Ecosystem variability and early human habitats in eastern Africa

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The role of savannas during the course of early human evolution has been debated for nearly a century, in part because of difficulties in characterizing local ecosystems from fossil and sediment records. Here, we present high-resolution lipid biomarker and isotopic signatures for organic matter preserved in lake sediments at Olduvai Gorge during a key juncture in human evolution about 2.0 Ma—the emergence and dispersal of Homo erectus (sensu lato). Using published data for modern plants and soils, we construct a framework for ecological interpretations of stable carbon-isotope compositions (expressed as δ13C values) of lipid biomarkers from ancient plants. Within this framework, δ13C values for sedimentary leaf lipids and total organic carbon from Olduvai Gorge indicate recurrent ecosystem variations, where open C4 grasslands abruptly transitioned to closed C3 forests within several hundreds to thousands of years. Carbon-isotopic signatures correlate most strongly with Earth’s orbital geometry (precession), and tropical sea-surface temperatures are significant secondary predictors in partial regression analyses. The scale and pace of repeated ecosystem variations at Olduvai Gorge contrast with long-held views of directional or stepwise ari-diffic tion and grassland expansion in eastern Africa during the early Pleistocene and provide a local perspective on environmental hypotheses of human evolution.

Climate-dependent ecosystem characteristics, such as habitat and water availability, likely influenced natural selection during human evolution (1). For example, woody plants may have influenced thermoregulatory and dietary adaptations in hominins and other terrestrial mammals since the Pleistocene (2–4) about 2.6 Ma. Unfortunately, in many cases, reconstructions of ecosystem characteristics and climate at hominin archaeological sites are limited by poor preservation and coarse temporal resolution. Moreover, discontinuities are common in terrestrial sediment sequences. As a result, much of the environmental context of human evolution has been interpreted based on regional and global conditions reconstructed from marine records (5, 6).

The role of savannas in human evolution remains a subject of debate (5–8). This debate stems, in part, from the historically imprecise definition of savanna for modern and ancient ecosystems and the difficulties of estimating plant community compositions—particularly woody cover—from sediments. Recently, the work by Cerling et al. (7) estimated plant community compositions based on present day relationships between woody cover and carbon-isotope compositions for soil carbonates and soil organic matter (SOM). This approach offers insights into ecosystem structures at hominin archaeological sites (e.g., Omo-Turkana Basin), but it is limited to environments supporting ancient soils (paleosols).

Here, we extend the approach in the work by Cerling et al. (7) to include lipid biomarkers archived in lake sediments deposited between about 2.0 and 1.8 Ma at an important hominin archaeological site—Olduvai Gorge. In addition to including key junctures in human evolution (8), this time interval is associated with important changes in tropical climate, including strengthening of east–west (Walker) atmospheric circulation across the Indian and Pacific Oceans (9). Weakened Walker circulation before about 2.0 Ma was similar to conditions projected to accompany the continued rise in greenhouse gas concentrations during the coming century (10). To examine connections among ocean and atmospheric circulation, regional climate, and plant community composition, we also compare our organic carbon signatures to reconstructions of polar ice volume and sea-surface temperatures (SSTs) in the Atlantic and Indian Oceans.

Background

Site Descriptions. Olduvai Gorge is just south of the equator in northern Tanzania (2° 48′S, 35° 06′E), where it cuts across a 50-km rift platform basin to expose a 2.0 million y sequence of lake and river sediments (Fig. 1). The basin formed on the western margin of the East African Rift System in response to extension tectonics and the growth of a large volcanic complex (11, 12). During the early Pleistocene, the basin area covered an estimated 3,500 km2 and included a saline–alkaline lake near its center (12). Sediments from this central lake are composed primarily of reworked volcanic material and air-fall tuffs (11). For our study, we use samples recovered from outcrop exposures near the center of the paleolake that preserve a stratigraphic record of continuous deposition (11).

Today, annual precipitation patterns at Olduvai Gorge and surrounding regions of eastern Africa are defined by monsoon circulation by two major convergence zones (13)—the Intertropical Convergence Zone (ITCZ) and the Interoceanic Confluence (IOC). The ITCZ marks convergence of regional trade winds, whereas the IOC marks zonal confluence of water vapor derived from the Atlantic and Indian Oceans (Fig. 1). Seasonal migrations of the ITCZ and the IOC result in an annual cycle consisting of two rainy seasons separated by arid conditions that last from May to September. Long rains (March to May) produce the largest proportion of total annual precipitation; short rains (October to December) are more variable but also correlate with total annual precipitation (14). Today, Olduvai Gorge experiences mean annual precipitation (MAP) of about 550 mm; several independent proxy archives suggest that MAP ranged between about 400 and 900 mm during the early Pleistocene (15–17).

We compare our data with coeval records for alkane-de- riv ed SSTs from the eastern Atlantic and western Indian Oceans (18–20) (Fig. 1). Ocean Drilling Program (ODP) site 662 (1° 23′ S, 11° 44′ W, 3,824 m water depth) is in the eastern Atlantic Ocean


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in the Gulf of Guinea. ODP site 722 (16° 37′ N, 59° 48′ E, 2,028 m water depth) is in the northwestern Indian Ocean. Today, SSTs at both sites are sensitive to monsoon-driven seasonal upwelling (21–23), but surface sediment calibrations indicate that alkenone signals reflect mean annual SSTs (22, 23).

**Sedimentary Organic Matter.** Organic matter in lake sediments derives from bacteria, algae, and plants (24), and it integrates contributions from the surrounding watershed (25–28). In contrast, organic matter in soils depends more strongly on local sources and preservation (29, 30), and it can vary spatially over scales of 10 m^2 or less (25).

Biomarkers are molecular fossils that have structures with biological specificity (31). Those biomarkers from plants and algae carry isotopic signals derived from terrestrial and aquatic sources, respectively. For instance, long straight-chained hydrocarbons, such as nonacosane (nC29) and nC31, occur abundantly in leaves (32) and indicate sedimentary inputs from terrestrial plants (33). Although somewhat less specific, certain shorter-chained hydrocarbons (e.g., nC17 and nC19) indicate contributions from algae and cyanobacteria (31).

**Carbon Isotopes in Leaves, Biomarkers, and Soil Organic Matter.** Photosynthetic carbon-isotopic fractionation is defined between atmospheric carbon dioxide (δ^13C_{CO2}) and leaf tissues (δ^13C_{leaf}), and its magnitude varies with plant functional type and water availability (34, 35):

\[ \varepsilon_{\text{CO2/leaf}} = \left( \frac{\delta^{13}C_{\text{CO2}} + 1,000}{\delta^{13}C_{\text{leaf}} + 1,000} \right) - 1. \]

We note that ε-values are expressed in permil, which is a unit of parts per thousand. Variability in ε_{\text{CO2/leaf}}, which is approximately equivalent to negative Δ_{\text{leaf}} values (widely used in ecological literature) (34), is well-constrained for different photosynthetic pathways (35), but these modern relationships are not easily applied to ancient plants because of limited preservation of leaf tissues through time. Relatively recalcitrant leaf lipids, such as nC31, afford an opportunity to circumvent this challenge provided that fractionation between δ^{13}C_{\text{leaf}} and nC31 (δ^{13}C_{31}) during biosynthesis can be documented for subtropical and tropical plants (36).

We evaluated carbon-isotopic relationships between soil organic matter (δ^{13}C_{SOM}), leaf tissues, and leaf lipids using published data for 64 plant species and 288 soils from nearly 300 tropical and subtropical localities (Fig. 2). For C_3 plant soil systems, we find that nC31 is δ^{13}C-depleted by about 7‰ (n = 45) with respect to leaf tissue, whereas SOM is δ^{13}C-enriched by about 2‰ (n = 184) relative to leaves. Thus, in C_3 ecosystems, there is an isotopic difference (ε_{SOM31}) between nC31 and SOM equal to about 9‰:

\[ \varepsilon_{\text{SOM31}} = \left( \frac{\delta^{13}C_{\text{SOM}} + 1,000}{\delta^{13}C_{31} + 1,000} \right) - 1. \]
In C4 plant soil systems, both nC31 and SOM are 13C-depleted with respect to leaf tissue by about 10‰ (n = 19) and 1‰ (n = 104), respectively. Accordingly, δ13C_SOM equals about 9‰ in both C3 and C4 ecosystems. Individual boxes contain interquartile ranges (IQRs). Bold vertical lines within boxes mark median values. C, mean values. Horizontal whiskers mark minimum and maximum values, except values outside of 1.5 IQR (10). Notch half-width values indicate confidence in differentiating median values.

Here is based on data from xeric woodlands and shrublands, tropical deciduous forests, and C4 grasslands, and it may not be representative for other ecosystems (36).

The fractional abundance of C3 plants is inversely related to C4 plants in tropical ecosystems (25, 37). However, the relationship between woody cover (f_wood) and C4 abundance is non-linear (7), because herbaceous C3 plants can occur in both open and wooded ecosystems (38). As a result, for δ13C_SOM values between near-total C3 composition (−30‰) and negligible C3 cover (−14‰), we follow the approach in the work by Cerling et al. (7) to estimate f_wood (where −13 ≤ δ13C_SOM ≤ −31‰):

f_wood = (sin(−1.06688 − 0.08538 δ13C_SOM))^2.

Structural Classification for Ancient Ecosystems. The broad functional definition for savannas as a continuous herbaceous understorey with irregular distributions of trees or bushes does not account for differences in f_wood (39). Therefore, we adopt definitions for African plant communities defined by the United Nations Educational, Scientific and Cultural Organization (UNESCO) (40). According to this classification scheme, (i) forests display continuous tree cover (>10 m) with interlocking crowns and poorly developed understorey, (ii) woodlands—including bush/shrublands—display open or closed stands of shrubs or trees (up to 8 m) with at least 40% woody plant cover and understorey with grasses and other herbs, (iii) wooded grasslands display 10–40% woody plant cover and well-developed groundcover with grasses and other herbs, (iv) grasslands display less than 10% woody plant cover and well-developed groundcover with grasses and other herbs, and (v) deserts display sparse groundcover and sandy, stony, or rocky substrate. UNESCO does not distinguish between forests and woodlands in terms of woody plant cover, but here, we consider forests to display greater than 80% woody plant cover (7, 39).

The evolutionary implications of orbital forcing on environmental change were recognized over a century ago (41) but remain controversial today (3–6). Marine sediments just off African
shores document orbital rhythms in terrestrial inputs during the Pleistocene (5), and a growing number of terrestrial sequences hint at a similar pacing for environmental changes in eastern Africa (42, 43). Marine sequences are often indirectly or too poorly constrained in time to infer relationships between key junctures in human evolution and terrestrial conditions or change (6). Lithostratigraphic patterns in lake margin sediments at Olduvai Gorge reveal five episodes of lake expansion between ca. 1.85 and 1.74 Ma, suggesting that lake level changes may have tracked orbital precession (43). Here, we use sedimentary organic matter signatures in high-resolution and temporally well-constrained lake sediments to evaluate the magnitude and timing of ecosystem changes associated with lake level changes.

Results and Discussion

Ecosystem Change and Woody Cover. We observe repeated shifts in $\delta^{13}$C$_{C13}$ values between about $-36\%$ and $-20\%$ (Fig. 4), which track closely with orbitally paced lake margin lithostratigraphic patterns, suggesting that ecosystem changes at Olduvai Gorge were also influenced by orbital cycles (Fig. 5). Total organic carbon (TOC) $\delta^{13}$C values ($\delta^{13}$C$_{TOC}$) show a smaller isotopic range of about $9\%$ and correlate tightly with $\delta^{13}$C$_{C13}$ values ($r^2 = 0.86$); $\delta^{13}$C$_{TOC}$ values follow terrestrial plant inputs but are attenuated, likely by algal or macrophytic inputs. Taken together, $\delta^{13}$C$_{C13}$ and $\delta^{13}$C$_{TOC}$ values suggest rapid local ecosystem shifts between closed C$_3$ woodlands and open C$_4$ grasslands. These changes were comparable with extreme events, such as the greening of the Sahara about 120,000 y ago, that accompanied the dispersal of modern humans out of Africa (44).

Carbon-isotope evidence for pronounced ecosystem shifts at Olduvai Gorge contrasts with previous reconstructions for eastern Africa that proposed that ecosystems were stable at local to regional scales in the early Pleistocene (15, 45, 46) and generally lacked closed woodlands near hominin archaeological sites since 6 Ma (7). Dramatic and rapid changes in $\delta^{13}$C$_{C31}$ values highlight ecosystem instability in this region; furthermore, $\delta^{13}$C$_{C13}$ values indicate that closed woodlands dominated local landscapes for up to 20% of the time.

Differences in the interpretation of ancient ecosystems, in addition to problems related to savanna heterogeneity, can stem from inherent proxy biases (6). For instance, $\delta^{13}$C$_{SOM}$ values can overrepresent C$_4$ inputs as a result of $^{13}$C enrichment during organic matter decomposition (47). Values for $\delta^{13}$C$_{C31}$ can also overrepresent C$_3$ inputs as a result of inorganic carbon (e.g., bicarbonate) assimilation by macrophytes, although $\delta^{13}$C$_{C31}$ values in arid environments are more likely biased to wet conditions (when plants synthesize most leaf lipids) (48). Although specific mechanisms responsible for differences among ecosystem proxies cannot necessarily be reconciled here, we suggest that carbon-isotopic signals for leaf lipids can complement $\delta^{13}$C$_{SOM}$ values, which otherwise can skew to C$_4$—and thus, arid—signals on seasonal and longer timescales.

Biogeochemical Variability at the Ecosystem Scale. Organic matter in lake sediments incorporates inputs from both aquatic and terrestrial photosynthetic organisms and can vary in proportion with productivity and deposition in a lake and the surrounding watershed. At Olduvai Gorge, $\delta^{13}$C$_{TOC}$ values correlate strongly with TOC ($\%$TOC; $r^2 = 0.84$) but show no clear relationship with algal vs. terrestrial plant inputs (Fig. 4):

$$P_{al} = \frac{(nC_{17} + nC_{19})}{(nC_{17} + nC_{19} + nC_{29} + nC_{31})}.$$ 

The abundance ratio of pristane vs. phytane is constantly near 2.5, suggesting that organic carbon deposition was dominated by terrestrial plant input (31). These observations corroborate strong

![Fig. 4. Biomarker and isotopic signatures for organic matter preserved in lake sediments at Olduvai Gorge. (A) Leaf lipid $\delta^{13}$C values for nC$_{17}$ ($\delta^{13}$C$_{fl}$). (B) TOC $\delta^{13}$C values ($\delta^{13}$C$_{TOC}$). (C) TOC percentages (%TOC). (D) Diagrammatic depiction of relative lake level changes at Olduvai Gorge based on lake margin lithostratigraphy (43). (E) Ratios of algal lipids (nC$_{17}$ + nC$_{19}$) relative to algal and terrestrial plant lipids (nC$_{17}$ + nC$_{19}$ + nC$_{29}$ + nC$_{31}$). Higher values reflect relatively increased algal inputs (31). (F) Ratios of pristane (Pr) to phytane (Ph) in lake sediments, values above two generally reflect a dominance of terrestrial plant inputs (31). (G) Ratios of macrophytic lipids (nC$_{23}$ + nC$_{29}$) relative to macrophytic and terrestrial plant lipids (nC$_{23}$ + nC$_{29}$ + nC$_{29}$ + nC$_{31}$; that is, $P_{pr}$. Higher values reflect relatively increased macrophytic inputs (50). (H) Values of $\delta^{13}$C for the macrophytic lipid nC$_{29}$ ($\delta^{13}$C$_{Paq}$). Horizontal gray bands highlight periods of time characterized by $\delta^{13}$C$_{C31}$ values higher than about $-28\%$ (i.e., open grassland and wooded grassland ecosystems).]
weakly with both chemical signals. Identifying organic facies or correlations with other biogeochemical and paleoecological proxies is challenging. Instead, these ratios are useful for estimating the relative paleo-abundance of different classes of molecules. They do not directly indicate a proportion of biotic contributions, although they can be informative about ecosystem changes. In lake sediments from Olduvai Gorge, δ13C values for macrophytes (e.g., nC23 and nC25) but limited long-chain homologs compared with terrestrial plant inputs (50):

\[ P_{\text{m}} = \frac{(nC_{23} + nC_{25})}{(nC_{23} + nC_{25} + nC_{29} + nC_{31})} \]

In lake sediments from Olduvai Gorge, δ13C values correlate weakly with both \( P_{\text{m}} \) (\( r^2 = 0.17 \)) and \( nC_{25} \) δ13C values (\( r^2 = 0.19 \)), suggesting that macrophytes did not significantly contribute to terrestrial plant inputs (50). \( P_{\text{m}} \) and \( P_{\text{alg}} \) are measures of relative abundance of molecules. They do not directly indicate a proportion of biomass from different organisms; instead, these ratios are useful for identifying organic facies or correlations with other biogeochemical signals.

**Mechanisms of Ecosystem Change.** Atmospheric \( p\text{CO}_2 \) concentrations, temperature, seasonality, and water availability are potential determinants of \( C_3 \) vs. \( C_4 \) plant abundance (38). Since the mid-Pleistocene, records of \( p\text{CO}_2 \) correlate strongly with polar ice volume changes (51, 52), which were obliquity paced before ~1 Ma (5). Lake sediment δ13C values for Olduvai Gorge correlate weakly with reconstructed polar ice volumes (\( r^2 = 0.16 \)) based on marine oxygen-isotopic records (9, 19), suggesting that ecosystem changes in this region did not track 41,000-yr glacial cycles. If polar ice volume is a representative proxy for \( p\text{CO}_2 \) during the early Pleistocene, then local ecosystem changes were not exclusively tied to \( p\text{CO}_2 \) changes. This conclusion contrasts with suggestions of a dominant role for \( p\text{CO}_2 \) in southern African ecosystems during the early Pleistocene based on speleothem carbonate δ13C values (53), but it is in agreement with marine oxygen-isotopic evidence for eastern African climate sensitivity to polar ice volume only after 1.0 Ma (54). Values for δ13C values correlate strongly with precession (\( \omega_p \)) and thus, do not support
temperature as primary determinant of ecosystem change, because $\omega_p$ negligibly influences mean annual temperatures (55). Similarly, paleosol carbonates indicate that mean annual temperatures varied by less than about $\pm 5^\circ$C at and around Olduvai Gorge during the early Pleistocene (56, 57). Strong correlation between $\delta^{13}C_{\text{TOC}}$ and $\omega_p$ also suggests that biotic (e.g., herbivory) or abiotic disturbances, such as fire, were not primary determinants of ecosystem change, although they may have served as feedback mechanisms that accelerated changes. In agreement with a variety of other studies (58, 59), we suggest that changing $C_3$ and $C_4$ plant abundances at Olduvai Gorge varied with orbital precession in response to water availability.

Mechanisms of Hydroclimatic Change. Cycles of about 21,000 yr are common in a variety of hydroclimatic proxy records in eastern Africa since the Pliocene (5), and $\delta^{13}C_{\text{TOC}}$ values correlate strongly with $\omega_p$ ($r^2 = 0.61$) in single-factor regression (SI Appendix). Although specific mechanisms responsible for these cycles remain unclear, the timing and magnitude of local and regional hydroclimatic changes are consistent with theoretical effects of $\omega_p$ on monsoon strength (60) (that is, higher summer insolation would enhance land–ocean temperature contrasts, resulting in stronger monsoons and increased precipitation).

Insolation alone cannot account for the magnitude of hydroclimatic change in eastern Africa (61). Previous reconstructions based on pollen and oxygen-isotope compositions of soil carbonates suggest that MAP fluctuated between ~400 and 800 mm at Olduvai Gorge and surrounding regions during the early Pleistocene (15–17, 43). However, in climate simulations, insolation variability accounts for MAP fluctuations of less than 200 mm and mostly affects long rains (60, 61). Thus, precipitation amounts in the past must have been impacted by multiple factors, the same as they are today (13).

Today, precipitation in eastern Africa responds sensitively to SSTs in the Indian Ocean and Atlantic Ocean (62). In particular, intensifications of short rains (up to 200 mm) accompany coordinated warm and cold SST anomalies in the western Indian Ocean and eastern Atlantic Ocean (63–65), respectively, as a result of transcontinental surface pressure gradients across Africa and monsoon displacement of the IOC from west to east (66). Partial regressions reveal that SSTs for ODP sites 662 (SST662) and 722 (SST722) are significant ($P < 0.01$) secondary predictors that are statistically independent of covariance with $\omega_p$ and the combination of $\omega_p$, SST662, and SST722 explains 73% of the variability in $\delta^{13}C_{\text{TOC}}$ values in a multiple regression model. During the early Pleistocene, both SST662 and SST722 show strong $\omega_p$ and 41,000-yr (obliquity) periodicity (20), but only SST662 shows a consistent relationship with monsoon-driven upwelling (20). Because upwelling in the eastern Atlantic correlates positively with monsoon strength during late boreal summer (20–22), we suggest that obliquity-paced cooling in the eastern Atlantic Ocean and monsoon strengthening (and therefore, stronger westerly winds) resulted in more frequent eastward displacements of the IOC and intensification of short rains in eastern Africa.

Ecosystems and Hominin Evolution. Fossil evidence for pronounced aridification and faunal turnover in eastern Africa between about 2.0 and 1.8 Ma has sparked hypotheses linking the emergence and dispersal of the genus Homo to climate-driven ecosystem change (2–6). Fossil evidence for cranial expansion in premontane Homo (e.g., H. erectus sensu lato) has been linked to irregular resource distributions (67), and our carbon-isotopic data are consistent with enhanced ecosystem variability as a context for encephalization (Fig. 5). During the early Pleistocene, strong ecosystem preferences are not apparent between transitional (e.g., H. habilis) and archaic (e.g., Paranthropus boisei) hominins (68); however, isotopic and fossil data suggest that transitional species accessed a broad spectrum of dietary resources compared with archaic species (68–70). Among primates, quality (i.e., energy density) of dietary resources correlates strongly with brain size (67). Assuming that dietary resources were primarily unrelated to technological innovations by transitional species (4, 68), we hypothesize that ecosystem variability favored hominin species with large brains that allowed for versatile foraging strategies and dietary diversity.

Conclusions

This study presents high-resolution biomarker and $\delta^{13}C$ records of ecosystem variability from lake sediments at Olduvai Gorge that were deposited during an interval of pronounced shifts in vertebrate community and global climate reorganization about 2.0–1.8 Ma. Values of $\delta^{13}C_{\text{TOC}}$ indicate rapid and repeated ecosystem restructuring between closed $C_3$ woodlands and open $C_4$-dominated grasslands. Our $\delta^{13}C$ records reveal coupled fluctuations between ecosystem and precession. Additional variability is explained by differences in SST between the Atlantic and Indian Oceans. These observations suggest aridity-controlled, as opposed to carbon dioxide- or temperature-controlled, woody plant cover in eastern Africa during the early Pleistocene. We conclude that highly variable ecosystems accompanied the emergence and dispersal of the genus Homo. Our study also builds on soil data to construct an interpretive framework for ecosystem reconstruction based on leaf lipids.

Materials and Methods

Reconstructions for Polar Ice Volume. We use the approach in the work by Bintanja and van de Wal (71), which assumes that a global composite record of benthic $\delta^{18}O$ values (LR04 Stack) accurately tracks polar ice volume during the early Pleistocene (19).

Multiple Regression Analysis. We used rank transformation (72) and Fourier cross-correlation (73) to compare nonlinear, time-shifted, and unevenly sampled proxy records (SI Appendix). Because $\omega_p$ correlates most strongly with $\delta^{13}C_{\text{TOC}}$ in single-factor analyses ($r^2 = 0.61$), we constrain multiple regression models for $\delta^{13}C_{\text{TOC}}$ values to always include $\omega_p$. This approach is justified, because the influence of $\omega_p$ on climate in eastern Africa is well-supported by theory and other observations (10, 61). Because $\omega_p$ is correlated with other factors, care is required in evaluating additional influences on $\delta^{13}C_{\text{TOC}}$ values. We assessed the influence of other factors on $\delta^{13}C_{\text{TOC}}$ values using multivariate partial regression models that account for covariance between $\omega_p$ and other factors. Partial regression models with SST662 (partial $r^2 = 0.17$) and SST722 (partial $r^2 = 0.11$) as secondary predictors are the only models with notable explanatory power for $\delta^{13}C_{\text{TOC}}$ values. The following equation shows the $\delta^{13}C_{\text{TOC}}$ relationship shared with $\omega_p$, SST662, and SST722 ($r^2 = 0.73$):

$$
\delta^{13}C_{\text{TOC}} = 34.7 (\pm 2.9) + 1.4 (\pm 0.1)\text{SST662} - 1.4 (\pm 0.2)\text{SST722} - 20.6 (\pm 6.8).
$$

Lipid Extraction and Purification. Freeze-dried and ground lake sediments were Soxhlet-extracted with dichloromethane:methanol (9:1 vol/vol) for 12 h. Total lipid extracts were then separated into apolar and polar fractions over alumina with hexanes and methanol, respectively. Apolar molecules were separated into saturated and unsaturated fractions over 5% (wt/wt) silver nitrate-imregnated alumina with hexanes and dichloromethane, respectively. Finally, unsaturated apolar compounds were separated with a 5-Å molecular sieve to isolate n-alkanes.

Isotopic Analysis. All $\delta^{13}C_{\text{TOC}}$ values were measured after decarbonation of ground lake sediments with excess 2N hydrochloric acid (74). Residual materials were combusted in an elemental analyzer, and $\delta^{13}C_{\text{TOC}}$ values were measured in a ThermoFinnigan Delta+ XP. Standard reference materials of known $\delta^{13}C_{\text{TOC}}$ values, including polyethylene foil (NIST 8540), were used throughout sample runs to ensure accuracy. SD (1σ) equaled 0.3%.
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Supporting Information Appendix

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</table>

$^a$Positive shifts indicate time-lag in relation to $\delta^{13}$C$_{TOC}$ values.

$^b$Polar ice volumes from global benthic $\delta^{18}$O$_{LR04}$ values (12).
Dataset description. We review 38 references to form a compilation of $\delta^{13}$C values for soil organic matter ($\delta^{13}$C$_{\text{SOM}}$), leaf tissues ($\delta^{13}$C$_{\text{leaf}}$) and leaf lipids ($\delta^{13}$C$_{\text{31}}$) that includes 64 plant species and 288 soils and from over 289 subtropical and tropical geographic sites (13-50). Data derive from sites with mixed C$_3$/C$_4$ ecosystems and mean annual precipitation of 250 to 5000 mm. Means were calculated for plant species or soil cores (0-10 cm) for each site to remove internal variability. We caution that our $\varepsilon_{\text{SOM/31}}$ values are not necessarily applicable on a global scale and future additions to our compilation will provide additional refinements for our calculations.

Age estimates and model uncertainties. We construct an age model for lake sediments from Olduvai Gorge using dated tie points for Bed I sediments (SI Figure 1). Individual ages derive from $^{40}$Ar/$^{39}$Ar dating, tephrocorrelation or magnetic stratigraphy, or a combination of techniques (1-8). Sediments from Bed I at geologic locality 80 do not show evidence for depositional hiatuses or surface erosion (1,5); therefore, we adopt the approach of Hay and Kyser (ref. 5) and apply consistent sedimentation rates for non-tuff sediments between dated tie points.

We do not orbitally-tune our record because local conditions at Olduvai Gorge may not be regionally or globally correlative (51). Using this strategy, we also avoid any assumptions about phase relationships between the effects of $\omega_p$ on seasonal solar heating (insolation) and hydroclimate change (52). Nevertheless, $\omega_p$ shows tight amplitude modulation with $\delta^{13}$C$_{\text{TOC}}$ values (SI Figure 2).

We use the approach of Bintanja and van de Wal (ref. 53) and assume that a global composite record of benthic $\delta^{18}$O values (LR04 Stack) traces polar ice volume during the early Pleistocene (12).

We use previously published age models for Ocean Drilling Program (ODP) sites 662 and 722 as constructed from $\delta^{18}$O values, biological and magnetic stratigraphy (10-12). Both ODP records are orbitally-tuned with respect to the LR04 Stack (12). However, absolute differences between orbitally-tuned age estimates and depth-derived age estimates (54) average less than 0.002 Ma.

We interpolate SST records at an interval of 2.0 kyr. Interpolation follows original sampling resolutions for site 662 (1.8 kyr) and site 722 (2.0 kyr), corresponding to average
sedimentation rates of about 6.7 and 3.1 cm kyr\(^{-1}\), respectively (10-12). Models for both sites yield age estimates in close agreement with well-constrained radiometric ages for the top (1.778 ± 0.003 Ma) and bottom (1.945 ± 0.004 Ma) of the Olduvai subchron (55).

**Correlation and regression analyses.** Proxy records (time series) from terrestrial and marine sediments are difficult to compare, in part, due to methodological differences for estimates of age and age uncertainty. For instance, time series from terrestrial sediments often cannot be orbitally-tuned because of ambiguity regarding phase-relationships or correlations between local, regional and global signals (51-56). Time series from marine sediments can be orbitally-tuned, but ambiguity about phase-relationships persists because of ambiguous synchronicity between local, regional and global signals (51, 57).

Precise phase-relationships remain unresolved in the absence of a common absolute timescale (51, 54), but we compare time series from terrestrial and marine sediments using rank- and Fourier transformation methods. We use rank-transformations to account for asymmetric and uneven data distributions and to provide robust estimates (Spearman) for monotonic relationships between time series (58). We estimate average time-lags between rank-transformed time series using cross-correlation, which measures how closely two signals resemble each other when shifted forward or backward through time (SI Figure 2). A robust approach for calculating cross-correlations between uneven time series is with the Lomb-Scargle algorithm for Fourier transformation (59):

\[
r_{\alpha\beta}(\tau) = FT^{-1}(FT\{\alpha\} FT^*\{\beta\})
\]

The terms \(FT\), \(FT^*\) and \(FT^{-1}\) denote a Fourier transform, its complex conjugate and inverse, respectively, and \(r_{\alpha\beta}(\tau)\) is the peak cross-correlation between \(\alpha\) and \(\beta\) at a time-lag of \(\tau\) kyr. Then, we evaluate cross-correlations between time series for lags from −10 to 20 kyr to calculate peak cross-correlations (SI Table 1):

\[
peak\ cross\-correlation = \max\{r_{\alpha\beta}(\tau)\}
\]

We use rank- and Fourier transformed time series at peak lags for our multivariate partial regression models (60). In all cases, peak lags occur in less than 5 kyr, and we conclude that correlations between \(\delta^{13}C_{TOC}\) and \(\omega_P\), \(SST_{662}\) and \(SST_{722}\) (10-12) and reconstructed polar ice
volumes from global benthic \( \delta^{18}O \) values (12) are robust within depth-derived age uncertainties for dated tie points (SI Figure 1).
References.


44. Terwilliger V, et al. (2008) Reconstructing palaeoenvironment from $\delta^{13}$C and $\delta^{15}$N values of soil organic matter: a calibration from arid and wetter elevation transects in Ethiopia. *Geoderma* 147:197.


