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Evolution and dispersal of the genus *Homo*: A landscape approach

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ABSTRACT

The notion of the physical landscape as an arena of ecological interaction and human evolution is a powerful one, but its implementation at larger geographical and temporal scales is hampered by the challenges of reconstructing physical landscape settings in the geologically active regions where the earliest evidence is concentrated. We argue that the inherently dynamic nature of these unstable landscapes has made them important agents of biological change, creating complex topographies capable of selecting for, stimulating, obstructing or accelerating the latent and emerging properties of the human evolutionary trajectory. We use this approach, drawing on the concepts and methods of active tectonics, to develop a new perspective on the origins and dispersal of the *Homo* genus. We show how complex topography provides an easy evolutionary pathway to full terrestrialisation in the African context, and would have further equipped members of the genus *Homo* with a suite of adaptive characteristics that facilitated wide-ranging dispersal across ecological and climatic boundaries into Europe and Asia by following pathways of complex topography. We compare this hypothesis with alternative explanations for hominin dispersal, and evaluate it by mapping the distribution of topographic features at varying scales, and comparing the distribution of early *Homo* sites with the resulting maps and with other environmental variables.

1. Introduction

The timing, geographical location and causes of the origins of the genus *Homo* (which is usually presumed to have split from one of the australopithecine lines) and the subsequent expansion of our lineage in Europe and Asia are the foci of ongoing interest and debate. The broad consensus is that the genus originated in Africa between two and three million years ago (Ma), followed by a widespread dispersal of *Homo* to lower and middle latitudes in Europe and Asia at or after about 1.8 Ma (Grine et al., 2009; Joordens et al., 2013). The presumption is that australopithecine adaptations were more narrowly confined by ecological, physical or climatic conditions to habitats in Africa, and that these constraints ceased to impede dispersal of the *Homo* lineage, either because it had acquired a new adaptive capacity that was able to overcome them, or because environmental change had removed them. Given uncertainties about the confounding effects of differential visibility, we cannot be sure that australopithecines were not more widely distributed outside Africa (or within it) (e.g., Dennell, 2003, 2008; Dennell and Roebroeks, 2005). Nevertheless, the pattern of *Homo* dispersal seems to have been genuinely different, expanding into new territory, albeit with total population sizes that appear to have remained small (Sherry et al., 1997; Huff et al., 2010). We therefore take the existing pattern as a legitimate starting point for exploring the relationship between external environmental variables and the distribution of known hominin sites, while recognizing the ever-present uncertainties posed by factors of differential survey and preservation.

A variety of explanations have been proposed to explain these broad differences in distribution, drawing variously on external environmental factors, particularly climate change, or intrinsic changes in biological or cultural potential. In this paper we propose an approach to *Homo* dispersal which introduces spatio-temporal variation in the physical landscape as an important factor. We draw, in particular, on the role of complex topography and its relationship to active tectonics as a potential additional factor driving the hominin evolutionary trajectory, an approach variously referred to as 'the tectonic landscape model' or the 'complex

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topography hypothesis' (King and Bailey, 2006; Reynolds et al., 2011; Winder et al., 2013; see also the debate in Thorpe et al., 2014 and Winder et al., 2014). We summarize the features of the model and further develop it to provide an explanation of dispersal in the *Homo* lineage, which, we argue, avoids some of the difficulties raised by alternative explanations. We explore the implications of this model by comparing the distribution of landscape features, hominin site locations, and other environmental variables, and outline the difficulties of implementing such an approach and remaining issues in need of further investigation.

2. Background

Since Darwin (1859, 1872) and Wallace (1876, 1880), dispersal has been conceived of as a process integral to biological evolution, with the clear implication that both dispersal and evolution should be explicable in relation to the same principles. According to modern biological theories of dispersal (e.g., Bowler and Benton, 2005; Dytham, 2009), species that expand beyond the margins of their pre-existing habitat tend to move into areas closely similar to those previously occupied, and do so because of habitat deterioration in the pre-existing territory, or because environmental changes have made available new territory with similar conditions. Expansion into different habitats may also occur but the dispersing species is only likely to persist if it is able to evolve new adaptations under the selective pressures of the new environmental conditions before becoming locally extinct. In the case of *Homo* expansion, a range of explanations drawing to greater or lesser extent on one or other of these variants has been proposed, and we identify four principal types.

The first and the simplest type of explanation is one in which climate change acts directly as an external driver, either by expanding favourable habitat conditions that facilitate dispersal, or by causing environmental deterioration in the ancestral habitat and forcing populations to disperse elsewhere (Hughes et al., 2007; Maslin and Christensen, 2007; Osborne et al., 2008; Agustí et al., 2009; Carto et al., 2009; DeMenocal, 2011; Abbate and Sagri, 2012). We refer to this as a Type 1 explanation, with two variants. The notion that populations expand when favourable climatic conditions expand (Type 1a explanation) seems intuitively obvious, and the progressive expansion of more open habitats and grasslands has been widely canvassed as a contributing factor to hominin dispersal at the largest spatial–temporal scale (Dennell and Roebroeks, 2005; Holmes et al., 2006; Holmes, 2007). The idea of dispersal driven by climatic deterioration into new habitats (Type 1b explanation) seems less obvious given the initial costs and risks for a species moving into a new and potentially more hostile environment to which it is not already well adapted. Both variants of this climatic hypothesis face difficulties, due to the relatively coarse chronological resolution of the fossil and

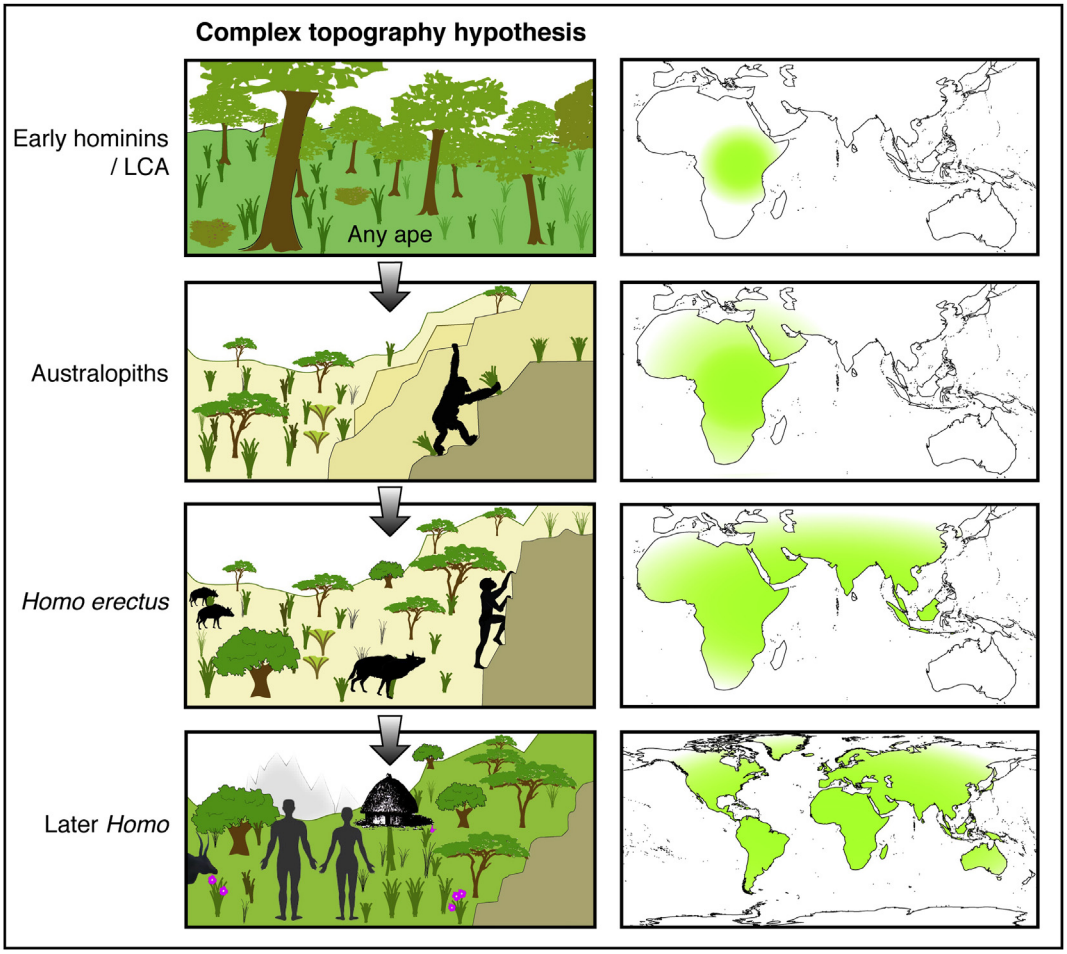

Figure 1. Schematic showing the basic trajectory of human evolution according to the complex topography hypothesis (left) and the corresponding changes in rough range extents (right). The shaded areas on the range maps (shown as green in the colour versions) are indicative only: they are not intended to imply specific claims about the occupation or absence of hominins from specific regions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)