

Environment and Climate of Early Human Evolution

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Abstract

Evaluating the relationships between climate, the environment, and human traits is a key part of human origins research because changes in Earth's atmosphere, oceans, landscapes, and ecosystems over the past 10 Myr shaped the selection pressures experienced by early humans. In Africa, these relationships have been influenced by a combination of high-latitude ice distributions, sea surface temperatures, and low-latitude orbital forcing that resulted in large oscillations in vegetation and moisture availability that were modulated by local basin dynamics. The importance of both climate and tectonics in shaping African landscapes means that integrated views of the ecological, environmental, and tectonic histories of a region are necessary in order to understand the relationships between climate and human evolution.

INTRODUCTION

Understanding the interactions between humans and their environments is a core part of human origins research. The study of human evolution, which concerns the origin of all species that are more closely related to modern humans than to chimpanzees or bonobos, involves understanding the development of the suite of morphological and behavioral traits that are thought to characterize humans, such as terrestriality, bipedalism, dietary flexibility, tool use, omnivory, larger brains, long-distance migrations, and the birth of dependent children. To understand the adaptive significance of these human features, we need to characterize the selection pressures that early humans experienced and to place those pressures in the context of the changes in Earth's atmosphere, oceans, and landscapes over the past 10 Myr.

The oldest hominin fossils date to 7–6 Ma (**Figure 1**) (Lebatard et al. 2008, Simpson et al. 2015). This timing agrees with genetic estimates calibrated by mutations per generation, which place the human-chimpanzee split as early as 8–7 Ma (Langergraber et al. 2012), but slightly precedes genetic estimates calibrated using the fossil record, which suggest the split occurred after 6.3 Ma (Patterson et al. 2006). Although there is debate over which fossils should be included among the earliest humans (Wood & Harrison 2011), this review takes an inclusive approach that starts at 8 Ma (**Figure 1**). Most of the records for these fossils, as well as environmental records, come from eastern Africa, which dictates the geographic focus of the review; however, the story of how climate and environmental change have influenced human evolution is much bigger and needs to consider data sets from elsewhere in Africa (South Africa, Chad), Europe, and Asia, as

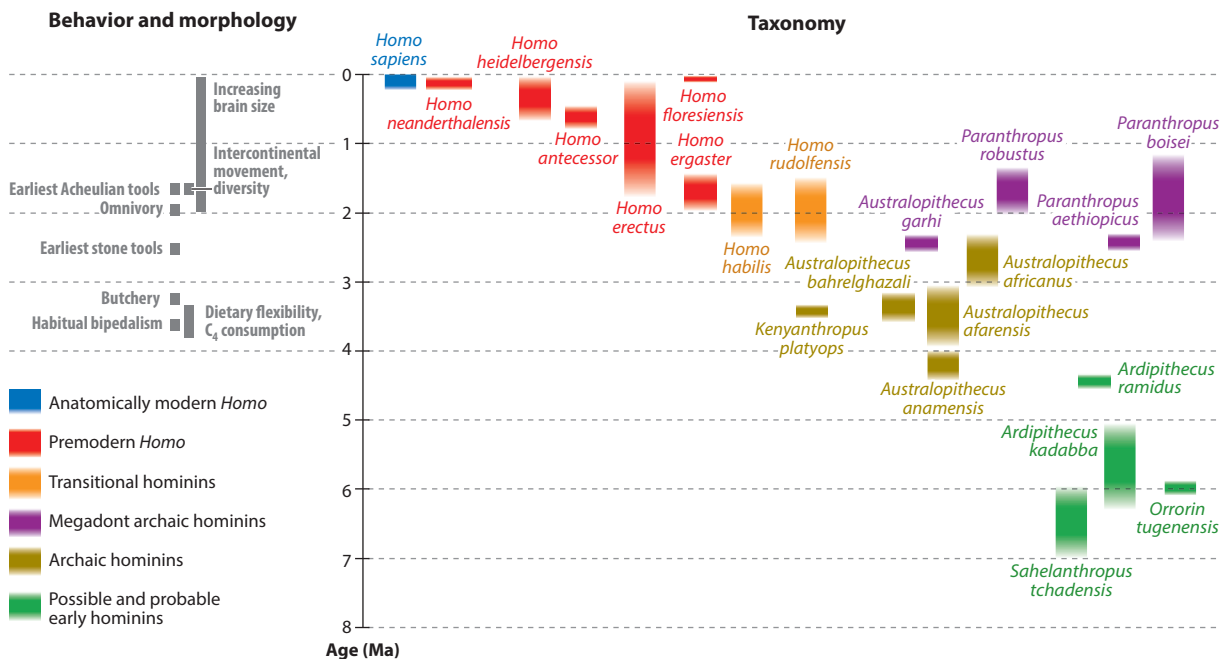


Figure 1

Schematic of hominin taxonomy adapted with permission from Wood & Loneragan (2008) and modified using information in Simpson et al. (2015). Some of the significant behavioral and morphological changes among hominins since 4 Ma, based on studies by Antón et al. (2014), Braun et al. (2010), Cerling et al. (2013b), Lepre et al. (2011), McPherron et al. (2010), Raichlen et al. (2010), Semaw et al. (2003), and Wynn et al. (2013), are noted.

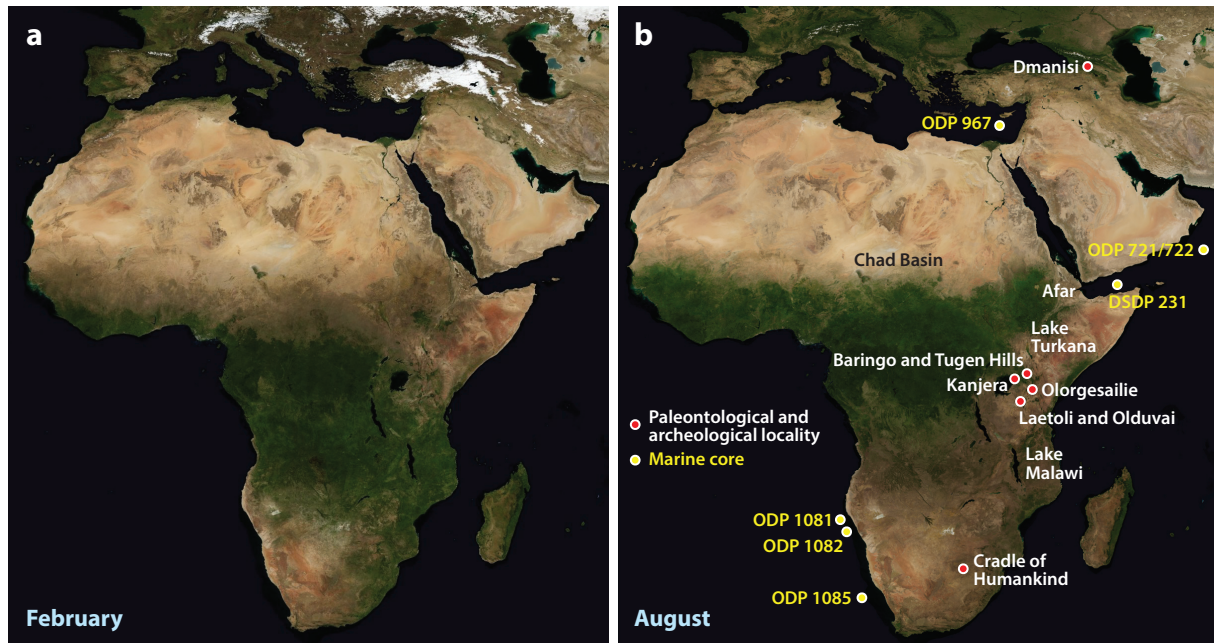


Figure 2

Imagery from NASA Earth Observatory (Stöckli et al. 2005) from (a) February 2004 and (b) August 2004, demonstrating the seasonal distribution of vegetation (*green*) in Africa today. The locations of sites discussed in the text are marked on panel *b*. Abbreviations: DSDP, Deep Sea Drilling Project; ODP, Ocean Drilling Program.

well as places where hominins might have lived that are not preserved or have yet to be discovered (**Figure 2**). I focus this review on the African records because most of the major events in early human evolution (prior to 1 Ma) occurred in Africa (MacLachy et al. 2010); I highlight eastern Africa because it contains the most abundant and well-dated climate, environmental, and fossil records. However, further work in northern Africa, the expanding ability to constrain the ages of fossil localities in South Africa, and the growing number of records from Europe mean that the field will increasingly need to expand its focus and build on studies that take continent-wide and intercontinental approaches (e.g., deMenocal 2004, Reed & Russak 2009, van der Made 2011).

The environment has been considered as a factor in most of the major changes in human evolution, including the transition from arboreal to terrestrial behaviors, bipedalism, megadontia, dietary changes to include a broader array of food types, tool use, increasing brain size, extended home ranges, and migrations (e.g., Antón et al. 2014, Braun et al. 2010, van der Made 2011, Vrba 1985, White et al. 2009). Many of these changes have been viewed in terms of local or regional environmental variables, including vegetation (extent of forests versus grasslands), hydrological balance, temperature, shade, variability and instability of climate and landscapes, and changes in the physical landscape such as habitat fragmentation, topography shifts, and the appearance of lakes (Antón et al. 2014, Cerling et al. 2011, deMenocal 2004, Domínguez-Rodrigo 2014, Passey et al. 2010, Potts 2013, Sepulchre et al. 2006, Trauth et al. 2007, White et al. 2009). Ecological considerations such as interspecific competition, community dynamics, fire, seasonality, and plant-herbivore dynamics are also important to human evolution (e.g., Cerling et al. 2013a, Grove 2012) but usually do not get as much attention.

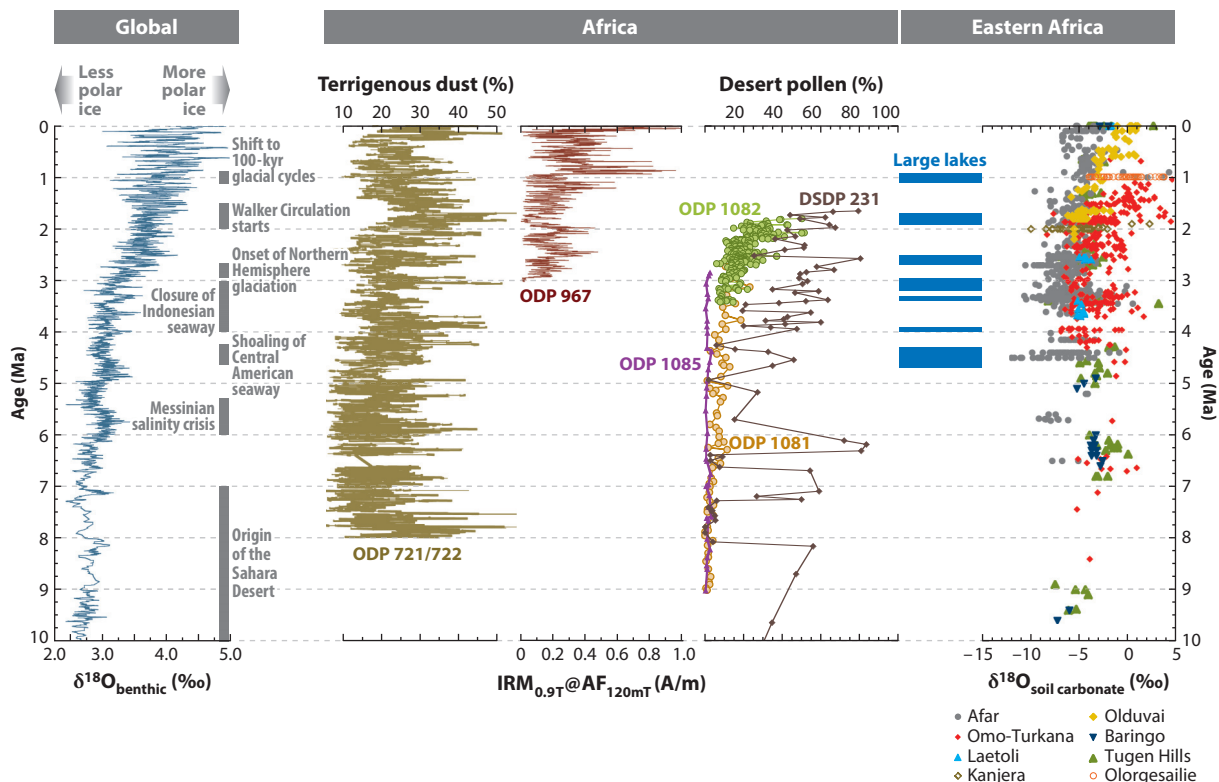


Figure 3

Compilation of data and events characterizing some of the global climate changes and variations in African hydroclimate during the past 10 Myr. The benthic $\delta^{18}\text{O}$ data are plotted as a 5-point running average reported relative to VPDB, from a global compilation of benthic (bottom-dwelling) foraminifera by Zachos et al. (2001), and represent polar ice volume and global temperatures. The timing of relevant events is plotted on the basis of information in Bickert et al. (2004), Cane & Molnar (2001), Haug et al. (2001), Imbrie et al. (1992), Ravelo et al. (2004), and Zhang et al. (2014). Dust records, representing dust supply from the Sahara, northeast Africa, Arabia, and Mesopotamia, are from the Mediterranean (ODP Site 967) and Arabian (ODP Sites 721 and 722) Seas. Environmental magnetic data ($\text{IRM}_{0.9\text{T}}@AF_{120\text{mT}}$, which is a good proxy for hematite content) are plotted from ODP Site 967 to represent the history of dust deposition (Larrasoana et al. 2003), whereas the percentage of terrigenous material is plotted for ODP Sites 721 and 722 (deMenocal 1995). The proportion of pollen from plants representative of semidesert or desert environments is used as a proxy for aridity and is plotted for DSDP Site 231 in the Gulf of Aden (Bonnefille 2010) and for ODP Sites 1081, 1082, and 1085 in the Atlantic Ocean off the western coast of Africa (Dupont et al. 2005, 2013; Hoetzel et al. 2013). Only plants from the families Chenopodiaceae and Amaranthaceae, halophytic herbs and shrubs widespread in arid regions, are considered in this category for Sites 231 and 1085 (Bonnefille 2010, Dupont et al. 2013), whereas a combination of semidesert and desert elements that includes Amaranthaceae and Chenopodiaceae is plotted for Sites 1081 and 1082 (Dupont et al. 2005, Hoetzel et al. 2013). Major lake phases for eastern Africa are plotted based on the criteria articulated by Trauth et al. (2007), who consider them to represent region-wide wet intervals. The soil carbonate $\delta^{18}\text{O}$ values are plotted relative to VDPB; see **Supplemental Material** for references (follow the **Supplemental Material** link in the online version of this article or at <http://www.annualreviews.org>). See **Figure 2** for the locations of cores and sites referenced here and **Supplemental Material** for the data plotted. Abbreviations: DSDP, Deep Sea Drilling Project; ODP, Ocean Drilling Program; VPDB, Vienna Pee Dee Belemnite.

Supplemental Material

Interactions between hominins and their environment need to be placed within the context of both global and regional climate change that occurred in the past 10 Myr, a time interval when Earth's climate became cooler and more variable (**Figure 3**) (Zachos et al. 2001). Feakins & deMenocal (2010) provided a thorough overview of Cenozoic climate in Africa, to which the reader is directed, but some of the main features of global climate that are relevant to the

discussion of human evolution include the decrease in global atmospheric CO₂ concentrations and expansion of C₄ grasses in the late Miocene, the mid-Pliocene warm interval, the closures of the Indonesian and Central American seaways in the Pliocene and Pleistocene, the onset and intensification of Northern Hemisphere glaciation by 2.75 Ma, the development of North Atlantic Deep Water in the early Pleistocene, the development of Walker Circulation between 2.0 and 1.5 Ma (when the east-west temperature gradient in the Pacific Ocean was established), and the mid-Pleistocene Revolution at ~1.0 Ma (during which glacial-interglacial cycles intensified) (**Figure 3**). The specific impacts of these global phenomena on African climate are an area of active study and are particularly relevant as climate scientists work on understanding how African environments will respond to present and future climate change.

Many reviews exist on human evolution and climate, in part because the field is constantly being updated with new fossils, behavioral data from archaeology, environmental and climate proxy data, and theories on how these data can (or should) be related to one another (e.g., deMenocal 2004, Kingston 2007, Maslin et al. 2014, Potts 2013). This review aims to synthesize some of the main data sets and narratives that are used to evaluate the environmental and climatic influences on human evolution. My approach to the review reflects my own research on this topic, as a field geologist and isotope geochemist who has worked primarily in eastern Africa. It is not comprehensive but instead provides a perspective that should complement existing reviews. I first review the kinds of data sets that are used to understand the dynamics between climate, paleoenvironments, and human evolution. I then review some of the main themes that arise when exploring these dynamics: (a) grasslands and open environments, (b) hydroclimate, (c) tectonics, and (d) variability and instability.

NATURE OF THE RECORD

Our understanding of human evolution comes from fossils and archaeology, which provide small, limited windows into the physiology, life histories, and behaviors of individuals and populations of human ancestors. In eastern Africa, hominin and other mammalian fossils are most commonly recovered from fluvio-lacustrine sequences that are intercalated with volcanics in basins that formed as part of the East African Rift System (e.g., Feibel et al. 1989). In South Africa they are found primarily in karst terrain and cave deposits (e.g., Dirks & Berger 2013), whereas in Chad they occur along lake margins (Lebatard et al. 2008). In the majority of these cases, hominins are among the least abundant mammalian fossils recovered from a locality.

Our understanding of climate and environment comes from multiple sources: excavations where hominin fossils and artifacts are recovered and from adjacent or nearby strata (e.g., Barboni 2014, Behrensmeyer et al. 2002, Bobe et al. 2007, Cerling et al. 2011, Deino et al. 2006, White et al. 2009), from drill sites in lacustrine and marine settings (e.g., deMenocal 1995, Scholz et al. 2007), and, soon, from terrestrial drilling projects (Cohen et al. 2009). Sedimentology provides the most basic information on depositional setting, paleogeography, and taphonomy of the record. Proxy records can be developed from the assemblage of fossil animals (taxonomy, species richness, relative abundances, faunal assemblages); the morphology of these animals (hypsodonty, mesowear, ecomorphology); the remains of plants (macrofossils, pollen, phytoliths, seeds); the isotopic composition of the mammalian teeth; and the geochemistry of the sediments, which may include the isotopic composition of soil carbonates and leaf waxes, the geochemistry of clays, and the distribution of biomolecules (see sidebar, Carbon Isotopes).

Proxies from fluvial, lacustrine, and marine records integrate data from different temporal and spatial scales and therefore provide different kinds of information about environmental and climate change. Proxy data from fossil and archaeological sites or nearby outcrops may be the best

CARBON ISOTOPES

Carbon isotopes are used as indications of the proportion of C_3 and C_4 vegetation preserved in soil carbonates, fossil teeth, and leaf waxes and are expressed using δ notation, where $\delta^{13}C = \left(\frac{{}^{13}C/{}^{12}C_{\text{sample}}}{{}^{13}C/{}^{12}C_{\text{reference}}} - 1 \right) \times 1,000$. For $\delta^{13}C$ values, Vienna Pee Dee Belemnite (VPDB), a marine carbonate, is used as a reference, such that materials with ${}^{13}C/{}^{12}C$ greater than that of VPDB yield a positive $\delta^{13}C$ value and materials with ${}^{13}C/{}^{12}C$ less than that of VPDB have a negative $\delta^{13}C$ value. Most terrestrial materials have $\delta^{13}C$ values lower than that of VPDB. (See Cerling 2014 for a review of how stable isotopes are used to reconstruct hominin paleoenvironments.)

way to evaluate the environmental context of hominin behaviors and morphologies, as they reflect the environmental conditions of the specific landscapes and ecosystems with which hominins interacted. Although some records, like the isotopic composition of teeth, capture information on very short timescales (less than 5 yr), the difficulty of placing these records within a highly resolved absolute timescale (10^3 to 10^5 yr) can make it challenging to connect them to specific climate phenomena (see Behrensmeyer et al. 2007 for a full discussion). Extensive lacustrine records, whether studied in outcrop or by core, do not provide information on the environments of hominins themselves, as hominins would interact only with shallow lakes or the margins of deep lakes, but they do provide valuable indications about how a specific place responds to climate change and yield information on orbital influences on continental environments (e.g., Ashley 2007, Bergner et al. 2009, Deino et al. 2006) in ways that most fluvial sediments cannot (see McDougall et al. 2005 for an exception). Finally, marine cores also provide useful perspectives because they can yield records with excellent temporal resolution ($<10^3$ yr) that integrate environmental and climate signals over large regions, although they do have their own taphonomic biases that must be considered (see discussions in Bonnefille 2010, deMenocal 1995, Dupont et al. 2013).

In all of these records, age control is a critical element in telling the story of how environmental and climate change is related to human evolution. Time can be measured using radiometric techniques; the ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ isotope system is most widely used in eastern Africa, given the prevalence of volcanic ashes and lava (e.g., Deino 2012, McDougall et al. 2005), but recent advances in carbonate U-series geochronology have made it possible to date fossils from South African cave sites and to generate climate and environmental records from these same sites (Pickering et al. 2013). Geochemical correlation of volcanic tephra is another key tool used to date and correlate hominin sites and climate records, due to the widespread nature and distinct geochemistry of many volcanic ashes (e.g., Feakins et al. 2007). In addition to tephra geochemistry, dating of deep-sea cores relies on biostratigraphy of marine fauna, orbital tuning, and magnetostratigraphy (e.g., deMenocal 1995, Larrasoana et al. 2003). Magnetostratigraphy is used to further constrain the age of outcrop and core records, on the basis of major reversals (e.g., Herries et al. 2006) and, in some cases, shorter polarity excursions (e.g., Lepre et al. 2011). Cosmogenic and luminescent dating has been critical to providing age control at sites or in strata where volcanic lithologies and carbonates are not available, or as a complement to other techniques (e.g., Lebatard et al. 2008, Pickering et al. 2013). In all cases sedimentation rates are used to estimate the age of a horizon (or fossil) between dated horizons.

GRASSLANDS AND OPEN ENVIRONMENTS

The story of human evolution is hard to discuss without considering the extent of grasslands and open environments. The influence of open versus closed environments on the development of

human morphology and behavior is mentioned as early as 1925 (Dart 1925), and it continues to be actively debated today (e.g., Cerling et al. 2011, Domínguez-Rodrigo 2014, White et al. 2009). Vegetation is a key component of habitat and the selection pressures on all terrestrial organisms, as it can affect diet, shelter, body plan, mobility, and predator-prey interactions. In studies of human evolution, vegetation has been important in considering the reasons for the development of terrestrial lifestyles, bipedalism, dietary change, and stone tool use (Domínguez-Rodrigo 2014, Plummer et al. 2009, Wheeler 1991, White et al. 2009). The nature of vegetation change in Africa has been recently reviewed (Bonnefille 2010, Barboni 2014, Jacobs et al. 2010), and the reader should consult these texts for more thorough treatments. Generally, over the past 10 Myr in Africa, open environments have become more prevalent and woody cover has decreased; however, the nature and the timing of this trend have varied by location and the changes were not unidirectional. A compilation of proxy data indicative of open environments shows how the nature and timing of vegetation change vary by region (**Figure 4**).

Regional Trends

In the late Miocene, African vegetation was diverse and heterogeneous, ranging from evergreen and deciduous forests to seasonally dry woodlands and wooded savannas as well as widespread grasslands (Bonnefille 2010, Jacobs et al. 2010). The global expansion of C₄ plants was one of the most significant ecological transitions that occurred in the past 10 Myr, and some of the earliest evidence for this transition comes from Africa (Cerling et al. 1997). Isotope records from soil carbonate, fossil teeth, and leaf waxes indicate that C₄ plants were present and in some cases were significant parts of African ecosystems by 9 Ma and gradually increased in abundance through the Pliocene and Pleistocene (**Figure 4**) (Cerling et al. 1997, Dupont et al. 2013, Feakins et al. 2013, Uno et al. 2011), although C₄ plants were not abundant in southwestern Africa in the late Miocene, likely due to cooler growing season temperatures resulting from winter rainfall in the region (Dupont et al. 2013, Ségalen et al. 2006). The late Miocene global expansion of C₄ grasses evident in regions with warm growing seasons, typically in monsoon-dominated climates, has been explained in terms of decreasing *p*CO₂, increasing aridity, and increasing fire frequency (e.g., Cerling et al. 1997, Edwards et al. 2010, Hoetzel et al. 2013). Explanations involving lower *p*CO₂ had gone out of favor in the past 15 years because alkenone-based reconstructions indicated that there was no decline in *p*CO₂ during the late Miocene (Pagani et al. 1999). However, new alkenone-based reconstructions and data from isotopic vital effects in coccoliths indicate that global *p*CO₂ did drop in the late Miocene, placing a renewed emphasis on the potential role of *p*CO₂ in the late Miocene expansion of C₄ plants (**Figure 4**) (Bolton & Stoll 2013, Zhang et al. 2013).

Amid diversity in vegetation during the Pliocene and Pleistocene, faunal assemblages, phytolith and pollen distributions, and carbon isotope data from soil carbonates, tooth enamel, and leaf waxes indicate an increase in the proportion of both open environments and C₄ resources at and near hominin sites between 4 and 1 Ma (e.g., Barboni 2014; Bobe et al. 2007; Bonnefille 2010; Cerling et al. 2011; Feakins et al. 2005, 2013; Reed 1997; Reed & Russak 2009; Wynn 2004). However, the timing and nature of this shift toward open environments varied spatially (**Figures 4 and 5**) (e.g., Bobe et al. 2007, Levin et al. 2011, Reed & Russak 2009). A large proportion of data on these changes comes from the Omo-Turkana Basin in southern Ethiopia and northern Kenya. Soil carbonate $\delta^{13}\text{C}$ and faunal abundance data from Omo-Turkana are often cited as representative of vegetation change in eastern Africa over the past 5 Myr and then related to global climate phenomena (e.g., deMenocal 2004, Maslin et al. 2014), in part because they provide a long record of environmental change that is associated with a rich archaeological and hominin fossil record (e.g., Braun et al. 2010, Lepre et al. 2011, Wood & Leakey 2011). However, as I describe below,

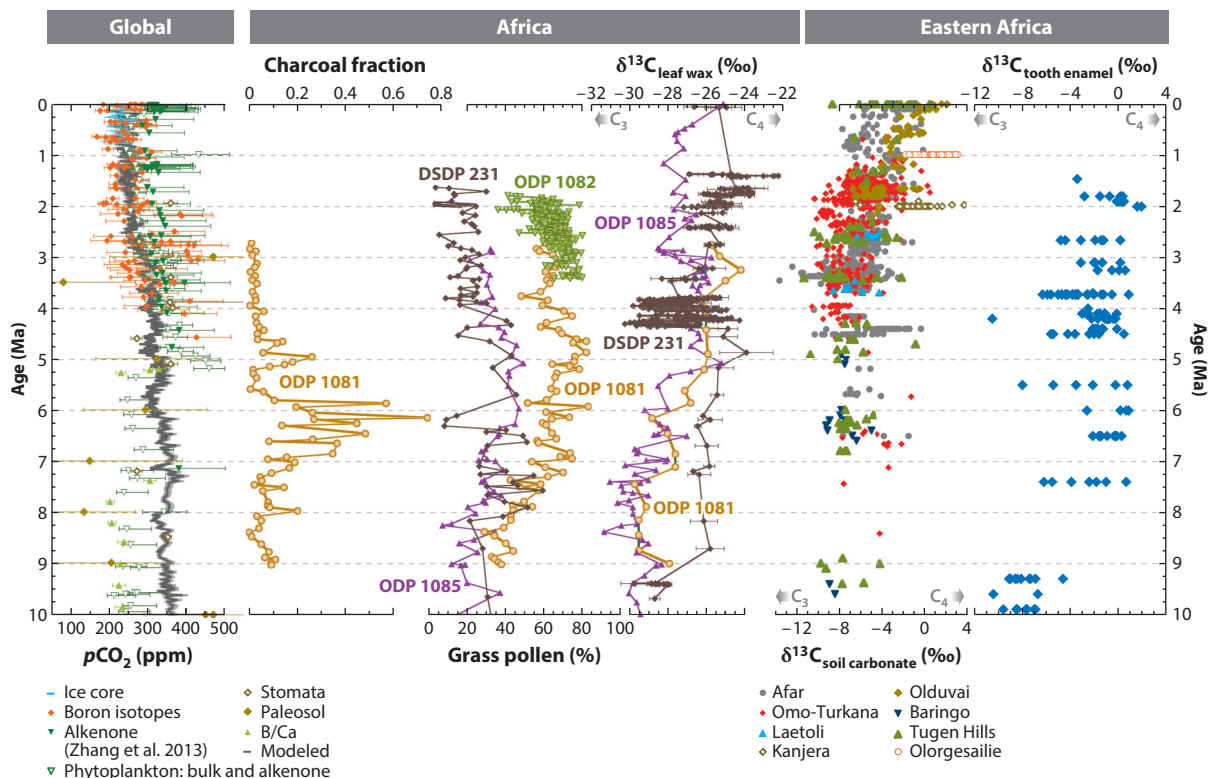


Figure 4

Compilation of data relevant to vegetation change in Africa during the past 10 Myr. The plotted estimates for atmospheric carbon dioxide concentrations ($p\text{CO}_2$) are from alkenone-, boron isotope- and ice core-based $p\text{CO}_2$ reconstructions reported by Bartoli et al. (2011), Hönlisch et al. (2009), Lüthi et al. (2008), and Zhang et al. (2013), in addition to the reconstructions from paleosols, alkenones, boron isotopes, stomata, and B/Ca ratios compiled by Beerling & Royer (2011). Modeled CO_2 concentrations are from van de Wal et al. (2011). The upper and lower bounds for each $p\text{CO}_2$ estimate are plotted as error bars. The charcoal abundance (the fraction of charcoal relative to the sum of pollen, charcoal, and spores) from ODP Site 1081 represents fire activity (Hoetzel et al. 2013). The proportion of grass pollen (family Poaceae) and the leaf wax $\delta^{13}\text{C}$ data from DSDP Site 231 and ODP Sites 1081, 1082, and 1085 are from Bonnefille (2010), Dupont et al. (2005, 2013), Feakins et al. (2013), Hoetzel et al. (2013), and Maslin et al. (2012). The $\delta^{13}\text{C}$ data from leaf waxes are reported relative to VPDB and are from long-chain $n\text{-C}_{31}$ alkanes for ODP Sites 1081 and 1085 (Dupont et al. 2013, Maslin et al. 2012, Hoetzel et al. 2013) and from C_{30} n -alkanoic acid for DSDP Site 231 (Feakins et al. 2013). Soil carbonate $\delta^{13}\text{C}$ values from eastern Africa are reported relative to VPDB and are derived from references cited in **Figure 3**. The tooth enamel $\delta^{13}\text{C}$ values of fossil Proboscidea from eastern Africa are plotted to indicate the dietary transition to C_4 resources; data from *Deimotherium* and *Prodeimotherium* are excluded because they are browsers. Abbreviations: DSDP, Deep Sea Drilling Project; ODP, Ocean Drilling Program; VPDB, Vienna Pee Dee Belemnite. See **Supplemental Material** for a full list of references (follow the **Supplemental Material** link in the online version of this article or at <http://www.annualreviews.org>).

▶ Supplemental Material

careful examination of these data demonstrates the importance of considering local basin dynamics before linking the observed environmental change in a particular basin to regional and global climate events (Bobe et al. 2007, Lepre 2014, Levin et al. 2011).

Case Study: The Omo-Turkana Basin

Pliocene and Pleistocene sedimentary strata are preserved primarily in three parts of the Omo-Turkana Basin: at the north end of the basin, the Shungura Formation records environments

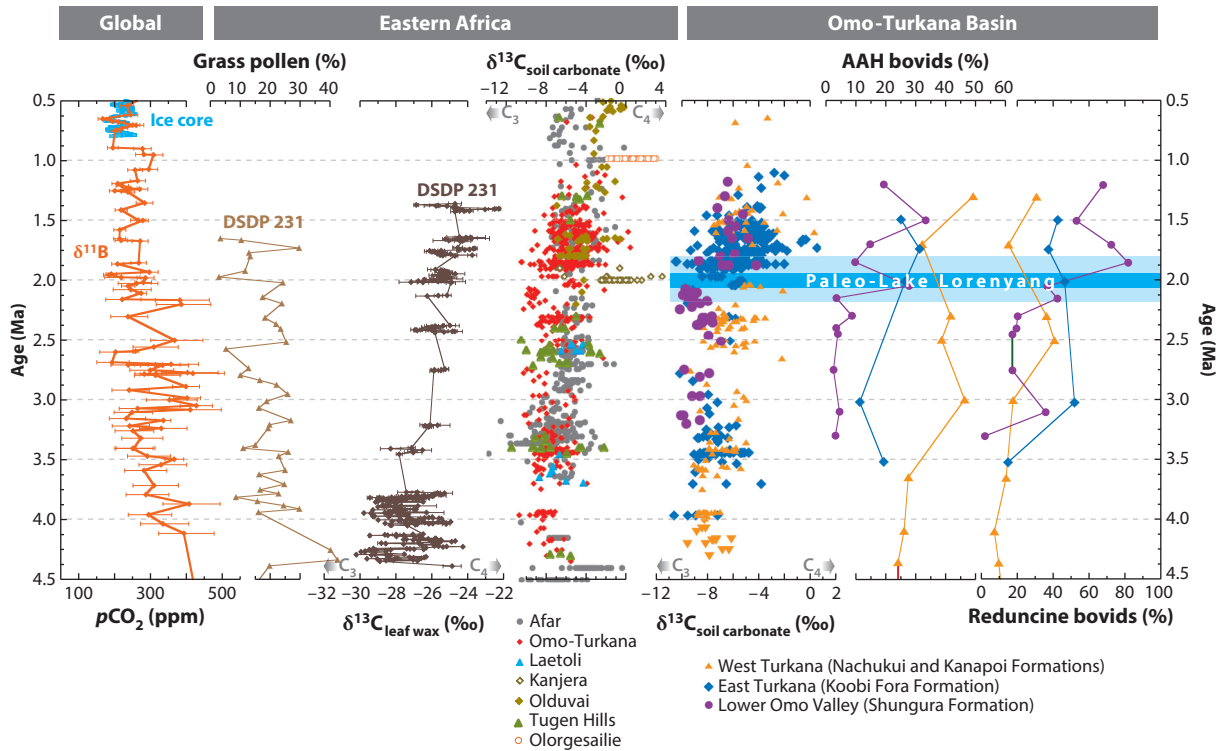


Figure 5

Compilation of data characterizing vegetation change in eastern Africa during the past 4.5 Myr. References for CO₂, pollen, leaf wax δ¹³C, and soil carbonate δ¹³C values are the same as in **Figure 4**. Soil carbonate δ¹³C data from the Omo-Turkana Basin are replotted and separated by basin position. The proportions of grazing fossil bovids relative to all fossil bovids from the Omo-Turkana Basin are from Bobe et al. (2007); the AAH bovids are indicative of seasonally arid grasslands, and the reduncine bovids are indicative of wet open habitats. The timing of the extent of paleo-Lake Lorenyang is from Lepre (2014); darker blue shading represents its presence in the lower Omo River basin, and lighter blue shading represents its extent in the northwest portion of the Turkana Basin. All δ¹³C values are reported relative to VPDB. Abbreviations: AAH, Alcelaphini, Antilopini, and Hippotragini; DSDP, Deep Sea Drilling Project; ODP, Ocean Drilling Program; VPDB, Vienna Pee Dee Belemnite.

along the axis of the paleo-Omo River as it emerged from the Ethiopian highlands, whereas on the west and east sides of the basin, respectively, the Nachukui and Koobi Fora Formations record a combination of lacustrine, fluvial, and basin margin depositional contexts (Brown & Feibel 1991, Feibel et al. 1989). Bovids from west Turkana indicate a steady rise in Alcelaphini, Antilopini, and Hippotragini (AAH) proportions relative to the total bovid population since the late Miocene, and the fraction of AAH is greater than or equal to that of Reduncini during any given time interval (**Figure 5**) (Bobe et al. 2007, Harris et al. 1988) (see sidebar, Bovids as Indicators of Paleoenvironments). On the east side of the lake, proportions of AAH also increased through time, but Reduncini usually outnumbered AAH. The bovids from the Shungura Formation have the most striking distribution patterns and have received the most attention (Bobe 2011, Bobe & Behrensmeyer 2004, Bobe et al. 2007, deMenocal 2004); at ~2.0 Ma there are increases in both AAH and Reduncini, when compared with the abundances of nongrazing bovid tribes, which reflect a shift from wooded to open environments on the floodplain of the lower Omo River Valley. The open environments indicated by the change in bovid distributions include an increase in both seasonally

BOVIDS AS INDICATORS OF PALEOENVIRONMENTS

Fossil antelopes or bovids are used as indicators of environment because the distribution of extant bovid tribes is sensitive to habitat type; the abundance of Alcelaphini (e.g., wildebeest), Antilopini (e.g., gazelle), and Hippotragini (e.g., oryx) bovids (i.e., AAH bovids) is used as an indicator of seasonally dry grasslands, bushlands, and woodland-grassland mosaics, whereas the abundance of Reduncini (e.g., waterbuck) is indicative of moist, open habitats where there is fresh grass (see Bobe et al. 2007 for explanation). The habitat preference of these bovids is considered to be relatively unchanged over the Pliocene and Pleistocene, making their distributions in the fossil record robust indicators of habitat (DeGusta & Vrba 2003, Sponheimer et al. 1999, Vrba 1988).

arid and wet grasslands. This shift in bovid abundances coincides with the appearance of a large lake, paleo-Lake Lorenyang, which formed in response to a major tectonic reorganization of the hydrology of the Omo-Turkana Basin (**Figure 5**) (Bobe et al. 2007, Bruhn et al. 2011, Lepre 2014).

The long-term trend toward open environments indicated by the bovid data is consistent with soil carbonate carbon isotope records from eastern Africa (**Figure 5**) that indicate an increased proportion of C_4 plants and a decrease in woody cover in floodplain and lakeshore soils since 4 Ma (Cerling et al. 2011, Levin et al. 2011). Sampling of coeval soil carbonate records from different parts of the Omo-Turkana Basin shows that the distribution of C_3 and C_4 plants varied by basin position, with more C_3 plants and greater woody cover in the Shungura Formation than in the Nachukui and Koobi Fora Formations; this is consistent with the environmental heterogeneity indicated by the bovids (**Figure 5**) (Bobe et al. 2007, Cerling et al. 1988, Levin et al. 2011, Quinn et al. 2007, Wynn 2004) (see sidebar, C_3 and C_4 Plants). General increases in C_4 plants are also observed in soil carbonate $\delta^{13}C$ and phytolith records from other parts of eastern Africa (Barboni 2014, Cerling 1992, Levin et al. 2004, Rossouw & Scott 2011) and in the $\delta^{13}C$ values of leaf waxes from deep-sea cores, which sample a broader area of land and environments (Feakins et al. 2005,

C_3 AND C_4 PLANTS

C_3 and C_4 refer to photosynthetic pathways that differ in the way that CO_2 is fixed by a plant. C_4 plants have the ability to concentrate CO_2 in a bundle sheath cell, giving them the advantage over C_3 plants in conditions of low atmospheric carbon dioxide concentrations (pCO_2), high temperature, and high water stress. In Africa, the majority of C_4 plants are grasses, and C_3 plants include cool-growing season grasses and dicots (Tieszen et al. 1979, Young & Young 1983). Growing season temperature, atmospheric pCO_2 , temperature, herbivory, and fire are some of the primary controls on C_4 abundance; a combination of these factors is responsible for the success of C_4 grasses relative to both C_3 grasses and C_3 woody vegetation (Bond et al. 2003, Ehleringer et al. 1997).

The carbon isotope signatures of C_3 and C_4 plants are distinct; on average, $\delta^{13}C$ values for C_4 plants are $\sim 14\%$ more positive than those for C_3 plants, although this difference varies by light level, water stress, and species (Cerling et al. 2003). These isotopic distinctions in plants are incorporated into leaf waxes, soil components, and animal tissues that are preserved in the geologic record such that $\delta^{13}C$ values of soil carbonates, fossil teeth, organic matter, and leaf waxes can be used to estimate the proportions of C_3 and C_4 plants in the geologic record (see Cerling 2014 for a review). Phytoliths of C_3 and C_4 grasses are also distinct, and they provide another way to detect the proportions of C_3 and C_4 grasses in sedimentary archives (see Rossouw & Scott 2011 for a case study from Laetoli, Tanzania).

2013), but the timing and magnitude of change vary by site (**Figure 5**) (e.g., Cerling et al. 2011, Levin et al. 2011).

The combination of soil carbonate $\delta^{13}\text{C}$ data, leaf wax $\delta^{13}\text{C}$ data, and faunal records of grasslands in the Shungura Formation is commonly used as evidence for an increase in aridity (e.g., Bobe 2011; deMenocal 2004, 2011; Maslin et al. 2014; Sepulchre et al. 2006), but these inferences should be tempered given the highly local nature of the faunal record, the relatively high proportion of reduncine bovids throughout the Omo-Turkana Basin, and the increases in indications of both seasonally arid and wet, open habitats in the Shungura Formation after ~ 2 Ma. It is important to emphasize that the presence of open indicators does not necessarily indicate a dry environment; in fact, grasses usually succeed in places and seasons where there is water, particularly in the shallow subsurface. This is clearly seen in the inverse correlation between the proportions of pollen from grass (Poaceae) and from arid-adapted halophytic herbs or shrubs (Chenopodiaceae and Amaranthaceae) in the marine core from Deep Sea Drilling Project (DSDP) Site 231 (Bonnefille 2010). Studies of African ecosystems today highlight the importance of considering a combination of factors that determine the extent of grasses (including C_4 vegetation) and woody cover, which include the seasonality of rainfall; the timing of the rainy season; the intensity of rainfall; the stability of the landscape; atmospheric $p\text{CO}_2$; and the presence of herbivores, fire, and canopy cover (Bond et al. 2003, Good & Caylor 2011, Guan et al. 2014, Staver et al. 2011).

Drivers of Variation in C_4 Vegetation

A combination of the above factors (e.g., timing and amount of rainfall, disturbance, fire, atmospheric $p\text{CO}_2$) is likely responsible for giving C_4 grasses the advantage over C_3 plants on the floodplains of large rivers during the Pliocene and Pleistocene, where C_3 plants might otherwise have the advantage over C_4 grasses in terms of canopy cover, temperature, water availability, and resistance to disturbance (Bond et al. 2003, Ehleringer et al. 1997). Although aridity is often cited as the explanation for the increase in C_4 plants (Edwards et al. 2010, Schefuß et al. 2003), there is limited terrestrial evidence for increased aridity that coincides with times of increases in C_4 vegetation in eastern Africa during the Pliocene and Pleistocene. Many of the records that are used as measures of paleoaridity, such as the prevalence of arid-adapted bovids, actually track the distribution of vegetation and not aridity. Some of the most direct evidence for terrestrial paleoaridity in eastern Africa comes from paleoprecipitation estimates derived from depth to calcic horizons in paleosols exposed on the west and east sides of Lake Turkana; these estimates indicate a general decrease in mean annual precipitation between 4.5 and 1.4 Ma amidst considerable scatter (ca. 400 mm) at any given time interval (Wynn 2004). Soil carbonate oxygen isotope data may also reflect increased aridity in the Omo-Turkana Basin (e.g., Cerling et al. 1988, Levin et al. 2011, Wynn 2004), but the lack of parallel changes in the oxygen isotope records in the Awash Basin indicate that increased aridity may not be the sole driver of increases in C_4 vegetation in eastern Africa (**Figure 5**) (Levin et al. 2011). See the next section for a more complete discussion of hydroclimate.

Among the other possible drivers, we do not have records that document changes in the seasonal distribution of rainfall, the extent of fire, or the amount of disturbance in eastern Africa that span the past 5 Myr. However, a group of recent studies provide evidence for a decrease in atmospheric $p\text{CO}_2$ during the past 5 Myr and particularly at the Pliocene–Pleistocene transition (Bartoli et al. 2011, Hönlisch et al. 2009, Martinez-Boti et al. 2015). Atmospheric $p\text{CO}_2$ has not been considered as a factor during Plio–Pleistocene increases in C_4 vegetation because high-resolution $p\text{CO}_2$ estimates were not available, but recent boron isotope records indicate that atmospheric $p\text{CO}_2$ was consistently below 300 ppm after 3 Ma, which coincides with the onset of

Northern Hemisphere glacial cycles (Bartoli et al. 2011, Hönisch et al. 2009, Martinez-Boti et al. 2015). This drop may have been a factor in giving C_4 plants an advantage over woody C_3 vegetation in floodplain environments, considering that C_4 plants are favored when $pCO_2 < 350$ ppm and growing season temperatures exceed $25^\circ C$ (Ehleringer et al. 1997). Temperatures greater than $25^\circ C$ are reasonable considering clumped isotope measurements of soils from Turkana that indicate soil temperatures in excess of $30^\circ C$ between 4 and 1 Ma (Passey et al. 2010). The sensitivity of C_3 and C_4 plant distributions to pCO_2 between glacial-interglacial cycles is an important consideration in interpretations of lacustrine records in eastern Africa (e.g., Street-Perrott et al. 2004); given similar oscillations in pCO_2 during the early Pleistocene (e.g., Martinez-Boti et al. 2015), C_3 and C_4 plant distributions may have also responded to changes in pCO_2 during the early Pleistocene, giving C_4 plants a selective advantage during glacial intervals when pCO_2 was low. Likewise, recent increases in pCO_2 are considered possible triggers for afforestation and a loss of savanna in Africa today and in the near future (Higgins & Scheiter 2012). In sum, the distribution of grasses and woody cover in Africa over the past 10 Myr is not solely a function of aridity but instead is a response to a suite of variables that includes atmospheric pCO_2 , length of rainy season, mean annual precipitation, fire regime, and the amount of disturbance. The influence of these variables on the vegetation of any particular site depends on its position on the landscape (e.g., riparian zone, lake margin) and climate regime.

HYDROCLIMATE

The effects of global climate change on African landscapes during the past 10 Myr are often discussed in terms of aridity and water availability (deMenocal 2004; Dupont et al. 2005, 2013; Sepulchre et al. 2006; Zhang et al. 2014). The distribution of vegetation and animals in Africa today depends not only on the amount of rainfall but also on its intensity and seasonal distribution (**Figure 2**) (e.g., Good & Caylor 2011, Guan et al. 2014, Kingdon 1988, White 1983). Topography, latitude, position relative to the Intertropical Convergence Zone (ITCZ), monsoon dynamics, ocean temperatures, and ocean upwelling all affect the hydroclimate of Africa, which can vary over short distances, between seasons, and on both decadal and millennial scales. Trends toward more arid climates have been central to hypotheses of human evolution and faunal change in Africa (deMenocal 2004, Reed 1997, Vrba 1985), but transitions between dry and wet phases and their effect on vegetation and geography (e.g., greenness of the Sahara, extent of the coastline) have been highlighted recently in discussions of the biogeography of early humans and in considerations of how climate variability affects speciation events (Larrasoña et al. 2013, Maslin et al. 2014, Potts 2013, Trauth et al. 2007). Generating records that link the impacts of hydroclimate on human environments to regional and global climate events is a key part of understanding the relationship between climate and human evolution.

The interplay between insolation changes at low latitudes and the effects of high-latitude forcing is at the heart of most descriptions of African paleoclimate (deMenocal 2004, Maslin et al. 2014, Trauth et al. 2009). Major global climate events that affected hydroclimate in Africa during the past 10 Myr include the Messinian salinity crisis (6–5.3 Ma), the onset and intensification of Northern Hemisphere glaciation at ~ 2.75 Ma, the onset of Walker Circulation at 2.0–1.5 Ma, and the mid-Pleistocene Revolution after ~ 1.0 Ma, when glacial-interglacial cycles shifted from 41-kyr to 100-kyr periodicity (**Figure 3**) (Bickert et al. 2004, Imbrie et al. 1992, Ravelo et al. 2004). Changes in the nature of Earth's rotation affect its position relative to the Sun and the amount of solar radiation it receives. These orbital fluctuations vary at different periodicities: a 100-kyr cycle due to variations in the shape of Earth's path around the Sun (eccentricity), a 41-kyr cycle that results from the tilt of Earth's axis (obliquity), and a 20-kyr cycle in the wobble of

Earth's rotation (precession) (Berger 1988). Variation in all of these parameters influences the degree of high-latitude glaciations (Imbrie et al. 1992), but in the tropics the precessional cycle has the biggest influence as it affects the season when Earth comes closest to the Sun and can amplify the hydrological cycle when this occurs in the boreal summer months (Clement et al. 2004, Kutzbach & Liu 1997). In the simplest case, wet intervals are expected during times of high insolation, but this can be complicated given the variation in topography, vegetation, and monsoon dynamics, in addition to ocean feedbacks and changes in polar ice distributions that affect tropical climate (deMenocal 1995, Kutzbach & Liu 1997). The African Humid Period, at 11–5 ka, is the most recent example of an insolation maximum during the boreal summer and is documented in lakes and in marine dust and hydrogen isotope records (see Tierney et al. 2011 and references therein); it represents one of many humid events that likely occurred in Africa since the Miocene and may serve as a good analog for earlier wet periods, in terms of the rapidity and the drastic nature of changes in vegetation and geography. Such wet intervals would have critically affected biogeography and may have influenced migrations among hominins (e.g., Larrasoña et al. 2013).

Marine Records

The long view of African hydroclimate is constructed primarily from dust, pollen, and leaf wax hydrogen isotope (δD) records from marine cores off the coast of Africa, sapropels from the Mediterranean, and lacustrine archives (e.g., deMenocal 1995, Dupont et al. 2013, Feakins 2013, Larrasoña et al. 2003, Marlow et al. 2000, Scholz et al. 2007). deMenocal (2004) summarized the dust records off of western and eastern Africa from the past 5.3 Myr, including cores from Ocean Drilling Program (ODP) Sites 721 and 722 off of Arabia, which indicate the existence of orbitally paced wet-dry cycles since the Miocene, increases in the amplitude and period of these cycles at intervals (2.8 ± 0.2 , 1.7 ± 0.1 , and 1.0 ± 0.2 Ma) that correspond to the onset of Northern Hemisphere glaciation and intensification of glaciation, and a long-term aridification trend starting after 2.8 Ma (**Figure 3**). A reevaluation of the dust flux records by Trauth et al. (2009) highlighted the role of low-latitude insolation effects, in addition to high-latitude events, on the monsoon dynamics that influence these dust records and documented how cores in the Mediterranean and the Arabian Sea are sensitive to different aspects of African climate (**Figure 3**). The amount of Chenopodiaceae and Amaranthaceae in the pollen record from DSDP Site 231, in the Gulf of Aden, also shows a general trend of increase in arid-adapted vegetation in eastern Africa, amid variability throughout the record (**Figure 3**) (Bonnefille 2010). In South Africa, the story of aridity and vegetation change is linked to the presence and intensity of upwelling of the Benguela Current, which responds to high-latitude forcing because it is linked to water temperatures in the South Atlantic and ice sheet dynamics in Antarctica (Dupont 2011). Benguela upwelling was established by 10 Ma (Krammer et al. 2006), and its intensification through the Pliocene and Pleistocene was associated with increased aridity in southern Africa (**Figure 3**) (Dupont et al. 2005, 2013; Marlow et al. 2000). In sum, although the timing of trends in aridity varies by region and record, there are many indications for large swings in moisture availability in most archives that reflect the cycling between wet and dry intervals in Africa since the late Miocene (Bonnefille 2010, deMenocal 2004, Dupont 2011, Feakins 2013, Larrasoña et al. 2003, Scholz et al. 2007).

Continental Records

Linking these big-picture changes in hydroclimate, deduced primarily from marine cores, to specific landscapes associated with hominins is the key to figuring out how they might affect human evolution. Mammalian herbivore abundances and soil carbonate carbon isotope values

are often cited as evidence for long-term trends in the aridification of eastern Africa (deMenocal 2004, Maslin et al. 2014, Sepulchre et al. 2006, Spiegel et al. 2007, Wynn 2004). However, these records are flawed measures for regional aridity because, as discussed above, C_4 plants are sensitive to variables other than aridity, grazing fauna can indicate both dry and wet grasslands, and both of these measures are highly sensitive to local basin dynamics (Bobe et al. 2007, Levin et al. 2011). Oxygen isotope records from soil carbonates have been used as measures of moisture availability and generally exhibit trends of increasing $\delta^{18}O$ values, which are consistent with general aridification from the early Pliocene to today (**Figure 3**) (Levin et al. 2004), but the roles of local and regional influences on these records still need to be established (Levin et al. 2011). Depth to carbonate was used by Wynn (2004), as described above, to provide a measure of aridity but it is not widely used in eastern Africa. The oxygen isotope record of fossil teeth also provides perspective on paleoaridity at fossil localities, and although this has been applied to several fossil sites (Bedaso et al. 2010, Braun et al. 2010, White et al. 2009), a compilation of data has not been integrated into a single story.

Although the long-term aridity trends can be difficult to identify, there is an increasing number of studies that document the nature of wet-dry oscillations in Africa, whether by fluctuations within lakes (Deino et al. 2006, Kingston et al. 2007, Magill et al. 2013, Scholz et al. 2007, Wilson et al. 2014), changes in the distribution of lakes (Trauth et al. 2007), intervals of fluvial deposition (McDougall et al. 2005), or isotopic compositions of speleothems (Hopley et al. 2007). Detailed lithologic and isotopic studies of lacustrine intervals provide the most direct views of the hydroclimate of terrestrial systems in the Pliocene and Pleistocene in Africa and the adaptive conditions for hominins living at the margins of these lakes. This is in contrast to marine records, which are far removed from the hominins themselves but are integrated over large regions. As an example, well-dated packages of fluvial and lacustrine deposition in the Baringo Basin between 2.69 and 2.58 Ma indicate wet and dry cycles at 23-kyr periodicities and likely reflect the intensification of the southwest African monsoon in response to orbital variation in insolation (Deino et al. 2006, Kingston et al. 2007). Correlation between diatomites and dust flux minima in the cores from ODP Sites 721 and 722 indicates that lake intervals in the Baringo Basin are consistent with records of regional humidity (Deino et al. 2006, Kingston et al. 2007). Lithologic and isotopic studies from Turkana and Olduvai also recognize lake expansion and contraction in the early Pleistocene, and the timing is consistent with orbital forcing of monsoon dynamics that result in wet-dry cycles in eastern Africa (Ashley 2007, Joordens et al. 2011, Lepre et al. 2007, Magill et al. 2013). In addition to orbital forcing, detailed lacustrine records have also recorded severe droughts, such as the megadrought at 175–145 ka identified in a core from Lake Malawi, which might have been important bottleneck for early *Homo sapiens* (Scholz et al. 2007) and could be an analog for other extreme intervals of drought and high climate variability that would have exerted distinct selection pressures on early humans and other mammals.

In contrast to detailed studies of specific lake basins, the occurrence of lakes in eastern Africa has also been used as an indication of regional wet intervals. Using a compilation of sedimentological data from eastern Africa, Trauth et al. (2007) identified wet phases in eastern Africa that occurred at 400-kyr periodicities prior to 2.7 Ma and at 800-kyr periodicities after 2.7 Ma and were coincident with periods of increased monsoon intensity at times of insolation maxima as indicated by dust abundance and sapropel formation in the Mediterranean. Trauth et al. (2007) argued that the synchronicity of these intervals with global climate transitions at 2.7–2.5, 1.9–1.7, and 1.1–0.9 Ma reflects that these wet lake phases and rapid shifts in moisture availability were influenced by high-latitude forcing, which compresses the ITCZ and increases the region's sensitivity to insolation forcing (Trauth et al. 2007). Although these wet phases have been studied in detail in some basins, more work needs to be done to generate detailed, high-resolution records of specific lake basins,

as has been done in Baringo, Turkana, and Olduvai (see references in previous paragraph), so that they can be placed into the framework of local basin dynamics and specifically linked to records of human evolution (Bergner et al. 2009, Lepre 2014).

TECTONICS: UPLIFT AND LANDSCAPES

Tectonic activity sets the stage for all aspects of the record of human evolution because it controls topography, landscape, sedimentation, and erosion. Despite evidence for some uplift and doming in southern Africa into the late Miocene (see the review in Partridge 2010), most tectonic activity in Africa in the last 10 Myr has centered on the East African Rift System (EARS), a series of fault-bounded valleys and uplifted plateaux that extends from the Afar Triple Junction in Ethiopia to the Zambezi Valley in southern Africa (Chorowicz 2005). The first evidence for volcanism and some extension in the EARS occurred at 45–36 Ma, but there are clear indications of widespread volcanism and active rifting throughout the EARS by 15–10 Ma (e.g., Chorowicz 2005, Ebinger et al. 2000, McDougall & Brown 2009, Roberts et al. 2012). The timing of uplift in eastern Africa and elevation of the highlands is the subject of active study. Whereas some studies have indicated that many topographic features of the EARS, like the southern Ethiopian Highlands and East Africa Plateau (the high-elevation area centered on Lake Victoria), were established by 15 Ma (e.g., Pik et al. 2008, Wichura et al. 2010), others have suggested that significant uplift occurred much later in other parts of the EARS, for example, between 10 and 6 Ma in the Ethiopian Plateau (Gani et al. 2007) and after 7 Ma on the western and eastern flanks of the central Kenya rift (Spiegel et al. 2007). The sum of the data shows that mountain building, extension, basin development, and volcanic activity started in the Eocene and continue today, but that the timing and specific histories of topographic change in the EARS can vary dramatically over very small distances.

Modeling studies have shown that changing topography has a significant impact on moisture transport in Africa and that the specific impact varies considerably by region, in part reflecting the diversity of climate regimes in Africa today (e.g., Sepulchre et al. 2006). Although it is tempting to make simple connections between uplift and aridification, the histories of both uplift and hydroclimate in Africa during the past 10 Myr vary tremendously by specific location, and this variation must be considered before linking records of aridity and uplift history. The growing number of tectonic and paleoenvironmental data sets and improved climate models mean that we can move away from generalizations about change over an entire region (or continent) and instead compare data about uplift and environmental histories in specific places.

In addition to placing controls on regional climate, tectonic and volcanic activity provide critical controls on both (a) the location and timing of deposition and (b) the distribution of water, plants, and animals at different points in time. The record of human evolution in eastern Africa exists because rifting has created accommodation space for sediments to accumulate relatively rapidly and because the current climate and tectonic conditions have promoted incision, such that many of these sediments are exposed and have allowed fossil discovery. Although cave and open-air records in South Africa, Chad, Georgia (Dmanisi), Java, and China are notable exceptions, the record of early human evolution is primarily a record of life and death in a rift setting. The nature of basin development and rift segmentation in the EARS established controls on the landscapes with which early humans interacted. See the review by Bailey & King (2011), which explores the history of landscape change in Africa and potential for hominin movement.

Tectonic and volcanic activity also exerts strong controls on the proxies that are used as records of climate and environmental change because they are responsible for sediment supply, subsidence, and physical barriers to water. The influence of tectonics on lacustrine records is nicely demonstrated by studies like those by Behrensmeyer et al. (2002) and Bergner et al. (2009), who

conducted detailed lithofacies and mapping studies of well-dated fluviolacustrine sequences to parse out intervals of deposition that were controlled by climate or tectonics. Detailed studies like these can identify and explain temporal disparities in regional wet periods, as some lakes can be full and others regressive at the same time due to different responses to orbitally driven changes in insolation, latitudinal position of basins, or tectonic controls (Bergner et al. 2009). Likewise, studies of tectonic and volcanic events over larger regions (hundreds of kilometers) demonstrate how paleogeographic changes can place first-order controls on the basin-wide histories of environmental change (e.g., Bobe et al. 2007, Bruhn et al. 2011, Lepre 2014, Levin et al. 2011). Such studies illustrate the extreme care that must be taken in describing the tectonic controls on a record before attributing either cycles or long-term trends to specific climate phenomena. Given the impact of tectonic and volcanic activity on landscapes, building the tectonic histories of each basin should be a requisite step before linking continental records of environmental change to regional or global climate phenomena.

VARIABILITY AND INSTABILITY

Variability and instability have become key components in understanding human evolution and are increasingly viewed as having exerted greater selection pressures on hominins (and other fauna) than did long-term trends or stepwise shifts in climate and vegetation (e.g., Antón et al. 2014, Grove 2012, Potts 2013, Trauth et al. 2007). Likewise, the existence of extreme climate states, such as the megadrought in Lake Malawi at 175–145 ka (Scholz et al. 2007) and megalakes in the Sahara (Bouchette et al. 2010), would have had significant effects on habitat, range, and selection pressures (Compton 2011, Larrasoña et al. 2003, Maslin et al. 2014, Trauth et al. 2010). The influence of variability on human evolution is often discussed in terms of orbital cycles, but seasonal variability, especially the length and timing of dry seasons, may have also exerted important selection pressures on hominins and other fauna, as it certainly affects the distribution of vegetation in Africa today (e.g., Guan et al. 2014). The influence of seasonal rainfall on vegetation in Africa today is evident by comparing the images in **Figure 2**.

Spatial variability and heterogeneity are also essential to understanding the environmental dynamics of human evolution and relating them to climate change (Kingston 2007). Terrestrial environments, especially in rift basins, can be highly variable, which becomes important in understanding the range of the resources available to early hominins, in reconstructing biogeography, and in determining whether a paleoenvironmental record is representative of a greater area. Lateral variability has been documented in fluvial and lacustrine settings in eastern Africa on scales ranging from hundreds of meters to thousands of kilometers (Bobe et al. 2007; Levin et al. 2004, 2011; Owen et al. 2011; Quinn et al. 2007). The record from the Shungura Formation, discussed above, provides a great example of how it is possible to identify distinct environments on a landscape. The sedimentological, faunal, and isotopic data all indicate the existence of a wooded, riparian zone in the lower Omo River Valley between 4 and 2 Ma (Bobe et al. 2007, Brown & Feibel 1991, Levin et al. 2011), which might have served as an important refugium from more open environments that were prevalent elsewhere in the Omo-Turkana Basin (Vrba 1988).

Instability is also part of this story, and it can be caused by rapid change in an environment due to changes in tectonic, climatic, or depositional regimes. Active floodplains, lake margins, and volcanic terrains, like those that are prevalent in rift settings and where hominin activity is recorded, are unstable by nature. Instability, as a function of grazing, fire, and disturbance, regulates vegetation in Africa (Bond et al. 2003, Staver et al. 2011), and habitat instability is increasingly considered as an influence on human evolution; part of becoming human might have involved adaptations to unpredictable and unstable environments (Antón et al. 2014, Potts 2013).

COINCIDENCE AND CONTEXT

Many studies that probe the links between human evolution and climate change rely on the co-occurrence of events or trends. Although there is an increasing focus on studying mechanisms that connect human evolution and environmental change, and a lessening focus on the co-occurrence of events, the emphasis on temporal links still dominates the literature. Any study that relies on co-occurrence must do so with great care. These links are extremely tempting, but it is critical to fully understand the context of the records that are used to link human evolution to climate and/or environmental phenomena. Here are two examples that should make workers cautious of such links:

1. **Stone tools and global climate change.** The timing of specific cultural landmarks or events is often used to link climate and human evolution; however, we need to understand the context of the evidence for cultural events. Early tool use provides a great example; the co-occurrence of the earliest evidence for stone tools at 2.6 Ma at Gona in the Afar rift (Semaw et al. 2003) with the onset of Northern Hemisphere glaciation and 400-kyr eccentricity maxima is cited when making links between human evolution and climate change (e.g., deMenocal 2004, 2011; Trauth et al. 2007). However, before making these connections, it is critical to consider why stone tools show up in the archaeological record at 2.6 Ma. The earliest tools at Gona are very mature, and it is unlikely that they were among the first tools manufactured by hominins (Rogers & Semaw 2009). Instead, their appearance at Gona at 2.6 Ma might reflect the availability of raw material; they occur in the sedimentary record when cobble conglomerates brought by the ancestral Awash River become regular features of the landscape and when hominins would have had increased access to such raw materials (Quade et al. 2004, Stout et al. 2005). Although climate change might have played a role in the early use of stone tools, the current data can link the earliest evidence for stone tools only to the deposition of large cobble conglomerates at Gona (Rogers & Semaw 2009).
2. **Omo-Turkana: representative of the region?** Records from the Omo-Turkana Basin are frequently cited in compilations that link global and regional climate change to human evolution, because they provide insight into environmental change from a place with one of the richest records for human evolution (Bobe et al. 2002; deMenocal 2004, 2011). The fossil bovid and soil carbonate $\delta^{13}\text{C}$ data indicate that the environments in the lower Omo River Valley became more open after ~ 1.9 Ma (**Figure 5**) (Bobe et al. 2007, Levin et al. 2011). Although the agreement of multiple proxies makes this observation robust, the Shungura Formation is not necessarily representative of environments throughout eastern Africa, as it was a large fluvial system with a riparian zone that had been buffered from the spread of C_4 grasses that occurred elsewhere in eastern Africa (and in the Omo-Turkana Basin). The Omo riparian zone was inundated with a large lake, paleo-Lake Lorenyang, at ~ 2.0 Ma, after volcanic impoundment in the basin (Bruhn et al. 2011, Lepre 2014). After the lake retreated, the basin never returned to its predammed state (Brown & Feibel 1988, Feibel et al. 1991). Although it is tempting to link the environmental changes in the Shungura Formation and elsewhere in the Omo-Turkana Basin at ~ 1.9 Ma to coincident changes in global climate, such connections are misleading because the volcanic and tectonic events in the basin likely placed a first-order control on environmental change at this time.

These two examples highlight the importance of establishing the local context for the data that are used to understand human evolution in relationship to environmental and climate dynamics. Although this point has been made by others (e.g., Barboni 2014, Behrensmeyer 2006, Behrensmeyer et al. 2007, Bergner et al. 2009, Lepre 2014), it is easy to dismiss when the ages of climate, environmental, and evolutionary events coincide. Instead, as a field, we should heed

Behrensmeyer et al.'s (2007) assertion that the null hypothesis should be that small-scale processes control the observed trends in hominins and other fauna, until proven otherwise. Testing this null hypothesis is becoming increasingly tractable due to the constant recovery of new fossils, the huge growth in the kinds of paleoenvironmental proxies used to characterize climate and environmental change, the advent of refined dating techniques to put fossils and paleoenvironmental results into an integrated framework, and the increased sophistication of climate models to develop mechanisms for how organisms and complex terrain might respond to climate forcing.

SUMMARY POINTS

1. There are clear, long-term trends toward more open environments in eastern Africa over the past 10 Myr. However, the timing of this increase varies by location, and the distribution of open environments varies greatly, both spatially and temporally.
2. The distribution of C₄ grasses in Africa is not simply a function of aridity but instead likely reflects a combination of factors including atmospheric CO₂ concentrations, fire, herbivory, and the timing of rainy seasons.
3. Oscillations between extreme wet and dry intervals, and associated swings in vegetation, during the last 10 Myr were likely just as important to human evolution as long-term environmental trends; they would have dramatically affected corridors for movement and availability of resources and were likely instrumental in adaptations to variability and genetic bottlenecks among early humans.
4. Climate change during the past 10 Myr in eastern Africa was mostly influenced by a combination of both orbitally paced low-latitude fluctuations in insolation and global events relating to polar ice volume and tropical ocean temperature gradients, whereas environmental change in southern Africa was mostly influenced by the variations in the extent of polar ice and its impact on ocean temperatures.
5. Active tectonics and volcanism play a critical role in human evolution in terms of setting first-order controls on landscapes, habitat fragmentation, and creation of barriers to movement, but many elements of African topography were likely established by 10 Ma.
6. Local, tectonic factors always need to be considered before linking evolutionary or environmental change to global or regional climate phenomena.

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