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# 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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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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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  $-500\text{-m}$  and  $-600\text{-m}$  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, deme topography, 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](http://www.ncdc.noaa.gov/data-access/paleoclimatology-data)).

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- Wang X, et al. (2004) Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. *Nature* 432(7018):740–743.
- McIntyre A, Molfino B (1996) Forcing of Atlantic equatorial and subpolar millennial cycles by precession. *Science* 274(5294):1867–1870.
- Johnson TC, et al. (2002) A high-resolution paleoclimate record spanning the past 25,000 years in southern East Africa. *Science* 296(5565):113–132.
- Haug GH, Hughen KA, Sigman DM, Peterson LC, Röhl U (2001) Southward migration of the intertropical convergence zone through the Holocene. *Science* 293(5533):1304–1308.
- Trauth MH, Deino AL, Bergner AGN, Strecker MR (2003) East African climate change and orbital forcing during the last 175 kyr BP. *Earth Planet Sci Lett* 206:297–313.
- Sepulchre P, et al. (2006) Tectonic uplift and Eastern Africa aridification. *Science* 313(5792):1419–1423.
- Hodell DA, et al. (2008) An 85-ka record of climate change in lowland Central America. *Quat Sci Rev* 27:1152–1165.
- Scholz CA, et al. (2007) East African megadroughts between 135 and 75 thousand years ago and bearing on early-modern human origins. *Proc Natl Acad Sci USA* 104(42):16416–16421.
- Kingston JD, Hill A, Marino BD (1994) Isotopic evidence for neogene hominid paleoenvironments in the Kenya rift valley. *Science* 264(5161):955–959.
- Salzburger W, Bocklaer BW, Cohen AS (2014) Ecology and Evolution of the African Great Lakes and their Faunas. *Annu Rev Ecol Syst* 45:519–545.
- Versfelt J, Rosendahl BR (1989) Relationship between pre-rift structure and rift architecture in Lakes Tanganyika and Malawi, East Africa. *Nature* 337:354–357.
- Specht TD, Rosendahl BR (1989) Architecture of the Lake Malawi Rift, East Africa. *J Afr Earth Sci* 8:355–382.
- Genner MJ, et al. (2007) Age of cichlids: New dates for ancient lake fish radiations. *Mol Biol Evol* 24(5):1269–1282.
- Brown ET, Johnson TC, Scholz CA, Cohen AS, King JW (2007) Abrupt change in tropical African climate linked to the bipolar seesaw over the past 55,000 years. *Geophys Res Lett* 34, 10.1029/2007GL031240.
- Tierney JE, Russell JM, Sinninghe Damsté JS, Huang Y, Verschuren D (2011) Late Quaternary behavior of the East African monsoon and the importance of the Congo Air Boundary. *Quat Sci Rev* 30:798–807.
- Schefuss E, Kuhlmann H, Mollenhauer G, Prange M, Pätzold J (2011) Forcing of wet phases in southeast Africa over the past 17,000 years. *Nature* 480(7378):509–512.
- Lyons RP, Scholz CA, Buoniconti MR, Martin MR (2011) Late Quaternary stratigraphic analysis of the Lake Malawi Rift: East Africa: An integration of drill-core and seismic-reflection data. *Palaeogeogr Palaeoclimatol Palaeoecol* 303:20–37.
- Cohen AS, et al. (2007) Ecological consequences of early Late Pleistocene megadroughts in tropical Africa. *Proc Natl Acad Sci USA* 104(42):16422–16427.
- Lyons RP, Kroll CN, Scholz CA (2011) An energy-balance hydrologic model for the Lake Malawi Rift Basin, East Africa. *Global Planet Change* 75:83–97.
- Raymo ME, Lisiecki LE, Nisancioglu KH (2006) Plio-Pleistocene ice volume, Antarctic climate, and the global  $\delta^{18}\text{O}$  record. *Science* 313(5786):492–495.
- Tierney JE, et al. (2008) Northern hemisphere controls on tropical southeast African climate during the past 60,000 years. *Science* 322(5899):252–255.
- Elderfield H, et al. (2012) Evolution of ocean temperature and ice volume through the mid-Pleistocene climate transition. *Science* 337(6095):704–709.
- Russell JM, et al. (2014) Glacial forcing of central Indonesian hydroclimate since 60,000 y B.P. *Proc Natl Acad Sci USA* 111(14):5100–5105.
- Singarayer JS, Burrough SL (2015) Interhemispheric dynamics of the African rainbelt during the late Quaternary. *Quat Sci Rev* 124:48–67.
- Trauth MH, Maslin MA, Deino A, Strecker MR (2005) Late Cenozoic moisture history of East Africa. *Science* 309(5743):2051–2053.

26. Pokras EM, Mix AC (1987) Earth's precession cycle and Quaternary climatic change in tropical Africa. *Nature* 326:486–487.
27. deMenocal PB, Tierney JE (2012) Green Sahara: African humid periods paced by earth's orbital changes. *Nature Education Knowledge* 3(10):12.
28. Kutzbach JE, Liu Z (1997) Response of the African monsoon to orbital forcing and ocean feedbacks in the Middle Holocene. *Science* 278:440–444.
29. Liseiecki LE, Raymo ME (2005) A Pliocene-Pleistocene stack of 57 globally distributed benthic  $\delta^{18}\text{O}$  records. *Paleoceanography*, 10.1029/2004PA001071.
30. Seehausen O (2006) African cichlid fish: A model system in adaptive radiation research. *Proc Biol Sci* 273(1597):1987–1998.
31. Wagner CE, Harmon LJ, Seehausen O (2012) Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* 487(7407):366–369.
32. Johnson TC, et al. (1996) Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* 273(5278):1091–1093.
33. Scholz CA, Rosendahl BR (1988) Low lake stands in lakes Malawi and tanganyika, East Africa, delineated with multifold seismic data. *Science* 240(4859):1645–1648.
34. Stone JR, Westover KS, Cohen AS (2011) Late Pleistocene paleohydrography and diatom paleoecology of the central basin of Lake Malawi, Africa. *Palaeogeogr Palaeoclimatol Palaeoecol* 303:51–70.
35. Templeton AR, Robertson RJ, Brisson J, Strasburg J (2001) Disrupting evolutionary processes: The effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proc Natl Acad Sci USA* 98(10):5426–5432.
36. Allender CJ, Seehausen O, Knight ME, Turner GF, Maclean N (2003) Divergent selection during speciation of Lake Malawi cichlid fishes inferred from parallel radiations in nuptial coloration. *Proc Natl Acad Sci USA* 100(24):14074–14079.
37. Loh YHE, et al. (2013) Origins of shared genetic variation in African cichlids. *Mol Biol Evol* 30(4):906–917.
38. Nichols P, et al. (2015) Secondary contact seeds phenotypic novelty in cichlid fishes. *Proc Biol Sci* 282(1798):20142272.
39. Genner MJ, Turner GF (2014) Timing of population expansions within Lake Malawi haplochromine cichlid fish radiation. *Hydrobiologia* 748:121–132.