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Editorial

Environmental variability and hominin dispersal



The collection of papers in this Special Issue explores the complex relationship between prehistoric environments and the pattern of hominin dispersals. Working within an evolutionary framework, the focus of the issue is the broad hypothesis that environmental variability acted as a significant factor in determining the timing and direction of hominin dispersal events. Arguably, dispersals themselves have had a significant impact on the course of hominin evolution, affecting both biological and behavioral adaptations; this collection of papers explores various aspects of dispersal along a broad timeframe, from the Pliocene to the Pleistocene, and from Africa to Eurasia. Most of the authors use some form of quantitative modeling as a tool for exploring ideas about dispersal, highlighting the growing importance of computational approaches in today's research environment. The first three contributions (Potts and Faith, Trauth et al., Grove et al.) present predictive models linking the timing of hominin dispersals to periods of high variability evinced in either orbital insolation parameters or records of fluctuation in African lake levels. The fourth contribution (Winder et al.) explores the impact of tectonics on habitat suitability. Macdonald and colleagues test encephalisation in primates as a possible factor facilitating increased range size and the ability to handle seasonal variability in resource availability. The final three contributions to the issue explore specific dispersal events and are presented in chronological order from the Pliocene evidence for early hominin dispersal within Africa offered by the discovery of *Australopithecus bahrelghazali* (Macho), to the environmental context that favoured initial hominin dispersal into Western Europe (Agusti et al.) and finally, to anatomically modern human dispersal and a test of different out-of-Africa models (Reyes-Centeno et al.).

Potts and Faith establish a broad framework of periods of high and low climate variability based on eccentricity and precession cycles. Their model predicts 32 high variability stages of different durations over the past 5 million years. Climate proxies such as regional evidence from deep-sea records (monitoring dust flux and sapropel reflectance as climate proxies) and local terrestrial records from hominin occupied regions in East Africa (lake levels) are used to test the predictive framework. Eight of the more prolonged phases are tested against the paleoanthropological record, specifically the timing of speciation and extinction events (e.g., the appearance for *Australopithecus anamensis*, *Paranthropus aethiopicus*, and early *Homo*), cultural innovation (e.g., the appearance of Oldowan, Acheulean, and both Middle and Late Stone Age industries), and the initial dispersal of *Homo* from Africa into East Asia. Via simulation, these authors develop a valuable null model to establish a statistical basis for the

association of high variability phases with key events in hominin evolution.

The variability selection hypothesis predicts that environmental instability, produced by phases of high climate instability, should correlate with these events. Potts and Faith note that five stratigraphic records in East Africa associated with hominin occupations (Turkana, Hadar, Olduvai, Ologesailie, and Tugen Hills) provide evidence of landscape variability in response to pronounced phases of high climate instability. Furthermore, evidence from the Nihewan Basin (China) together with the East African data confirms that initial hominin expansion out of Africa correlates with a protracted phase of climate variability (Potts and Faith's period H14, from 1.9 to 1.7 Ma). This evidence, and other examples provided in the article, suggests that environmental instability may be an important factor driving various milestones in hominin evolution.

Trauth and colleagues examine orbital forcing of climate transitions (alternating periods of climate stability and instability) at different timescales. The timing of climate transitions in East Africa is established using lake records correlated with the orbital record. A novel age modeling technique designed to deal with hiatuses and other abrupt changes in sedimentation rates (Trauth, 2014) is employed to model the age structure of the stratigraphic sequences, with fluctuations in lake levels used to identify unstable periods. Three transitions from stable to unstable periods are considered in detail in the article: a Mid-Holocene wet–dry transition in the Chew Bahir basin, between 11 and 4 ka; the transition between MIS 5 and 4 in the Naivasha Basin; and the Early Mid-Pleistocene transition at Ologesailie. The mechanisms underlying the transitions and their impact on the East African landscape are discussed in detail.

Although the transitions from stable to unstable conditions are shown in all cases to be correlated with decreases in orbitally-induced insolation, Trauth and colleagues develop a useful deconstruction of the major forces acting to create fluctuations in lake levels at the three very different scales that they examine. At the longest timescale (i.e., millions of years), conditions for lake formation are provided by tectonic activity as basins are formed or destroyed. On the scale of tens to hundreds of thousands of years, and in situations where tectonics promote lake formation, lake levels are governed primarily by orbital parameters. At millennial timescales, climate fluctuations such as Dansgaard-Oeschger and Heinrich events are imprinted on the broader insolation fluctuations of the orbital cycles, governing finer-scale hydrological budgets. This multi-scalar synthesis has the potential to be highly valuable in relating environmental instability to the conditions experienced by hominins on the ground.

Grove and colleagues develop a dispersal hypothesis based on two well-established bodies of research in evolutionary biology: temporal heterogeneity in environments as promoter of plasticity in adaptation, and plasticity as a recurrent trait in species characterised as successful dispersers. The Accumulated Plasticity Hypothesis (APH) thus involves two stages: initial selection for increased tolerance during periods of high climate variability, followed by dispersal during subsequent periods of low climate variability when populations are equipped with levels of tolerance that are above those required to survive in their natal environments. This hypothesis is considered to apply particularly to latitudinal or altitudinal expansions, with the prediction that hominin dispersals should occur immediately following abrupt transitions from high to low variability conditions. Using the results of a simple evolutionary algorithm that demonstrates the validity of this mechanism in theory (Grove, 2014), a series of predictions are tested empirically using a precipitation–evaporation proxy from Lake Tana (Ethiopia) for the timeframe between 79 and 146 ka. Based on the theoretical underpinnings of the APH, a dispersal window is identified between c. 97 and c. 112 ka, a period that, given moderate dispersal speeds, aligns with archaeological evidence for the initial dispersal of *Homo sapiens* from Africa to the Levant. Grove and colleagues discuss this postulated dispersal scenario in conjunction with recent genetic dating of the *H. sapiens* diaspora out of Africa. Although further testing is required, the alignment of moisture fluctuations, archaeological occupations, and genetic data provides preliminary empirical support for the APH.

The three papers discussed above use orbital precession, modulated by eccentricity, to predict cycles of climate variability, refining the predictions with the aid of climate proxies such as records of lake level fluctuation. Different interpretations of the lake data are offered in these contributions, however. Potts and Faith, for example, follow Owen et al. (2008) in describing highly variable climate conditions at Olorgesailie between 0.5 and 1.2 Ma (phase H9 in their predictive climate model). Dynamic oscillations in lake levels are indicated, particularly from 1.1 to 0.9 Ma. Trauth and colleagues, on the other hand, describe a relatively long episode of stability at Olorgesailie between 1.15 and 0.95 Ma, followed by a long dry spell interrupted by rapid climate oscillations between 0.75 and 0.49 Ma. Similarly, the period between 97 and 112 ka at Lake Tana is marked by low climate variability in the record analysed by Grove and colleagues, whereas a similar timeframe at lake Naivasha, between 76 and 106 ka, is described by Trauth and colleagues as a series of wet episodes punctuated by severe drought events centered at ~91, 88, 83, 78, and 73 ka.

Clearly, the interpretation of lake level stratigraphy and sedimentation rates affects age estimates of the timing of climate events, although it should be noted that it is the duration of phases of high climate variability that differs in these cases and their estimated occurrence times overlap. Some of the larger disparities in the chronologies presented by Potts and Faith and by Trauth and colleagues result from the use of different age models for the sedimentary sequence at Olorgesailie. As age models increase in sophistication for both palaeoenvironmental cores and archaeological deposits, it will be important to examine the implications of different assumptions about sedimentation rates and the treatment of hiatuses for conclusions regarding hominin evolution. In other instances, it will be important to determine whether the differences in interpretations presented by various authors in this issue are the result of genuine regional asynchrony, are due to theoretical differences, or are merely the result of taphonomic factors.

Comparisons between the Lake Tana record and that from the Peqiin Cave speleothem provided by Grove and colleagues suggest that regional asynchrony may be a very real factor, and one that

should inform future efforts in dispersal modelling. Theoretical differences are also certainly present. Potts and Faith view dispersal events as likely to occur during periods of high variability, whereas the APH—also built upon the strong foundations provided by the variability selection hypothesis—suggests that dispersal should occur immediately after periods of high variability. Reconciling these positions with further empirical data should form a major focus of subsequent investigations.

Winder and colleagues expand the theme of tectonics and their importance for human evolution, stressing not the potential for tectonic activity to create water sources per se, but the fact that areas of complex topography might have been generally conducive to hominin occupation. These authors present the “tectonic landscape model” that focusses on topographic variability as a driver of hominin evolution and dispersal (Reynolds et al., 2011). Tectonic activity, which maintains and renews topographic complexity, pools resources and creates tactical opportunities for predators. Topographic complexity may itself act as an agent of selection, and the authors argue that it provides an evolutionary pathway towards full terrestriality in the African landscapes of our ancestors. These authors thus provide a predictive model of hominin dispersal using variables such as ‘topographic roughness’ as predictors of habitat suitability for early *Homo*. The value of this model is that it not only identifies the geological underpinnings of habitat types conducive to hominin dispersal, but is able to map the changing geographic extent of such habitats. The authors are thus able to describe pathways (connected, topographically complex regions) that hypothetically facilitated the dispersal of early *Homo* out of Africa and across Eurasia.

Macdonald and colleagues explore factors that enabled hominin dispersal into seasonally variable, high-latitude environments. Given the consistently high energetic demands of neural tissue, seasonal variation in the availability of food sources provides an environmental risk factor, especially for the relatively large-brained primates. The nutritional demands of larger brains, however, are counterbalanced by increased cognitive ability, which could have enabled encephalised primates to maintain seasonal food intake despite resource variability. The authors ask whether encephalisation might thus be a factor conditioning the potential for hominin dispersal. To test the relationship between brain size and seasonality, the authors conduct a comparative analysis of extant, non-human primates, searching for correlations between geographic and environmental variables and relative and absolute brain size. The results show that larger-brained primates do not tend to occupy more diverse geographical ranges than their smaller-brained cousins; instead, primates with relatively larger brains are restricted in distribution in equatorial West Africa, and although such primates are more widely distributed in Central and South America, they encounter less environmental variability there. The authors suggest, therefore, that the evolutionary transformation of a “cognitive buffer” into a “cultural buffer” (a temporally and spatially extended memory store and more elaborate technology) was what allowed hominins to overcome environmental constraints such as seasonality.

The only known occurrence of *A. bahrelghazali* is located in Chad, Central Africa, far from the clusters of contemporaneous, Pliocene hominin localities in East and South Africa. *A. bahrelghazali*, therefore, presents a rare opportunity to study early hominin dispersals from a unique perspective for this very early timeframe. *A. bahrelghazali* had low-crowned, bunodont teeth with relatively thin enamel which precludes a diet based on abrasive foods. Despite this, dietary reconstructions point to an eclectic, C₄-dominated diet consistent with evidence for relatively open habitats at

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