

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 biological 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 highstands 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 | tropical paleoclimatology | East African rift | cichlid fish | quaternary

Insolation forcing of tropical convection and shifts in the Intertropical Convergence Zone (ITCZ) are considered principal mechanisms driving tropical climate variability on geologic time scales (1–5). However, instrumental records show that the ITCZ over land is poorly characterized compared with the oceans (Fig. 1), and the transport of oceanic moisture to the hinterlands is complex, because topographic barriers redirect winds and block advection to the continental interiors (6). To document moisture transport onto the continents over geological time scales, terrestrial records of tropical paleoclimate with the length and continuity of ocean drilling records are required. Continental drilling in long-lived tropical lakes provides continuous, high-resolution paleoclimate records that extend well past the last glacial maximum (7, 8), and augment shorter, well-dated records from outcrops. Lakes of great antiquity also contain numerous endemic species—notably, cichlid fishes—whose modern assemblages evolved in concert with changing climates, and which figure prominently into models of speciation and diversification (9, 10).

Lake Malawi and Its Catchment

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,

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.

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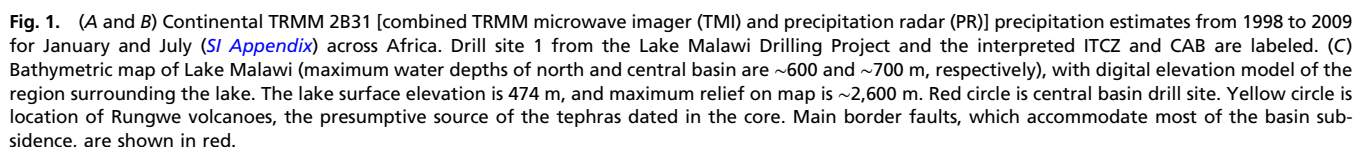
Data deposition: The paleoclimate proxy data and geochronology data have been deposited with the NOAA paleoclimatology database of the National Centers for Environmental Information: <https://www.ncdc.noaa.gov/paleo/study/19424>.

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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

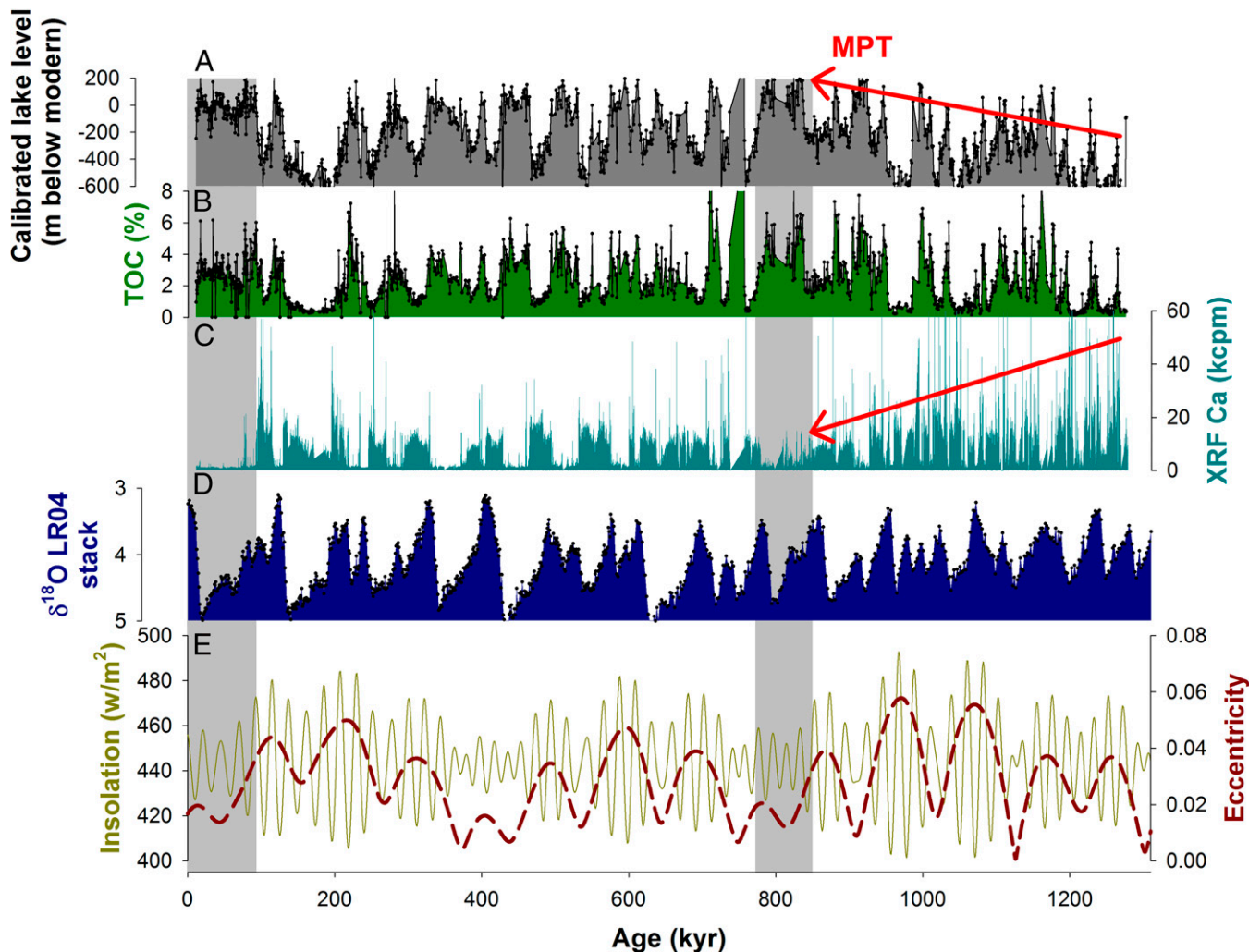


Fig. 2. Comparison of Malawi paleo-lake level reconstructions with eccentricity, insolation (low latitude), and the LR04 benthic stack (high latitude). Gray bars represent intervals of low (400 ky) eccentricity when Malawi lake level stabilized at highstand conditions. Red arrows represent the presence of the MPT in Malawi, from frequent low lake levels before ~900 ka to frequent high lake level conditions after. (A) Calibrated lake level from PC(1) from Malawi site 1 (see *SI Appendix*, Fig. S7, and supplemental text for calibration routine). (B) Bulk TOC measurements from site 1. (C) Calcium abundance from scanning X-ray fluorescence (kcpm = thousand counts per minute). (D) $\delta^{18}\text{O}$ LR04 benthic stack (29). (E) Eccentricity and insolation from 10 °S.

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. 24). 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 – 10^5 -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

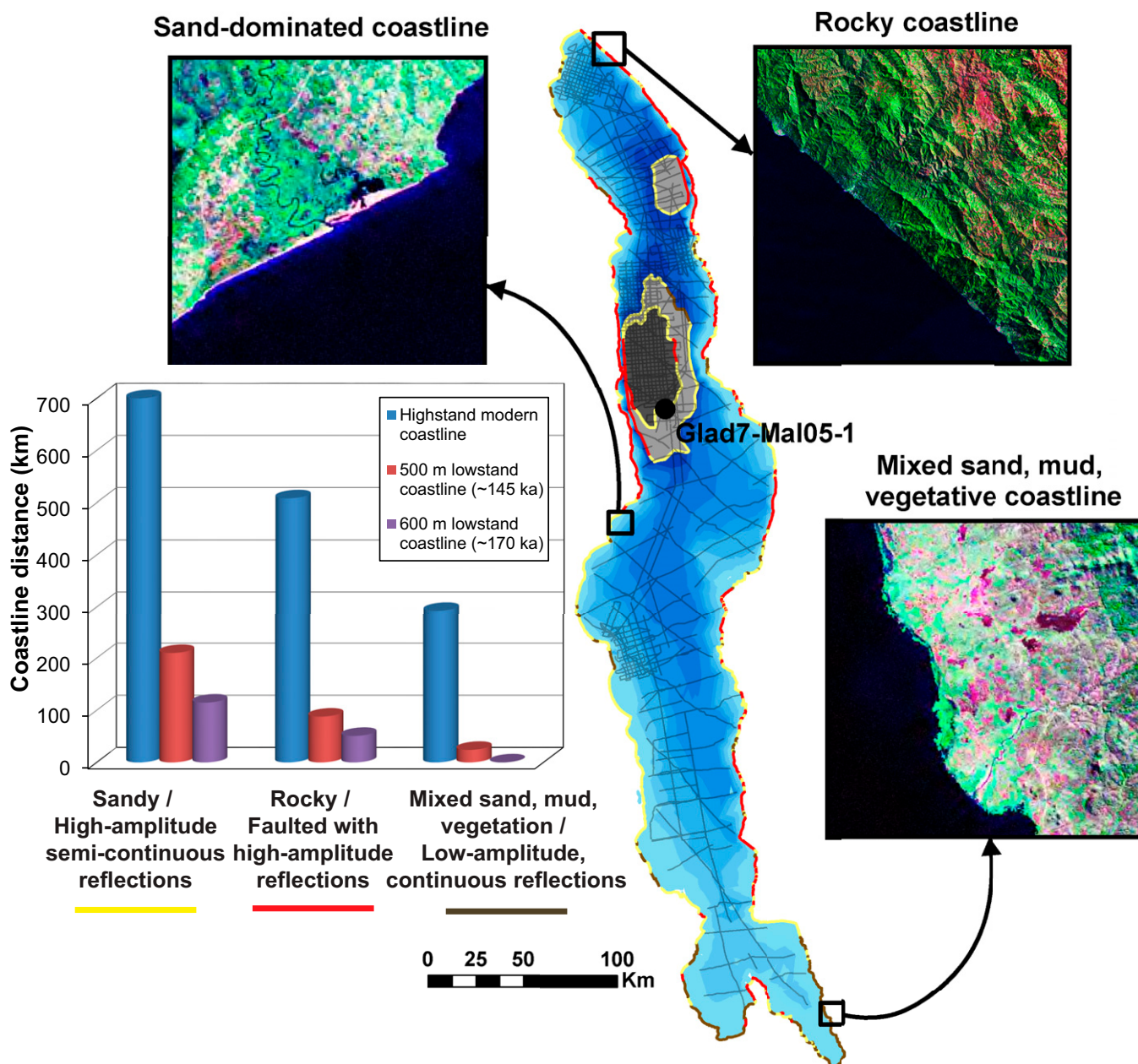


Fig. 3. Lake Malawi bathymetry with seismic tracklines shown. The modern shoreline is annotated with a three-term coastline classification scheme interpreted from GeoCover Landsat data (bands 7, 4, 2) and World Wind's NLT Landsat visible color data set (bands 1, 2, 3). (Insets) GeoCover Landsat data 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 core 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, demography, 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 would provide ecological opportunities for secondary contact between lacustrine and riverine cichlids that are consistent with genetic polymorphism contributions from outside the lake (37) and

formation of phenotypic novelty from hybridization (38). Through ecological opportunities, founder effects, genetic bottlenecks, drift, hybridization, and/or sexual selection, the new populations would differentiate rapidly to distinct species multiple times during the history of the lake. The atmosphere-controlled lake-level variability described here likely promoted rapid speciation of cichlids by changing habitat availability, total lake surface area, and through geographic isolation of parts of the species flock (Fig. 3). This analysis is consistent with DNA similarity of cichlid species in Lake Malawi, where multiple rapid 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, $\delta^{13}\text{C}$ of bulk sediment, Ca, and L^* (*SI Appendix*, Fig. S1). Total organic carbon is most sensitive during times of high and intermediate lake level, $\delta^{13}\text{C}$ 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 resampled 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-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; *SI Appendix*), Ar–Ar dates on two thin tephra (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-squared polynomials to develop an age model for the entire site 1 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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