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Invited review

Hominin evolution in settings of strong environmental variability

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A R T I C L E I N F O

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A B S T R A C T

Investigations into how climate change shaped human evolution have begun to focus on environmental dynamics, i.e., the nature and tempo of climate and landscape variability, an approach that de-emphasizes static reconstructions of early hominin habitats. The interaction among insolation cycles is especially apparent in the paleoenvironmental records of the East African Rift System, where the longest records of human evolution are preserved. However, environmental indicators such as deep-sea oxygen isotopes, terrestrial dust flux, paleosol carbon isotopes, and lake sediments do not point consistently to any simple trend or climate driver of evolutionary change. Comparison of environmental indicators cautions against an exclusive focus on any given end-member of environmental fluctuation (driest or wettest, warmest or coolest), and argues for the impact of the entire range of variability in shaping evolutionary change. A model of alternating high and low climate variability for tropical Africa further implies that specific environmental indicators reflect different aspects of East African environmental dynamics. The model may thus help reconcile some of the conflicting interpretations about the environmental drivers of hominin evolution. First and last appearances of hominin lineages, benchmark biogeographic events, and the emergence of key adaptations and capacities to alter the surroundings are consistently concentrated in the predicted longest intervals of high climate variability. The view that emerges is that important changes in stone technology, sociality, and other aspects of hominin behavior can now be understood as adaptive responses to heightened habitat instability.

1. Introduction

In recent decades the relationship between environmental and evolutionary change has become prominent in the thinking of Earth scientists and biologists interested in human evolution. As researchers have investigated this relationship, the goal has largely focused on whether evolutionary events have corresponded in time and space with particular types of environmental events.

Evolutionary events include morphological change, speciation (i.e., the division of a lineage into two distinct species), lineage extinction, and the origin of novel behaviors and ecological interactions. Environmental events include directional shifts in habitat (e.g., drying, cooling) and also increases or decreases in environmental variability. Because adaptive evolution, lineage divergence, and extinction are the results of evolutionary processes that play out over extended periods of time, the co-occurrence between environmental and evolutionary events can be expected to take place within intervals spanning 10^3–10^5 years rather than in exact 'instants' in time.

Although the analysis of temporal associations is helpful, the ultimate goal of this research is to understand the processes by which environment may have affected the major features of human evolutionary history. The co-occurrence between environmental and evolutionary events is, by itself, insufficient in building this understanding. It is essential to point explicitly to how environmental change led to particular genetic, demographic, and other mechanisms that drive evolutionary responses. That human evolution has largely been unaffected by the external environment also needs to be considered, an idea sometimes referred to as the evolution-environment 'null hypothesis' since it implies that evolutionary change can, and has, taken place at various times independent of environmental change (National Research Council, 2010; Potts, 2012a). The hypothesis that environmental events have indeed influenced evolutionary change is, nonetheless, consistent with natural selection as the process that has shaped the adaptations of organisms, including hominins. It is also consistent with habitat expansion, fragmentation, and disappearance as factors involved in the origination, divergence, and extinction of populations.

Although it is sometimes said that Darwin established a link between climate and evolution, his scenario of human origins

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(Darwin, 1871) was devoid of the idea that environmental change directly stimulated the variety of evolutionary events that happened over the course of human evolution. Throughout much of the 20th century, paleoanthropologists followed his lead. Rather than focusing on external environmental stimuli, researchers favored intrinsic explanations of human evolution (e.g., Bartholomew and Birdsell, 1953; Washburn, 1960), in which a single environmental transition from forest to grassland set the stage for the emergence of bipedal walking and tool use. This earliest shift in way of life then laid the foundation for meat-eating, hunting, brain expansion, control of fire, food sharing, complex social interactions, and language, among other novel adaptations that characterize how human ancestors interacted with the world. Such explanations have generally looked no further than prior adaptations to explain, through complex feedback, how evolutionary developments early in time could account for the evolution of later ones as ancestral hunter-gatherers gradually overcame the challenges of the African savanna and Eurasian ice ages (e.g., Klein, 1989; Wilson, 1978; Wolpoff, 1980; see Potts, 2012a for further discussion).

A heightened interest in extrinsic explanations, by contrast, developed in the 1980s (Laporte and Zihlman, 1983), especially through the writings of Elisabeth Vrba (1985a,b, 1988, 1992, 1995a,b; Vrba et al., 1989, 1995). Such explanations focus on factors external to the organism in explaining how evolutionary change was initiated, and in accounting for the tempo and mode of evolution, the turnover of species (originations and extinctions), and the specific adaptations that emerged in particular intervals of time.

The most prominent statements that invoke extrinsic causes of human evolutionary change are the turnover-pulse hypothesis of Vrba (see references above), the variability selection hypothesis proposed by Potts (1996a,b, 1998a,b, 2007, 2012a,b), the aridity hypothesis developed by deMenocal (1995, 2004, 2011) and deMenocal and Bloemendal (1995), and the deep-lakes hypothesis of Trauth and colleagues (Trauth et al., 2005, 2007, 2010). A variety of other studies published in recent years offer variations on the themes established by these four main hypotheses and identify factors responsible for creating spatial and temporal variability in habitats and fossil assemblages (e.g., Bailey et al., 2011; Kingston, 2007; Cerling et al., 2011; Hopley and Maslin, 2010; Passey et al., 2010).

This suite of hypotheses is obviously Africa-oriented and heavily weighted toward East Africa. Two reasons why Africa-based researchers have been so active in proposing environment-evolutionary linkages are: (1) the relatively precise geochronological resolution of lengthy stratigraphic sequences, especially in East Africa, which preserve hominins, other fossil organisms, and multiple paleoenvironmental indicators; and (2) the totality of paleontological and archeological evidence, which strongly implies that Africa was the source of many of the critical transitions in human evolution, including the origin of the hominin clade; each genus within the clade; the extant human species; and key adaptations including bipedality, stone technology, and several other behavioral innovations.

The purpose of this article is to review the data sets that have led to the most prominent ideas linking environmental and evolutionary change. It also identifies the areas of agreement and disagreement among these ideas and data interpretations. A framework for tropical African climate variability is proposed as a way of reconciling the diverse data sets; it thus has promise as an analytical tool for evaluating environment-evolutionary linkages, particularly relevant to East African hominins and contemporaneous organisms. This predictive framework describes how intervals of high and low climate variability alternated over the past several million years, and provides insights into the adaptive history of African hominins, including the emergence of *Australopithecus*, *Homo*, and *Homo sapiens*.

2. The problem of explaining one-time evolutionary outcomes

Since the purpose here is to review environmentally-based explanations of human evolution, attention must be given to a simple fact of our evolutionary history that creates an apparently insurmountable challenge in searching for testable explanations of any kind. Hominin evolution has yielded only a single surviving species, *H. sapiens*. If the point of paleoanthropology is solely to explain how *H. sapiens* emerged, human evolution becomes a singular, hard-to-comprehend phenomenon, a unique event largely intractable to scientific analysis. The flaw in this characterization is that almost all evolutionary phenomena can be narrowly construed as one-time outcomes. The evolution of any lineage could be defined as a singular phenomenon, thus creating a scientific predicament since scientific explanations require the analysis of phenomena that are, in some sense, repeatable and capable of examination as multiple instances for which explanatory factors or variables can be explored and tested. However, the evolutionary events that define any given clade, including hominins, are comprised of recurrent instances of adaptive change, multiple episodes of speciation and extinction, and a series of biogeographic events (e.g., dispersals, range expansions and contractions) that can be examined in relation to various types of environmental change or shifts in climate mode.

Thus the problem with the claim that hominin evolution represents a one-time evolutionary outcome is that it ignores the multitude of events that have occurred in the hominin clade and in the ancestry of *H. sapiens*. It is this series of events, or natural experiments, which enables researchers to assess multiple instances and patterns of evolutionary change and to test for explanatory variables. Table 1 offers a synopsis of several of the key adaptive and phylogenetic events in hominin evolution. The timing of speciation and extinction events and the onset (i.e., the increase and spread) of novel adaptations can be estimated by first appearance datums (FADs) and last appearance datums (LADs), indicated by the first or last in a particular sample of fossils that has morphological similarity (thus defining a lineage distinct from others) or by archeological indicators that denote a novel behavior or ecological innovation.

The overarching picture of hominin evolution entails the emergence of a small-bodied bipedal ape, probably in tropical/subtropical latitudes of Africa, followed by 6 million years of multiple episodes of species diversification and extinction; the evolution of adaptations that temporarily improved how species of *Australopithecus*, *Paranthropus*, and *Homo* interacted with their surroundings; and, ultimately, the survival of a single African species that has become cosmopolitan and capable of pervasive modification of its surroundings. Any explanatory model of hominin evolution that includes the physical and biotic environment needs to account for the evolutionary pressures underlying the adaptive properties of the diverse hominin species, the suite of extinctions, and, ultimately, the survival of a species that practices an astonishing degree of niche construction via cultural buffering of its environment (Laland et al., 2001; Odling-Smee et al., 2003; Potts, 1996a, 2012a).

The fact that hominin evolution has entailed numerous phylogenetic and adaptive events (Tables 1 and 2) does not mean that paleoanthropologists are close to having a sufficiently rich data set of events that is well-resolved in time and space and which might then lead to a straightforward understanding of human evolution. The pace and nature of paleoanthropological discoveries denote