossil *Giraffa* from the Kanapoi, Nachukui and Koobi Fora Formations had a similar diet ($\delta^{13}C$ = -11.4 ± 1.1 (n =38); G:M:B = 0:0:100). Thus, *Giraffa* has not significantly changed its diet from 4 Ma to present.

African sivatheres were large bodied, short-necked giraffids that changed diet over time with associated morphological changes (43). *Sivatherium* specimens older than 2.35 Ma have a $\delta^{13}C$ = -10.4 ± 1.6‰ (n = 10; G:M:B = 0:10:90) indicating a diet dominated by C_3-biomass; *Sivatherium* specimens from 2.35 to 1.9 have a $\delta^{13}C$ = -4.6 ± 2.5‰ (G:M:B = 0:80:20; n = 5); *Sivatherium* specimens younger than 1.9 Ma have a $\delta^{13}C$ = -1.2 ± 2.3 (G:M:B = 67:33:0; n = 9). Thus, between 3 and 1.5 Ma *Sivatherium* changed from a C_3-browsing to a C_4-grazing giraffid. The sample size so far is too small to determine the details of the timing of this change.

Artiodactyla: Hippopotamidae. In East and Central Africa *Hippopotamus amphibius*, the extant hippo, has a diet that ranges from C_3-dominated to C_4-dominated (44-46). The 186 modern *H. amphibius* sampled have an average $\delta^{13}C_{1750}$ value of -2.1 ± 2.6‰ (G:M:B 36:61:3) indicating a predominantly mixed diet although approximately 40% of modern hippos have a grazing diet.

Two genera of hippos have been recognized in the Kanapoi, Nachukui, and Koobi Fora Formations. Early workers identified these as *Hippopotamus* and *Hexaprotodon* (47) but the latter is referred to cf. *Hippopotamus* (48) pending selection of a new name for this genus. In this paper we group *Hippopotamus* and cf. *Hippopotamus* as *Hippopotamus* sensu lato.

The Pliocene and earliest Pleistocene hippos in the Kanapoi, Nachukui, and Koobi Fora Formations (4.3 to 2.35 Ma) have an average $\delta^{13}C$ value of -3.3 ± 2.9 (G:M:B = 23:71:6, n = 48). However, hippos 2.35 to 1.0 Ma in age have an average $\delta^{13}C$ value of -1.1 ± 1.4‰ (G:M:B = 49:51:0). Thus, through the past 4.3 Ma hippos in East Africa have had diets that are strongly biased towards C_4-vegetation, with overall G:M:B proportions between *ca*. 75:25:0 to *ca*. 25:75:0. Although many hippos are predominantly C_4-grazers, occasional opportunistic individuals, both modern and fossil, have isotopic values that record a very high fraction (i.e., >75%) of C_3 biomass in the diet such that they are considered to be C_3-browsers.

Artiodactyla: Suidae. The three genera of suids in East and Central Africa— *Hylochoerus* (the forest hog), *Phacochoerus* (warthog), and *Potamochoerus* (bush and

red river hogs)—have different $\delta^{13}C$ dietary niches (49) with average $\delta^{13}C_{1750}$ values of -14.1 ± 3.3‰ (n = 26), -0.1 ± 2.4‰ (n = 101), and -10.9± 3.9‰ (n = 46), respectively; these genera have corresponding G:M:B proportions of 0:0:100; 80:18:2, and 2:22:76, respectively. *Hylochoerus* is a C_3-hyperbrowser (i.e., $\delta^{13}C_{1750}$ < -12‰) in forested regions (Ituri, Kahuzi-Biega, Kibale, Mt. Kenya, Aberdares); many individuals from these forests have $\delta^{13}C_{1750}$ values < -14‰ indicating a diet derived from closed canopy understory (49, 50). *Potamochoerus* is a C_3-hyperbrowser in the Kahuzi-Biega and Ituri closed forests.

Four lineages of suids are found in the Plio-Pleistocene of East Africa: *Nyanzachoerus—Notochoerus*, *Kolpochoerus–Hylochoerus*, *Metridiochoerus—Phacochoerus*, and *Potamochoerus*. Evolutionary trends of suids related to dental changes from 4 to 1 Ma were discussed by Harris and Cerling (49). *Notochoerus* specimens were predominantly a mixed C_3-C_4 feeder between 4.3 and 4.0 Ma ($\delta^{13}C$ = -3.4 ± 2.7, G:M:B = 25:75:0; (n = 8), but were predominantly C_4-grazers by 2.0 Ma (Upper Burgi Member in the Koobi Fora Formation; $\delta^{13}C$ = -0.7 ± 0.5; G:M:B = 83:17:0, n = 12). *Kolpochoerus* and *Metridiochoerus* were predominantly grazers throughout the intervals sampled with high C_4-grazer proportions (G:M:B = 82:18:0 (n = 38) and 93:7:0 (n = 67, respectively)). By 2.0 Ma, the region had three sympatric genera of suids that were C_4-grazers. Of these, the *Nyanzachoerus-Notochoerus* lineage became extinct, the *Kolpochoerus-Hylochoerus* lineage exploited more closed habitats and became C_3-browsers in the past 1 Ma, and the *Metridiochoerus-Phacochoerus* lineage continued as C_4-grazers.

Perissodactyla: Equidae. Today, African equids are represented by species of the genus *Equus*. Extant *Equus* is a C_4-grazer with an average $\delta^{13}C_{1750}$ value of 1.3 ± 1.4‰ (n = 147) with G:M:B proportions of 91:8:1. The most positive $\delta^{13}C$ value is 3.7‰, approximately one per mil less enriched in ^{13}C than the most positive alcelaphin. This difference in isotope values for equids compared to alcelaphins, both widely thought to be pure C_4-grazers, may be related to the difference in isotopic enrichment by hind-gut fermenting equids compared to ruminating bovids (see 18, 38).

Fossil equids in the Nachukui and Koobi Fora Formations are represented by two genera. The hippionin *Eurygnathohippus* (51, 52) is present from before 4 Ma to *ca*. 1.5 Ma; it is a C_4-grazer with an average $\delta^{13}C$ value of -0.3 ± 1.2‰ (n =33) and G:M:B proportions of 79:21:0. *Equus* is present in the Omo-Turkana Basin from 2.3 Ma onwards; its average $\delta^{13}C$ value is -0.1 ± 1.1‰ (n = 39) with G:M:B proportions of 82:18:0. Thus, there is virtually no difference in diets of the two equid lineages based on stable isotope evidence.

Of the two C_4-grazing equids present in the Nachukui and Koobi Fora Formations, *Eurygnathohippus*, representing the *Hipparion* lineage, became extinct in Africa during the middle Pleistocene (52). *Equus* has been a C_4-grazing equid since its first appearance in Africa during the late Pliocene.

Perissodactyla: Rhinocerotidae. The two extant genera of rhinos in East and Central Africa, *Diceros* and *Ceratotherium*, have distinctly different diets. *Diceros* is a C_3-browser with an average $\delta^{13}C_{1750}$ value of enamel of -10.2 ± 1.2‰ (n = 145; G:M:B = 0:6:94) while *Ceratotherium* is a C_4-grazer with a $\delta^{13}C_{1750}$ value of +1.4 ± 1.2‰ (n = 13; G:M:B = 100:0:0).

Many of the fossil rhinocerotids analyzed were so fragmentary that identification to genus was not possible. We grouped analyses into "B" (values with $\delta^{13}C < -5‰$) and "G" (values with $\delta^{13}C > -5‰$); this resulted in a clear separation into two groups as no analyses were between -1‰ and -7‰. "Rhino B" and "Rhino G" had an average $\delta^{13}C$ values of -10.1 ± 1.2‰ (n = 17; G:M:B 0:6:94) and 0.3 ± 0.8 (n = 19; G:M:B = 100:0:0), respectively. These values are indistinguishable from those of modern *Diceros* and *Ceratotherium*, respectively. However, many Miocene rhinos in East Africa, older than those sampled here, had C_3-C_4 mixed diets (53).

Thus, the fossil record of rhinos in the Nachukui and Koobi Fora Formations comprises two groups of rhinos with similar $\delta^{13}C$ values to the two modern extant rhinos.

Proboscidea; Deinotheriidae. Deinotheres are an extinct family of proboscideans that were present in Africa for the past 25 or so million years, becoming extinct in the early to middle Pleistocene. Deinotheres from the Nachukui and Koobi Fora Formations are C_3-browsers, with an average $\delta^{13}C$ of -12.7 ± 0.8 (n = 28; G:M:B = 0:0:100). *Deinotherium* has, in most stratigraphic intervals, the most ^{13}C-depleted $\delta^{13}C_{enamel}$ of any fossil taxon in the basin.

Proboscidea; Elephantidae. *Loxodonta* is the only extant elephantid genus in Africa. *Loxodonta* is a C_3-browser to C_3-C_4-mixed feeder (54). Modern *Loxodonta* is represented by two species. The savanna elephant, *Loxodonta africana* has an average $\delta^{13}C_{1750}$ value of -9.2 ± 2.4‰ (G:M:B = 0:24:76; n = 225); the forest elephant, *Loxodonta cyclotis*, has a $\delta^{13}C_{1750}$ value of -14.1 ± 1.3 (G:M:B = 0:0:100; n = 55).

Two elephant genera are recorded in the stratigraphic intervals under discussion: *Elephas* and *Loxodonta*. *Elephas* was more abundant than *Loxodonta* from 4 to 1 Ma in the Turkana Basin. *Elephas* had a C_3-C_4-mixed diet from 4.3 to 4.0 Ma ($\delta^{13}C$ = -2.7 ± 1.1‰ (n = 7; G:M:B = 0:100:0)) but had evolved into a C_4-grazer by the early Pleistocene ($\delta^{13}C$ = -0.4 ± 1.2‰ (n=17; G:M:B = 82:18:0)). *Loxodonta* shows a similar trend: for the lowest stratigraphic intervals, from 4.0 to 2.35 Ma, *Loxodonta* was a mixed C_3-C_4- feeder (average $\delta^{13}C$ = -2.1 ± 1.6 (n=12; G:M:B = 17:83:0) whereas it was a C_4-grazer for the period from 2.35 to 1.9 Ma (average $\delta^{13}C$ = 0.1 ± 0.4 (n = 5; G:M:B = 100:0:0)).

The two elephantids present in the Turkana Basin from 4 to 1 Ma were both mixed C_3-C_4-feeders at 4 Ma and gradually changed their diets to become C_4-grazers by 2 Ma. *Elephas* became extinct in the middle to late-Pleistocene; *Loxodonta* persists but extant *Loxodonta* is a C_3-browser to C_3-C_4- mixed feeder.

Proboscidea: Gomphotheriidae. *Anancus* is the only gomphotheriid recovered from this stratigraphic interval, becoming extinct in the basin in the Pliocene. A single *Anancus* tooth from the sub-A stratigraphic interval has a $\delta^{13}C$ value of -0.1‰, indicating a C_4-grazing diet.

6. Comparison of dietary guilds. The fossil record has only rare specimens of the bovid tribes Neotragi and Cephalophini. Therefore, we have used the modern collections for comparison but in Figures 3 and 4 we have excluded the modern and fossil Neotragini and Cephalophini from the analysis. Figure S3 shows that modern the fractions of C_4-

grazing, mixed C_3-C_4, and C_3-browing taxa have similar proportions for the 30 modern ecosystems, whether including all taxa (Figure S3A) or excluding the Neotragini and Cephalophini (Figure S3B) in the analysis. All data from Dataset I.

7. Datasets

7.1. Dataset I. Dataset I includes $\delta^{13}C$ values as measured for >1900 modern individual mammals from East and Central Africa. Geographic origin, estimated year of death, and ecosystem groupings presented. $\delta^{13}C$ values presented as the original data for enamel, keratin, or collagen, with the equivalent $\delta^{13}C$(enamel), and the enamel value corrected to $\delta^{13}C_{1750}$ (see text). Data is from this study and references (18, 29-37, 44–45, 49–50, 54–56). Geographic location and date of death is estimated from information provided by collector and vary in degree of accuracy.

7.2 Dataset SI II. Dataset II includes $\delta^{13}C$ values for fossils collected from the Kanapoi, Nachukui, and Koobi Fora Formations in the Omo-Turkana Basin, Kenya. Data is from this study and from references (37, 49, 54, 57–58)

8. Supplementary Information References

1   White F (1983) *The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa by F White*. Natural Resources Research Report XX, UNESCO, Paris, France.

2   Cerling TE, Brown FH (1982) Tuffaceous marker horizons in the Koobi Fora region and the lower Omo Valley. *Nature* 299: 216– 221.

3   Brown FH, Feibel CS (1986) Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. *J Geol Soc London* 143(2): 297–310.

4   Harris JM, Brown FH, Leakey MG (1988) Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Natural History Museum of Los Angeles County, Contributions in Science* 399: 1–128.

5   Harris JM, et al (1988) Stratigraphy and paleontology of the Nachukui Formation, Lake Turkana region, Kenya. *Natural History Museum of Los Angeles County, Contributions in Science* 399: 1–128.

6   Leakey MG, Feibel CS, McDougall I, Walker A (1995) New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376: 565–571.

7   Leakey MG, Feibel CS, McDougall I, Ward, C, Walker, A (1998) New specimens and confirmation of an early age for Australopithecus anamensis. *Nature* 393:62–66.

8   Feibel CS (2003) Stratigraphy and depositional setting of the Pliocene Kanapoi Formation, lower Kerio valley, Kenya. *Natural History Museum of Los Angeles County, Contributions in Science* 498: 9–20.

9   Brown FH, Haileab B, McDougall I (2006) Sequence of tuffs between the KBS Tuff and the Chari Tuff in the Turkana Basin, Kenya and Ethiopia. *J Geol Soc London* 163: 185–204.

10   McDougall I, Brown FH (2006) Precise 40Ar/39Ar geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. *J Geol Soc London* 163: 205–220.

11   McDougall I, Brown FH (2008) Geochronology of the pre-KBS Tuff sequence, Omo Group, Turkana Basin. *J Geol Soc London* 165: 549–562.

12   Lepre CJ, Kent DV (2010) New magnetostratigraphy for the Olduvai Subchron in the Koobi Fora Formation, northwest Kenya, with implications for early Homo. *Earth Planetary Sci Lett* 290: 362–374.

13   Joordens JC, et al. (2011) An astronomically-tuned climate framework for hominins in the Turkana Basin. *Earth Planet Sci Lett* 307: 1–8.

14   Brown FH, Mcdougall I (2011) Geochronology of the Turkana depression of northern Kenya and southern Ethiopia. *Evolutionary Anthropology: Issues, News, and Reviews* 20.6: 217-227.

15   McDougall I, et al (2012) New single crystal ^{40}Ar/^{39}Ar ages improve timescale for deposition of the Omo Group, Omo-Turkana Basin, East Africa. *J Geol Soc London* 169: 213–226.

16   McDougall I (2014) K/Ar and ^{40}Ar/^{39}Ar Isotopic dating techniques as applied to young volcanic rocks, particularly those associated with hominin localities. In: Cerling TE (ed) *Treatise of Geochemistry Volume 14: Archaeology and Anthropology*, Elsevier, New York. p. 1–15.

17   Cerling TE, Omondi P, Macharia AN (2007) Diets of Kenyan elephants from stable isotopes and the origin of confiscated ivory in Kenya. *Afr J Ecol* 45: 614–623.

18   Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120: 347–363.

19   Lee-Thorp JA, Sealy JC, van der Merwe NJ (1989) Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Jour Archaeol Sci* 16: 585–599.

20   Francey RJ, et al. (1999) A 1000-year high precision record of d13C in atmospheric CO2. *Tellus* 51: 170–193.

21   Keeling RF, Piper SC, Bollenbacher AF, Walker SJ (2010) Monthly atmospheric 13C/12C isotopic ratios for 11 SIO stations. In *Trends: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, Oak Ridge National* Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A.

22   Pratt DJ, Greenway PJ, Gwynne MD (1966). A classification of East African rangeland, with an appendix on terminology. *J Appl Ecol*: 369-–382.

23   Cerling et al (2011) Woody cover and hominin environments in the past 6 million years. *Nature* 476: 51–56.

24   Ratnam J (2011) When is a 'forest'a savanna, and why does it matter? *Global Ecol Biogeogr* 20.5: 653–660.

25   Sankaran M (2005) Determinants of woody cover in African savannas. *Nature* 438: 846–849.

26   Bond WJ (2008) What limits trees in C4 grasslands and savannas? *Ann Rev Ecol Evol Syst* 39: 641–659.

27   Lloyd J, et al (2008). Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate. *Tree Physiol* 28(3): 451–468.

28   Good SP, Caylor KK (2011) Climatological determinants of woody cover in Africa. *Proc Nat Acad Sci* 108: 4902–4907.

29   Koch PL, Behrensmeyer AK, Fogel ML (1990) The isotopic ecology of plants and animals in Amboseli National Park, Kenya. *Ann Report Director, Geophys Lab*. Carnegie Inst, Washington DC. p. 163–171.

30   Bocherens H, Koch PL, Mariotti A, Geraads D, Jaeger JJ (1996) Isotopic biogeochemistry (13C 18O) of mammalian enamel from African Pleistocene hominid sites. *Palaios* 11: 306–318.

31   Nelson SV (2013) Chimpanzee fauna isotopes provide new interpretations of fossil ape and hominin ecologies. *Proc Royal Soc B: Biol Sci* 280: 20132324. doi.org/10.1098/rspb.2013.2324

32   Martin JE, Vance D, Balter V (2015) Magnesium stable isotope ecology using mammal tooth enamel. *Proc Nat Acad Sci* 112: 430–435.

33   Kingston JD (2011) Stable isotopic analyses of Laetoli fossil herbivores. (ed Harrison, T) *Paleontology and geology of Laetoli: Human evolution in context*. Springer Netherlands, p. 293-328.

34   van der Merwe NJ (2013) Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna. *S Afr Jour Sci* 109(11/12): 1-14.

35   Ambrose SH, DeNiro MJ (1986) The isotopic ecology of East African mammals. *Oecologia* 69: 395–406.

36   Cerling TE, Harris JM, Leakey MG, Mudida N (2003) Stable isotope ecology of Northern Kenya, with emphasis on the Turkana Basin, Kenya. In: MG Leakey and JM Harris (eds). *Lothagam: the Dawn of Humanity in Africa*. Columbia Univ. Press. p. 583–603.

37   Cerling TE, et al (2011) Diet of Paranthropus boisei in the early Pleistocene of East Africa. *Proc Nat Acad Sci* 108: 9337–9341.

38   Passey BH, et al (2005) Carbon isotopic fractionation between diet, breath, and bioapatite in different mammals. *Jour Archaeol Sci* 32: 1459–1470.

39   Cerling TE, Harris JM, Passey BH (2003) Dietary preferences of East African Bovidae based on stable isotope analysis. *Jour Mammal* 84: 456–471.

40   Sponheimer M et al (2003). Diets of southern African Bovidae: stable isotope evidence. Jour Mammal 84: 471–479.

41   Bobe R (2011) Fossil mammals and paleoenvironments in the Omo-Turkana Basin. *Evol Anthro* 20: 254-263.

42   Bibi F, Souron A, Bocherens H, Uno K, Boisserie JR (2013) Ecological change in the lower Omo Valley around 2.8 Ma. *Biol Lett* 9(1), 20120890.

43   Cerling TE, Harris JM, Leakey MG (2005) Environmentally driven dietary adaptations in African mammals. In Ehleringer JR, Dearing MD, Cerling TE (eds). *History of Atmospheric CO$_2$ and the Impacts on Plants, Animals, and Ecosystems*. Springer, New York. p. 258–272.

44   Cerling TE, et al (2008) Stable isotope ecology of modern Hippopotamus amphibius in East Africa. *Jour Zool* 276: 204–212.

45   Boisserie JT et al (2005) Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and microwear of tooth enamel. *Palaeogeogr Palaeoclim Palaeoecol* 221: 153–174.

46   Souron A, Balasse M, Boisserie JR (2012) Intra-tooth isotopic profiles of canines from extant Hippopotamus amphibius and late Pliocene hippopotamids (Shungura Formation, Ethiopia): insights into the seasonality of diet and climate. *Palaeogeogr Palaeoclim Palaeoecol* 342: 97–110.

47   Coryndon SC (1977) The taxonomy and nomenclature of the Hippopotamidae (Mammalia, Artiodactyla) and a description of two new fossil species. *Proc Koninklijke Nederland Akad Wetenschappen* 80: 61–68.

48   Boisserie JR (2005) The phylogeny and taxonomy of the Hippopotamidae (Mammalia: Artiodactyla): A review based on morphology and cladistical analysis. *Zool Jour Linnean Soc* 143:1–26.

49   Harris JM, TE Cerling (2002) Dietary adaptations of extant and Neogene African suids. *Jour Zool* 256: 45–54.

50   Cerling TE, Hart JA, Hart TB (2004) Stable isotope ecology in the Ituri Forest. *Oecologia* 138: 5–12.

51   Bernor RL, Harris JM (2003) Systematics and evolutionary biology of the Late Miocene and early Pliocene Hipparionine horses from Lothagam, Kenya. In (Harris JM, Leakey MG, eds.), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York. pp. 387–438

52   Bernor RL, Armour-Chelu MJ, Gilbert H, Kaiser TM, Schulz E (2010) Equidae, In (Werdelin L and Sanders WE, eds) *Cenozoic Mammals of Africa*. University of California Press, p. 685–721.

53   Uno KT, et al (2011) Late Miocene to Pliocene carbon isotope record of differential diet change among East Africa herbivores. *Proc Nat Acad Sci* 108: 6509–6514.

54   Cerling TE, Harris JM, Leakey MG (1999) Browsing and grazing in modern and fossil proboscideans. *Oecologia* 120: 364–374.

55   Cerling TE, Viehl K (2004) Seasonal diet changes of the giant forest hog (Hylochoerus meinertzhagani Thomas) based on the carbon isotopic composition of hair. *Afr Jour Ecol* 42: 88–92.

56   Levin NE, Simpson SW, Quade J, Cerling TE, Semaw S, SR Frost SR (2008) Herbivore enamel carbon isotopic composition and the environmental context of Ardipithecus at Gona, Ethiopia. *Geol Soc Amer Spec Pap* 446: 215–234.

57   Harris JM, Cerling TE, Leakey MG, Passey BH (2008) Stable isotope ecology of fossil hippopotamids from the Lake Turkana Basin region of East Africa. *Jour Zool* 275: 323–331.

58   Braun DR et al. (2010) Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proc Nat Acad Sci* 107: 10002–10007.

59   Climatological Statistics for East Africa (1975) *Climatological Statistics for East Africa*. East African Meteorological Department, Nairobi.

60   Altmann J, Alberts SC, Altmann SA, Roy SB (2002) Dramatic change in local climate patterns in the Amboseli basin, Kenya. *Afr J Ecol* 40:248–251.

61   National Climatic Data Center (2014) National Climatic Data Center. Available at: http://www.ncdc.noaa.gov/cdo-web/datatools/findstation [Accessed June 7, 2014].

62   Yineger H, Kelbessa E, Bekele T, Lulekal E (2008) Floristic composition and structure of the dry Afromontane forest at Bale Mountains National Park, Ethiopia. *Ethiopian J Sci* 31:103–120.

63   Yusuf H, Treydte AC, Demissew S, Woldu Z (2011) Assessment of woody species encroachment in the grasslands of Nechisar National Park, Ethiopia. *Afr J Ecol* 49:397–409.

64   Ndey JA, Smith KH, Antoninova M (2014) Vegetation & Climate. *Garamba, Conservation in Peace and War*, eds Smith KH, Kalpers J, Arranz L, Ortega N, (Self-published) pp 3–18.

65   Makana J-R, Thomas SC (2005) Effects of Light Gaps and Litter Removal on the Seedling Performance of Six African Timber Species. *Biotropica* 37: 227–237.

66   Makana J, Hart TB, Liengola I, Ewango C, Hart JA (2004). Ituri forest dynamic plots, Democratic Republic of Congo. *Flora of Tropical East Africa*. Balkema Publishers, Leiden. p. 492-505.

67   Hartter J, Ryan SJ, Southworth J, Chapman CA (2011) Landscapes as continuous entities: forest disturbance and recovery in the Albertine Rift landscape. *Landscape Ecol* 26: 877–890.

68   Egeru A et al. (2014) Assessing the spatio-temporal climate variability in semi-arid Karamoja subregion in north-eastern Uganda. *Inter Jour Environ Stud* 71: 490–509.

69   Yamagiwa J et al. (2012) Long-Term Research on Grauer's Gorillas in Kahuzi-Biega National Park, DRC. (eds Kappeler PM, Watts DP) *Life History, Foraging*

Strategies, and Ecological Differentiation from Sympatric Chimpanzees. Long-Term Field Studies of Primates. Springer Berlin Heidelberg, Berlin, Heidelberg, p. 385–412.

70   Ngatia LW et al. (2014) Seasonal patterns in decomposition and nutrient release from East African savanna grasses grown under contrasting nutrient conditions. *Agri Ecosys Environ* 188: 12–19.

71   Apio A, Muwanika V, Plath M (2009) Seasonal variation in reproductive behaviour of bushbuck (Tragelaphus scriptus Pallas, 1766) in an equatorial savannah ecosystem. *Afr J Ecol* 47: 592–597.

72   Henschel P, Abernethy KA, White LJT (2005) Leopard food habits in the Lopé National Park, Gabon, Central Africa. *Afr J Ecol* 43: 21–28.

73   Demeke Y, Bekele A (2000) Population estimates and threats to elephants Loxodonta africana (Blumenbach 1797) in the Mago National Park, Ethiopia. *Trop Zool* 13: 227–237.

74   Jacobs MJ, Schloeder CA (2002) Fire frequency and species associations in perennial grasslands of south-west Ethiopia. *Afr J Ecol* 40: 1–9.

75   Boutton TW, Tieszen LL, Imbamba SK (1988) Biomass dynamics of grassland vegetation in Kenya. *Afr J Ecol* 2 6:89–101.

76   Ogutu JO, Piepho HP, Dublin HT (2012) Ostrich recruitment dynamics in relation to rainfall in the Mara–Serengeti ecosystem. *Ostrich* 83: 119–136.

77   Averbeck C, Plath M, Wronski T, Apio A (2012) Effect of human nuisance on the social organization of large mammals: group sizes and compositions of seven ungulate species in Lake Mburo National Park and the adjacent Ankole Ranching Scheme. *Wildl Biol* 18: 180–193.

78   Rasmussen HB, Wittemyer G, Douglas-Hamilton I (2006) Predicting time-specific changes in demographic processes using remote-sensing data. *Jour Appl Ecol* 43: 366–376.

79   Thompson BW (1966) The mean annual rainfall of Mount Kenya. *Weather* 21: 48–49

80   Ogutu JO, Owen-Smith N, Piepho HP, Kuloba B (2012) Dynamics of ungulates in relation to climatic and land use changes in an insularized African savanna ecosystem. *Biodiversity Conserv* 21: 1033–1053.

Table S1. Locations, climate parameters, and dominant biomes of modern sites in East and Central Africa.

Abbrev[1]	location[2]	Country[3]	MAT[4]	MAP[5]	lat[6]	long[7]	elev[8]	Ref[9]	vegetation description[10]	UNESCO[11]
ABER	Aberdares	Kenya	11.6	1420	0.4 S	36.8 E	2700*	59	evergreen montane forest	forest
AMBO	Amboseli	Kenya	24.0	350	2.6 S	37.2 E	1140	60	grassland to wooded grassland	wooded grassland
ATHI	Athi plains	Kenya	19.4	850	1.5 S	37.1 E	1640	61	grassland to wooded grassland	wooded grassland
AWSH	Awash	Ethiopia	25.0	480	8.9 N	40.0 E	1050	61	acacia wooded grassland with riparian woodland	riparian with wooded grassland
BALE	Bale Mtns	Ethiopia	9.0	1220	6.9 N	39.6 E	3500*	96	Afro-Alpine forest to moorland	Afro-alpine
CHYU	Chyulu Hills	Kenya	21.0	650	2.6 S	37.9 E	1850*	45	wooded grassland to grassy woodland	wooded grassland
ETHR	Ethiopian Rift lakes	Ethiopia	20.2	510	6.0 N	37.7 E	1540	63	wooded grassland	wooded grassland
GMBA	Garamba	DRC	24.4	1250	4.0 N	29.5 E	800	64	grassland to woodland, gallery forests	wooded grassland
ITRI	Ituri Forest	DRC	22.4	1640	1.8 N	29.9 E	800	65,66	evergreen forest	closed canopy forest
KBLE	Kibale	Uganda	19.0	1660	0.5 N	30.5 E	1250*	67	evergreen forest	open to closed canopy forest
KCST	Kenya Coast	Kenya	25.3	1230	3.3 S	39.9 E	30	59	coastal lowland forest	open to closed forest
KDPO	Kidepo	Uganda	25.1	810	3.9 N	33.8 E	1120	68	wooded grassland	wooded grassland
KZBG	Kahuzi-Biega	DRC	20.1	1610	2.3 S	28.6 E	2000*	69	evergreen montane forest	closed canopy forest
LAIK	Laikipia	Kenya	21.8	640	0.3 N	36.9 E	1700	70	wooded grassland	wooded grassland
LEDW	Lake Edward	Uganda, DRC	25.3	680	0.2 S	29.9 E	924	71	forest to wooded grassland	wooded grassland
LOPÉ	Lope	Gabon	25.5	1490	0.5 S	11.5 E	400	72	rainforest	closed canopy forest
MAGO	Omo / Mago	Ethiopia	26.0	830	5.5 N	36.3 E	600	73,74	semi-desert bushland with riparian forest	riparian with wooded grassland
MARA	Masai Mara	Kenya	20.5	1000	1.4 S	35.0 E	1600	75,76	grassland, with riparian woodland	wooded grassland
MBRO	Lake Mburo	Uganda	21.3	890	0.6 S	31.0 E	1300	77	wooded grassland to grassy woodland	wooded grassland / grassy woodland
MERU	Meru NP	Kenya	23.5	380	0.1 N	38.2 E	500	59,78	wooded grassland with riparian woodland	riparian with wooded grassland
MTKE	Mt Kenya	Kenya	7.4	1250	0.3 S	37.2 E	2700*	79	evergreen forest	forest
NAKG	Nakuru - shore	Kenya	17.7	870	0.4 S	36.1 E	1850	59,80	alkali grassland	grassland
NBNP	Nairobi NP	Kenya	18.8	910	1.4 S	36.8 E	1700	59	grassland to woodland	mixed woodland to grassland
RFTV	Kenya Rift Valley	Kenya	17.3	620	0.5 N	36.1 E	1900	59	grassland to woodland	mixed woodland to grassland
SAMB	Samburu	Kenya	23.5	380	0.6 N	37.5 E	880	59	semi-desert bushland with riparian woodland	riparian with wooded grassland
SIME	Simean Mtns	Ethiopia	8.7	1600	13.1 N	38.4 E	3200*	61	Afro-Alpine forest to moorland	Afro-alpine
TANA	lower Tana River	Kenya	27.5	475	1.9 S	40.1 E	40	59	semi-desert bushland with riparian forest	riparian with wooded grassland
TRKG	Turkana - grassland	Kenya	29.2	180	4.0 N	36.2 E	370	59	alkali grassland	grassland
TRKX	Turkana - regional	Kenya	29.2	180	4.2 N	36.3 E	400	59	semi-desert bushland with riparian woodlands	dwarf shrubland
TSVO	Tsavo region	Kenya	24.9	550	3.4 S	38.6 E	530	59	semi-desert bushland with riparian woodland	riparian with wooded grassland

1   abbreviation
2   locality
3   country
4   Mean annual temperature
5   Mean annual precipitation
6   latitude
7   longitude
8   reference elevation (*sites with high variability in elevation)
9   Reference for climate parameters
10   colloquial description of vegetation
11   UNESCO classification for African vegetation (Ref 1).

Table S2. $\delta^{13}C_{1750}$ values for modern East African large mammal by species (except *Madoqua* and *Phacochoerus*) in this study; also classified by the percentage of individuals that are C_4-grazers (G), mixed C_3-C_4 (M), or C_3-browsers (B) based on the isotope values ($\delta^{13}C_{1750}$ values > -1‰, > -1‰ and < -8‰, and <-8‰, respectively). See Dataset I for complete data.

Taxon	number	$\delta^{13}C_{1750}$ (±1σ)	percent		
			G	M	B
Artiodactyla					
Bovidae					
Aepycerotini					
Aepyceros melampus	66	-3.9 ±2.6	15	77	8
Alcelaphini					
Alcelaphus buselaphus	54	3.3 ±1.3	100	0	0
Beatragus hunteri	2	2.0 ±0.4	100	0	0
Connochaetes taurinus	67	3.0 ±1.2	100	0	0
Damaliscus lunatus	18	3.2 ±1.0	100	0	0
Antilopini					
Eudorcas thomsonii	22	-1.6 ±2.4	55	45	0
Litocranius walleri	17	-10.9 ±1.0	0	0	100
Nanger granti	73	-8.5 ±3.2	1	36	63
Nanger soemmerringii	1	-10.5	0	0	100
Ourebia ourebi	6	-2.6 ±4.5	0	0	100
Bovini					
Syncerus caffer	167	0.9 ±3.3	84	13	4
Caprini					
Capra walie	1	-11.1	0	0	100
Cephalophini					
Cephalophus adersi	2	-10.6 ±3.3	0	0	100
Cephalophus callipygus	4	-11.7 ±4.0	0	25	75
Cephalophus dorsalis	2	-13.9 ±0.9	0	0	100
Cephalophus leucogaster	2	-13.3 ±0.3	0	0	100
Cephalophus natalensis	6	-11.4 ±1.3	0	0	100
Cephalophus nigrifrons	13	-14.3 ±1.5	0	0	100
Cephalophus sylvicultor	2	-13.1 ±0.8	0	0	100
Cephalophus weynsi	2	-12.7 ±2.5	0	0	100
Philantomba monticola	6	-12.0 ±1.6	0	0	100
Sylvicapra grimmia	16	-11.1 ±1.1	0	0	100
Hippotragini					
Hippotragus equinus	4	2.0 ±3.0	75	25	0
Hippotragus niger	5	3.9 ±0.3	100	0	0
Oryx beisa	29	0.8 ±1.9	90	10	0
Neotragini					
Madoqua sp.	52	-10.4 ±1.7	0	10	90
Neotragus batesi	1	-24.1	0	0	100
Neotragus moschatus	13	-12.6 ±0.7	0	0	100
Oreotragus oreotragus	9	-10.9 ±1.4	33	67	0
Raphicerus campestris	12	-10.7 ±1.0	0	0	100
Reduncini					
Kobus ellipsiprymnus	55	1.9 ±1.3	96	4	0
Kobus kob	17	2.3 ±1.0	100	0	0
Redunca fulvorufula	4	2.3 ±1.0	100	0	0
Redunca redunca	14	0.7 ±4.0	71	29	0
Tragelaphini					

Taurotragus oryx	35	-8.5 ±2.0	0	31	69
Tragelaphus buxtoni	5	-11.4 ±1.0	0	0	100
Tragelaphus euryceros	5	-14.9 ±0.9	0	0	100
Tragelaphus imberbis	18	-9.2 ±2.0	0	28	72
Tragelaphus scriptus	48	-12.1 ±1.7	0	0	100
Tragelaphus spekei	5	-13.1 ±5.1	0	20	80
Tragelaphus strepsiceros	10	-9.6 ±2.2	0	20	80
Giraffidae					
Giraffa camelopardalis	61	-10.6 ±1.6	0	7	93
Okapia johnstoni	2	-19.5 ±0.1	0	0	100
Hippopotamidae					
Choeropsis liberiensis	1	-15.2	0	0	100
Hippopotamus amphibius	186	-2.1 ±2.6	36	61	3
Suidae					
Hylochoerus meinertzhageni	26	-14.1 ±3.3	0	0	100
Phacochoerus sp.	101	0.1 ±2.4	80	18	2
Potamochoerus larvatus	23	-8.7 ±4.2	4	39	57
Potamochoerus porcus	23	-13.1 ±2.0	0	4	96
Tragulidae					
Hyemoschus aquaticus	1	-13.9	0	0	100
Perissodactyla					
Equidae					
Equus burchellii	129	1.5 ±1.3	96	4	0
Equus grevyi	28	-0.6 ±2.2	68	29	4
Rhinocerotidae					
Ceratotherium simum	13	1.4 ±1.2	100	0	0
Diceros bicornis	145	-10.2 ±1.2	0	6	94
Proboscidea					
Elephantidae					
Loxodonta africana	225	-9.2 ±2.4	0	24	76
Loxodonta cyclotis	55	-14.1 ±1.3	0	0	100

TABLE S3. Percentages of APP taxa that are C_4-grazers (G), mixed C_3-C_4 feeders (M), and C_3-browsers (B) based on stable isotopes for ecosystems considered in this study. N is the total number of large mammal taxa analyzed in each locale/ecosystem.

Locale	Ecosystem	N	G	M	B
ABER	forest	10	10	20	70
AMBO	wooded grassland	10	50	30	20
ATHI	wooded grassland	11	36	18	45
AWSH	riparian with wooded grassland	9	44	22	33
BALE	Afro-alpine	6	0	50	50
CHYU	wooded grassland	9	33	33	33
ETHR	wooded grassland	9	44	22	33
GMBA	wooded grassland	8	50	25	25
ITRI	closed canopy forest	10	0	0	100
KBLE	open to closed canopy forest	5	20	0	80
KCST	open to closed forest	7	14	14	71
KDPO	wooded grassland	7	71	0	29
KZBG	closed canopy forest	5	0	0	100
LAIK	wooded grassland	15	47	13	40
LEDW	wooded grassland	8	50	13	38
LOPE	closed canopy forest	5	0	20	80
MAGO	riparian with wooded grassland	10	40	30	30
MARA	wooded grassland	13	38	31	31
MBRO	wooded grassland / grassy woodland	8	75	13	13
MERU	riparian with wooded grassland	11	45	18	36
MTKE	forest	9	0	33	67
NAKG	grassland	8	75	25	0
NBNP	mixed woodland to grassland	11	36	27	36
RFTV	mixed woodland to grassland	10	50	20	30
SAMB	riparian with wooded grassland	12	42	17	42
SIME	Afro-alpine	5	0	0	100
TANA	riparian with wooded grassland	14	36	36	29
TRKG	grassland	6	83	17	0
TRKX	dwarf shrubland	9	33	0	67
TSVO	riparian with wooded grassland	14	43	21	36

Table S4. Average δ¹³C values for fossil APP (Artiodactyla, Perrisodactyla, and Proboscidea) taxa in the Turkana Basin by time interval, and average δ¹³C values for equivalent taxa in East and Central Africa.

Taxon used	N	4.3 to 4.0	4.0 to 3.4	3.4 to 3.0	3.0 to 2.5	2.5-2.35	2.35 to 1.9	1.9 to 1.5	1.5 to 1.3	1.3 to 1.0	Modern	N	δ¹³C
Artiodactyla											**Artiodactyla**		
Bovidae											Bovidae		
Aepycerotini	67	-4.3	-0.5	-2.2	-2.0		-0.2	-1.2	-1.1	-1.4	Aepycerotini	66	-3.9
Alcelaphini	129	1.0	-0.2	0.8	1.1	1.0	1.2	1.1	1.0	2.0	Alcelaphini	141	3.1
Antilopini	38	-7.6	-2.0	-2.9	-0.9		-2.1	-0.7	-2.5		Antilopini	122	-7.7
Bovini	21		-2.6	-2.7	-1.9		-0.2	0.7	1.0	2.1	Bovini	167	0.9
Caprini											Caprini	1	-11.1
Cephalophini											Cephalophini	63	-12.5
Hippotragini	17			-3.6	-2.2		0.5	0.6	-0.3		Hippotragini	38	1.3
Neotragini	1	-11.6									Neotragini	84	-10.4
Reduncini	43				-0.2	-0.8	-0.2	0.5	0.3	0.6	Reduncini	90	1.8
Tragelaphini	43	-7.8	-9.3	-6.0	-7.3	-3.0	-4.0	-5.6	-6.0	-4.1	Tragelaphini	126	-10.6
Camelidae											Camelidae		
Camelus	2			-10.0	-7.3						domestic only		
Giraffidae											Giraffidae		
Giraffa	38	-11.5	-12.2	-11.2	-11.6	-12.8	-11.2	-11.6	-10.8		*Giraffa*	61	-10.6
											Okapia	2	-19.5
Sivatherium	24	-10.2		-10.9	-9.8		-4.6	-1.5	0.9		*Sivatherium*		Extinct
Hippopotamidae											Hippopotamidae		
Hippopotamus s.l.	115	-3.0	-4.4	-3.7	-2.9	-2.3	-0.9	-1.4	-1.3	0.0	*Hippopotamus*	186	-2.1
Suidae											Suidae		
Kolpochoerus	38				-1.7		0.2	-0.6	-0.4		*Hylochoerus*	26	-14.1
Metridiochoerus	67				-0.2		-0.3	-0.2	0.1	0.0	*Phacochoerus*	101	0.1
Notochoerus	28	-3.9	-2.8	-1.4	-0.8		-0.7	-1.6			*Notochoerus*		Extinct
Nyanzachoerus	7	-2.3	-2.7	-2.9							*Nyanzachoerus*		Extinct
											Potamochoerus	46	-10.9
Tragulidae											Tragulidae		
											Hyemoschus	1	-13.9
Perissodactyla											**Perissodactyla**		
Equidae											Equidae		
Equus	39						0.0	0.2	-0.6	-0.7	*Equus*	157	1.1
Eurygnathohippus	33	1.2	-0.9	-1.3	-0.1		0.7	-0.3	-0.2		*Eurygnathohippus*		Extinct
Rhinocerotidae											Rhinocerotidae		
Rhino G	19	-0.2	-0.8	0.1		-0.3	0.9	0.3		1.3	*Ceratotherium*	13	1.4
Rhino B	17	-10.2		-11.9	-9.3		-8.9				*Diceros*	145	-10.2
Proboscidea											**Proboscidea**		
Deinotheriidae											Deinotheriidae		
Deinotherium	28	-12.6	-13.0	-11.1	-13.3	-13.2	-12.6	-11.8			*Deinotherium*		Extinct

	Count									
Gomphotheriidae										
Anancus	1	-0.1								
Elephantidae										
Elephas	43	-2.7	-2.1	-0.6	-0.7	-2.5	0.1	-0.4	-1.5	-0.2
Loxodonta	18	-2.3	-2.1	-1.8	0.4		0.1	0.3		
Total number of taxa		17	14	18	19	8	19	20	15	10
(ex. Neotragini and Cephalophini)		(16)	(14)	(18)	(19)	(8)	(19)	(20)	(15)	(10)

Gomphotheriidae		
Anancus		Extinct
Elephantidae		
Elephas		Extirpated
Loxodonta	280	-10.2
All East/Central Africa	21	
	(19)	
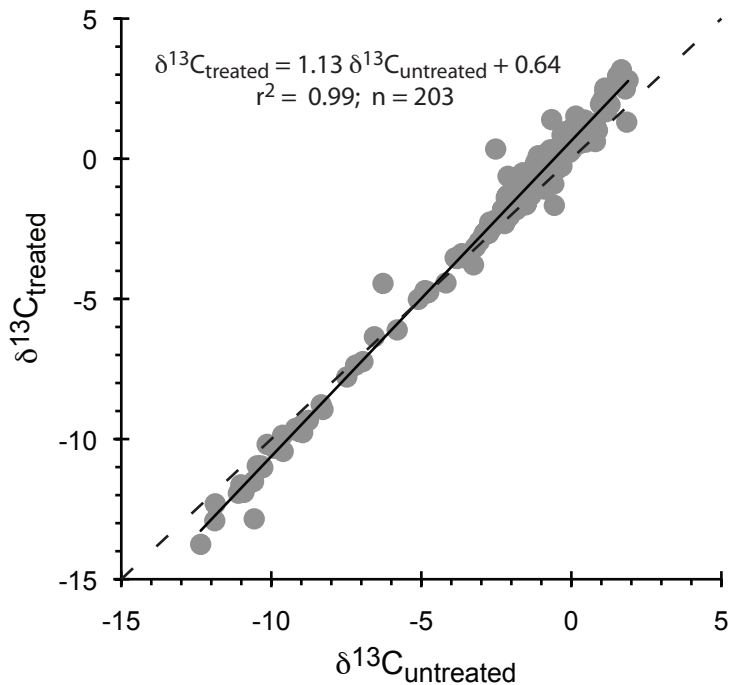
Figure S1. $\delta^{13}C$ comparing results for treated and untreated sample powders.
The least squares best-fit is shown as a solid line; the 1:1 line is shown as a dashed line.
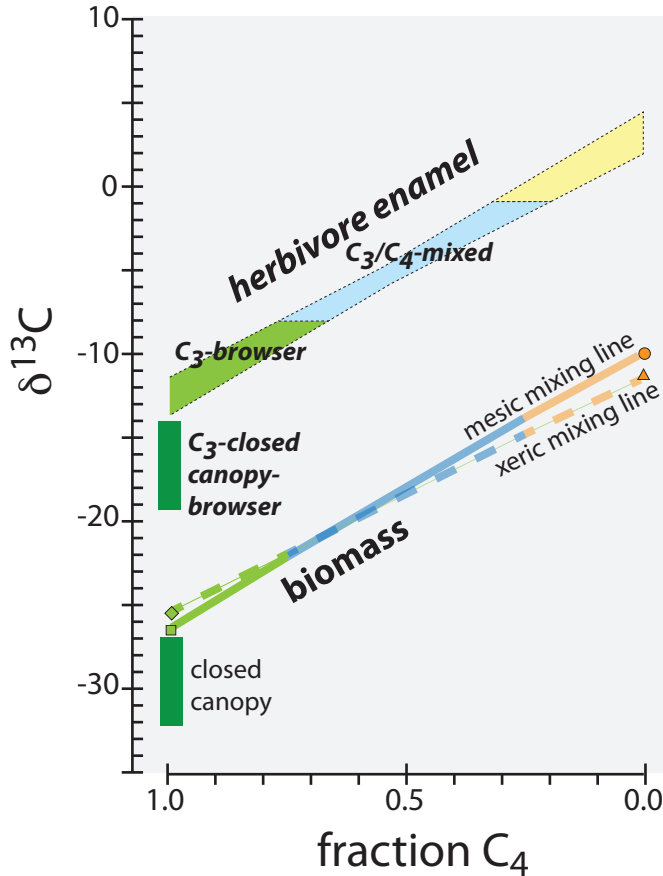
Figure S2. Mixing lines for vegetation from xeric and mesic biomes (lower lines) based on $\delta^{13}C_{1750}$ values on previously published data (23, 86): xeric (lower dashed line) is based on C_3 and C_4 plants from Samburu, Mpala, and Turkana with end-member $\delta^{13}C_{1750}$ values of -25.6 (green diamond) and -11.2‰ (orange triangle), respectively; mesic (lower solid line) is based on C_3 and C_4 plants from the Aberdares (forest) and the Athi plains (wooded grassland to grassland) with $\delta^{13}C_{1750}$ values of -26.6 (green square) and -10.2‰ (orange circle), respectively; closed canopy is based on C_3 plants from the Ituri Forest. Isotope enrichment (23, 28) of ^{13}C from biomass to tooth enamel ranges from 13.3‰ (suids) to 14.6‰ (bovid ruminants) and results in the upper shaded mixing line for enamel; the thickness of the line is due to the uncertainty in end-member values for C_3 and C_4 plants in xeric and mesic ecosystems and to the range in isotope enrichment values. Diets derived from closed canopy vegetation are considered to have $\delta^{13}C_{1750}$ enamel values < -14‰ (dark green); C_3-browsers are from -14‰ to -8‰ (green); mixed C_3/C_4 are from -8‰ to 1‰ (blue); and C_4-grazers are > -1‰ (yellow).
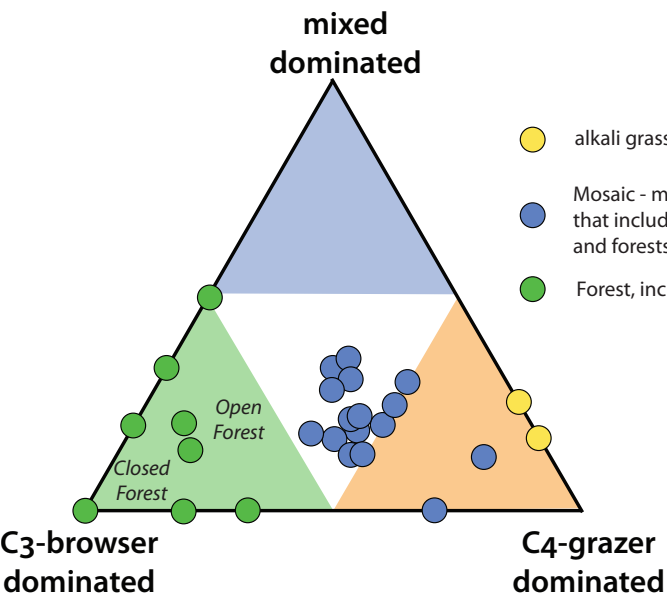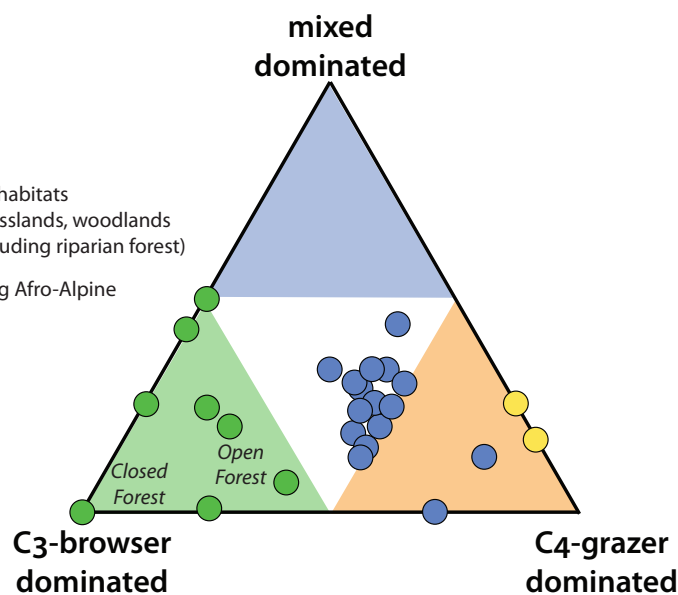
Figure S3. Ternary plot of Artiodactyla-Perrisodactyla-Proboscidea (APP) C_3-browsing, mixed C_3-C_4, and C_4-grazing taxa from the modern sites considered in this study. Each taxon in each locality is represented by the average $\delta^{13}C$ value for that respective taxon (data from Dataset SI I). The green, blue, and orange triangles represent regions where > 50% of the taxa are C_3-browsers, C_3-C_4 mixed feeders, or C_4-grazers, respectively. A. All APP taxa. B. APP taxa, but excluding Neotragini and Cephalophini.

Figure S4. Percent G:M:B (shaded yellow, blue, and green, respectively) of APP major lineages through time in the Kanapoi, Koobi Fora, and Nachukui Formations. Modern fractions shown on the left side for each lineage. Compiled from Datasets I and II.
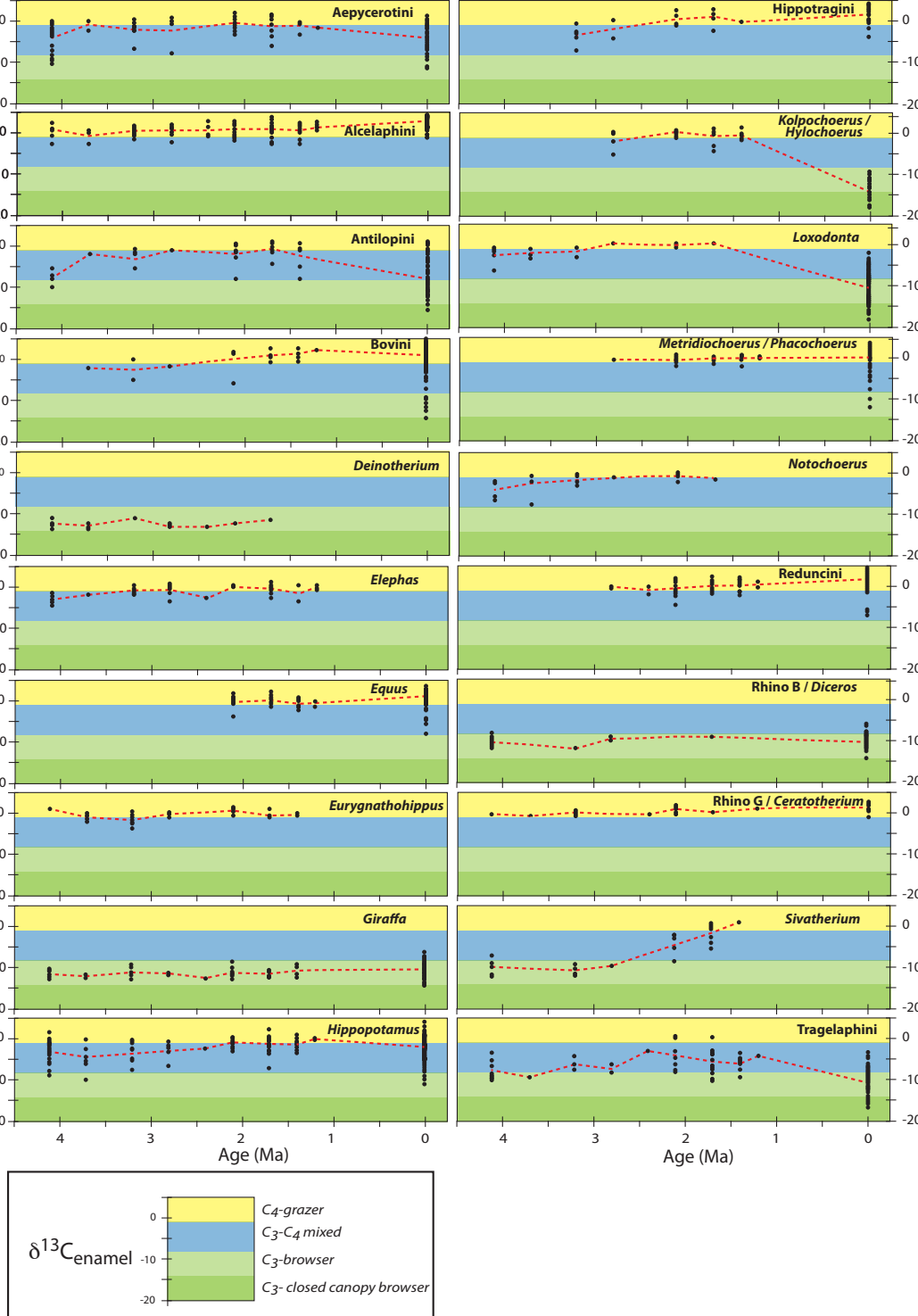
Figure S5. δ¹³C values of major APP lineages through time in the Kanapoi, Koobi Fora, and Nachukui Formations (from Dataset II); modern values includes all samples from East and Central Africa in Dataset I for each taxon plotted. Shaded fields (yellow, blue, green, dark green) show C₄-grazers, C₃-C₄-mixed feeders, C₃-browsers, and C₃-closed canopy browsers, respectively.