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Invited review

East African climate pulses and early human evolution

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ABSTRACT

Current evidence suggests that all of the major events in hominin evolution have occurred in East Africa. Over the last two decades, there has been intensive work undertaken to understand African palaeoclimate and tectonics in order to put together a coherent picture of how the environment of East Africa has varied in the past. The landscape of East Africa has altered dramatically over the last 10 million years. It has changed from a relatively flat, homogenous region covered with mixed tropical forest, to a varied and heterogeneous environment, with mountains over 4 km high and vegetation ranging from desert to cloud forest. The progressive rifting of East Africa has also generated numerous lake basins, which are highly sensitive to changes in the local precipitation-evaporation regime. There is now evidence that the presence of precession-driven, ephemeral deep-water lakes in East Africa were concurrent with major events in hominin evolution. It seems the unusual geology and climate of East Africa created periods of highly variable local climate, which, it has been suggested could have driven hominin speciation, encephalisation and dispersal out of Africa. One example is the significant hominin speciation and brain expansion event at ~1.8 Ma that seems to have been coeval with the occurrence of highly variable, extensive, deep-water lakes. This complex, climatically very variable setting inspired first the *variability selection hypothesis*, which was then the basis for the *pulsed climate variability hypothesis*. The newer of the two suggests that the long-term drying trend in East Africa was punctuated by episodes of short, alternating periods of extreme humidity and aridity. Both hypotheses, together with other key theories of climate-evolution linkages, are discussed in this paper. Though useful the actual evolution mechanisms, which led to early hominins are still unclear and continue to be debated. However, it is clear that an understanding of East African lakes and their palaeoclimate history is required to understand the context within which humans evolved and eventually left East Africa.

1. Introduction

Human evolution is characterised by speciation, extinction and dispersal events that have been linked to both global and/or regional palaeoclimate records (deMenocal, 1995; Trauth et al., 2005; Carto et al., 2009; Castañeda et al., 2009; Armitage et al., 2011; Donges et al., 2011; Shultz et al., 2012). However, none of these records fully explain the timing or the causes of these human evolution events (Maslin and Christensen, 2007; Trauth et al., 2009; Potts, 2013). This is primarily due to global and regional palaeoclimate records not being representative of the climate of the East Africa (Shultz and Maslin, 2013). Understanding the climate of East Africa is essential because, despite the dispersal of hominins out of Africa after two million years ago (Agusti and Lordkipanidze, 2011) current evidence suggests the majority of hominin species originated in East Africa (Antón and Swisher, 2004; Wood, 2014).

Environmental pressures have long been assumed to play a key role in hominin speciation and adaptation (Maslin and Christensen, 2007) and a number of iconic theories have been developed to frame and develop the discussion of hominin evolution. Table 1 tries to put these key theories into the context of overarching evolutionary theory. Though the split between *phylogenetic gradualism* and *punctuated equilibrium* is artificial it does provide a starting point with which to discuss theories of early human evolution. In Table 1, gradualism has been split into constant and variable evolution rates to reflect the full range of current opinions;

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Table 1
Early human evolutionary theories placed in the context of overall evolutionary theory and modes of climatic change.

			CLIMATE STRESS			
			None	Long-term state change	Threshold event	Variability
EVOLUTIONARY FORM	Phyletic Gradualism	constant	Red Queen (Van Valen 1973)	*Allopatic speciation*		
		variable	Red Queen (Van Valen 1973)	Turnover-pulse hypothesis (Vrba 1985) Savannah hypothesis	*Allopatic speciation*	Variability selection hypothesis (Potts 1998) Pulsed-climate variability hypothesis (Maslin & Trauth 2009)
	Puncuated Equilibrium		Court Jester (e.g. Impact event) (Bamosky 2001)	Aridity hypothesis (de Menocal 1995)	Court Jester (Bamosky 2001) *Allopatic speciation*	Pulsed-climate variability hypothesis (Maslin & Trauth 2009)

though attempts have been made to combine *phylogenetic gradualism* and *punctuated equilibrium*, such as *punctuated gradualism* (Malmgren et al., 1983), these have not been included as they are not widely accepted.

The first key environmental theory to explain bipedalism was the *savannah hypothesis*, which suggested that hominins were forced to descend from the trees and adapted to life on the savannah facilitated by walking erect on two feet (Lewin and Foley, 2004). This theory was refined as the *aridity hypothesis*, which suggested that the long-term trend towards increased aridity and the expansion of the savannah was a major driver of hominin evolution (deMenocal, 1995, 2004; Reed, 1997). A key addition to this theory was the suggestion that during periods when aridification accelerated, due to thresholds in the global climate system, then thresholds in evolution were reached and major hominin speciation events occurred (deMenocal, 1995).

The *turnover pulse hypothesis* (Vrba, 1988) was originally developed to explain discrete patterns in ungulate speciation, and suggests that acute climate shifts drove adaptation and speciation. Vrba (1988) recognised that environmentally-induced extinctions hurt specialist species more than generalist species. Hence when there is an environmental disruption, the generalists will tend to thrive by utilizing new environmental opportunities and by moving elsewhere to take advantage of other areas that have lost specialist species. The specialists will experience more extinctions, and therefore an increased speciation rate within their group. This would lead to more rapid evolution in isolated areas, i.e., allopatric speciation, whereas the generalists will become more spread out.

The *variability selection hypothesis* advocates the role of environmental unpredictability in selecting for behavioural or ecological flexibility (Potts, 1998, 2013; Grove, 2011a,b). This theory develops the original *turnover pulse hypothesis* but instead splits species into their varying ability to adapt and evolve to a more variable and unpredictable environment. The *variability selection hypothesis* emphasises the long-term trends toward a drier and more variable climate. It however struggles to explain the current palaeoanthropological evidence that suggests a pulsed/threshold nature of hominin speciation and migration events. A direct development of the *variability selection hypothesis* is the *pulsed climate variability hypothesis*, which highlights the role of short periods of extreme climate variability specific to East Africa in driving hominin evolution (Maslin and Trauth, 2009). It is the palaeoclimate evidence for this later framework, the *pulsed climate variability hypothesis*, which is discussed in this review along with how the other evolutionary theories may be applied given the new context (see Fig. 1).

2. Formation and development of the East Africa rift system

On a regional scale, tectonics can cause significant changes in climate, hydrology and vegetation cover. In East Africa, long-term climatic change is controlled by tectonics, with the progressive formation of the East African Rift Valley leading to increased aridity and the development of fault graben basins as catchments for lakes (Fig. 2). Rifting begins with updoming at the site of future separation, and downwarping away from the site. This is followed by rifting and separation as half grabens (land that has subsided with a fault on one side) are formed on either side of the rift. While the early stages of rifting in East Africa were characterised by general updoming and downwarping, faulting during the later stages progressed from north to south.

Volcanism in East Africa may have started as early as 45–33 Ma in the Ethiopian Rift (Trauth et al. (2005, 2007) while initial uplift may have occurred between 38 and 35 Ma (Underwood et al., 2013). There is evidence for volcanism as early as 33 Ma in northern Kenya, but magmatic activity in the central and southern rift segments in Kenya and Tanzania did not start until between 15 and 8 Ma (e.g., Bagdasaryan et al., 1973; Crossley and Knight, 1981; McDougall and Watkins, 1988; George et al., 1998; Ebinger et al., 2000). The high relief of the East African Plateau developed between 18 Ma and 13 Ma (Wichura et al., 2010). Major faulting in Ethiopia occurred between 20 and 14 Ma and was followed by the development of east-dipping faults in northern Kenya between 12 and 7 Ma (Fig. 3). This was superseded by normal faulting on the western side of the Central and Southern Kenya Rifts between 9 and 6 Ma (Baker et al., 1988; Blisniuk and Strecker, 1990; Ebinger et al., 2000). Subsequent antithetic faulting of these early half grabens between about 5.5 and 3.7 Ma then generated a full-graben (a block of subsided land with faults on either side) morphology (Baker et al., 1988; Strecker et al., 1990). Prior to the full-graben stage, the large Aberdare volcanic complex (elevations in excess of 3500 m), an important Kenyan orographic barrier, was established along a section of the eastern rim of the EARS (Williams et al., 1983). By 2.6 Ma, the Central Kenyan Rift graben was further segmented by west-dipping faults, creating the 30-km-wide intrarift Kinangop Plateau and the tectonically active 40-km-wide inner rift (Baker