Water, plants, and early human habitats in eastern Africa

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Water and its influence on plants likely exerted strong adaptive pressures in human evolution. Understanding relationships among water, plants, and early humans is limited both by incomplete terrestrial records of environmental change and by indirect proxy data for water availability. Here we present a continuous record of stable hydrogen-isotope compositions (expressed as δD values) for lipid biomarkers preserved in lake sediments from an early Pleistocene archaeological site in eastern Africa—Olduvai Gorge. We convert sedimentary leaf- and algal-lipid δD values into estimates for ancient source-water δD values by accounting for biochemical, physiological, and environmental influences on isotopic fractionation via published water-lipid enrichment factors for living plants, algae, and recent sediments. Reconstructed precipitation and lake-water δD values, respectively, are consistent with modern isotopic hydrology and reveal that dramatic fluctuations in water availability accompanied ecosystem changes. Drier conditions, indicated by lower δD values, are associated with expanded woody cover across the ancient landscape. Estimates for ancient precipitation amounts, based on reconstructed precipitation δD values, range between approximately 250 and 700 mm y⁻¹ and are consistent with modern precipitation data for eastern Africa. We conclude that freshwater availability exerted a substantial influence on eastern African ecosystems and, by extension, was central to early human proliferation during periods of rapid climate change.

paleohydrology | plant waxes | carbon isotopes

The role of water and ecosystem change in human evolution remains a subject of active debate (1–3), but experts widely acknowledge that these factors likely shaped early human (hominin) foraging strategies and diet (4) approximately 2.0–1.8 million years ago (Ma). According to marine records, this juncture occurred during an interval of protracted grassland expansion across eastern Africa (1). In contrast, coeval terrestrial records from hominin archaeological sites such as Olduvai Gorge indicate recurrent fluctuations between open-grassland and closed-woodland ecosystems (5). Although such ecosystem fluctuations are commonly interpreted in relation to aridity, grassland expansion is sensitive to multiple factors (6), and proxy signals more closely linked to meteoric waters could strengthen interpretations.

Here we use δD values for lipid biomarkers preserved in lake sediments to reconstruct source-water δD values at Olduvai Gorge during the early Pleistocene. In modern lake basins, precipitation and lake-water δD values correlate strongly with δD values for leaf- and algal-lipids, respectively, after accounting for isotopic fractionation during lipid biosynthesis (7). Present and past source-water δD values reflect the combined influences of vapor-source, transport history, and aridity, ultimately linking local hydrologic patterns to atmospheric and oceanic-circulation dynamics (8).

Sample Locality. Olduvai Gorge is incised into the eastern margin of the Serengeti Plain in northern Tanzania (Fig. 1). Gorge walls expose a thick sequence of volcanioclastic sediments and tuff accumulated in lake and lake-margin environments (9, 10). Between approximately 2.0 and 1.8 Ma, a perennial saline-alkaline lake (paleolake Olduvai) occupied the center of the closed basin (9–11). Lake-margin stratigraphy suggests paleolake Olduvai responded sensitively to local and regional precipitation patterns during this 200,000-y interval (9–12). Stable carbon-isotope compositions (expressed as δ¹³C values) of leaf-lipids preserved in the lake sediments vary by more than 15‰, suggesting that pronounced ecosystem fluctuations accompanied lake-level fluctuations (5). Here we measure leaf-lipid δD values in a subset of the same lake sediment outcrop. All samples are from locality 80 (Bed 1), which accumulated near the depocenter of paleolake Olduvai (10) and was exposed by stream incision during the late Pleistocene (9).

Precipitation Patterns in Eastern Africa. In eastern Africa, precipitation patterns reflect interactions between regional highlands and two convergent boundaries (Fig. 1). The Intertropical Convergence Zone (ITCZ) and closely associated African rainbelt (13) mark north–south convergence of monsoon airstreams. The Interoceanic Confluence (IOC; also referred to as the Congo Air Boundary) marks east–west convergence of air masses derived from the Indian and Atlantic Oceans (14). Both the ITCZ and IOC migrate in response to insolation-driven surface heating patterns (13), yielding two rainy seasons. In eastern Africa, the “long rains” (March to May) account for more than 50% of annual totals (15). Precipitation during the “short rains” (October to December) is more variable but correlates strongly with annual totals (16).

Precipitation δD values (δDrain) reflect the origins and histories of the related air masses that produce it. In eastern Africa, δDrain values correlate inversely with precipitation amounts due to the influences of vapor-source, transport history, and “amount” effects (17). Today the Indian Ocean is the primary vapor source to eastern Africa (13); the Atlantic Ocean and continental surface-water evaporation are important secondary sources. Transport history and amount effects result in δDrain values that differ between the rainy seasons (18). On average, δDain values for the long rains are less negative (~20‰) than for the short rains (~28‰); in central eastern Africa, the average annual δDain value is approximately ~22‰ (19–22).

Leaf-Lipid Apparent Fractionation Factors. Plant-water δD values reflect soil-water δD values (δDsoil) (7). Isotopic relationships between δDsoil and δDrain values can be influenced by surface evaporation in arid and semiarid regions (8), but plant-water δD values remain relatively constant across a wide range of δDsoil values.


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The median δ13C values published in lake sediments from Olduvai Gorge (5). Therefore, we use these values to reconstruct δDsoil values.

The relative influences of biochemical, physiological, and environmental processes on δDwater values are difficult to account for in interpretations of δD31 values. For instance, our δ31/model value for C3 woody plants does not distinguish by canopy height, despite observed differences between modern trees and shrubs (SI Appendix). Similarly, annual δDrain values do not distinguish seasonality. In eastern Africa, annual and rainy-season δDrain values can differ in excess of 20‰ (SI Appendix), although >85% of annual precipitation occurs during rainy seasons (15). Thus, to the extent that plant growth takes place in rainy seasons, annual δDrain values can overestimate δDsoil values during lipid biosynthesis.

Although propagated uncertainty in εlandscape values (SI Appendix) represents a substantial portion of the variability in modern δD31 values across central eastern Africa (approximately 60‰), sedimentary δD31 values capture space- and time-integrated signals that attenuate variability of individual plants or species (7, 31).

Thus, uncertainty in εlandscape values largely reflects ecosystem-scale differences in transpiration and phenology (7), which are at least partially accounted for by ε31/model values, provided living plants are representative of their ancient counterparts. Despite some significant shortcomings in the state of the art, εlandscape values provide a useful interpretational framework to account for biological and physical influences on leaf-lipid δD values—a factor often overlooked in hydrological reconstructions.

Algal-Lipid Apparent Fractionation Factors. Aquatic photosynthetic organisms acquire hydrogen for lipid biosynthesis from ambient waters (7). Therefore, algal δD values reflect lake-water δD values—which integrate precipitation, groundwater, run-off, and evaporation—as modified by biosynthetic fractionation.

We calculate “landscape” apparent fractionation factors (εlandscape) using ε31/model values and relative PFT abundances (Fig. 2) estimated from δ13C values for nC31 (δ31C31) in lake sediments (5). Leaf-lipids represent relative PFT abundances in basins ranging from small lakes (31) to expansive river systems (32), despite differences in basin morphology, transport, and burial processes (33). We multiply each ε31/model value by relative PFT abundance (i.e., fwoody, fherb, and fgram for woody plants, herbs, and graminoids, respectively) to calculate εlandscape values:

εlandscape = fwoody(−109‰) + fherb(−124‰) + fgram(−146‰).

Finally, we apply εlandscape values to sedimentary δD31 values to reconstruct δDsoil values.

We reevaluate a global compilation of published leaf-δD values for living plants (SI Appendix) to determine representative εlipid/water values for different PFTs relevant to this study. We target subtropical and tropical taxa in clades most representative of plants in eastern Africa since the early Pleistocene (27, 28). Leaves of subtropical and tropical plants commonly contain the leaf-lipid hentriacontane (nC31) (29, 30), and nC31 is also abundant in lake sediments from Olduvai Gorge (5). Therefore, we use published δD values for nC31 (δD31) to determine εlipid/water values applicable to sedimentary δD31 values from Olduvai Gorge.

We define PFTs in terms of photosynthetic pathway and growth habit: C3 woody plants, C3 herbs, and C4 graminoids. We determine representative εlipid/water values—termed ε31/model values—from published δD31 values using modeled annual δDrain values (64/31/model) (21, 22). Measured annual δDrain values rarely accompany published leaf-lipid δD values but, when available, generally coincide with δD31/model values (7, 21).

Collectively, ε31/model values average −124‰ (Eaverage). Among individual PFTs the median ε31/model value for C4 graminoids is most negative (−146‰ ± 8‰, n = 95 confidence interval; n = 51). The median ε31/model value for C3 herbs (−124‰ ± 10‰; n = 24) is more negative than for C3 woody plants (−109‰ ± 8‰; n = 84).
Biochemical fractionation, in turn, incorporates biological and physical factors (7). Culture studies indicate that algal $\varepsilon_{\text{lipid/water}}$ values vary between species (34), but space- and time-integration seems to minimize these effects in sediments (7).

Field studies indicate that algal $\varepsilon_{\text{lipid/water}}$ values vary in relation to salinity and must be accounted for when interpreting algal-lipid $\delta D$ values (35). The response of algal $\varepsilon_{\text{lipid/water}}$ values to salinity is markedly consistent at 0.9‰ ± 0.2‰ ppt⁻¹ (7). Heptacosane ($nC_{17}$) is a general biomarker for algae (36) and is abundant in lake sediments from Olduvai Gorge. Modern studies establish an apparent fractionation between freshwater and $nC_{17}$ equal to −172‰ (7), and we use this value to determine algal $\varepsilon_{\text{lipid/water}}$ values at different salinities—termed $\varepsilon_{\text{lake}}$ values:

$$\varepsilon_{\text{lake}} = 0.9(\text{salinity}) - 172\%e.$$

We construct a basic lake-water evaporation model to constrain $\varepsilon_{\text{lake}}$ values in the past (SI Appendix). Briefly, we estimate the total solute load for paleolake Olduvai on the basis of stratigraphic evidence for maximum lake area (approximately 200 km²) (10) and lake level (approximately 5 m) (12) during the early Pleistocene and fossil evidence for minimum salinity (approximately 20 ppt) (9). Then, we infer changes in lake level from Pleistocene and fossil evidence for minimum salinity (approximately 20 ppt) (9) and lake level (approximately 5 m) (12) during the early Pleistocene could weaken this interpretational link (1, 13). Modern $\delta D_{\text{lake}}$ values correlate weakly with reconstructed $\delta D_{\text{soil}}$ values (after 500 km²) (14). Reconstructed $\delta D_{\text{lake}}$ values range from −150‰e to −120‰e (Fig. 4).

Interpretations and Discussion

Precipitation in Eastern Africa. Historical precipitation patterns serve as a framework for interpreting reconstructed hydrologic patterns over timescales of 10⁷ to 10⁸ thousand years (38), although regional tectonism and the intensification of zonal atmospheric (Walker) circulation during the early Pleistocene could weaken this interpretational link (1, 13). Modern $\delta D_{\text{rain}}$ values reveal a regional meteoric waterline (RMWL) for eastern Africa (Fig. 5):

$$\delta D_{\text{rain}} = 7.9\delta^{18}O_{\text{rain}} + 11.3\%e.$$
because of sparse measurements, but available data suggest comparable effects at seasonal, annual, and interannual timescales (44, 45). In eastern Africa, available rainy-season δD\textsubscript{\text{rain}} values correlate inversely with precipitation at a slope of $-0.125 \% \text{ mm}^{-1}$ (SI Appendix). If modern sensitivity is representative for the past, and changes in vapor-source and transport history were important, then a 29%e range in δD\textsubscript{soil} values translate to 225 mm precipitation range; the full 54%e range translates to 415-mm precipitation range.

Historical data for annual δD\textsubscript{\text{rain}} values ($-22%e$) (19, 39) and mean annual precipitation (MAP) (550 mm) (9, 15) provide a local reference point from which to project reconstructed δD\textsubscript{soil} values. Because rainy seasons account for approximately 85% of MAP in northern Tanzania (15), we use an amount effect for rainy-season months to reconstruct MAP in the past:

$$\text{MAP} = (\text{δD}_{\text{soil}} + 22\%e)/(-0.13\%e \text{ mm}^{-1}) + 550 \text{ mm.}$$

MAP estimates for the full range of δD\textsubscript{soil} values are from $-700$ to $-250$ mm. This range is consistent with reconstructions based on pollen spectra ($-750$ mm) (46) and soil carbonates ($-400$ mm) (47) during wetter and drier intervals, respectively. Woody cover strongly covaries with MAP today in eastern Africa (6):

$$f_{\text{woody}} = (0.14(\text{MAP}) - 14.2)/100.$$

We find a similar relationship between our estimates of MAP and woody cover (5). For instance, in the modern calibration, MAP of 700 mm yields an $f_{\text{woody}}$ value of 0.84, which is consistent with a δ13C\textsubscript{31}-derived (−36.3%e) $f_{\text{woody}}$ value of 0.90 (5). These observations suggest amount effects influenced δD\textsubscript{rain} values more than changes in vapor-source or transport history at Olduvai.

Fig. 4. Leaf- and algal-lipid δD values and reconstructed source waters with respect to sedimentary δ\textsubscript{TOC}. (A) Measured δD\textsubscript{31} (hollow circles) and reconstructed δD\textsubscript{soil} values (black circles) with respect to δ\textsubscript{TOC}. For reference, a gray line marks the linear regression for values based on the average δ\textsubscript{13C}\textsubscript{31} (40). (B) Measured δD\textsubscript{31} (hollow circles) and reconstructed δD\textsubscript{lake} values (black circles) with respect to δ\textsubscript{TOC}. A gray line marks the linear regression for values based on a freshwater δ13C\textsubscript{31} value of $-172%e$. A wide range in δD\textsubscript{soil} values (and, by inference δD\textsubscript{\text{rain}} values) indicates pronounced changes in vapor source, transport history, amount of precipitation, or a combination thereof. Today, changes in vapor source account for up to 10%e variability in δD\textsubscript{\text{rain}} values (40). Sea-surface temperatures in vapor-source regions influence δD\textsubscript{\text{rain}} values by approximately 1%e $\text{ °C}^{-1}$ (42), accounting for up to 5%e variability during the early Pleistocene (43). Transport history is difficult to constrain (44) but can account for up to 10%e variability today. Together, changes in vapor source and transport history can account for nearly half of the variability in δD\textsubscript{soil} values in eastern Africa. If so, changes in the amount of precipitation account for the remaining variability (29%e in δD\textsubscript{soil} values).

The relationship between modern δD\textsubscript{\text{rain}} values and amount of precipitation is difficult to evaluate in many tropical regions. A gray line marks the linear regression for values based on the average δ13C\textsubscript{31} (40). Waterline (dashed line). A large black circle marks the point defined by a single reconstructed δD\textsubscript{soil} value from published δ13C\textsubscript{31} values in closely associated lake-margin sediments (SI Appendix). Propagated uncertainties are shown. (SI Appendix). We also plot the global meteoric waterline (dashed line). A large black circle marks the point defined by a single reconstructed δD\textsubscript{soil} value from published δ13C\textsubscript{31} values in closely associated lake-margin sediments (SI Appendix). A gray line marks the linear regression for values based on the average δ13C\textsubscript{31} (40). We also plot the global meteoric waterline (dashed line). A large black circle marks the point defined by a single reconstructed δD\textsubscript{soil} value from published δ13C\textsubscript{31} values in closely associated lake-margin sediments (SI Appendix).
Gorge and highlight the importance of using \( \delta_{\text{landscape}} \) values to reconstruct hydrologic patterns from leaf-lipid \( \delta D \) values.

**Lake-Water Evaporation in Eastern Africa.** Loss of lighter isotopic species (H\(_2\)\(^{16}\)O) during evaporation progressively enriches residual lake waters in D\(^{18}\)O and H\(^{18}\)O. In eastern Africa, lake-water \( \delta D \) values (\( \delta D_{\text{lake}} \)) and \( \delta^{18}O \) values (\( \delta^{18}O_{\text{lake}} \)) define an isotopic trajectory—called a local evaporation line (LEL)—with a slope that is lower than that of the RMWL (8). LEL slopes are primarily a function of relative humidity (\( h \)); in general, very low \( h \) values (e.g., 0.25) result in slopes close to 4, whereas higher \( h \) values result in slopes closer to 6 (8). Modern \( \delta D_{\text{lake}} \) and \( \delta^{18}O_{\text{lake}} \) values yield an LEL for eastern Africa:

\[
\delta D_{\text{lake}} = 5.6\delta^{18}O_{\text{lake}} + 1.6\%e.
\]

Modern \( \delta^{18}O_{\text{lake}} \) values range from approximately \(-30\%e \) in humid regions of eastern Africa to \(+80\%e \) or higher in extremely arid regions (48–53).

The LEL defines source-water composition at its intersection with the RMWL. For modern waters in eastern Africa, LEL and RMWL intersect at a source-water \( \delta D \) value of \(-22\%e \) (Fig. 5), which closely matches historical data (19–22). In closed basins, lake waters derive primarily from precipitation (54).

**Tracing Isotopic Hydrology at Olduvai Gorge.** To compare modern and ancient lake-waters, we pair reconstructed \( \delta D_{\text{lake}} \) values with published \( \delta^{18}O_{\text{lake}} \) values that were determined from authigenic clays (12) in associated sediments (SI Appendix). Reconstructed \( \delta D_{\text{lake}} \) and \( \delta^{18}O_{\text{lake}} \) values show close agreement with the modern LEL (Fig. 5). Further, reconstructed \( \delta D_{\text{lake}} \) and \( E / I \) values strongly correlate, suggesting lake-water compositions shifted largely owing to changes in precipitation. Evaporation rates decrease at high salinity because of the decreased activity of water in high ionic-strength solutions. As a result, potential evaporation can exceed lake-water evaporation by up to 100-fold (54). Thus, although reconstructed \( \delta D_{\text{lake}} \) values vary only slightly more than \( \delta^{18}O_{\text{lake}} \) values, changes in source-water and amount of precipitation would have been accompanied by large changes in potential evaporation. Reconstructed lake evaporation relative to meteoric input (\( E / I \)) based on our data suggest higher evaporation during intervals of reduced precipitation (\( E / I = 2.9 \)) than during increased precipitation (\( E / I = 1.3 \)) and are consistent with historical and modeled \( E / I \) values for eastern Africa (SI Appendix).

**Water Availability and Ecosystem Dynamics.** Reconstructed \( \delta D_{\text{rain}} \) and \( \delta D_{\text{lake}} \) values reveal strong relationships between water and carbon-isotopic data for ecosystem type. Lower \( \delta D_{\text{rain}} \) and \( \delta D_{\text{lake}} \) values, which reflect increased MAP and decreased evaporation, respectively, correspond with increased woody cover (\( f_{\text{woody}} = 0.90 \)). Although the organic carbon-derived indicators we use to determine \( \delta^{18}C_{\text{lake}} \) and \( \delta^{18}C_{\text{soil}} \) may be codependent (55), reconstructed values for \( f_{\text{woody}} \) and lake level are consistent with independent indicators for ecosystem type and paleolake level (Fig. 3). Much like today (6), aridity was a dominant control on ecosystem change in eastern Africa during the Pleistocene.

Contrasting proxy records have fueled debate about the pace and patterns of environmental change in eastern Africa during the Pleistocene. Pollen and fossil abundance records suggest expansion of arid-adapted species beginning near 2.0 Ma and culminating around 1.8 Ma (56, 57). Marine dust-flux records and soil-carbonate \( \delta^{13}C \) values also suggest shifts toward more arid conditions around 1.8 Ma (1), although geomorphic evidence suggests regionally wetter conditions (1).

Lipid biomarkers from Olduvai Gorge point to rapid changes in plants and water between approximately 2.0 and 1.8 Ma, and we suggest this environmental variability both influenced and can reconcile proxy records. For instance, increased seasonality can lead to C\(_4\) graminoid expansions (58) but can also lead to unrepresentatively positive C\(_3\)-like \( \delta^{13}C \) values in soil carbonates (59). Similarly, rapid wet-to-dry transitions can simultaneously produce both increased dust and elevated lake-levels (60). Over the past several million years, modulation of marine dust-flux records from the Arabian Sea has been tightly coupled with orbital eccentricity, resulting in distinct intervals of exceptionally high-amplitude variability during orbital-eccentricity maxima (1). We hypothesize that high-amplitude, orbital precession-paced environmental variability, as opposed to gradual or stepwise aridification, characterized eastern Africa during the early Pleistocene.

**Water and Early Human Evolution.** In semiarid regions, precipitation primarily determines water availability (15). Today, water availability shapes primate behaviors through its influence on vegetation and resource distributions (4, 61). For example, regions with MAP <700 mm do not support chimpanzee populations (62). Water likely shaped behavioral adaptations in the genus Homo (63). Our evidence for dramatic variability is consistent with water as a strong selective pressure in human evolution (1, 2). However, thermoregulatory and dietary constraints function at microhabitat scales (64), and many hominin fossil sites—including Olduvai Gorge (9)—are associated with ephemeral or saline water sources (65). Our reconstructions of precipitation and lake-chemistry in- dicate that, even during maximum lake expansion, lake waters at Olduvai Gorge were likely not potable (12). Groundwater-fed freshwater springs could have aided hominin existence and proliferation (65).

**Conclusions**

This study presents a continuous record of \( \delta D \) values for lipid biomarkers from lake sediments at Olduvai Gorge that were deposited during a key juncture in human evolution, ~2.0–1.8 Ma. We pair sedimentary leaf-lipid \( \delta D \) values with corresponding \( \delta^{18}C \) values to account for physiological and environmental influences on reconstructed precipitation \( \delta D \) values. We use a basic lake-water evaporation model to account for the influence of salinity on algal-lipid \( \delta D \) values and reconstructed lake-water \( \delta D \) values. Sedimentary leaf- and algal-lipid \( \delta D \) values show a weak relationship, but “corrected” values correlate strongly. We compare reconstructed precipitation and lake-water \( \delta D \) values with isotopic data for environmental waters in modern eastern African to estimate ancient precipitation amounts and evaporative losses, respectively. Our results indicate Olduvai Gorge received approximately 250 mm of MAP during arid intervals and ~700 mm during wetter intervals. Given the magnitude and variability in water availability revealed by our reconstructions, we hypothesize freshwater springs were important for hominin subsistence in highly variable environments.

**Materials and Methods**

**Lipid Extraction and Purification.** Lipid biomarkers in lake sediments were extracted and separated according to Magill et al. (5).

**Isotopic Analysis.** Lipid \( \delta D \) values were measured by gas chromatography–isotope ratio monitoring–mass spectrometry. Hydrogen gas of known \( \delta D \) value was used as reference. Samples were coinjected with internal standards of known \( \delta D \) values (\( nC_{41}, \) androstane, and squalane). Uncertainty (1σ SD) for \( nC_{41} \) was 4‰.

**Age Model.** Our age model is constrained using previously published \(^{40}\)Ar/\(^{39}\)Ar, magnetic stratigraphy, and tuff correlation dates (5).

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Magill et al.
Supporting Information Appendix
Magill CR, Ashley GM and Freeman KH

Supporting Information (SI) Table of Contents:
Dataset description.......................................................... 2
Salinity reconstructions...................................................... 2
Monthly and regional amount effects................................. 3
Evaporative balance reconstructions................................. 4
Uncertainty in $e_{\text{landscape}}$ values.................................5
Determination of environmental water $\delta^{18}O$ values........5
SI Figures........................................................................... 6
References.......................................................................... 12
**Dataset description.** We compile and review published leaf-lipid δD data to form a compilation ($n=159$) of 76 plant species from 31 sites (1-13). Sites are located within 5 biomes and have mean annual precipitations ranging from 183 mm to more than 1200 mm. Leaf-lipid data derive from living subtropical and tropical plants belonging either to the monocot clade or the two largest dicot clades (rosid and asterid) in ecosystems with discontinuous woody cover and herbaceous understory. We calculate species means for individual sites to remove within-species variability (14). We use modeled annual δD rain values to calculate representative ε_lipid/water values because measured δD rain values rarely accompany published leaf-lipid δD values.

**Salinity reconstructions.** Today, saline-alkaline lake waters in eastern Africa show remarkably consistent trends in major solute compositions of water (15). In closed basins, water chemistry is primarily a function of dissolved Cl$^-$, Na$^+$, CO$_3$–HCO$_3$–, and K$^+$ species (16). The presence of distinctive minerals such as trona (NaHCO$_3$·Na$_2$CO$_3$·2H$_2$O) in Bed I lake sediments suggests a similar water chemistry for paleolake Olduvai (17,18).

Species diversity and composition of aquatic organisms are influenced by the interplay between salinity and habitat availability (19,20). Fossil remains of two fish taxa (*Clarias* sp. (catfish) and *Orechromis* sp. (tilapia)) occur in Bed I sediments from about 1.835 Ma (18,21). Today, catfish similar to those occurring in Bed I sediments (*e.g.*, *C. gariepinus* and *C. lazera*) survive at salinities of up to 20 ppt in shallow benthic habitats (22,23). Extant tilapias can survive in open waters at salinities of up to 40 ppt (24), but most species reproduce in littoral habitats of between 4 and 5 m depth at salinities of 20 ppt or less (21,24-26).

In shallow saline-alkaline lakes, salinity is controlled primarily by water level fluctuations over long timescales ($10^1$ to $10^3$ kyr)(27-29). Solute balance is largely a function of mineral precipitation and solute diffusion at water-sediment interfaces (30,31), and we use a conservative solute balance for paleolake Olduvai during deposition of Bed I sediments.

Paleolake Olduvai occupied an elliptical conic basin with high surface area-to-volume ratio (32,33). Today, closed basins with similar morphology show strong correlations between water level and surface area (27,34). Stratigraphic evidence in lake-margin deposits suggests a maximum water level of about 5 m (18,33), which is consistent with fossil occurrences of tilapia (21). During maximum expansion, paleolake Olduvai extended to 15 km in average diameter (32).
Relative lake levels correlate strongly with sedimentary total organic carbon (%TOC) in many shallow lakes in eastern Africa (35, 36). Although this relationship may not be purely mechanistic, in part, low lake levels result in low %TOC values due to selective removal of unstable organic compounds during bacterial respiration and to sediment dilution (36). Thus, we interpret %TOC values as a reflection of relative lake levels.

Reconstructed levels for paleolake Olduvai agree closely with independent records for lake level (lithological and faunal) during deposition of Bed I sediments (18, 33, 37, 38).

We develop a conservative lake-water evaporation model for paleolake Olduvai based on the strong empirical relationship between observed and modeled salinity in modern saline-alkaline lakes (27, 34) (SI Figure 2):

\[ S = 55000 \left( \frac{E}{D} \right) \left( \frac{0.55}{U} \right) \left( \frac{\sqrt{A_L}}{D} \right)^{2/3} \]

Here, \( S \) is salinity in parts per million, \( E \) is annual potential evaporation in feet, \( D \) is average lake level in feet, \( U \) is the coefficient of variation for lake area change (about 1.75 for shallow lakes in eastern Africa) (34, 39, 40) and \( A_L \) is lake area in square miles. Thus, based on stratigraphic evidence for average lake level (about 6.5 feet) (18, 32) and area (about 70 square miles) (32, 33) during maximum lake expansion, we calculate a salinity of about 20 ppt for paleolake Olduvai during maximum lake expansion, which is consistent with faunal evidence for salinity (SI Figure 1). Evidence for wave or current action at several localities in lake sediments from central parts of the paleolake Olduvai basin suggest lake levels ranged between a maximum of 1 to 2 m (average depth of about 1.5 feet) (18, 32) during lake contraction with lake areas of about 10 square miles (32, 33); thus, we calculate salinity of about 105 ppt during lake contraction, which is consistent with mineralogical evidence for high salinity during low lake levels (e.g., trona and gaylussite) (18, 32). Overall, reconstructed salinity primarily fluctuates between about 20 and 80 ppt during and is consistent with the range of modern fluctuations in nearby lakes considered as chemical and sedimentary analogues for paleolake Olduvai (e.g., Natron and Nakuru) (15, 18, 39, 40).

**Monthly and regional amount effects.** Amount effects are strongest in tropical regions and function via re-evaporation and diffusive exchange during precipitation events (41). Thus, amount effects are sensitive to relative humidity and precipitation rate (42), resulting in monthly and regional variability (43). Modeled monthly \( \delta D_{\text{rain}} \) values (44) and precipitation averages (45)
for rainy seasons and the climatologically important (46,47) months that precedes them (February (long rains) and September (short rains)) from 48 stations in central eastern Africa show amount effects of about −0.125‰ mm⁻¹ (SI Figures 3 and 4). Interestingly, the x-intercept for short rains is about 10‰ more negative than for long rains. Thus, amount effects for central eastern Africa are broadly consistent with those for Central America (about −0.125‰ mm⁻¹)(ref. 48) and for tropical and coastal regions receiving less than 750 mm of MAP (about −0.145‰ mm⁻¹)(ref. 49).

**Evaporative balance reconstructions.** Isotopic mass balance for evaporative loss in well-mixed lakes with constant volume is equal to (50):

\[
I \delta_{\text{input}} = Q \delta_{\text{outflow}} + E \delta_{\text{evaporation}}
\]

(1)

\(I\) is input, \(Q\) is outflow and \(E\) is lake evaporation. Variables \(\delta_{\text{input}}\), \(\delta_{\text{outflow}}\) and \(\delta_{\text{evaporation}}\) represent isotopic compositions of input, outflow and evaporation, respectively. Since \(\delta_{\text{outflow}}\) is similar to the composition of lake water (\(\delta_{\text{lake}}\)):

\[
E/I = (\delta_{\text{input}} - \delta_{\text{lake}})/(\delta_{\text{evaporation}} - \delta_{\text{lake}})
\]

(2)

Values for \(\delta_{\text{evaporation}}\) cannot be measured directly, but fractionation between \(\delta_{\text{evaporation}}\) and \(\delta_{\text{lake}}\) depends on temperature, boundary layer and atmospheric conditions. Assuming negligible resistance to mixing (51):

\[
\delta_{\text{evaporation}} \approx (\alpha^* \delta_{\text{lake}} - h (\delta_{\text{input}} - \varepsilon^*) - \varepsilon)/(1 - h + 10^{-3} \varepsilon_K)
\]

(3)

Here, \(\alpha^*\) is equilibrium isotopic fractionation between lake-water and vapor and \(h\) is relative humidity. The variable \(\varepsilon\) equals the sum of equilibrium (\(\varepsilon^*\)) and kinetic (\(\varepsilon_K\)) fractionations. We calculate \(\varepsilon^*\) for deuterium using the empirical equation (52):

\[
\varepsilon^* = 1158.8 (T^3/10^8) - 1620.1 (T^2/10^6) + 794.84 (T/10^3) - 161.04 + 2.9992 (10^9 / T^3)
\]

\(T\) is lake surface temperature in Kelvin. We also calculate \(\varepsilon_K\) for deuterium (53):

\[
\varepsilon_K = 12.5 (1 - h)
\]

(5)

Next, we substitute equation (3) into equation (2):

\[
E/I = (\delta_{\text{input}} - \delta_{\text{lake}})/(-\varepsilon^* - \varepsilon_K) = (\delta_{\text{lake}} - \delta_{\text{input}})/\varepsilon
\]

(6)

We calculate the ratio of lake evaporation to input for Olduvai Gorge during arid and wetter intervals. We define \(\delta_{\text{lake}}\) based on reconstructed \(\delta_{\text{lake}}\) values, but must define several other variables based on historical observations:

1. Mean annual \(\delta D_{\text{input}}\) value equals −22‰ (refs. 44, 53-57).
2. Mean annual \( h \) rose to 75% during wetter intervals but fell to 55% during arid intervals (47, 58). Mean annual \( h \) is currently about 65% (ref. 58).

3. Mean annual temperature of 23°C with little seasonal variability (18).

Then, we use equation (8) to calculate \( E/I \) of 2.9 (\( \delta_{\text{lake}} = +59 \% \)) during arid intervals and 1.3 (\( \delta_{\text{lake}} = +16 \% \)) during wetter intervals. Values vary by less than 0.5 if mean annual \( h \) is used to calculate \( E/I \). These values are in close agreement with modeled \( E/I \) (0.5° × 0.5°) (ref. 59) near Olduvai Gorge using prescribed MAP values of 250 mm (\( E/I = 3.2 \)) and 700 mm (\( E/I = 1.3 \)) (ref. 60).

**Uncertainty in \( \varepsilon_{31/\text{model}} \) values.** We propagate uncertainty in \( \varepsilon_{\text{landscape}} \) values (95% confidence intervals, \( \sigma_{\text{landscape}} \)) using a linear combination of 95% confidence interval values for individual C\(_4\) graminoids (±8‰, \( \sigma_{\text{gram}} \)), C\(_3\) herbs (±10‰, \( \sigma_{\text{herb}} \)) and C\(_3\) woody plants (±8‰, \( \sigma_{\text{woody}} \)) and modeled annual \( \delta_{\text{D rain}} \) values (±6‰, \( \sigma_{\text{rain}} \)) (ref. 60). We account for uncertainty in \( \delta^{13}C_{31} \)-based estimates of relative plant functional type abundances (about 20%) (ref. 61) by multiplying respective standard error values by 1.2:

\[
\sigma^2_{\text{landscape}} = 1.2\sigma^2_{\text{gram}} + 1.2\sigma^2_{\text{herb}} + 1.2\sigma^2_{\text{woody}} + 3\sigma^2_{\text{rain}}
\]

Thus, \( \sigma_{\text{landscape}} \) is equal to about 20‰.

**Determination of environmental water \( \delta^{18}O \) values.** In this study, we use a single soil carbonate sample (nodule with sparry calcite) from the eastern lake-margin of Olduvai Gorge that has a \( \delta^{18}O \) value of −6.2‰ (62) to determine \( \delta^{18}O_{\text{rain}} \) values. We assume a mean annual soil temperature (MAst) of 25°C in order to calculate apparent fractionation values for oxygen isotopes between environmental water and soil carbonate minerals (\( \varepsilon_{\text{carb/water}} = (R_{\text{carb}} / R_{\text{water}}) - 1 \)) (refs. 62, 63). Uncertainty of ±5°C in MAsT results in about 1‰ uncertainty in \( \delta^{18}O_{\text{rain}} \) values.

We determine apparent fractionation values for oxygen isotopes between environmental water and clay minerals (\( \varepsilon_{\text{clay/water}} = (R_{\text{clay}} / R_{\text{water}}) - 1 \)) according to bond-type calculations of Savin and Lee (ref. 64) from structural formulas. Our determination of \( \delta^{18}O_{\text{lake}} \) values derives from a single sediment sample composed of 97% illite and 3% analcime (w/w). Mean annual temperature at Olduvai Gorge during the deposition of Bed I sediments has been estimated as 14-16°C (refs. 18, 62), as compared to about 22°C in the present, and we use 15°C to calculate
$\epsilon_{\text{clay/water}}$ values. Bulk clay minerals show a $\delta^{18}$O value of 27.1‰, to which we apply a $\epsilon_{\text{clay/water}}$ value of 24.8‰.
SI Figure 1: Published δD values for the lipids $nC_{31}$ (δD$_{31}$) and $nC_{29}$ (δD$_{29}$)(1-13), cross-plotted by photosynthetic pathway and growth habit.

- **C$_4$ graminoids**: $\delta D_{31} = 0.94 \delta D_{29} - 26\%$ \hspace{1cm} $r^2 = 0.88$
- **C$_3$ herbs**: $\delta D_{31} = 1.1 \delta D_{29} + 15\%$ \hspace{1cm} $r^2 = 0.88$
- **C$_3$ woody plants**: $\delta D_{31} = 1.0 \delta D_{29} + 1\%$ \hspace{1cm} $r^2 = 0.81$
SI Figure 2: Bathymetric contours (lines) and reconstructed salinity (shading) for paleolake Olduvai. Bold outlines represent ancient shorelines during expanded and contracted phases (18, 33, 66). Fish fossils constrain salinity to 20 ppt or less during maximum lake expansion (21-26), and we use 20 ppt for our conservative lake water evaporation model. Bathymetric contours occur at approximately 0.5 m intervals.
SI Figure 3: Modeled monthly $\delta$D$_{\text{rain}}$ values (44) versus measured monthly precipitation ($P$ in mm) (ref. 45) for rainy seasons from 48 stations in central eastern Africa (SI Figure 4). Short rains ($n=6200$) and long rains ($n=6335$) show amount effects of about $-0.125\%$ mm$^{-1}$:

‘Long rains’: $\delta$D$_{\text{rain}} = -0.132 P - 2\%$  
($r^2 = 0.87$; bold regression)

‘Short rains’: $\delta$D$_{\text{rain}} = -0.138 P - 12\%$  
($r^2 = 0.90$; dashed regression)

Bold vertical lines represent uncertainty in modeled monthly $\delta$D$_{\text{rain}}$ values (95% confidence interval) and dotted horizontal lines represent average monthly precipitation variability. Long rains include the months February (F), March (Ma), April (A) and May (M); short rains include the months September (S), October (O), November (N) and December (D) (refs. 46, 67).
SI Figure 4: Measured (65) versus modeled (44) monthly δD_{rain} values for eastern African sites with at least 2 years of rainy season precipitation data (Dar es Salaam, Tanzania; Entebbe, Uganda; Muguga, Kenya). One ‘short rains’ data point (marked x) has been omitted from linear regression analysis because it is an outlier (jackknife estimate).

‘Long rains’: Modeled δD_{rain} = 0.9621 δD_{rain} − 2‰  \quad (r^2 = 0.91; n = 12)

‘Short rains’: Modeled δD_{rain} = 0.9362 δD_{rain} − 3‰ \quad (r^2 = 0.80; n = 11)
**SI Figure 5:** Geographic locations of the 48 stations used to calculate amount effects for eastern Africa.
SI Figure 6: Alternative $\varepsilon_{\text{landscape}}$ values based on modified proportions of trees versus shrubs in $C_3$ woody plants. We use median $\varepsilon_{31/\text{model}}$ values for $C_4$ graminoids ($\varepsilon_{\text{gram}} = -146\permil$), $C_3$ non-woody plants ($\varepsilon_{\text{herb}} = -124\permil$), $C_3$ shrubs ($\varepsilon_{\text{shrub}} = -87\permil$) and $C_3$ trees ($\varepsilon_{\text{tree}} = -121\permil$) (refs. 1-13).

$$\varepsilon_{\text{landscape}} = f_{\text{gram}} \varepsilon_{\text{gram}} + f_{\text{herb}} \varepsilon_{\text{herb}} + f_{\text{shrub}} \varepsilon_{\text{shrub}} + f_{\text{tree}} \varepsilon_{\text{tree}}$$

Taken together, the $\varepsilon_{31/\text{model}}$ value for combined $C_3$ woody plants is $-109\permil$. Alternative scenarios yield $\varepsilon_{\text{landscape}}$ values that vary by up to $15\permil$, although differences are nominal for relative $C_3$ woody plant abundances of less than about 50%.
References.


