Capturing climate variability during our ancestors' earliest days

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Climate's role in shaping the environmental and evolutionary history of our earliest ancestors remains an actively debated topic. In PNAS, Magill et al. (1, 2) present records of terrestrial habitat and hydroclimate variation and pacing from Olduvai Gorge sediments during a key interval of our ancestors' divergence and dispersal approximately 2.0 Ma. Although there is general consensus that ecosystem variability shaped resource and landscape distributions on the East African landscape, causing changes in early *Homo* foraging strategies and diet (3–5), the temporal linkages between climate and environmental changes and hominin evolution remain far more contentious (6). Here, Magill et al. constrain some of these temporal linkages by extracting paleoclimate records of terrestrial plant community change and hydrological cycle dynamics from well-dated, continuously deposited lake sediments associated with hominin archaeological sites. These new archives of terrestrial ecosystem variability reveal distinct orbital pacing in precipitation that drove abrupt changes in the local plant community and shaped the landscape's water availability during an important interval of hominin evolution.

In subtropical Africa, the period between 2.8 and 1.0 Ma saw increased climate variability and aridity, with a fundamental junction in the hominin taxonomic tree (7). Fossil evidence from this time also suggests an increased diversity of hominin species and gradual increases in brain size and tool development (7). The coincidence of climate variability with hominin evolution and cognitive development has fueled suggestions and hypotheses about how the emergence and dispersion of the genus *Homo* is linked to climate-driven ecosystem change.

Detailed stratigraphic control is required to understand the temporal and causal relationships between climatic variations and changes in *Homo* diversity, evolutionary events, and adaptation in East Africa. Throughout the Olduvai region, the terrestrial sediments in which most hominin and faunal materials are recovered come from distinct stratigraphic intervals and locations (8). The main advantage of these sedimentary archives is that they directly relate to the terrestrial environment in which the organisms lived. Although the region has many volcanic beds that can be quantitatively dated, constraining time in terrestrial sediments is notoriously tricky, as sediments can reflect limited intervals of time or less discrete durations of time (6). Further, terrestrial sedimentation is often laterally discontinuous, making correlations across beds and regions difficult. These characteristics of terrestrial sediments make deconvolving the temporal relationships between climate and evolution difficult. As a result of the stratigraphic limitations of terrestrial sediments, much of the environmental and climatic framework of hominin evolution has been recovered from marine sediments off the Horn of Africa (9). Constraining time is much easier in marine sediments given their continuous sedimentation; however, deep marine cores are far removed from the Olduvai ecosystem and cannot be directly tied to the Olduvai sediments. In their two contributions, Magill et al. (1, 2) extract climate archives from ancient Lake Olduvai sediments. By using lake sediments in the basin where early hominins were living, Magill et al. capture an integrated ecosystem signal and take advantage of the best qualities of terrestrial and marine records: local environmental and climate information and high temporal constraints given continuous sediment deposition. This stratigraphic control allows an unprecedented glimpse into the climate dynamics and orbital controls surrounding early hominin evolution in the Olduvai region.

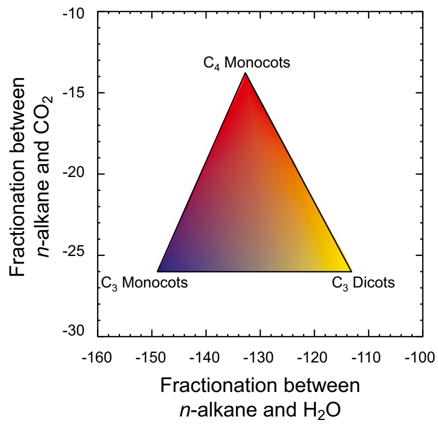

Fig. 1. Carbon and hydrogen isotope fractionations (ε) between leaf wax lipids and carbon dioxide and source water for different plant types. Carbon and hydrogen isotope data for modern C_3 and C_4 plants are compiled from Tipple and Pagani (19) and Sachse et al. (18), respectively. C_3 dicots include trees, shrubs, and forbs, whereas monocots include only grasses.

From the Olduvai sediments, Magill et al. extract terrestrial plant leaf wax lipids (*n*-alkanes) at high temporal resolution and measure the carbon and hydrogen isotope ratios of these plant compounds. *n*-Alkanes are straight-chain hydrocarbons produced by nearly all terrestrial plants (10). The carbon isotope ratios of plant materials reflect the photosynthetic pathway (C_3 vs. C_4) a plant uses to fix CO_2 from the atmosphere (Fig. 1). In this case, grasses and woody plants possess different photosynthetic pathways and thus very distinct carbon isotope values that allow for open grassland and closed canopy forest ecosystems to be distinguished (3) from lipids preserved in lake sediments. In the Olduvai lake record, Magill et al. report several oscillations between grasslands and forests (1). Although a variety of previous records from the region have observed shifts between from forests to open grasslands (3, 9, 11–15), none have shown such enormous ecosystem variability at regular intervals as is seen in this record. As an example, the terrestrial ecosystem surrounding Lake Olduvai oscillated from forest to open grassland and then back to forests on the order of every 20,000 y. This quick and large environmental variability could have been a strong selective force on early transitional hominin species and their dietary resources.

Although the marked oscillations between plant communities is striking, the pace at which these oscillations occur suggests orbital parameters and the regional climate factors controlled by these parameters played a key role in shaping the landscape on which our ancestors developed. From the marine record during this time, increases in regional climate variability are coincident with intensification of high-latitude glaciations paced by the 41,000-y obliquity cycle (4), yet the precessional ∼21,000-y harmonic is also observed in many East African paleoclimate archives (i.e., ref. 16). Changes in monsoonal strength has been purposed to explain the precessional signal in these records (4), yet the specific climatic mechanism responsible for these cycles

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remains uncertain. Magill et al. find their carbon isotope values have the strongest correlation to Earth's ∼21,000-y precessional cycle. They note the amount and timing of monsoonal precipitation in eastern Africa responds to sea surface temperatures in the Indian and Atlantic Oceans. Previous research has found temperature records from both ocean basins to respond strongly to obliquity, but only the Atlantic records respond strongly to precessionally driven upwelling (17). From this, Magill et al. put forth a hypothesis that combines multiple lines of evidence to explain the strong precessional signal in their carbon isotope record as a response to changes in the intensity of late season monsoonal precipitation. This hypothesis suggests moisture stresses drove cycles between forests and grasslands and shaped the ecosystems in which early *Homo* species emerged.

In their second contribution, Magill et al. use the hydrogen isotopic signature of leaf wax *n*-alkanes to reconstruct hydrologic cycle dynamics within the Olduvai region (2). The hydrogen isotope value relates to the isotopic ratio of the water available to the plant (i.e., source water) and to the plant-water dynamics during biosynthesis (18); thus, the interpretation of hydrogen isotope values is more nuanced than that of carbon isotopes. Another confounding factor in the interpretation of hydrogen isotope values is that plants with different growth forms (i.e., grass, forb, shrub, tree) and photosynthetic pathways (i.e., C_3 vs. C_4) have slightly different net isotopic fractionations between source water and leaf waxes (18). Although the understanding of the mechanisms behind these fractionation differences is nascent, it has been linked to differences in lipid biosynthesis between the photosynthetic pathways and leaf morphology (i.e., monocot vs. dicot) (18). Fig. 1 shows the relationship between carbon and hydrogen isotopes for the different photosynthetic pathways and plant functional types and demonstrates why differences between plant types and communities should be considered when interpreting hydrogen isotope data. This approach has been used to separate the variation in hydrogen isotope values as a result of plant community composition or hydrologic cycle changes (19).

Magill et al. use terrestrial biomarkers to provide insights into plant community change and hydrologic dynamics during a key period of hominin evolution in East Africa.

In their record, Magill et al. find relatively minor variation in the hydrogen isotope ratio (−148‰ to −132‰), which is surprising considering their carbon isotope values suggest plant community turnover associated with major changes in hydrology (2). To account for the attenuating effects of plant type on hydrogen isotope values, they model a landscape hydrogen fractionation by using their estimates of the plant community composition. As shown in Fig. 1, a change from woody forests to open C_4 grassland would be accompanied by an ∼−20‰ shift in the ecosystem hydrogen isotope values even without any change in source water isotope value. By using the carbon isotopes to constrain plant community makeup, the authors can better approximate changes in the hydrologic cycle during the time period of interest. The authors are able to take this approach another step further by combining ancient ecosystem-corrected leaf wax estimates of precipitation and paleolake water levels with modern East African climate and precipitation data. By using this approach and model, they find large variations in the amounts of precipitation received in the region during the arid and wetter intervals between 1.83 and 1.92 Ma. Given the large magnitude and variation of water delivery to the region, the authors argue that hominins living on this landscape likely relied on freshwater springs. Notably, many hominin fossils sites in Olduvai Gorge and other regions are associated with freshwater oases (20), which is consistent with the authors' model (2).

In their two contributions, Magill et al. (1, 2) use terrestrial biomarkers to provide insights into plant community change and hydrologic dynamics during a key period of hominin evolution in East Africa. The authors use a continuous section of lake sediments from the Olduvai basin and capture an integrated regional ecosystem signal at high temporal resolution. This regional perspective paints a fundamentally different, but complementary, picture of the climate dynamics and orbital controls surrounding early hominin evolution in the Olduvai region compared with local terrestrial and global marine climate archives. This biomarker approach provides a new framework for the application of plant biomarkers in the reconstructions of regional terrestrial environments on geologic and human timescales.

1. Magill CR, Ashley GM, Freeman KH (2013) Ecosystem variability and early human habitats in eastern Africa. *Proc Natl Acad Sci USA*, 10.1073/pnas.1206276110.
2. Magill CR, Ashley GM, Freeman KH (2013) Water, plants, and early human habitats in eastern Africa. *Proc Natl Acad Sci USA*, 10.1073/pnas.1209405109.
3. Cerling TE, et al. (2011) Woody cover and hominin environments in the past 6 million years. *Nature* 476 (7358):51–56.
4. deMenocal PB (2004) African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth Planet Sci Lett* 220:3–24.
5. McNabb J (2005) Environmental hypotheses of Pliocene human evolution. *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence*, eds Behrensmeyer AK, Bobe R, Alemseged Z (Springer, Dordrecht, The Netherlands), pp 25–50.
6. Potts R (2007) Paleoclimate and human evolution. *Evol Anthropol* 16:1–3.
7. deMenocal PB (2011) Anthropology. Climate and human evolution. *Science* 331(6017):540–542.
8. Hay RL (1976) *Geology of the Olduvai Gorge: A Study of Sedimentation in a semiarid basin* (Univ California, Berkeley).
9. Feakins SJ, deMenocal PB, Eglinton TI (2005) Biomarker records of late Neogene changes in northeast Africa vegetation. *Geology* 33:977–980.
10. Eglinton G, Hamilton RJ (1967) Leaf epicuticular waxes. *Science* 156(3780):1322–1335.
11. Bobe R, Behrensmeyer AK (2004) The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus Homo. *Palaeogeogr Palaeoclimatol Palaeoecol* 207:399–420.
12. Cerling TE (1992) Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeogr Palaeoclimatol Palaeoecol* 97:241–247.
13. Feakins SJ, Eglinton TI, deMenocal PB (2007) A comparison of biomarker records of northeast African vegetation from lacustrine and marine sediments (ca. 3.40 Ma). *Org Geochem* 38:1607–1624.
14. Wynn JG (2000) Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, Northern Kenya. *J Hum Evol* 39(4):411–432.
15. Wynn JG (2004) Influence of Plio-Pleistocene aridification on human evolution: Evidence from paleosols of the Turkana Basin, Kenya. *Am J Phys Anthropol* 123(2):106–118.
16. Rossignol-Strick M (1985) Mediterranean quaternary sapropels, an immediate response of the African monsoon to variation of insolation. *Palaeogeogr Palaeoclimatol Palaeoecol* 49:237–263.
17. Cleaveland L, Herbert T (2007) Coherent obliquity band and heterogeneous precession band responses in early Pleistocene tropical sea surface temperatures. *Paleoceanography* 22:PA2216.
18. Sachse D, et al. (2012) Molecular paleohydrology: Interpreting the hydrogen-isotopic composition of lipid biomarkers from photosynthesizing organisms. *Annu Rev Earth Planet Sci* 40:221–249.
19. Tipple BJ, Pagani M (2010) A 35 Myr North American leaf-wax compound-specific carbon and hydrogen isotope record: Implications for C_4 grasslands and hydrologic cycle dynamics. *Earth Planet Sci Lett* 299: 250–262.
20. Ashley GM, et al. (2010) Paleoenvironmental and paleoecological reconstruction of a freshwater oasis in savannah grassland at FLK North, Olduvai Gorge, Tanzania. *Quat Res* 74:333–343.