Continuous 1.3-million-year record of East African hydroclimate, and implications for patterns of evolution and biodiversity

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The transport of moisture in the tropics is a critical process for the global energy budget and on geologic timescales, has markedly influenced continental landscapes, migratory pathways, and biologic evolution. Here we present a continuous, first-of-its-kind 1.3-My record of continental hydroclimate and lake-level variability derived from drill core data from Lake Malawi, East Africa (9–15° S). Over the Quaternary, we observe dramatic shifts in effective moisture, resulting in large-scale changes in one of the world’s largest lakes and most diverse freshwater ecosystems. Results show evidence for 24 lake level drops of more than 200 m during the Late Quaternary, including 15 lowstands when water levels were more than 400 m lower than modern. A dramatic shift is observed at the Mid-Pleistocene Transition (MPT), consistent with far-field climate forcing, which separates vastly different hydroclimate regimes before and after ∼800,000 years ago. Before 800 ka, lake levels were lower, indicating a climate drier than today, and water levels changed frequently. Following the MPT high-amplitude lake level variations dominate the record. From 800 to 100 ka, a deep, often overfilled lake occupied the basin, indicating a wetter climate, but these hightands were interrupted by prolonged intervals of extreme drought. Periods of high lake level are observed during times of high eccentricity. The extreme hydroclimate variability exerted a profound influence on the Lake Malawi endemic cichlid fish species flock; the geographically extensive habitat reconfiguration provided novel ecological opportunities, enabling new populations to differentiate rapidly to distinct species.

Lake Malawi

Lake Malawi (Nyasa) is one of the world’s largest and oldest lakes, and is situated at the southern end of the East African Rift System. The hydrologically open, freshwater ecosystem spans 6° of latitude (9–15° S), and has a length of ∼580 km and a maximum depth of 700 m (Fig. 1). Lake morphometry is a consequence of crustal subsidence induced by slip along large border faults that define the three main structural segments in the Malawi rift (11, 12) (Fig. 1). Steep slopes adjacent to border faults characterize the asymmetric central and northern basins (∼700 and ∼600 m water depth, respectively), whereas the southern part of the lake is an extended shallow-dipping ramp, with maximum water depth of ∼400 m. Rocky shorelines interspersed with pocket beaches are prominent along the coasts, especially along border fault margins. Lake Malawi is home to >1,000 species of mainly endemic cichlid fishes (13), more than any other lake in the world, as well as numerous endemic invertebrates, and its sediment record is a proven climate archive (3, 14). Because of its anoxic hypolimnion, changing climates, and which figure prominently into models of speciation and diversification (9, 10).

Significance

Lake Malawi is one of the world’s oldest and deepest lakes, with >1,000 species of endemic cichlid fish; its water bottom anoxia prevents bioturbation of deep-water sediments, which preserve exceptional paleoclimate signals. The Lake Malawi Drilling Project recovered the first continuous 1.3-My record of past climates of the African interior. These sediments show that the catchment experienced 24 dry periods over that time, when lake levels dropped more than 200 m. After ∼800,000 years ago, the lake was commonly deeper and overflowing, indicating wetter conditions, but lowstand intervals became more prolonged and extreme. These changes promoted the evolution of the endemic cichlid fishes, through shifting of habitats, and through isolation and restriction of populations.


The authors declare no conflict of interest.

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Data deposition: The paleoclimate proxy data and geochronology data have been deposited with the NOAA paleoclimatology database of the National Centers for Environmental Information: https://www.ncdc.noaa.gov/paleo/study/19424.

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finely laminated lacustrine sediments below 200 m water depth are exquisitely preserved (3), permitting studies of long-term high-resolution climate change. The watershed experiences a single rainy season, as the ITCZ passes over the lake during the austral summer (Fig. 1). Moisture transport over tropical Africa is controlled by the migration of the ITCZ and Congo Air Boundary (CAB; Fig. 1) (15, 16). As a result of its southern tropical position, elongated North/South configuration, and expansive catchment (∼128,000 km²), Lake Malawi is ideally positioned to record long-term, continental-scale paleoclimatic signals.

Hydroclimate Proxy Analyses

Drill cores from the central basin of Lake Malawi extend 380 m below lake floor at a water depth of 590 m, a site dominated by hemipelagic deposits sensitive to environmental variability (8, 17). Site survey and geochronological data demonstrate that sampled sediments represent continuous sedimentation over the last ∼1.3 My (SI Appendix, Figs. S1 and S2 and Table S1). A principal components analysis (PCA) of geochemical and sedimentological variables directly influenced by lake-level variations (8, 18) was computed, and the first principal component was calibrated to known lake levels to reconstruct a precision lake level history (SI Appendix, Fig. S1). Datasets contributing to the PCA include total organic carbon (TOC), δ¹³C of organic matter, saturated bulk density, carbonate abundance, and lightness of color (L*). Highstand sediments, deposited when the lake is at or near its current outlet level (maximum water depth ∼700 m), are characterized by high TOC, low density, low Ca, and low L* values, and are finely laminated (Fig. 2 and SI Appendix) (8, 17). Conversely, lowstand sediments are poor in organic matter, carbonate-rich, high density, and exhibit high L* values (SI Appendix, Fig. S1) (9, 18).

Evidence from diatoms, ostracodes, and other paleoecological indicators, as well as seismic-reflection data show lake levels dropped by as much as ∼600 m over the past 150,000 y (8, 17, 18). Here we extend the lake level reconstruction to the entire ∼1.3-My drill core record, revealing that there were 24 lowstands of more than 200 m below modern; at least 15 were very severe, when water levels were reduced more than 400 m (Fig. 2). Severe lowstands produced hydrologically closed, shallow, mildly saline and alkaline lakes. Terrestrial paleoclimate indicators, including charcoal recovered from the last 150,000 y, indicate drier conditions relative to modern, coincident with the severe lowstands (18). Hydrologic modeling of the catchment’s water budget indicates that a precipitation rate 50% of modern sustains equilibrium lake level during ∼200-m lowstands (assuming modern bathymetry) and a precipitation rate 39% of modern sustains ∼600-m lake levels (19); these simulations require major atmospheric reconfigurations during each of the 24 arid intervals and lowstands of more than 200 m (Fig. 2).

Patterns of environmental variability shift markedly at 800–900 ka (Fig. 2), indicating that the Mid-Pleistocene Transition (MPT) (20) was an important climate transformation in central and southern tropical Africa, as well as north of the equator (21, 22) (Fig. 2). This transition marks the boundary between two distinct hydroclimate regimes within the rift valley, likely related to changes in global climate cyclicity (20). Before the transition, Lake Malawi was dominated by low levels but also by high-frequency variability, particularly apparent in the Ca record (Fig. 2), and also indicated by thick sand deposits in this interval at the base of the drill core. Because the MPT, the amplitude of Malawi lake level fluctuations has been greater, with lowstands both more severe and sustained (Fig. 2).

During eccentricity minima every ∼400,000 y, the Lake Malawi Rift Valley filled to its spill point and deep lakes persisted in the basin. Over the ∼1.3-My record, this hydrologic overfilling occurred for unusually long durations twice: ∼950–760 ka and ∼60 ka to present. These intervals indicate diminished variability of tropical convection across Africa, manifested as a sustained positive water balance within the Lake Malawi catchment. That this relationship is not observed during the eccentricity minimum during Marine Isotope Stage (MIS) 11, centered at ∼400 ka, may result from greater age model uncertainties between ∼100 and 550 ka (SI Appendix, Fig. S2).

Causative Mechanisms for Climate Variability

The lake level response evolves over the length of the 1.3-My drill core record. Before ∼800 ka, the paleoclimate proxies indicate a basin occupied by a lake shallower than modern, with
Lake level shifts occurring every 10,000 y or less. Although that lake was shallower than the current one, the drill site was a distal and open water environment like today, dominated by hemipelagic sedimentation; this is evidenced by the broad expanse of high continuity, high amplitude, and uniformly stratified seismic facies that extend in all directions away from the drill site for many tens of kilometers (17). The high values of Ca and lower TOC in this interval, coupled with the continuous, high-amplitude seismic character in this part of Lake Malawi, indicate a large lake situated in a drier environment than observed in the catchment today. Although lake level changes were frequent in this interval, the amplitude of change was much less than what is observed post-800 ka. In the interval from the MPT (∼800 ka) until ∼100 ka, the rift valley was often filled with a deep lake that overflowed the basin, reflecting wetter conditions, compared with the pre-800 ka interval (Fig. 2A). However, the dominant signal since 800 ka is of much higher amplitude lake-level variability, albeit at a considerably slower cadence, with lake stages lasting more than 20,000 y. The intervals of hydrologic overfilling of the lake are interrupted by periods of extreme drought (8, 18), which were both more severe and longer in duration than those documented in the pre-800-ka period.

The change in the hydroclimate behavior at the MPT in Lake Malawi is consistent with some patterns of averaged global climate variability documented in marine benthic stack records (20). Indeed, the markedly deepened megadrought behavior over the last 450,000 y in particular, resembles the tempo of enhanced northern hemisphere glacial–interglacial variability during that time interval, and suggests a strong linkage to high-latitude forcing and Indo-Arabian monsoon dynamics, as indicated in some shorter tropical records (21, 23). The lack of steady precessional rhythms in this terrestrial hydroclimate record is consistent with recent modeling efforts (24) that suggest that moisture transport in southeastern Africa is a more complex and nuanced process than previously postulated, and orbital forcing alone (2, 5, 25–28) is insufficient to explain 10^4–5-y moisture variability over million-year time frames. Calibrated lake level [the first principal component, PC(1)] demonstrates cyclic behavior from ∼200 to ∼600 ka (Fig. 2) with some, but not all, fluctuations following a glacial–interglacial rhythm. The signal is not in phase with high-latitude signals, however (29), which may be a consequence of either a limited number of absolute ages within this section or the impact of other interacting forcing mechanisms such as precession. Although high-latitude forcing
in the catchment was likely important over the past 450,000 y, not all glacial and interglacial events had major influence on Malawi climate. During the Last Glacial Maximum (LGM, MIS 2), lake level was relatively high (Fig. 2) in a well-dated section of the core, close to its spill point, implying there was a comparatively small climate perturbation in the catchment. Additionally, before ∼800 ka, a well-dated section of the core, Malawi lake level varied at a much faster pace, consistent with conditions in a pre–100-ky world (Fig. 2). The response at this drill site reflects the varied sources of moisture feeding southern Africa. The long Lake Malawi record reflects multiple forcing mechanisms (24), representing the long-term variability in both the ITCZ and the Congo Air Boundary, and responding to the distinct moisture sources in the region, including the southern, equatorial, and northwestern Indian Ocean, as well as the eastern Atlantic Ocean via the Congo Basin.

**Implications for Evolution and Species Diversification**

The high-frequency, high-magnitude lake-level variability reported here has profound implications for the adaptive radiation, ecological diversification, and speciation of haplochromine cichlid fishes, because lake size and depth have significant correlation

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**Fig. 3.** Lake Malawi bathymetry with seismic tracklines shown. The modern shoreline is annotated with a three-term coastline classification scheme interpreted from GeoCover Landsat data (bands 7, 4, 2) and World Wind’s NLT Landsat visible color data set (bands 1, 2, 3). (Insets) GeoCover Landsat data showing examples of each coastline classification. The most recent −500 m (∼145 ka) lowstand is highlighted in light gray, and the −600 m (∼170 ka) lowstand is highlighted in dark gray. Note that Lake Malawi was relatively shallow and separated into two subbasins during the −500-m lowstand, and during many of the 24 major lowstands discussed in the text. The lowstand shorelines are classified in a similar three-term scheme based on interpretations of seismic facies from seismic-reflection profiles (SI Appendix, Fig. S8, and supplemental text). (Inset) Distributions of interpreted Lake Malawi coastline classifications in distance for both the modern lake and the lowstands (8, 17).
with the number of extant species (30, 31). Lake-level fluctuations substantially alter the extent of suitable habitat for both rocky and sandy substrate-dwelling species, have considerable impacts on the genetic structure of the fish populations, and are crucial for the evolution of these cichlid species flocks here and in other African Great Lakes (32). Whereas profound lake-level variations have been shown to influence cichlid evolution over short intervals (32, 33), our work demonstrates that such environmental shocks were not rare events, but persistent and recurring episodes over million-year time frames.

Interpretations of GeoCover Landsat data (bands 7, 4, 2) and World Wind’s NLT Landsat visible color data (bands 1, 2, 3) from modern Lake Malawi, as well as seismic facies (SI Appendix, Fig. S8) and ostracode data (8, 18) from lowstands, indicate that during ~500 m and ~600 m lake-level falls, the well-known mbuna cichlids that are restricted to the rocky coastlines of Lake Malawi would have lost 83% and 90% of modern rocky coastline habitat, respectively (Fig. 3 and SI Appendix). During severe lowstands, Lake Malawi likely experienced more mixing and eutrophic conditions, as evidenced by the drill diatom diatom record (18, 34). As lake level fell dramatically, rocky habitat was lost, and the mbuna flocks experienced local extinctions or possibly reticulation of microallopatric localized species lineages. Within isolated mbuna populations, genetic variation, deme topology, and spatial population dynamics would be impacted by contracting population sizes with genetic drift being increasingly important, decreasing genetic variation within but increasing genetic differentiation among local populations (35). Even without reticulation or hybridization, deeper mbuna lineages likely persisted, and populations were maintained with major genera represented; this is the case of modern Lake Malawi, where the maximum number of mbuna at any one shallow water rocky site is limited, and the vast majority of the species-level diversity is due to microallopatric differentiation, primarily by color pattern (36). As lake level rose following severe lowstands, connections and isolation of newly formed rocky habitat and the subsequent isolation by distance led to reinforcement by assortative mating and microallopatric speciation. Old rocky shoreline habitat, due to water depth changes, was less suitable for shallow water species due to altered selective regimes for color or food resources. Additionally, the lake at maximum depth was restricted to the rocky coastlines of Lake Malawi that are restricted to the rocky coastlines of Lake Malawi (Fig. 3). This analysis is consistent with DNA similarity of cichlid species in Lake Malawi, where multiple radiations have been observed over short time scales (39).

Materials and Methods

Scientific drilling was completed in March and April 2005 using the Malawi Lake Services barge Viphya, which was extensively modified for this drilling effort. To determine trends in lake-level indicators from drill-core analyses, PCA was performed on density, TOC, δ13C of bulk sediment, Ca, and L* (SI Appendix, Fig. S1). Total organic carbon is most sensitive during times of high and intermediate lake level, δ13C is more sensitive to lake level variability during times of very low lake level, and Ca is sensitive during times of intermediate and low lake level. Density and L* are physical properties used to quantify lithology, which varies with water depth at the drill site. Variables contributing to PCA were rescaled to the lowest-resolution data set (TOC) using an integration technique in AnalySeries. PC(1) represents 49% of the total variance, and the weights from all contributing variables are between 0.31 and 0.54.

Age-dating of the drill-core samples recovered from site GLAD7-Malosi-1 using U-series dates from holes 1B and 1C was accomplished using several different dating methods. The principal ages for the GLAD7-Malosi-1 drill cores were obtained by using 16 AMS radiocarbon dates (0–21 m), the occurrence of the Toba Ash (28 m, 75 ka; SI Appendix, Ar–Ar dates on two thin tephas (168 m, 242 m), paleomagnetic reversal stratigraphy, and magnetic paleointensity (165 m to the base of the core) correlations to the global stack (SI Appendix, Table S2). From these ages, we used a series of linked least-squares polynomials to develop an age model for the entire site record (SI Appendix, Fig. S2).

Data presented are downloadable from the National Oceanic and Atmospheric Administration Paleoclimatology website (www.ncdc.noaa.gov/data-access/paleoclimatology-data).

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Core collection

Scientific drilling was completed in March and April 2005 using the Malawi Lake Services barge *Viphya*, which was extensively modified for this drilling effort. A summary of the Lake Malawi Drilling Project core recovery is shown in Table S1. Hole 1C over-penetrated the upper sedimentary section, and thus a 6.5 m shift was applied to Hole 1C. The top of Hole 1B was adjusted to 19.5 meters below lake floor (mblf), in agreement with the driller’s logs.

Geochemical and geophysical analyses

The composite record from Site 1 was produced using drillers depth logs as well as density, L* values, and total organic carbon (TOC) records from both Holes 1B and 1C. Sample intervals vary among the geochemical and geophysical data sets at Drill Site 1 from millimeter-scale (L*) to 16 cm (TOC).

High-resolution digital imagery (pixel size is ~0.1 mm) of each core section was captured using a 1) DMT CoreScan Colour scanner and 2) a Geotek Geoscan-V scanner with polarizing filters on both the cameras and the light source at the National Lacustrine Core Repository (LacCore), University of Minnesota. To reduce total data volume, each image was resampled to 10% of its original size using the bicubic interpolation tool in Adobe Photoshop©, reducing sample intervals to ~1 mm. Red-Green-Blue (RGB) data were extracted from a 9-pixel-wide horizontal band from the center of each core section. RGB space was then converted to L*, a*, b* space, where L* represents the lightness of color in the core image. To eliminate high-frequency variability due to small gaps and cracks (dark values) a filter was applied to the final data set, where a given point was eliminated if its L* value fell outside two standard deviations of a 100-point running mean. Calcium (Ca), a proxy for calcium carbonate mineral abundance, was measured in 1-cm intervals using an ITRAX X-ray Fluorescence Core Scanner at the Large Lakes Observatory of the University of Minnesota-Duluth. The cores were exposed to X-radiation generated by a molybdenum source set to 30 kV and 15 mA. XRF counts per minute (cpm) correspond to Ca concentrations in NIST Standard Reference Materials. The 1C part of record had twice the exposure time relative to 1B, so the 1C counts were reduced by 50%. Saturated bulk density measurements were taken every 1 cm using a Gamma-Ray Attenuation Porosity Evaluator (GRAPE) on a Geotek multi-sensor logger at LacCore. Organic matter samples for TOC and δ¹³C were measured in 1-cm thick discrete samples at 16 cm intervals. They were pretreated with a vapor phase acidification (VAI) technique to remove inorganic carbon
phases and then analyzed using an ANCA elemental analyzer and accelerator mass spectrometer at the University of Miami Stable Isotope Laboratory.

**Age dating methodology**

Age dating of the drill-core samples recovered from site GLAD7-Mal05-1 using drill cores from holes 1B and 1C was accomplished using several different dating methods. The principal ages for the GLAD7-Mal05-1 drill cores were obtained by using 16 AMS radiocarbon dates (0-21 m), the occurrence of the Toba Ash (28 m, 75 ka) (S2), Ar-Ar dates on two thin tephras (168 m, 242 m), paleomagnetic reversal stratigraphy, and magnetic paleointensity (165 m to the base of the core) correlations to the global stack (Table S2). From these ages, we used a series of linked least-squared polynomials to develop an age model for the entire Site 1 record (Fig. S2).

**AMS Radiocarbon and Toba Ash detection**

The AMS radiocarbon dates are also detailed previously (9). Methods for the detection of the Toba ash are described in (S2).

**Ar-Ar dating**

Ar-Ar dating was completed at the Berkeley Geochronology Center. K-feldspar phenocrysts were separated from two thin tephra horizons for $^{40}$Ar/$^{39}$Ar dating using the total-fusion approach. Analyses of sample GLAD7-MAL05 1B-54E (167.84 mblf) were carried out on six relatively small grains, resulting in an age with a relatively large uncertainty, 0.59 ± 0.02 Ma (1σ). Sample GLAD7-MAL05 1B-83E-3 (241.53 mblf) yielded much more material and a resulting higher precision age, 0.915 ± 0.008 Ma (n = 28).

K-feldspar phenocrysts were separated from tephra samples using gentle hand-crushing, followed by dilute HF (5%, 3 min) and distilled water rinses. Grains were hand-picked under binocular microscope, and irradiated in two separate batches in the Cd-lined, in-core CLICIT facility of the Oregon State University TRIGA reactor (sample GLAD7-MAL05 1B-83E-3 for 0.1 hour, and sample GLAD7-MAL05 1B-54E for 0.5 hour). Sanidine from the Alder Creek Rhyolite was used as a mineral standard to evaluate neutron fluence, with a reference age of 1.202 ± 0.012 Ma (S3) adjusted for the FC age of 28.201 ± 0.046 Ma (S4). Standards and unknowns were placed in 2-mm diameter by 2-mm deep wells situated in a ring configuration centered on the 16.5 mm diameter, 2.5 mm thick aluminum disk (S5). Planar regressions were fit to the standard data and the $^{40}$Ar/$^{39}$Ar neutron fluence parameter, J, interpolated for the unknowns. Uncertainties in J (0.2–0.3%) are estimated based on Monte Carlo error analysis of the planar regressions. Reactor-induced isotopic production ratios for these irradiations were:
(36Ar/37Ar)Ca = 2.65 ± 0.02 × 10^{-4}, (38Ar/37Ar)Ca = 1.96 ± 0.08 × 10^{-5}, (39Ar/37Ar) Ca = 6.95 ± 0.09 × 10^{-4}, (37Ar/39Ar) K = 2.24 ± 0.16 × 10^{-4}, (38Ar/39Ar) K = 1.220 ± 0.003 × 10^{-2}, (40Ar/39Ar) K = 2.5 ± 0.9 × 10^{-4}. The 40K decay constants applied to age calculations were $\lambda_E = 5.810 ± 0.170 \times 10^{11}$/yr and $\lambda_\beta = 4.962 ± 0.086 \times 10^{10}$/yr (S6).

Following irradiation, single-crystal total-fusion analyses were performed at the Berkeley Geochronology Center using a Noblesse 5-collector Noble gas mass spectrometer and dedicated extraction line. Individual K-feldspar phenocrysts ~0.2–0.5 mm in maximum dimension (est. ~10–130 micrograms) were heated for 5–7 seconds to fusion in UHV using a CO2 laser at ~6 Watts with a 1.5 mm beam diameter. Evolved gasses were then exposed for ~60 seconds to a 50 cc SAES getter operated at 2.1 A and a cryosurface at -125°C to remove reactive species and water. The gas was then admitted to the mass spectrometer and measured by ion counting over a period of about eight minutes. This machine has ETP (Model 14143) ion counters at differential spacing of 1 and 2 m/e both above and below an axial Faraday cup, a configuration that permits simultaneous measurement of $^{40}$Ar, $^{39}$Ar, $^{37}$Ar, and $^{36}$Ar on individual ion counters. A brief peak hop was employed several times during the run to allow $^{38}$Ar to be measured on one of the ion counters. All electronic source and detector settings were held constant for the duration of mass spectrometry. $^{36}$Ar signals were normalized to the detector used for the $^{40}$Ar and $^{39}$Ar measurements by reference to relative gains evaluated by time-interpolation through periodic runs of atmospheric argon measured using the same source and detector settings as the unknowns (1–2 air runs every ~15 analyses; $^{40}$Ar delivered to the mass spectrometer per air aliquot = 2.5 X 10-15 moles; $^{40}$Ar/$^{36}$Ar = 298.56 ± 0.31; (S7)). Normalization of $^{39}$Ar, $^{38}$Ar and $^{37}$Ar signals were achieved by using the same air shots using a post-run test sequence invoking repeated measurement of $^{40}$Ar on relevant detectors. Procedural blanks bracketed every total-fusion analysis, and yielded approximately 5 × 10^{-17}, 9 × 10^{-19}, 3 × 10^{-19}, 7 × 10^{-18}, and 6 × 10^{-19} moles of at the measurement positions of $^{40}$Ar, $^{39}$Ar, $^{38}$Ar, $^{37}$Ar, and $^{36}$Ar, respectively.

Sample GLAD7-MAL05 1B-54E yielded only six K-feldspar crystals sufficiently large for analysis. Although all extractions were highly radiogenic (yielding >75%, mostly >90% radiogenic $^{40}$Ar), the small grain size and relatively young age resulted in large age uncertainties, from 5-40%. The probability density function of the results are shown below (Fig. S3). The observed distribution is sub-gaussian, with a slight skewing toward older ages, though the MSWD remains reasonable (0.78). The weighted-mean age of the six analyses is 0.59 ± 0.02 Ma (1σ analytical error). The high radiogenic content of the analyses precludes effective isochron correlation analysis, though for reference these data yield an inverse $^{36}$Ar/$^{40}$Ar vs. $^{39}$Ar/$^{40}$Ar isochron age of 0.58 ± 0.08 Ma, in agreement with the weighted-mean age, and a poorly defined $^{40}$Ar/$^{36}$Ar intercept of 1,000 ± 1,700.

Sample GLAD7-MAL05 1B-83E-3 yielded many more grains for analysis (n = 37) than the previous sample. The geochronological data are displayed in Fig. S4. While most analyses yielded >75% $^{40}$Ar*, six ranged from 14–64%, and may represent altered material (most of these also have relatively young ages). These are considered anomalous and excluded from further data analysis. The remaining population has a simple unimodal distribution but with a small shoulder of older ages. Tails toward older ages are often seen in single-crystal total-fusion analyses of late Cenozoic feldspars, and may represent excess $^{40}$Ar present in glass inclusions in some crystals. A robust outlier filter, eliminating grains with ages more than 2.0 nMads
(normalized deviations from the median) was employed to trim the population, resulting in removal of three analyses from the data set. The resulting analyses give a weighted-mean age of 0.915 ± 0.006 Ma (MSWD = 1.3, n = 28). For reference, an isochron from these data yields an age of 0.900 ± 0.008 Ma (MSWD = 0.81, \(^{40}\)Ar/\(^{39}\)Ar int = 394 ± 35), within 2σ error of the weighted-mean age. Analytical results are presented in Table S3.

**Paleomagnetic analyses**

To incorporate the paleomagnetic data, we employed an iterative approach of interpreting both the inclination and paleo-intensity records:

1) Used Ar-Ar dates to constrain first-order absolute age model “pins” for the full Site 1 record (from 165 to 384 m below lake floor).

2) Measured inclination and relative paleointensity for Site 1 (1B).

3) Identified major reversals and excursions in the inclination record (Fig. S5):
   Bruhnes/Matayama boundary = 222 m; Santa Rosa = 247 m; Upper Jaramillo = 271.5 m.

4) Following the establishment of the reversal stratigraphy, magnetic paleointensity was interpreted between the younger Ar-Ar date (~165 m) and the base of the core, with supporting interpretations from the inclination data. Magnetic paleointensity was determined from the ratio of natural remnant magnetization to anhysteretic remnant magnetization (NRM/ARM) (a measure of magnetic field intensity), were correlated to the global paleointensity stack (S8). Excursions in the paleomagnetic inclination record (Fig. S6) were identified using classifications from (S9, S10).

**PCA Computation and lake-level calibration**

In order to determine trends in lake-level indicators from drill-core analyses, principal component analysis (PCA) was performed on density, TOC, \(\delta^{13}\)C, Ca, and L* (Fig. S1). Total organic carbon is most sensitive during times of high and intermediate lake level, \(\delta^{13}\)C is more sensitive to lake level variability during times of very low lake level, and Ca is sensitive during times of intermediate and low lake level. Density and L* are physical properties used to quantify lithology which varies with water depth at the drill site. Variables contributing to PCA were re-sampled to the lowest resolution data set (TOC) using an integration technique in Analyseries©. The first principal component (PC(1)) represents 49% of the total variance and the weights from all contributing variables are between 0.31 and 0.54.

Seismic facies analysis and paleo-ecological indicators pinpoint lowstand magnitudes at Site 1 for several intervals over the last ~200,000 years (9, 17, 18). We plot PC(1) against these
lowstand magnitudes to generate a transform function to calibrate lake level over the entire Site 1 record (Fig. S7). This calibration is used to assess lowstand magnitudes throughout the late Quaternary (Fig. S7). Note that lowstands interpreted from seismic-reflection data reflect intervals of sustained lower lake level and not necessarily the most extreme, short-term events. However, the paleo-ecological data sets are higher resolution and can define higher frequency events.

Calibration of seismic facies

Interpretations of seismic facies from the paleo-shoreline of the most recent (centered at ~145 ka) -500 m lowstand surface (9, 17) indicate that rocky coastlines during lowstands are associated with a faulted, high-amplitude seismic-reflection character (Fig. 3, S8). Interpreted sandy coastlines have high-amplitude, continuous reflections while interpreted mixed mud/sand vegetated coastlines are characterized by low-amplitude, continuous reflections (Fig. S8). Interpretations of sandy coastline are supported by drill-core and seismic-reflection data at Drill Site 2 in Lake Malawi, where fine- to medium-grained sand found at the base of the drill core is interpreted as a transgressive beach deposit in the drill cores (Fig. S8) (9). This fining-upwards sedimentary package is associated with high-amplitude, continuous reflections in seismic data (17).

Presentation of TRMM results

A 12-year (1998 – 2010) processed compilation of NASA’s Tropical Rainfall Measuring Mission (TRMM) data for January and July were downloaded from B. Bohagen (http://www.geog.ucsb.edu/~bodo/TRMM/) to be used in Fig. 1 (S11). Combined Precipitation Radar (PR) and TRMM Microwave Imager (TMI) were used on product 2B31 with 4 km horizontal and 250 m vertical resolution.
Fig. S1. Paleoclimate proxy records used in the Principal Component Analysis. Vertical axis mcd = meters composite depth from all holes at site. Column on left is condensed high-resolution core image of all composited core from Site 1. See Suppl. Text.
Fig. S2. Age-depth relationships for the Lake Malawi Drilling Project Site 1, illustrating dates and age model approaches employed. The age model (blue solid line) is used to transform paleoclimate proxies, including PC(1), to age from depth, as presented in the main text.
Fig. S3. Probability density function for sample GLAD7-MAL05 1B-54E.
Fig. S4. Probability density function for sample GLAD7-MAL05 1B-83E-3.
**Fig. S5.** Inclination and paleointensity data for Malawi core 1B. The inclination record was demagnetized at 50 mT with a 50-point smooth. Geomagnetic excursions (sharp changes to positive values) are identified using classification from (S8). Here, the paleomagnetic intensity record is shown correlated to global composite paleointensity record SINT-2000 (S9).
Fig. S6. The SINT-2000 paleointensity stack (S8) with locations of excursions and reversals in the record (S8, S9). The numbered and lettered paleointensity features are identified in the Malawi record shown in Fig. S5.
Fig. S7. Calibration of PC(1) lake level with seismic lowstand indicators (plot of lowstand magnitude vs. PC(1) values). Intervals of known lowstand magnitudes from seismic facies and paleo-ecological data are shown in the inserted table.
**Fig. S8.** Interpretations of seismic facies from the paleo-shoreline of the most recent (~145 kyr) - 500 m lowstand surface and megadrought interval (9, 17). (a) A seismic profile showing low-amplitude continuous reflections, interpreted as a mixed-vegetative lowstand coastline. (b) The -500 m lowstand surface is characterized by high-amplitude continuous reflections, indicative of a sandy lowstand surface. (c) The seismic-profile shows the -500 m lowstand water depth is associated with a fault-scarp, indicative of a rocky lowstand coastline during the lowstand.
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**Table S1.** Drilling program summary
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Table S2. Age-depth data for Malawi Site 1, Holes 1B and 1C.
Table S3. Ar-Ar analyses of Malawi tephras.

References in Supplemental Information
S5. Best MG, Christiansen EH, Deino AL, Grommé CS, Tingey DG (1995) Correlation and emplacement of a large, zoned, discontinuously exposed ash flow sheet; the 40Ar/39Ar
chronology, paleomagnetism, and petrology of the Pahranagat Formation, Nevada. J. Geophys.

S6. Steiger RH, Jäger E (1977) Subcommission on Geochronology: Conventions on the use of


over the past two million years. Nature 435:802-805.

field variability recorded in Ocean Drilling Program cores. Physics of the Earth and Planetary
Interiors 156:194-204.

the Matuyama chron. Earth Planets Space 54:679-690.

S11. Bookhagen B, Burbank DW (2010) Toward a complete Himalayan hydrological budget:
Spatiotemporal distribution of snowmelt and rainfall and their impact on river discharge.