East African megadroughts between 135 and 75 thousand years ago and bearing on early-modern human origins

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The environmental backdrop to the evolution and spread of early Homo sapiens in East Africa is known mainly from isolated outcrops and distant marine sediment cores. Here we present results from new scientific drill cores from Lake Malawi, the first long and continuous, high-fidelity records of tropical climate change from the continent itself. Our record shows periods of severe aridity between 135 and 75 thousand years (kyr) ago, when the lake's water volume was reduced by at least 95%. Surprisingly, these intervals of pronounced tropical African aridity in the early late-Pleistocene were much more severe than the Last Glacial Maximum (LGM), the period previously recognized as one of the most arid of the Quaternary. From these cores and from records from Lakes Tanganyika (East Africa) and Bosumtwi (West Africa), we document a major rise in water levels and a shift to more humid conditions over much of tropical Africa after \approx 70 kyr ago. This transition to wetter, more stable conditions coincides with diminished orbital eccentricity, and a reduction in precession-dominated climatic extremes. The observed climate mode switch to decreased environmental variability is consistent with terrestrial and marine records from in and around tropical Africa, but our records provide evidence for dramatically wetter conditions after 70 kyr ago. Such climate change may have stimulated the expansion and migrations of early modern human populations.

human origins | Lake Malawi | paleoclimate | Pleistocene

he tropics are the heat engine that drives global circulation, as most solar energy received at the top of the atmosphere strikes the tropical latitudes. The climate behavior of the tropical ocean is well documented (1-4), but detailed records of the continental response to tropical climate change, especially from the low latitudes in Africa, are either relatively short (5, 6) or well dated, but punctuated (7, 8). The longest, most continuous signals of African climate variability have been extrapolated from distant marine sediment cores (9-11). Here we report continental evidence for several periods of pronounced tropical African aridity in the late-Pleistocene, surprisingly much drier than the Last Glacial Maximum (LGM), interpreted from recently acquired tropical lake drill cores. These events are potentially important benchmarks of climate change for interpreting the history of early modern human migrations and population dynamics (12-16) and understanding the evolution of extant endemic species of Africa (17).

The climate of tropical Africa is dominated by variability in effective moisture, rather than temperature as in higher latitudes, and is driven by the circulation of the African monsoon and the seasonal migration of the Intertropical Convergence Zone. In West Africa, the monsoon transfers moisture to the continental interior from the equatorial Atlantic, whereas East African moisture is obtained mainly from the Indian Ocean (18). Orbital precession has induced 19- to 23-thousand-year (kyr) fluctuations in insolation at the top of the atmosphere, and has prompted changes in tropical African climate during the Pleistocene (9-11, 19, 20). However, this forcing is moderated at times by tropical sea-surface temperatures (SSTs), which may be linked to high-latitude climate processes (21, 22). The variability of tropical African continental climate is documented over the past 25 kyr in lake and ocean sediment cores, as is the orbital forcing of North African climate (23). The modern precipitation of East Africa is linked to Indian and Pacific Ocean SSTs and the El Niño Southern Oscillation (ENSO) (18, 24), whereas the long-term forcing of equatorial East African climate has been attributed both to orbital processes (e.g., precession) (25) and to variations in ice volume at high latitudes (19). For instance, well dated deltaic deposits of the Kibish Formation appear to correlate to Mediterranean sapropels (8), which are controlled by insolation variations induced by orbital precession (9). However, subtropical North African, Arabian Sea, and Indian monsoon climate records suggest that ice volume exerts greater control on climate in those areas (26). Our work provides detailed, continuous records from the tropical latitudes of East Africa that help to constrain the history of climate controls in this region.

Long Lacustrine Records of Tropical African Climate

Lacustrine deposits provide long, continuous records of terrestrial climate change, and tropical lakes, because they are commonly perennially stratified with anoxic bottom waters, may GEOLOGY

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Abbreviations: LGM, Last Glacial Maximum; kyr, thousand years; TOC, total organic carbon. ^bTo whom correspondence should be addressed. E-mail: cascholz@syr.edu.

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Fig. 1. Study site locations in Africa. Bathymetric maps of Lakes Malawi, Tanganyika, and Bosumtwi showing locations of cores. Lake Bosumtwi contour interval, 10 m; solid line shows seismic profile location shown in Fig. 2. Shaded areas on Malawi and Tanganyika maps show the maximum extent of lowstand lakes described in text. (*Upper Inset*) Lake locations along with maximum northern and southern extent of the Intertropical Convergence Zone, as well as the location of Atlantic Ocean core GeoB 1016 (asterisk) on the Angola margin.

preserve finely laminated, high-resolution records. Lakes Malawi and Tanganyika in the East African Rift Valley are among the world's deepest and oldest lakes; together they span 11° of latitude in southern tropical East Africa and contain >80% of the surface freshwater on the African continent [supporting information (SI) Text]. In 2005, we drilled a series of continuous cores in Lake Malawi, which provides a highresolution sampling of southeast African climate over the past ≈1 million years. A similar program in West Africa in 2004 sampled sediments from Lake Bosumtwi, an 8-km diameter, 78 m deep, meteorite impact crater lake in Ghana. The sedimentary section of Lake Bosumtwi (6° N) consists of mostly laminated sediments, recording a 1.1-million-year history of the West African monsoon system. Lake Bosumtwi and its drainage basin sample only a small area of West Africa compared with Lake Malawi's extensive drainage, but the lake contains a proven archive of late-Quaternary climate variability (6). Finally, we also acquired a low-resolution sediment record that spans the past ≈ 100 kyr from a slow sedimentation rate site on an interbasinal ridge in Lake Tanganyika (Fig. 1). These three sets of lake cores provide temporally continuous and unprecedented spatial coverage of tropical African climate; here we consider the climate variability of this system over the past \approx 145 kyr from the Lake Malawi record, and over the past \approx 75–100 kyr from Lake Tanganyika and Lake Bosumtwi cores. We identify a series of low lake intervals in the Malawi record, and depth-calibrate the lake level history by correlating the geochemical and biostratigraphic anomalies in the dated cores to lowstand delta deposits observed in seismic reflection data (*SI Text*).

A Pan-African Climate Transition at \approx 70 kyr Ago

Nested seismic reflection site surveys were conducted in all three lake basins before drilling expeditions (SI Text), and the resulting seismic profiles show evidence for pronounced fluctuations in lake levels (Fig. 2). In each of the lakes, relatively shallow depositional sequence boundaries are observed and defined by erosional truncation of seismic reflections. Additionally, the uppermost depositional sequences in each lake basin are characterized by very low seismic amplitudes relative to deeper intervals (Fig. 2). The low amplitudes in the upper sequences correlate in sediment cores to hemipelagic silty clays characterized by low-density, high water content, which are commonly laminated. In contrast, the high-amplitude reflections that delineate the sequence boundaries are produced by high-density sediments, with low-water and low-organic carbon contents, or in the case of northern Lake Malawi, medium-grained and well sorted transgressive sands. Prominent angular unconformities are observed near the drill sites at subbottom depths of 38 m, 32 m, and 9.5 m in northern Lake Malawi, Lake Bosumtwi, and Lake Tanganyika, respectively (SI Text).

Lithostratigraphy, total organic carbon content (TOC), and saturated bulk density observed downcore in the three lakes constrain the first-order environmental variability over the past ≈ 100 kyr (Fig. 3) (*SI Text*). Ages on these cores were determined by accelerator mass spectrometry radiocarbon dating of bulk organic matter and luminescence dating (*SI Text* and SI Tables 1 and 2).

Drill site 2A in Lake Malawi is located in the northern basin of the lake, in 359 m of water (Fig. 1). Lake Malawi is perennially stratified and anoxic below 200-250 m water depth (27), and preserves thick intervals of laminated mud lacking benthic invertebrates (Fig. 3). The lithostratigraphy of site 2A consists of laminated and homogenous hemipelagic muds in the upper 36 m of the core, where TOC values average 2-5%. From 28.0-29.7 and 34.5-37 m subbottom, the fine-grained muds are enriched in carbonate due to the presence of authigenic calcite; the lower of these carbonate-rich sequences overlies a 2-m section of well sorted, medium-grained sand. Seismic reflection data acquired adjacent to this site reveal a series of buried progradational, lowstand delta deposits laid down during earlier stages of Lake Malawi (SI Text). Based on correlation to these low lake level indicators, the sand deposit observed in Malawi site 2A represents a transgressive sand sheet laid down when lake level rose from a low of 350 m below modern lake level, to a still stand \approx 200 m below modern lake level. Subsequently, lake level rose to close to the modern level between ≈ 50 and 35 kyr ago, then fell to 100 m below modern during the last glacial maximum, before rising to the modern highstand (SI Text). A very similar shallow unconformity and lithologic sequence is also observed in Lake Tanganyika (Fig. 3) (SI Text).

Drill site 5B in Lake Bosumtwi is situated near the center of the lake, in 74 m of water (Figs. 1 and 2) (28). Because Lake Bosumtwi rests within a young impact crater with a well defined rim, its drainage basin is limited and the drill site is dominated by hemipelagic sedimentation. The lake is presently closed and eutrophic, although during the early Holocene the lake overflowed the crater rim, producing a 211-m-deep lake (6). The water column is anoxic below 15 m depth, yielding thick intervals of varved sediment. The upper 32 m of sediment at drill site 5B in Lake Bosumtwi consists mainly of well laminated, organicrich, silty clay, containing an average TOC of \approx 5–15% (Fig. 3). From 3–5.5 m subbottom, we observe a section of dark grayblack homogenous mud with very high TOC values (>20%),



Lake Malawi Drill Site MAL05-2A

b 70 m water depth 32 m subbottom, (77.9+/ 6.1 kYr) 0.5 km 150 m subbottom

Lake Bosumtwi Drill Site BOS04-5B



Fig. 2. Cross-sections of shallow unconformities and drill sites. Yellow bars on seismic profiles indicate drilled extent at each location. (a) Lake Malawi site MAL05-2A. (b) Lake Bosumtwi site BOS04–5B. (c) Lake Tanganyika site T97-52V. (Insets) Full seismic profiles. Green arrows indicate reflection terminations diagnostic of subaerial exposure. Ages (kyr BP) of unconformities are shown in parentheses. (b Inset) The drill site location relative to annular moat of impact structure is shown; dashed line is the sediment-impact rock interface. See *SI Text*, SI Figs. 5–7, and SI Tables 1–3 for additional details.

which was deposited during the warm, humid, highstand conditions operative during the early Holocene (6, 23). Below 32 m subbottom, lithology, physical properties, and TOC change dramatically, with the section from 32-34 m containing dense, massive blue–gray clay, TOC values <1% and bulk density increasing 60% over background values. These profound contrasts in sedimentary properties, in conjunction with the erosional unconformity identified in seismic reflection data, indicate lake-wide desiccation during this interval.

The sampled unconformities documented in the seismic data and three sediment cores are dated by optically stimulated luminescence samples below the discontinuities, at 74.2 ± 5.3 kyr B.P. in Lake Malawi, 77.9 ± 6.1 kyr B.P. in Lake Bosumtwi, and 97.3 ± 5.7 kyr B.P in Lake Tanganyika (Figs. 2 and 3, and *SI Text* and SI Table 2). These ages are corroborated by linearly consistent radiocarbon ages in the uppermost sections of each core (Fig. 3 and *SI Text*). These stratigraphic surfaces document the dramatic rise in lake levels after 70 kyr ago, following the complete desiccation of Lake Bosumtwi, and lowstands lower than -350 m in Lake Malawi and -390 m in Lake Tanganyika. Based on hydrologic modeling of the three basins, the low lake stages reflect reduced net precipitation (P–E) of >65% in Bosumtwi and $\approx 60\%$ in Malawi and Tanganyika (29–31) (*SI Text*) relative to modern mean values.

East African Climate During the Past 145 kyr

To determine the duration of the severe low lake stands in East Africa, we examined drill site 1 in Lake Malawi, located in 593 m of water in the lake's central basin (Fig. 1) in a locality that was mainly submerged for the past ≈ 1 million years (SI Text). Age dates on this core were determined primarily by accelerator mass spectrometry radiocarbon dating of bulk organic matter and paleomagnetic and ¹⁰Be analyses, supplemented by a few luminescence dates (SI Text, SI Figs. 5 and 6, and SI Tables 1 and 2). The upper 35 m of core consists of massive and laminated organic-rich silty clays, which overlie a 4-m-thick unit of low-TOC, high Ca-carbonate, blue-gray massive clay that is correlative to the transgressive sand deposit observed at the base of site 2 cores in northern Malawi (Figs. 1 and 2). Between 35 and 88 m subbottom (the base of core 1C), we observe several intervals of dense, organic-poor, calcareous silty clay with abundant benthic ostracodes, indicative of dramatically lower lake levels (Fig. 4). The -350 m lowstand interval persisted from $\approx 78-74$ kyr ago (Fig. 4), based on hole 1C lithostratigraphy, physical properties, Ca and ostracode abundance, and our age model (Fig. 4 and SI *Text* and SI Fig. 6). Lake level subsequently rose to the -200 mlevel and stabilized briefly from 62-64 kyr ago, corresponding to the upper carbonate-rich sequence in the north basin, before the water level rise that led eventually to current hydrologically open conditions (Fig. 4). This and other low lake stage intervals interpreted from Malawi core 1C are depth-calibrated by correlation to lowstand delta deposits observed in seismic data and through examination of ostracode taxa within Malawi core 1C (SI Text and SI Fig. 7). Underlying the distinctive blue-gray clay layer at 38-41 m at site 1C is a 3.5-m-thick interval of dark laminated muds that reflects relatively higher lake levels between \approx 78 and \approx 85 kyr ago. Below this interval, we observe a 22-m-thick interval of dense, gray-blue, ostracode-rich, and sparsely laminated homogenous mud, deposited during a period of extremely low lake levels (>550 m below modern), prevalent between \approx 85 and \approx 110 kyr ago. Another severe low stage event is observed in this core between 77 and 82 m below lake floor, which is dated between 127 and 135 kyr ago (Fig. 4).

Causal Mechanisms for Tropical African Climate Variability

Increased insolation is generally thought to enhance convection and the intensity of tropical convergence, leading to an increase in precipitation over evaporation (32). Although tropical tem-



Fig. 3. Summary stratigraphy from three drill sites. Included are TOC, saturated bulk density, lithostratigraphy, and selected core imagery. (a) Lake Bosumtwi, West Africa (BOS04–5B). (b) Lake Malawi southern East Africa, (MAL05-2A). (c) Lake Tanganyika (T97-52V), southern East Africa. Red dashed lines indicate subbottom locations of each unconformity observed in the seismic data in Fig. 2. The unconformities are also reflected in the cores by reductions in TOC, increases in bulk density, and marked changes in lithostratigraphy. Radiocarbon dates (red asterisks) and infrared luminescence dates (blue asterisks) are shown above and below the unconformities (ages in kyr BP). See *SI Text*, SI Figs. 5 and 6, and SI Tables 1 and 2 for details of geochronology.

perature changes may be directly forced by precessiondominated insolation, recent climate modeling suggests that zonal and meridional gradients of atmospheric heating may control local hydrologic cycles (33, 34). Thus, the regional hydrology of tropical Africa may have responded to temperature change in ways that are not simply interpretable from the precession cycle alone. When precessional forcing is weak, as is the case during periods of low eccentricity (e.g., MIS stages 1 and 11), tropical coupling to high latitude processes may be enhanced (33). The timing of the onset of the severe arid events identified in our record is best constrained by Ca abundance, which occurs, with one exception, during insolation minima (Fig. 4 c and d). The Ca record indicates periods of calcite saturation and subsequent burial, which occurs during intervals of low lake level and high salinity, and when the dry season is extended and the rains are shortened and less intense. The strong link between Ca abundance and precession is evident between 145 and ≈ 60 kyr ago, but after this interval Ca is not preserved because the lake deepened and freshened. We interpret the interval between 145 and ≈ 60 kyr ago as a period of enhanced precession-scale variability in the hydrologic cycle, dominated by periods of extreme drought conditions, with shorter intervals of greater precipitation. We attribute this high variability to a peak in orbital eccentricity, which enhanced the amplitude of precession (Fig. 4 d and e).

The enhanced variability in African climate during the period \approx 145–75 kyr ago is also manifested in marine records from both the Atlantic (35-38) and Indian (39) Oceans, as well as from outcrops of diatomite beds deposited during the highstand intervals of paleolakes in the Central Kenva Rift (25). However, none of these records have indicated the relative intensity of aridity in interior East Africa during this period that is reflected especially in the Lake Malawi record. Continuous records of climate change from East Africa covering the period 0-150 kyr ago are sparse, but a series of cores from offshore West Africa, at about the same latitude as Lake Malawi, provide an important comparative low-resolution record of coastal climate during this time interval (36, 37). Cores from the Congo Fan and Angola margin also illustrate the pronounced precession-scale climate variability during the period 150-75 kyr ago, as the largest changes in abundance of Podocarpus, an Afromontane indicator, and dry woodland vegetation are observed with \approx 20-kyr periodicities (36, 37) (SI Text).

Few Indian Ocean records are available from the latitudes of Lakes Malawi and Tanganyika, but equatorial cores offshore Somalia that contain alkenone-based temperature records (39) also show pronounced quasi-precessional scale variability during



Fig. 4. Summary Lake Malawi lake level indicators, with orbital forcing and marine records. (a-c) Measurements from drill hole MAL-1C from the deep water (593 m) drill site. (a) TOC. High TOC values indicate highstand conditions, with predominantly laminated intervals, indicating bottom water anoxia. (b) Ostracode abundance, peaks with one asterisk indicate core intervals of profundal taxa, peaks with two asterisks indicate core intervals of littoral zone taxa, and lake shoreline close to the drill site. Ostracodes are only present when the lake is dramatically shallower, with oxygenated bottom waters. (c) Ca abundance, indicating intervals of calcium carbonate precipitation, which occurs during severe lowstands and periods of high salinity. See SI Text, SI Figs. 5 and 6, and SI Tables 1 and 2 for details of geochronology. (d) Mean insolation at 10 S° at the end of the dry season, start of the rains (October 1 to December 1). Vertical dotted lines indicate precession-dominated insolation minima, correlated with Ca and ostracode abundance, indicating calcite saturation. Although these proxies exhibit a precession-forced threshold response, the exact phasing between lake level and insolation is likely obscured by the broad latitudinal extent of the Malawi drainage (Fig. 1); as the Intertropical Convergence Zone migrates, the timing of the rainy season varies along the length of the basin (SI Text). Additional peaks in Ca and Ostracode abundance at ~75 and \approx 97 kyr ago suggest half-precessional cycles, observed at very low latitudes (40). (e) Malawi lake levels vs. Eccentricity. (f) Dry woodland pollen dominated by Brachystegia, from marine core GeoB 1016, West Africa (36), showing high-amplitude precessional variability at 140-75 kyr ago, comparable to climate signals observed in Lake Malawi.

the interval 150–75 kyr ago. Early modern human fossil discoveries in the Kibish Formation, southern Ethiopia, have prompted careful dating of those lacustrine deltaic sequences, which appear correlative to Mediterranean sapropels. Both the sapropels, which are deposited during wet periods in the Nile drainage, and the Kibish Formation highstand deltaic deposits, sourced by the Omo River, suggest the intensification of the African monsoon at approximately precessional-scale intervals (8, 9). Exceptionally well dated diatomite beds, which record peak highstand conditions, are exposed adjacent to Lake Naivasha, Central Kenya Rift. These occurrences over the interval $\approx 150-75$ kyr ago suggest the development of markedly wet climates every ≈ 11 kyr, corresponding to the half-precessional cycle prominent over the equator (25, 40, 41)

GEOLOGY

Most Central Kenya Rift lakes are located in an elevated part of the rift and are underlain by late Cenozoic volcanic substrate, both of which promote hydrologic seepage. However, Lakes Malawi, Tanganyika, and Bosumtwi are positioned in topographically low areas and are underlain by comparatively impervious Proterozoic crystalline rocks; hydrological modeling studies indicate negligible ground water outflow (29–31). Lakes Malawi and Tanganyika extend along >1,500 km of the western branch of the East African Rift, across seven discrete, independently deforming structural basins (42). Our lake levels records show coincident behavior in Lakes Malawi, Tanganyika, and Bosumtwi, and accordingly those shifts are driven by regional changes in the evaporation–precipitation balance in tropical Africa, and not by tectonic activity or deformation-enhanced ground water seepage.

After 70 kyr ago, we observe evidence for increased effective moisture in tropical Africa, manifested in the dramatic rise in water level in all three lakes. Whereas the decrease in eccentricity explains the diminished precession-scale climate variability since 70 kyr ago, it does not account for the long-term shift to overall higher lake levels in the late Pleistocene. Millennial scale climate variations, likely correlated to high-latitude Dansgaard-Oeschger (D-O) events, are observed in the Lake Malawi record during MIS 2-4^m, and may suggest a tropical link to high-latitude climate behavior after 70 kyr ago. To explain the change in precession-scale variability over the duration of our record in Lake Malawi and the change to wetter conditions post-70 kyr ago, we refer to an atmospheric general circulation model, coupled to a mixed-layer ocean model (33), which focuses on the hydrological cycle in the tropical latitudes during glacial versus precessional forcing modes. The results of the glacialforcing experiment demonstrate precipitation changes in the same direction over both land and ocean (SI Text and SI Fig. 8). Because the global temperature was reduced during the glacial period, precipitation also decreased globally, but with a small net increase in precipitation in the Southern Hemisphere tropics. This small increase is due to the southward shift of the austral summer Hadley cell, on account of more pronounced cooling in the northern hemisphere, which generates an increase in latitudinal temperature gradients. This simulation for instance explains the desiccation of equatorial Lake Victoria during the last glacial period (43). The precession-dominated climate simulation (33) (SI Text and SI Fig. 8) indicates a major contrast in precipitation response over land versus the oceans (SI Fig. 8). During the austral summer the Earth is at aphelion, at its maximum distance from the sun, and there is general cooling throughout the tropics. Because of the lower heat capacity of the continents, land-sea temperature contrast is reduced, convection is weakened over the continents, and there is a pronounced shift in precipitation from the land to the ocean, especially in the Southern Hemisphere. The marked contrast in the Southern Hemisphere precipitation between glacial versus precessiondominated climate is manifested in the zonal mean, annual mean change in precipitation over land in the two model runs (SI Text and SI Fig. 8). A similar precession experiment run with a high-eccentricity orbital geometry (44) would generate an even higher amplitude response, i.e., markedly dryer Southern Hemisphere climate, than the simulation discussed here (33).

These climate modeling studies support the concept that the high-eccentricity interval from $\approx 145-70$ kyr ago is responsible for generating the high precession-scale variability in East African Malawi and Tanganyika lake levels. Because of their great depths, parts of both lake systems remained continuously subaqueous throughout the high-variability interval that in-

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cluded periods of extreme drought. Smaller, shallower East African lakes, such as the paleo-lakes of the Central Kenya Rift (25), record the wettest intervals of this extreme precession-scale variability in their preserved highstand deposits. However, because the latter are clipped, punctuated records, the full spectrum of highstand-lowstand variability from equatorial and northern hemisphere tropical East Africa awaits collection of more continuous records from the time frame 150-70 kyr ago than are presently available. Additionally, determining the precise phasing of the severe drought intervals between Northern and Southern Hemisphere tropical Africa during this interval awaits more continuous and better-dated records (SI Text). However, the combined results from Malawi, Tanganyika, and West African Lake Bosumtwi suggest that the mode switch to high-latitude forcing and overall wetter, more stable conditions \approx 70 kyr ago was likely widespread across tropical Africa. Our observations also help constrain previously reported Pleistocene hyperarid intervals in Central and West Africa (45), evidenced by ancient pre-LGM dune fields in areas now covered with lowland rainforest vegetation. Whereas the LGM in tropical Africa was arid relative to the Holocene, the early-Late Pleistocene megadroughts that we document here were far more severe and more sustained. We cannot rule out the possibility that some component of the observed tropical aridity is due to high latitude influences; for instance, the earliest documented arid interval in our record from before 128 kyr B.P. overlaps with the penultimate glaciation. However the severity of the observed lowstands, especially those centered at \approx 75 and \approx 100 kyr B.P., during the period of enhanced eccentricity, strongly suggest a precessional control on tropical African climate during this interval, when glacial influence was relatively minor.

Implications for Early Modern Human Populations

The climatic shift away from mainly arid conditions, identified by the dramatic rise in African lake levels following ≈ 70 kyr ago,

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coincides with the marked expansion of early modern human populations, suggested from studies of modern mtDNA inherent in maternal lineages (12) and Y-chromosome analyses (13). Although still controversial, several early studies of mtDNA deduced that modern human ancestry is traceable to a single individual who lived in South or East Africa before 130 kyr ago (14). Similar studies demonstrate the importance of the founder effect, in that all modern-day non-Africans are descended from a small group of individuals who departed northeast Africa after the early Late Pleistocene (12). Coincident with the expansion of the African lineages is the expansion of early modern human populations that apparently experienced orders-of-magnitude increases by \approx 50 kyr ago (46).

Before 70 kyr ago, the tropical lake data sets indicate a period of heightened climate variability, when tropical refugia expanded and collapsed repeatedly. Whether a series of climatic crises before 70 kyr ago produced a true human population bottleneck is still uncertain (47). The question arises as to whether the observed change to a more hospitable climate after 70 kyr ago, the dramatic late-Pleistocene population expansion, and the only successful early-modern human African exodus are mere coincidence.

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