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Climatic variability, plasticity, and dispersal: A case study from Lake Tana, Ethiopia

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ABSTRACT

The numerous dispersal events that have occurred during the prehistory of hominin lineages are the subject of longstanding and increasingly active debate in evolutionary anthropology. As well as research into the dating and geographic extent of such dispersals, there is an increasing focus on the factors that may have been responsible for dispersal. The growing body of detailed regional palaeoclimatic data is invaluable in demonstrating the often close relationship between changes in prehistoric environments and the movements of hominin populations. The scenarios constructed from such data are often overly simplistic, however, concentrating on the dynamics of cyclical contraction and expansion during severe and ameliorated conditions respectively. This contribution proposes a two-stage hypothesis of hominin dispersal in which populations (1) accumulate high levels of climatic tolerance during highly variable climatic phases, and (2) express such heightened tolerance via dispersal in subsequent low-variability phases. Likely dispersal phases are thus proposed to occur during stable climatic phases that immediately follow phases of high climatic variability. Employing high resolution palaeoclimatic data from Lake Tana, Ethiopia, the hypothesis is examined in relation to the early dispersal of *Homo sapiens* out of East Africa and into the Levant. A dispersal phase is identified in the Lake Tana record between c. 112,550 and c. 96,975 years ago, a date bracket that accords well with the dating evidence for *H. sapiens* occupation at the sites of Qafzeh and Skhul. Results are discussed in relation to the complex pattern of *H. sapiens* dispersal out of East Africa, with particular attention paid to the implications of recent genetic chronologies for the origin of non-African modern humans.

1. Introduction

Hominin dispersals have become the focus of a steadily increasing body of research in evolutionary anthropology over the past two decades (e.g. Lahr and Foley, 1998; Anton et al., 2002; Hazelwood and Steele, 2004; Dennell and Roebroeks, 2005; Mellars, 2006a,b; Lycett and von Cramon-Taubadel, 2008; Shea, 2008, 2010; Lycett, 2009; Steele, 2009; Koenig and Borries, 2012). During this time the appreciation of the vital role played by climatic factors in hominin dispersals has greatly increased (e.g. Foley, 2002; Mithen and Reed, 2002; Nikitas and Nikita, 2005; Hughes et al., 2007; Gamble, 2009; Petraglia et al., 2010; Mueller et al., 2011), with the result that palaeoclimatic records have become indispensable to this field of study. Despite the growing literature on hominin dispersals, however, there is a generic lack of engagement with theoretical developments concerning dispersal dynamics in the parallel disciplines of zoology and evolutionary biology (e.g. Baker, 1965; Mayr, 1965; Vazquez, 2006; Sol, 2007). This contribution proposes a theory of hominin dispersals rooted in the evolutionary biology of fluctuating environments, and examines that hypothesis via a detailed analysis of the Late Pleistocene dispersal of *Homo sapiens* from East Africa into the Levant. Integral to the hypothesis are the findings that species subject to high levels of climatic variability can accumulate plastic adaptations, and that such adaptations are characteristic of successful dispersers. Utilising new high-resolution palaeoclimatic data from Lake Tana,

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Ethiopia, a chronology of dispersal from this area is developed and assessed against the chronologies of the extensively studied Levantine sites of Qafzeh and Skhul.

2. Climatic variability, plasticity, and dispersal

2.1. *The evolutionary biology of plasticity*

Plasticity has varying, complex definitions in evolutionary biology, but is understood in a broad sense here as "the ability of an individual organism to react to an environmental input with a change in form, state, movement, or rate of activity" (West-Eberhard, 2003: 34). Foundational research on evolutionary responses to climatic variability at a microevolutionary level was provided by geneticists focussing on the maintenance of polymorphisms (e.g. Levene, 1953; Dempster, 1955; Haldane and Jayakar, 1962; Cohen, 1966; Lewontin and Cohen, 1969; Gillespie, 1973). The principles derived by such research include the fact that, since reproduction is a multiplicative process, the overall fitness of a genotype across generations should be measured by the geometric rather than the arithmetic mean. As the geometric mean is more sensitive to variance than is the arithmetic mean, this principle has the corollary that temporal climatic variability can favour highly tolerant genotypes. Figure 1a shows the fitness of two genotypes over a continuum of climatic states; Genoytpe 2 is more tolerant than Genotype 1 by virtue of having non-zero fitness values across a greater range of climatic states. When subject to climatic change through time as plotted in Figure 1b, Genotype 2 thus has lower variance in fitness through time, as shown in Figure 1c. Genotype 1 has a higher *arithmetic* mean fitness over these ten generations, but Genotype 2 has a higher *geometric* mean fitness due primarily to its lower variance, and is therefore favoured by natural selection. To clarify, the point is not that increased tolerance of environmental variability is necessarily due to plasticity, but that plasticity will necessarily lead to increased tolerance of environmental variability, and will often be the most efficient way of doing so.

Although formulated at the microevolutionary level, there is abundant evidence that the 'geometric mean principle' also plays a prevalent macroevolutionary role (Moran, 1992; Simons, 2002; Lee and Doughty, 2003; Yoshimura et al., 2009; Grove, in press). In its macroevolutionary form, this basic logic strikes a chord with a number of more recent, palaeoanthropologically grounded hypotheses concerning the relationship between climatic variability and human evolution. The variability selection hypothesis (Potts, 1996, 1998, 2013; see also Grove, 2011a,b) suggests that, on geological timescales, hominin species accumulated adaptations that increased behavioural versatility in response to substantial climatic and environmental fluctuations. Kingston's (Kingston, 2007; Kingston and Harrison, 2007) shifting heterogeneity model couples the idea of versatile responses to "complex and dynamic adaptive landscapes" (Kingston, 2007: 48) with the observation that precession-driven shifts in seasonality in equatorial African environments would have affected vegetation physiognomy and faunal distribution patterns. The focus on latitudinal and altitudinal drift in hominin geographic ranges, with the resulting establishment of isolated refugia, recalls Vrba's (1992, 1999) habitat theory and outlines expectations concerning vicariance and speciation (see also Grove, 2012a). Extending the theme of precessional effects on low-latitude hominin populations, Trauth and colleagues' pulsed climate variability hypothesis (Trauth et al., 2007, 2010; Maslin and Trauth, 2009) focuses on the semi-precessional pulses of wetter and more variable conditions evinced in East African lake records.

2.2. *Plasticity and dispersal*

Though a number of hypotheses have been advanced regarding the details of the relationship between climatic variability and hominin evolution within Africa and elsewhere, research into the interactions between climate and dispersal remains focused on the basic paradigm that glacials and interglacials led to population

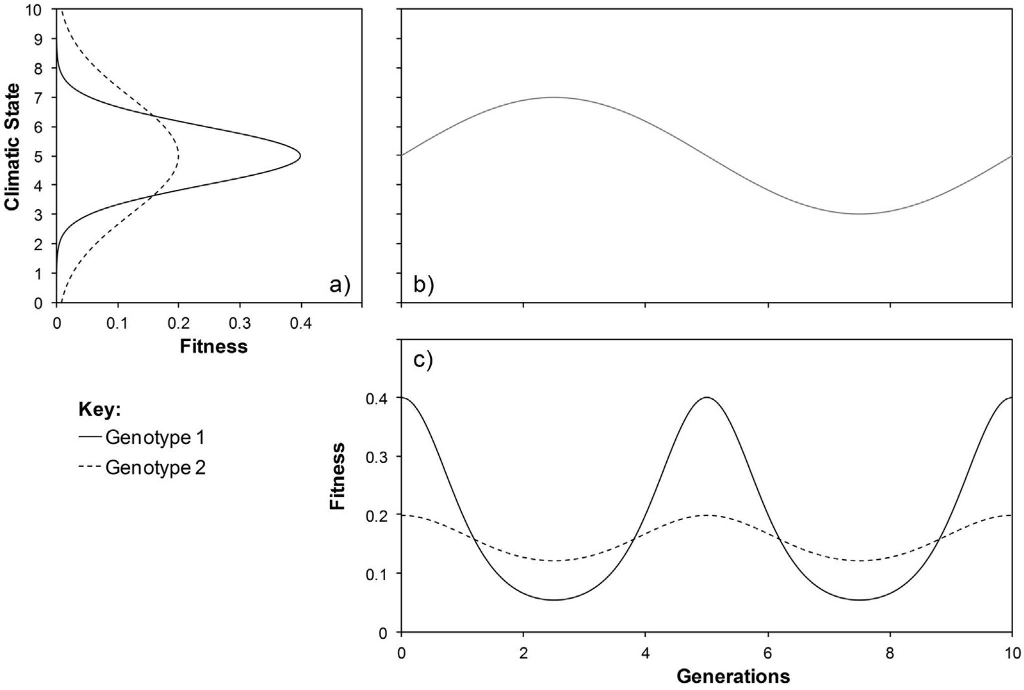

Figure 1. a) Shows the fitness of two genotypes over a continuum of climatic states, b) shows the oscillating climate they experience over time, and c) shows the variation in fitness over time experienced by each genotype.