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journal homepage: www.elsevier.com/locate/jhevolEvolution and dispersal of the genus *Homo*: A landscape approachIsabelle C. Winder^{a,*}, Maud H. Devès^b, Geoffrey C.P. King^{a,b}, Geoffrey N. Bailey^a, Robyn H. Inglis^a, Matthew Meredith-Williams^a^a Department of Archaeology, University of York, The King's Manor, York YO1 7EP, UK^b Institut de Physique du Globe de Paris, Sorbonne Paris Cité, Univ. Paris Diderot, CNRS, Paris, France

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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.

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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 wide-spread 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 palaeoenvironmental records and the consequent difficulties of establishing correlations in time between evolutionary and climatic changes.

A second type of explanation (Type 2) is one in which the evolutionary changes take place within an existing habitat. For example, it has been suggested that *Homo ergaster's* intrinsic biology – generalism, large brain and body, and long limbs – made colonization of more variable environments and range expansion possible by giving this species the cognitive capacity to adapt rapidly to new conditions and the strength and energy reserves to survive the adaptive process (Antón and Swisher III, 2004). A similar claim is that the development of new technologies and social structures in this period relaxed the selective pressures exerted by new environments, or 'forced' dispersal by strengthening inter-group competition (Carbonell et al., 1999, 2010). For this

type of explanation to be correct, we need to postulate some ongoing process of adaptation that would be expected to yield the traits needed for dispersal and range expansion. So far, there is no consensus on what kind of process this might be, what sort of selective pressures in the pre-existing habitat would have generated it, or whether it was triggered by intrinsic changes in behaviour or extrinsic environmental changes. Potts (1998a,b; 2007) has proposed a variant on the latter with the concept of variability selection, in which increased climatic variability selects for more adaptable behaviour, but this faces the same problem as other climatic explanations of specifying timing and linkage.

A third type of explanation (Type 3) is that climate change might also have acted to remove existing physical or ecological barriers, for example, by facilitating shorter sea crossings across the Mediterranean or the southern Red Sea at lowered sea level (e.g., Lambeck et al., 2011). The difficulties here are that these changes have recurred episodically throughout the Quaternary period, that the possibility of early Pleistocene sea crossings in the Mediterranean or the Red Sea remains controversial, and that in any case the primary land route through the Sinai Peninsula does not appear to have posed a physical or ecological barrier at any time in the period under discussion, although it does constitute a topographic bottleneck and constraint on dispersal.

Finally, simple demographic pressure may have driven dispersal (Type 4 explanation), but exploration of this possibility is hampered by our limited ability to reconstruct palaeodemography or to model demographic processes on the expanded time scales of the Pleistocene (Hawks et al., 2000; Monge and Mann, 2007; Dennell et al., 2011), and we do not pursue it further.

Here we develop an approach that draws on the concept of complex topography as an agent of selection to explore a Type 2 explanation as defined above – one that involves an ongoing process of adaptation within an existing habitat, which then facilitates subsequent range expansion into new territory. We present arguments and evidence in favour of this type of explanation, and we also evaluate it in comparison with Type 1 and Type 3 explanations. We have previously argued that specific configurations of topography and landforms resulting from active tectonics facilitated the transition from arboreal to ground-dwelling bipedalism, improved access to mobile prey, increased meat-eating, and expanded spatial and cognitive awareness (King and Bailey, 2006; Bailey et al., 2011; Winder et al., 2013, 2014). Here we develop this line of argument to suggest that comparable topographic conditions facilitated range expansion into new territory regardless of specific vegetation types or climatic zones.

3. The tectonic landscape model

The tectonic landscape model (Reynolds et al., 2011: 281) focusses on the potential role in human evolution of complex topography, meaning a land surface characterized by irregularities in surface morphology or 'roughness' (Bailey et al., 2011: 260). Rough land surfaces are commonly (though not uniquely) associated with tectonically active landscapes, characterized by ongoing earthquake activity, faulting and volcanism. Winder et al. (2013) draw attention to the following six characteristics of tectonically-created rough landscapes that make them peculiarly attractive candidates for early human evolution and settlement:

- Repeating earthquakes on fault zones create and accentuate basins at local and regional scales that trap water and sediment, and activate or re-activate spring lines, concentrating and renewing conditions of localized fertility and water supply.
- Continued activity rejuvenates and maintains these favourable conditions over long periods, making them less sensitive to the

vagaries of climate change in comparison with non-active regions.

- These same conditions also create *and renew* a complex topography of local and regional barriers, bottlenecks and enclosures of varying size that afford tactical advantages for early hominins, especially in relation to a growing dependency on meat-eating whether by scavenging or hunting.
- These topographic advantages afford both places for hiding and protection from competing predators and also opportunities for monitoring of and access to otherwise elusive or dangerous animal prey.
- Topographic roughness is often associated with marked changes in topographic elevation over relatively short distances – the two effects being the outcome of the same underlying tectonic processes – and this combination creates ecological diversity and a range of different resources within relatively circumscribed territory.
- Volcanic lava flows can have similar effects in trapping sediments, renewing soil nutrients and creating minor barriers, and the combination of local volcanic activity and faulting can be doubly advantageous in producing and sustaining the above characteristics.

We have elaborated these concepts elsewhere with supporting detail and applications in a variety of landscape settings in Europe,

Asia, Africa, Australia and North America (King and Bailey, 1985, 2006, 2010; King et al., 1994, 1997; Bailey et al., 2011, 2012; Bailey and King, 2011; Devès et al., 2014; Holdaway et al., 2015), and take this previous work as a starting point for the present discussion.

Dynamic landscapes driven by tectonic activity, rough and variable ('complex') topographies, and heterogeneous habitats that pack varied resources including water and stone outcrops into a relatively small area are especially characteristic of the active, tectonic landscapes of eastern and southern Africa (Bailey and King, 2011; King et al., 1994; Bailey et al., 2000, 2011; Reynolds et al., 2011). These areas are highly spatially variable in terms of local vegetation and climate as well as topography, especially in the African Rift proper. These would be attractive areas for hominin habitation, providing ready access to subsistence needs, as well as protection from major predators like lions and hyenas.

We cannot be certain that the tectonically created regions of eastern and southern Africa were uniquely favoured in these respects as the cradle of hominin evolution and the location of the Last Common Ancestor (LCA) between humans and our nearest relatives. As we demonstrate later, similar topographic features are also present in parts of western and northwestern Africa. However, east and southern Africa are distinctive in that they represent a geographically much more extensive region with variable but generally high rates of tectonic activity, and a large range and high

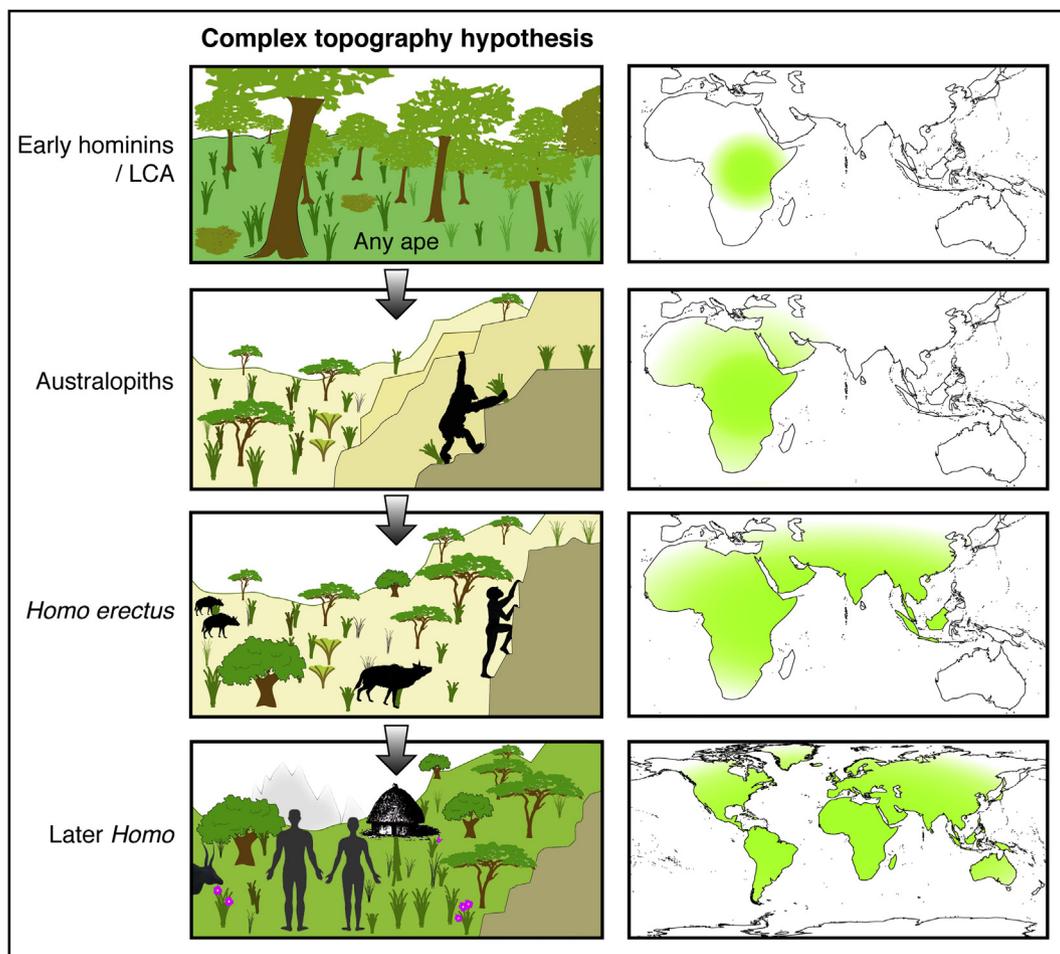


Figure 1. Schematic showing the basic trajectory of human evolution according to the complex topography hypothesis (left) and the corresponding changes in rough range extents (right). The shaded areas on the range maps (shown as green in the colour versions) are indicative only: they are not intended 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.)

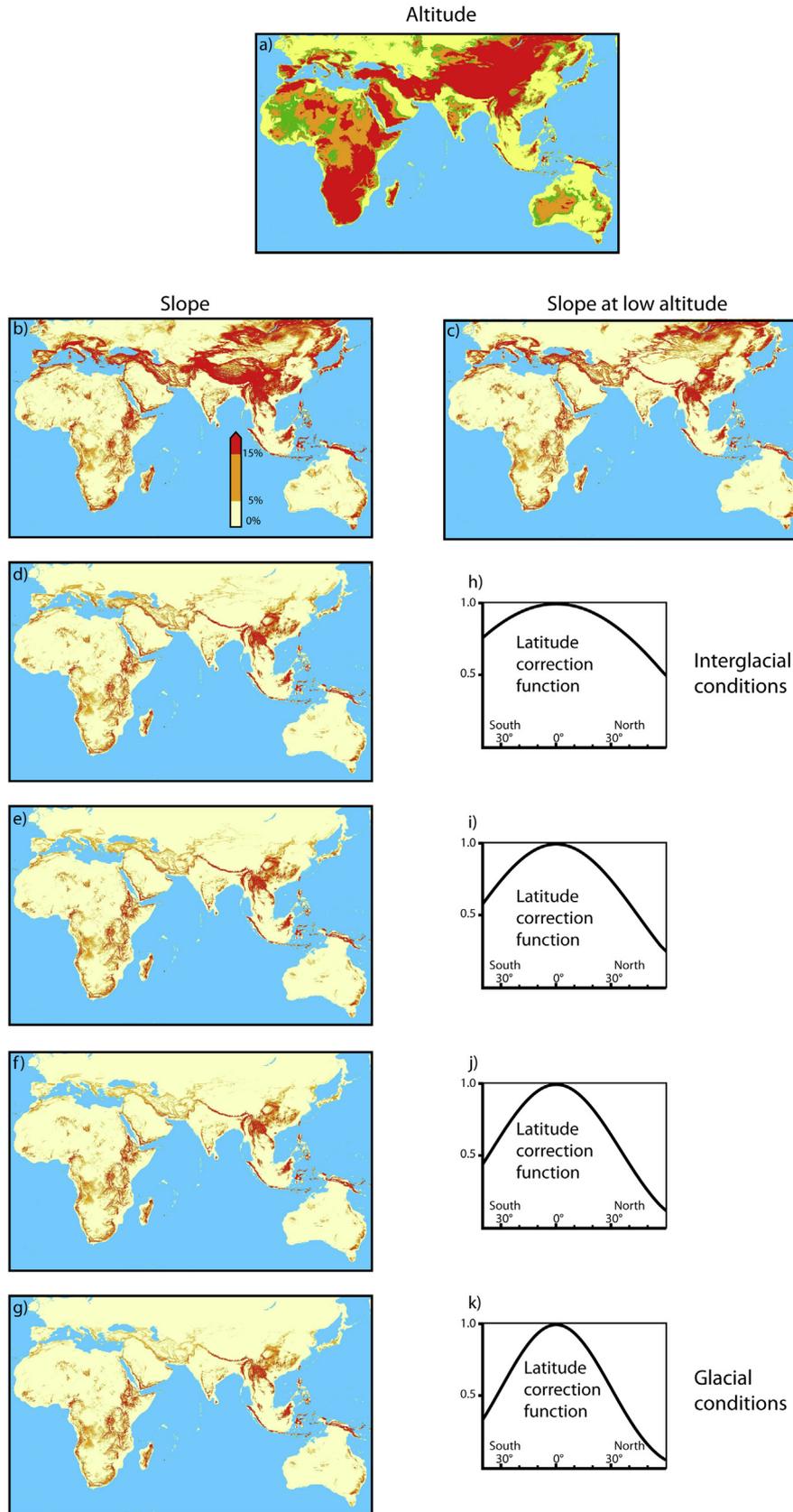


Figure 2. Maps of the physical landscapes of Africa and Eurasia, using SRTM3plus data with a spatial resolution of ~900 m and sea levels set at 100 m below the present level. These images show the steps taken in generating a map of attractive complex landscapes. (a) Map of terrain altitude; shading ranges from high = dark to very low = light; in the colour versions, red = high, orange = moderate, green = low and yellow = very low altitude. (b) Map of terrain complexity, in this case a slope map displayed on a scale from light shading (very low slopes) to dark (very high); in the colour version, the range is from yellow (very low slopes) through to red (very high). (c) The same map as in (b) but corrected for altitude on the assumption that very high altitudes in the northern hemisphere would have been inaccessible to early hominins because of adverse climatic conditions. Highest altitudes are

biomass of animal and mammalian resources, affording more opportunities for adaptive radiation (Bailey et al., 2011; Reynolds et al., 2011).

According to the complex topography hypothesis, the earliest hominins did not become terrestrial via a process of adaptation to semi-arborescence on the predator-rich savannah plains, as suggested by many competing hypotheses (see Winder et al., 2013, 2014 and references therein for a full discussion). Instead, we argue that exploiting rough and complex terrain provided a more favourable context for the evolution of hominin terrestriality, and one that is applicable to an ancestral ape with a wide variety of body forms (Winder, 2012). From this perspective, our ancestral arboreal locomotor anatomies, whether or not they featured upright posture, would have been better suited to a move onto these easily accessible, rough landscapes, as a first step towards fully developed terrestrial bipedalism (Fig. 1). From this starting point, the further evolution of the hominins can be seen as a process of increasingly active exploitation of these ‘complex’ landscapes, followed by expansion into similar landscapes in Europe and Asia, and ultimately beyond them.

Though ecologically and anatomically diverse, australopithecines typically display a combination of anatomical features that are usually associated with the development of some bipedal ground movement alongside the continuation of a semi-arboreal way of life – relatively long arms, though shorter than in the living African apes, for example, and anatomical modifications to the pelvis and lower limb facilitating an upright gait (Richmond et al., 2001; Harcourt-Smith, 2007). This combination is typically seen as resulting from ground dwelling alongside continued reliance on trees (Ward, 2007). However, we argue that these characteristics can be equally well explained, and perhaps better explained, as a coherent set of adaptations to ground dwelling in rough and complex topography without any necessary dependence on trees, rather than as a hybrid mixture that is neither fully arboreal nor fully ground dwelling. In particular, the combination of shorter arms, upright posture and foot arches would make a hominin well suited to the demands of climbing and scrambling in rough terrain, and perhaps better so than to movement in trees. Complex topography would thus have permitted ground dwelling through a simple pathway of evolutionary adaptation, encouraging expansion into a range of terrestrial niches and release from dependence on trees or their particular vegetational and climatic associations.

The challenges and opportunities associated with complex topography and spatially heterogeneous habitats would have further selected for cognitive development alongside biological adaptations, and thence to the tactical exploitation of rough terrain close to biomass-rich plains to trap animals such as ungulates without the need to abandon the safe areas afforded in complex topography. The first species to show clear adaptations to such a niche are arguably the early members of *Homo*, perhaps including *H. habilis* and *H. rudolfensis*, and more certainly *H. ergaster/erectus*. These species began to incorporate features associated with efficient running and striding, and have larger bodies and brains (Antón, 2003), all of which might have resulted from increased possibilities for meat-eating and permitted more wide-ranging movement from safe havens in rough terrain.

We do not attempt detailed linkages between specific hominin fossil taxa and particular stages in the early part of this trajectory,

both because there is ongoing disagreement about the taxonomic status of some of the earliest African fossils attributed to the *Homo* genus, and also because we consider it more helpful to think in terms of an adaptive radiation involving a mosaic of niches within the broader concept of a ‘complex topography niche,’ and a diversity of hominin anatomical adaptations, not all of which were necessarily on the main track to fully developed *Homo* (Winder et al., 2014). Our hypothesis does not require that all early hominin species followed an identical evolutionary trajectory through every stage, only that they all followed some parts of it. Many early forms may have moved away from this trajectory as they diverged, perhaps back into trees.

Similarly it does not follow from our hypothesis that other species that occupy rough habitats (for example, gorillas, wolves or chamois) should have evolved the same cognitive and biological adaptations as humans (though their failure to do so is sometimes cited as evidence against our hypothesis). The interaction between chance, the constraints of existing biological and anatomical structures, and selection is likely to have produced many different evolutionary trajectories, and what works for hominins does not necessarily have to be replicated in other species to be possible or true.

By the time of *Homo sapiens*, this process had produced humans who were not only highly adept in the tactical exploitation of complex topography but who also had sufficient adaptive flexibility to move far beyond their ancestral bounds into high latitudes, across oceans and into flatter and more arid regions posing new risks and challenges.

According to this hypothesis, a key to early *Homo* dispersal lies in the preference for rough landscapes close to smoother terrain, the smoother terrain providing the animal biomass to support a predatory way of life, the rougher terrain providing protection, tactical advantage and alternative food supplies. If this view is correct, then the following points follow. First, complex landscapes with the features described above should actually have existed and formed plausible pathways out of Africa that would have facilitated the substantial Pleistocene range expansion seen in early *Homo*. Second, there should be a reasonable fit between the distribution of these landscapes and the locations of early *Homo* sites in Eurasia. Third, palaeoenvironmental records associated with these sites should show a mixture of climatic and vegetational characteristics rather than a specific climatic or vegetational niche that would be required by alternative possible environmental hypotheses of the *Homo* niche, like those which might be developed around an emphasis on climatic variables or savannah vegetation (Type 1 and alternative Type 2 explanations). Finally, we should be able to show that the ‘release’ of hominin populations from Africa was not simply due to the removal of physical barriers that had previously prevented wider dispersal in the absence of evolutionary change (Type 3 explanation). We consider each of these in turn.

4. Materials and methods

4.1. Mapping landscape features

For mapping complex landscape features, we use measures of topographic roughness, defined as irregularities in surface morphology, using digital elevation models (DEMs) derived from satellite data. The full details of the concepts and the mathematical

filtered out using a linear function inversely proportional to altitude, with a value of 1 at sea level and 0 at ≥ 4000 m. Note that features such as the Tibetan plateau are removed. (d)–(g) The same map as in (c) but corrected for latitude using the four functions shown respectively in (h)–(k). These filter out regions at higher latitudes that are assumed to have been inaccessible to early hominins during different parts of the glacial cycle, with (d) showing full interglacial conditions when higher latitudes would have been most easily accessible in climatic terms, (g) glacial conditions when latitudinal adjustment would have been most extreme, and (e) and (f) showing intermediate positions in the glacial cycle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

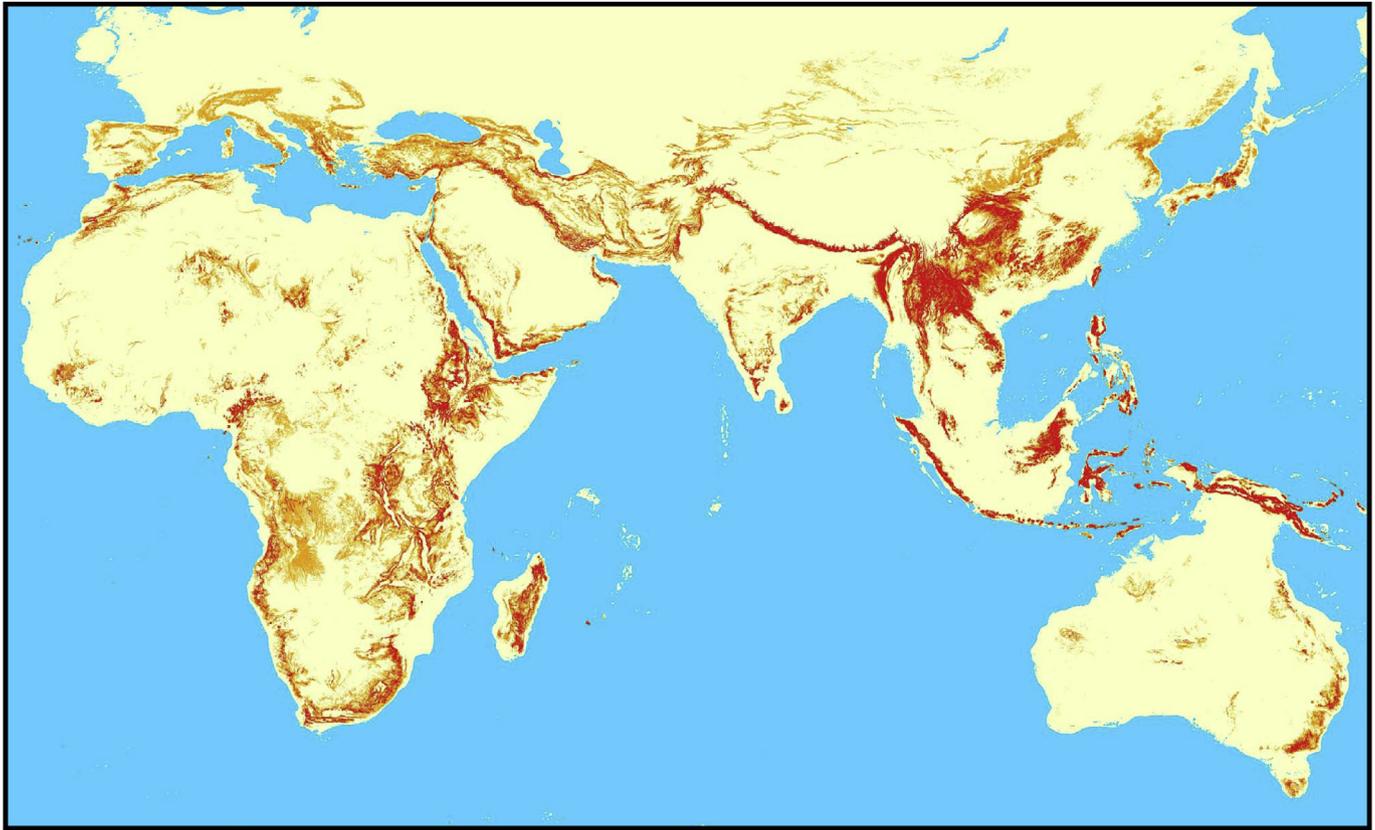


Figure 3. Larger version of the topographic map shown in miniature in Figure 2 (e); shading as for Figure 2.

methods for transforming digital elevation data into measures of roughness are set out elsewhere (King and Bailey, 2006; Bailey and King, 2011; Bailey et al., 2011; Reynolds et al., 2011), and in summary form here, and in the figure captions (Figs. 2, 3 and 5). The essential features that form the basis for the method are that:

- measures of roughness can be derived from DEMs, using slope angles
- roughness is scale-invariant, and roughness at large scales and coarse mapping resolution is typically associated with roughness at smaller scales

Roughness can occur at different scales, ranging from the large-scale roughness associated with major mountain ranges that can act as absolute physical barriers, to small-scale roughness associated with low ridges and surface irregularities. Roughness associated with tectonic activity can result in the juxtaposition of rougher terrain with flatter and smoother areas that act as sediment and water traps. These can occur at a range of spatio-temporal scales from relatively smooth and extensive plains abutting major mountain chains and their foothills to localized valleys and enclosures circumscribed by more or less impassable topographic barriers that can impede movement for many mammals and provide tactical advantage for hominins in avoiding predators or accessing mobile animal prey. We refer to this combination of features as ‘complex topography,’ and use roughness as a proxy measure for complexity in this sense. Here we begin with maps at a relatively low resolution that can show major variations at a world scale, focussing down to a regional scale at a later stage of the enquiry.

We make a further distinction between rough terrain associated with tectonic activity in rifts and at plate boundaries, resulting in

complex topography, and roughness associated with erosion along the edge of uplifted topography located above “hot spots” in the mantle that have undergone uplift because of thermal expansion. This latter involves a different geomorphological process comprising heavy erosion along the edges of the uplifting dome, and is especially well represented in South Africa (Burke, 1996; Bailey et al., 2011, Fig. 5). Unlike fault zones, where rough landscapes alternate with flatter basins, producing edge effects advantageous to *Homo* patterns of land use, the roughness associated with the edge of an uplifting dome is more uniformly rough, creating a heavily dissected landscape without intervening areas of flatter terrain. Similar effects are present in relation to hot spots in parts of Ethiopia and in the Indian subcontinent. This type of roughness is not easily distinguishable on low-resolution maps of large areas, and roughness maps at this scale need careful interpretation informed by knowledge of the regional tectonics.

These maps are, of course, maps of roughness as observed today, and an immediate question is how far these can be assumed to represent terrain characteristics as they might have existed during the earlier Pleistocene. There are three principles to keep in mind in addressing this question. The first is that high degrees of roughness and topographic complexity are associated with regions of active tectonics. Provided these features do not substantially change their position, ongoing activity associated with faulting, localized uplift and subsidence, and volcanism where present, will tend to reproduce and rejuvenate features of complex topography. Rates of activity may change over long time scales – for example, in some parts of the African Rift, notably Afar, the rift axis has changed position. However, in general, regions of complex topography today are likely to have been regions of complex topography far back into the Quaternary.

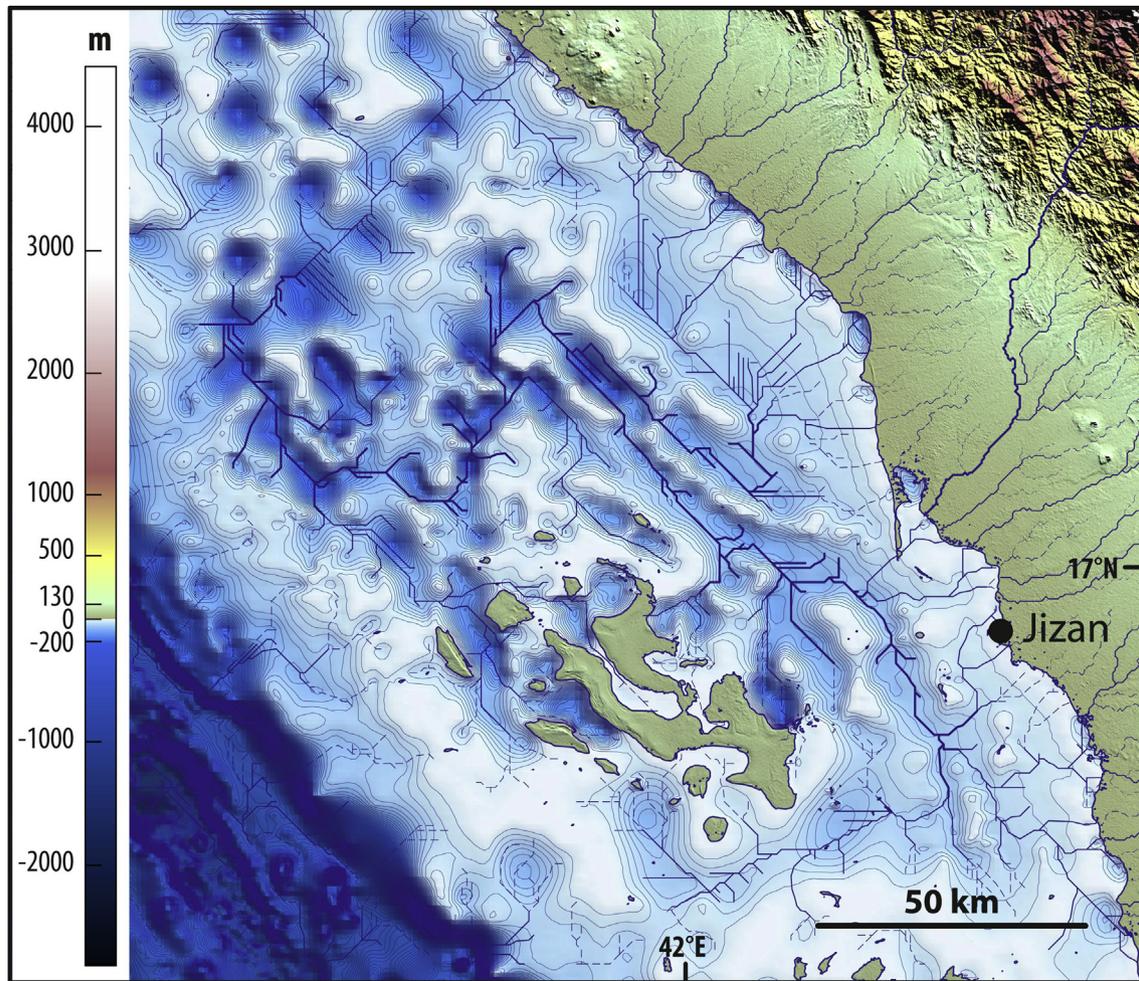


Figure 4. The topography of the submerged landscape in southwest Saudi Arabia in the region of Jizan and the Farasan Islands, based on bathymetry derived from SRTM30plus data. This region is subject to considerable tectonic disturbance resulting from large-scale rifting of the Red Sea and more localized salt tectonics, which are especially active on the coast and offshore. White areas (light blue on the colour image) show water depths shallower than -100 m. Bathymetry data are used to model the likely drainage network on the submerged landscape. The reconstruction indicates a landscape of deep solution hollows, fault-bounded valleys, and potential lake and sediment basins. Testing of these patterns using ship-based acoustic survey and sediment coring is currently in progress. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Differences in the scale and resolution of observation and mapping will affect what can be seen and how precisely it represents conditions on the ground. At the coarsest scale, that of continents and sub-continental regions, roughness maps provide a low-resolution map of differential topographic features that can be taken as a good if rather generalized proxy for past conditions. However, at this coarse scale of observation some regions that show up as relatively smooth and flat can turn out on closer inspection at a finer scale of observation to have features of complex topography of relevance to the home ranges and day-to-day activities of hominin populations on the ground (Holdaway et al., 2015). Conversely, as the scale of observation narrows down to smaller areas on scales of tens to hundreds of kilometres, so the likelihood increases that individual features of the topography will have changed. For example, zones of fault activity and fault scarps may shift to different parts of a regional landscape, remaining unchanged and rejuvenating lake basins surrounded by tactically advantageous topographic barriers for long periods in one part of the landscape, but creating and then destroying similar features in another part of the same landscape (e.g., King and Bailey, 2010, Fig. 8).

Interacting with variations in scale of observation is a third factor – varying rates of tectonic activity. In South Africa, rates of change are slow though active, and ongoing faulting is present; even quite localized features in the present-day landscape can be projected with some confidence back into the early Pleistocene (Partridge, 2010; Bailey et al., 2011). In parts of the Ethiopian Rift, rates are much higher and projection into the past of present-day features more difficult (Bailey et al., 2011). In the Kenyan Rift, the position is more variable. Under favourable circumstances, it is possible to combine dating of fault scarps to model fault motions in conjunction with dating of volcanic features, and thus to run the process of landscape evolution backwards so as to reconstruct the landscape as it would have appeared at some earlier time. Changing water levels in lakes, which can have a significant impact on local topography, mobility and access, can be further factored into the reconstruction. At a larger geographical scale, the Alpine-Himalayan belt has very high rates of tectonic activity and changes can be pronounced, even at the broadest scale of observation. For example, major features like the Sea of Marmara or the Gulf of Corinth, are less than 4 Ma and 1 Ma, respectively (Armijo et al., 2003).

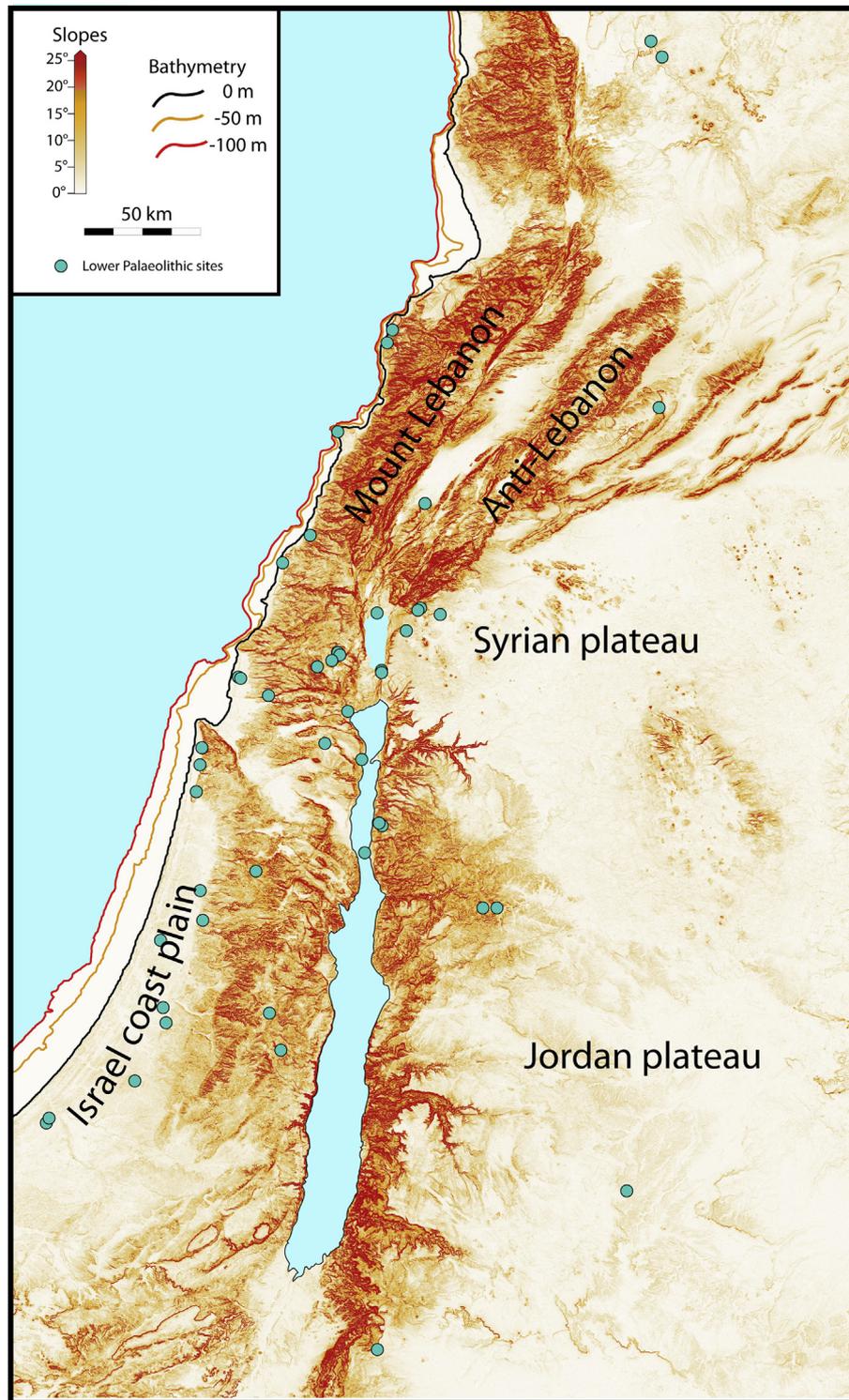


Figure 5. A higher resolution roughness map of the physical landscape in the Levant region, using data derived from Aster DEMs with a spatial resolution of ~90 m. Shading and construction as in Figure 2. At this scale, the map shows a near-continuous distribution of rough terrain and complex topography, with Lower Palaeolithic sites falling at or near edge-landscapes.

4.2. Site locations

For the comparison of landscape distributions with early hominin activity and vegetational and climatic variables, we rely on the locations of sites in Europe and Asia that have produced the earliest dated evidence of fossil remains of *Homo* (mainly *H. erectus*, but

also including finds like those from Dmanisi, variously assigned to *H. ergaster*, *Homo* spp. and the new species *Homo georgicus*), and associated floral and faunal data providing evidence of vegetational and climatic conditions (Tables 1 and 2). We also include some sites with well-dated stone tools in the >1 Ma time range, but have not attempted a comprehensive analysis because of large uncertainties

Table 1

A sample of key sites for early *Homo* in Europe and Asia. These sites include only localities either (a) with fossil finds attributed to *H. ergaster*, *H. erectus*, *H. habilis* or closely related species or (b) with well-known, securely dated stone tools over c. 1 Ma.^a

Site details	Finds	Date	Location	References
Pabbi Hills, Pakistan	Stone tools	Late Pliocene/Early Pleistocene	33.8°N, 70.8°E	Dennell (2008)
Riwat, Pakistan	Stone tools	1.9 Ma	33.5°N, 73.1°E	Dennell et al. (1988)
Longuppo, China	Early <i>Homo</i>	1.9 Ma	30.8°N, 109.7°E	Wanpo et al. (1995)
Modjokerto, Indonesia	<i>H. erectus</i>	1.8 Ma	7.5°S, 112.4°E	Swisher et al. (1994); locality given is the site of nearby Modjokerto settlement
Dmanisi, Georgia	Affinities to <i>H. ergaster</i> / <i>H. habilis</i>	1.8–1.7 Ma	41.3°N, 44.2°E	Gabunia et al. (2001); PBD
Yuanmou, China	<i>H. erectus</i>	Unknown, <1.7 Ma	24.9°N, 100.9°E	Zhu et al. (2003); PBD
Sangiran, Indonesia	<i>H. erectus</i>	1.66 Ma	7.4°S, 110.8°E	Swisher et al. (1994) and Van den Bergh (1999); PBD
Orce, Spain	Early <i>Homo</i> (contested)	1.4 Ma	37.7°N, 2.5°W	Duval et al. (2012); PBD (locality is Fuente Nueva 3)
'Ubediya, Israel	<i>Homo</i> sp.	1.4–1.0 Ma	32.7°N, 35.6°E	Gaudzinski (2004); PBD
Sima del Elefante, Spain	<i>Homo</i> sp.	1.2–1.1 Ma	42.4°N, 3.6°E	Carbonell et al. (2008)
Gongwangling, China	<i>H. erectus</i>	1.15–1.1 Ma	34.2°N, 109.5°E	Zhu et al. (2003); PBD
Sambungmahan	<i>H. erectus</i>	Unknown, <1 Ma	Approximately 7.4°S, 111.0°E	Delson et al. (2001) and Huffman (2001)
Chenjiawo, China	<i>H. erectus</i>	Unknown, <1 Ma	34.2°N, 109.3°E	Zhisheng and Kun (1989); PBD
Evron, Israel	Acheulian stone tools	~1–0.78 Ma	32.6°N, 35.1°E	Ron et al. (2003); PBD
Trinil, Indonesia	<i>H. erectus</i>	0.9 Ma	7.4°S, 111.3°E	Van den Bergh (1999); PBD
Monte Poggiolo, Italy	Oldowan stone tools	0.85 Ma	44.2°N, 11.9°E	Muttoni et al. (2011)
Kul'dara, Tajikistan	Stone tools	0.8 Ma	38°N, 69.5°E	Davis and Ranov (1999)
Kedung Brubus, Indonesia	<i>H. erectus</i>	0.8–0.7 Ma	7.4°S, 111.7°E	Van den Bergh (1999); PBD
Gesher Benet Ya'aqov, Israel	Acheulian stone tools	0.8–0.7 Ma	33.0°N, 35.4°E	Martínez-Navarro and Rabinovich (2011)
Treugol'naya cave, Russia	Stone tools	0.6–0.4 Ma	44.0°N, 41.0°E	Blackwell et al. (2005) and Hoffecker et al. (2003)
Zhoukoudian, China	<i>H. erectus</i>	0.55–0.3 Ma	39.7°N, 115.9°E	Grün et al. (1997)
Hexian, China	<i>H. erectus</i>	0.5–0.4 Ma	31.7°N, 118.4°E	Wu et al. (2006); PBD
Kocabas, Turkey	<i>H. erectus</i>	c. 0.5 Ma	37.8°N, 29.3°E	Kappelman et al. (2008)
Tham Khuyen, Vietnam	<i>H. erectus</i>	0.475 Ma	22.0°N, 106.4°E	Ciochon et al. (1996); PBD
Ceprano, Italy	Affinities to <i>H. erectus</i> / <i>H. heidelbergensis</i>	0.45 Ma	13.5°N, 41.5°E	Muttoni et al. (2009)
Fontana Ranuccio, Italy	<i>H. erectus</i> (?)	0.45 Ma	13.1°N, 41.9°E	Muttoni et al. (2009)
Nanjing, China	<i>H. erectus</i>	c. 0.3 Ma	39.3°N, 118.1°E	Xu (1999); locality given is nearby Tangshan town
Ngandong, Indonesia	<i>H. erectus</i>	0.25–0.1 Ma	7.3°S, 111.4°E	Van den Bergh (1999); PBD
Kashafrud, Iran	Oldowan stone tools	Unknown	35.7°N, 60.5°E	Sajjadi et al. (2007)

^a The finds from Narmada, Vertesszolos and other sites now usually attributed to *H. heidelbergensis* are excluded. The reference 'PBD' refers to a locality from the Paleobiology Database, at www.paleodb.org.

over dating and palaeoenvironmental associations in many cases. Nor do we attempt here large-scale mapping of vegetation and climate variability, though we note the possibility of pursuing such an approach as an independent body of mapped data that can be compared with our landscape distributions (Mithen and Reed, 2002; Field and Lahr, 2005; Field et al., 2007; Hughes et al., 2007; Dennell et al., 2011).

5. Results

5.1. Mapping landscapes and dispersal routes

In producing low-resolution maps of roughness at the world scale, we use slope angles as a proxy measure of roughness (Fig. 2b). In addition, we show maps that exclude complex topography in the northern hemisphere at high altitude (Fig. 2c) and high latitude (Figs. 2d–g and 3) on the assumption that the earliest *Homo* dispersals out of Africa would have avoided very cold climate regimes even if topographic conditions were otherwise favourable. We have further refined this modification to differentiate between glacial and interglacial conditions. These adjustments remove large areas of potentially usable complex topography in central Asia and northern Europe, and the northern margin of usable terrain is further depressed southwards during glacial conditions.

In all maps in Figures 2 and 3, the African Rift stands out with its high concentration and extent of complex landscapes, extending into parts of South Africa. Some of the roughness around the southern and western margins of South Africa is the result of erosion at the edge of an uplifting plate, as described earlier, but other regions in the South are demonstrably associated with active tectonics, and these are the regions typically associated with fossil and archaeological sites (Bailey et al., 2011; Reynolds et al., 2011). Elsewhere in Africa, regions of complex topography occur in relative isolation, the largest being in the northwest in association with the Atlas Mountains, with smaller patches in the central Sahara and in West Africa. Northwards, there is an almost unbroken chain of topographic complexity extending along both sides of the Red Sea, especially on the eastern margin associated with the Arabian escarpment. It is worth noting here that, in terms of topography, western Arabia would have provided an obvious and proximate zone of *Homo* dispersal from Africa, whether approached across the southern end of the Red Sea or from the north.

Looking eastwards, along the southern end of the Arabian Peninsula, complex topography disappears at this scale of observation, and if we are looking for a pathway eastwards into Asia, then the most attractive route appears to lie northwards from the Sinai Peninsula along the Syrio-Jordanian Rift and then eastwards around the margins of the Zagros arc into the north of the Indian

Table 2
Contextual information from the early *Homo* sites listed in Table 1, showing associations with climate and vegetation.

Site	Vegetation	Climate	References
Pabbi Hills, Pakistan	Fairly uniform open grasslands	Monsoonal, with marked seasonal contrast; cool and arid winters and warm and wet summers	Dennell (2008)
Riwat, Pakistan	Uncertain	Uncertain	–
Longuppo, China	Dense forest (including rainforest)	Subtropical climate	Ciochon (2009)
Modjokerto, Indonesia	Uncertain; marine deltaic or sea-coast location	Uncertain due to lack of specific locality/date	Huffman et al. (2006)
Dmanisi, Georgia	Mixed woodland, with patches of forest and steppe; lakeside	Warmer and drier than today	Gabunia et al. (2001)
Yuanmou, China	Mosaic including open grassland, bushland, forest, marsh and freshwater	Warm and humid in the Late Pliocene, shifting to dry and hot today	Yao et al. (2012) and Zhu et al. (2008)
Sangiran, Indonesia	Spatio-temporally variable and mosaic: patches include lakeside, marsh, wet grasslands, savannah, open and closed woodlands	Wet at c. 1.5–2 Ma, later drier, with a monsoonal climate; temperature has oscillated with glacial cycles	Bettis III et al. (2009)
Orce, Spain	Near a large water body, with mosaic habitats including a lot of open and semi-open and some closed humid contexts	Wetter (741 mm rain/year) and warmer (16.9 °C mean annual temperature) than present, with a summer drought	Blain et al. (2011)
'Ubediya, Israel	Marsh or shallow lake context; Mediterranean woodland in early occupation periods, grassland and savannah later (not African species)	Colder climate, with a drying trend through time	Belmaker (2006); Issar (2010)
Sima del Elefante, Spain	Open vegetation, with standing water nearby	Warm and humid, with short-lived cool shifts	Carbonell et al. (2008) and Van der Made (2013)
Gongwangling, China	Warm temperate forest, perhaps near areas of cold desert/steppe	Monsoonal and seasonal; hominins may have lived here only in warm seasons	Wang et al. (1997)
Sambungmahan, Indonesia	As at Sangiran (later period)	As at Sangiran (later period)	Jacob (1975)
Chenjiawo, China	Mosaic palaeoartic habitat, including warm forest and cool grassland	As at Gongwangling, but seemingly occupied all year round	Wang et al. (1997)
Evron, Israel	Water bodies, steppe, wet woodlands and bare rocky areas all present	Uncertain	Tchernov et al. (1994)
Trinil, Indonesia	Open woodland habitats	Probably cooler and drier than today	Van den Bergh et al. (2001)
Monte Poggiolo, Italy	Forests and steppes	Cool (spanning a minor glacial period) and seasonal	Messager et al. (2011) and Muttoni et al. (2011)
Kul'dara, Tajikistan	Tree-dominated, but with shrubs and herbaceous vegetation as well	Uncertain	Dodonov and Baiguzina (1995)
Kedung Brubus, Indonesia	Open woodland habitats	Probably dry in comparison to today; sea level fluctuates	Van den Bergh et al. (2001)
Gesher Benet Ya'aqov, Israel	A lacustrine context, with Mediterranean vegetation	Cool when first occupied, then warmer and drier	Rosenfeld et al. (2004)
Treugol'naya cave, Russia	High altitude woods and subalpine meadows in the earliest occupation levels; woods, steppes and meadows later	Cool and humid at initial occupation; variable in both temperature and humidity later	Doronichev (2008)
Zhoukoudian, China	Mixed C ₃ /C ₄ grasslands and woodlands	Deteriorating; getting colder and wetter, and with a more marked monsoon	Gaboardi et al. (2005)
Hexian, China	Mixed, but dominated by forest and woodland	A little cooler and rather wetter than today, but uncertain and variable	Wanpo (1982) and Xu (1984)
Kocabas, Turkey	Unknown (isolated fossil found during quarrying)	Unknown (isolated fossil found during quarrying)	–
Tham Khuyen, Vietnam	Mixed, including closed habitats, scrub and parkland vegetation and bamboo	Uncertain; faunas contain subtropical, tropical and temperate forms	Louys et al. (2007)
Ceprano, Italy	Deciduous and mixed forests	Interglacial conditions	Leroy et al. (2011)
Fontana Ranuccio, Italy	Forest, including deciduous and evergreen trees	Humid and warm	Corrado and Magri (2011)
Nanjing, China	As at Zhoukoudian, with broadleaved trees and open-habitat plants	Uncertain – probably a cold-inclined temperate climate	Wang et al. (2003) and Zhu and Zhang (2000)
Ngandong, Indonesia	Open or semi-open vegetation (not rainforest)	Slightly colder than today	Von Koeningswald (1975)
Kashafrud, Iran	Most likely grassland, though this is unconfirmed	Uncertain; warm/hot but lacustrine context	Biglari and Shidrang (2006)

subcontinent, around the Himalayan foothills into China, and southwards again at periods of lower sea level into the Malaysian Peninsula and Indonesia, albeit with some gaps in the chain of topographic complexity.

The Anatolian Peninsula is an important region at the junction of major fault boundaries with extensive areas of complex topography, and lies at a crossroads between Africa, Europe, and Asia, with opportunities for dispersal not only eastwards, but also northwards to the Caucasus, and westwards into Europe. Of particular interest is the impact of glacial conditions, which would tend to compress, fragment and isolate areas of complex topography in the north and the west, particularly in the southern

European peninsulas, in comparison with the zones that lie eastwards in Asia.

One question that emerges at this scale is the reality and effect of gaps in the chain of complex topography already noted both within Africa and beyond. One possibility is that distances were short enough that populations could easily bridge the gap regardless of conditions in the gap. A second possibility is that the intervening areas may have been made more easily habitable by other environmental factors. Climate change (a Type 1a explanation) may be relevant in crossings of the Sahara and the Arabian deserts, which have undergone periodic greening and extension of drainage networks during the Pleistocene (Osborne et al., 2008; Petraglia et al.,

2012; Drake et al., 2013). The status of these green periods in terms of the amount and frequency of water supply, the influence of local tectonic controls on water flow, and whether the environments created represented extensive and well-watered grasslands or semi-arid oases connected by more transitory streams is still under investigation. However, it appears that these green episodes and associated evidence of human activity lasted for less than 20% of the glacial interglacial cycle. If nothing else, these examples demonstrate the vulnerability of water supplies and other resources to over-riding climate change in regions that appear to lack the hydrological and micro-climatic advantages of active tectonics and complex topography.

A third possibility is that coastlines may have offered a pathway of connection, particularly along the North African coast, and around the southern end of the Arabian Peninsula, particularly in the southern Red Sea and the Persian–Arabian Gulf where the continental shelf is shallow. Coastal regions often have attractive topographic features because of the effects of sea-level change and coastal erosion, which can create complex topography at least at a small scale, and offer better water supplies than their more arid hinterlands, and a diversity of resources augmented by seafood. This possibility is difficult to evaluate because conditions visible today would have been very different during periods of low sea level when additional land was exposed. Little more can be said until more extensive investigation of these submerged landscapes has been undertaken. However, both theoretical expectations (Faure et al., 2002; Bailey and Flemming, 2008) and survey based on low-resolution bathymetry suggest many of these submerged landscapes presented areas of considerable topographic complexity and likely zones of concentrated water supplies and other resources. In the southern Red Sea, a key region on the southern dispersal route, the coastline would have extended seawards by c. 100 km at periods of maximum sea-level regression, exposing a landscape deformed by salt tectonics (Fig. 4), and recent high-resolution underwater survey demonstrates the presence of a complex topography with fault-bounded valleys and lake basins (Bailey et al., 2015).

This in turn raises a fourth possibility, that some of the patterning as shown in Figures 2 and 3 is obscured by the low resolution of mapping at this scale, and that some of the gaps have a greater degree of topographic complexity than is apparent on low resolution maps. We can examine this possibility by changing the scale of observation and looking more closely at smaller regions. We do this here for the southern Levant (Fig. 5), a key region on the dispersal pathway northwards. This map shows a near-continuous distribution of rough terrain and complex topography with many Lower Palaeolithic sites occurring throughout this region. Zooming in at yet higher resolution shows adjacent rougher and smoother terrain (Fig. 6). A more detailed and higher-resolution spatial analysis of the relationship between archaeological sites and large-mammal distributions in relation to seasonal factors of grazing and water supply in this region demonstrates that major concentrations of *Homo erectus* activity are located at critical topographic constrictions associated with basins of fertile animal grazing, where large mammals could be easily monitored and trapped during their seasonal movements (Devès et al., 2014).

5.2. The relationship between complex topography and hominin sites

In assessing this relationship, we confine our attention primarily to sites with dated finds of hominin fossils. It is hard to identify a single ‘earliest’ site for *Homo* in Eurasia. One contender is the Longgupo site in China, dated to 1.9 Ma (Wanpo et al., 1995), though both this date and its hominid attribution have since been

challenged (Schwartz and Tattersall, 1996; but see also Wanpo et al., 1996). Several sites in Java were originally dated to ~1.8 Ma (Swisher et al., 1994), though there have been claims that these dates are not secure (see discussion and references in Hyodo et al., 2002) or that the geological history of the region makes occupation before 1.7–1.6 Ma impossible, at least for the Sangiran dome, where many of the most famous fossil finds originate (Sémah et al., 2000). Perhaps more reliable is the evidence from Dmanisi in Georgia, dating to 1.7–1.8 Ma (Gabunia et al., 2000, 2001; Lordkipanidze et al., 2007). The fossil finds from Orce, in Spain, currently a contentious claimant to the title of the earliest site in Europe, are somewhat younger (at 1.65–1.4 Ma), but debatable (Toro-Morano et al., 2013). Taking these sites and other, more secure, evidence for hominin presence in the early–mid Pleistocene, however, we can compile a dataset that gives us a large enough sample to permit a preliminary test (Table 1; Fig. 7).

The sites show an association with regions of complex topography stretching from Spain in the west through the peninsulas of southern Europe to northern Anatolia, and then to the east to East Asia, with a few also further south in Indonesia. These Indonesian sites are in a region that can be accessed by following a continuous corridor of complex topography south from China. Similarly, sites in Spain and Italy can be reached by following a corridor from Anatolia through Europe. Both these routes may not have been continuously accessible at all times, the eastern one because of changes in sea level (Fig. 7 shows sea level at its lowest Pleistocene level) and the western one because of climatic changes associated with glaciation (Fig. 2g).

In evaluating this relationship, we recognize the potential bias introduced by taphonomic effects of differential preservation and visibility of evidence, and the charge that the correlation between early sites and regions of complex topography is not a genuine one, but is, rather, simply an artificial effect of heightened preservation and visibility. For example, caves, and exposure of earlier geological deposits by erosion, are both good for the visibility of early fossils and archaeological deposits, and both tend to be associated with rough terrain.

We have discussed this issue elsewhere (King and Bailey, 2006; Bailey and King, 2011; Bailey et al., 2011; Reynolds et al., 2011). Like others who have examined global patterns of early evidence, for example, Holmes (2007) in relation to bone collagen preservation, we recognize the potential effect of taphonomic factors. All attempts to examine correlations between sites of archaeological or fossil deposition and environmental variables, of whatever type and at whatever scale, must grapple with the problem of differential preservation and survey. It is only through an examination of many sites in their landscape settings with alternative hypotheses in mind, including taphonomic ones, and through field research designed to separate out the relative influence of different factors, that it will be possible to progressively distinguish between different hypotheses. Known sites may not be a complete or representative sample, but they are a necessary starting point, and we have provided examples elsewhere showing how detailed analysis demonstrates that differential preservation associated with geological exposures cannot be invoked to explain the occurrence of all known sites (e.g., Bailey et al., 2011: 272–3).

5.3. Alternative environmental hypotheses

One approach to resolving competing hypotheses is to examine the palaeoenvironmental records at the early *Homo* sites discussed (Table 2). If *Homo* dispersal were associated with a specific type of vegetational or climatic niche, we would expect to see evidence for a consistent association. Conversely, under the complex topography hypothesis, we would expect to see variable vegetational and

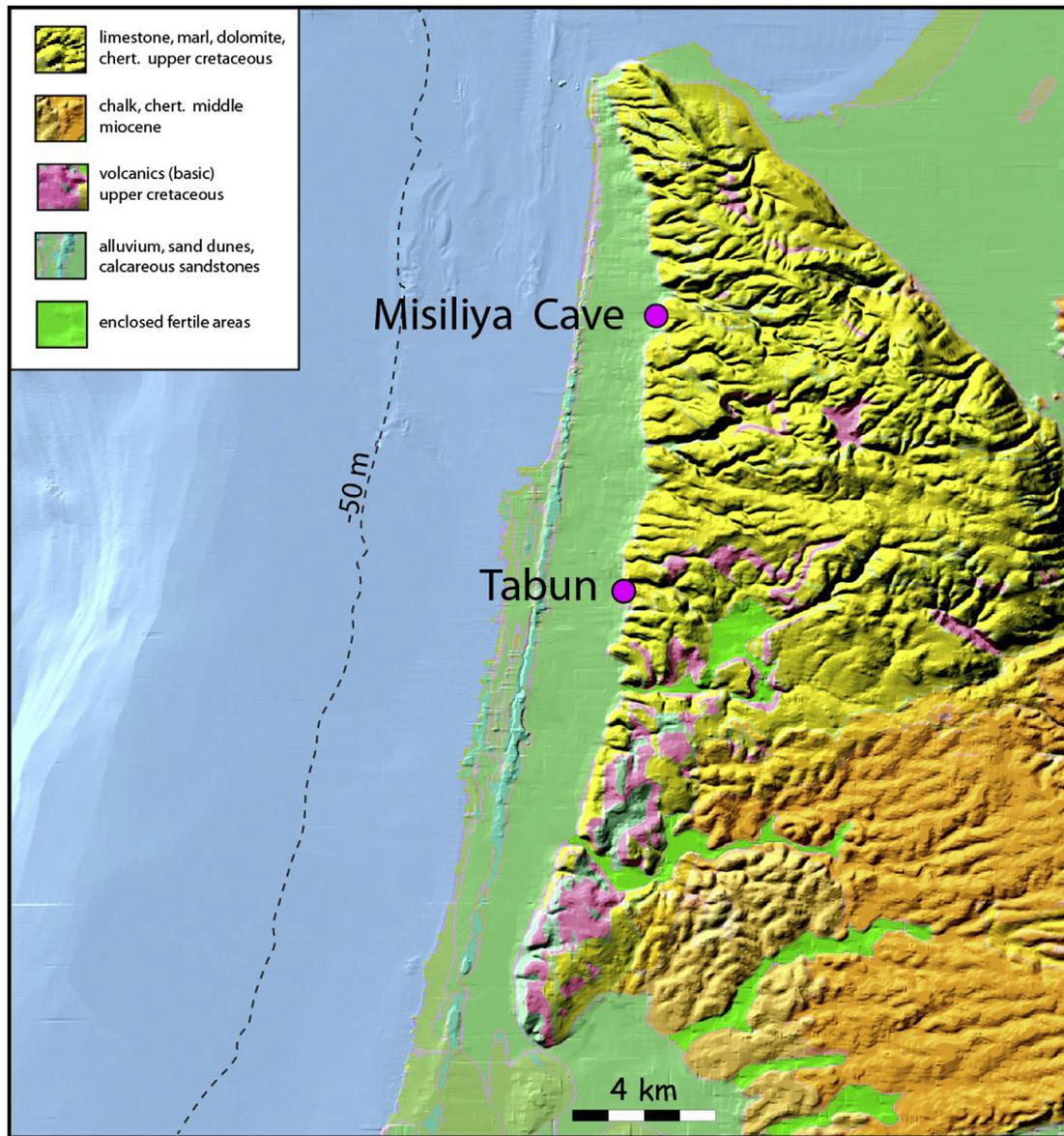


Figure 6. A more detailed view of part of the landscape shown in Figure 5. The contrast between contiguous areas of rough and smooth terrain and the location of archaeological sites in relation to these edge situations is clearly apparent.

climatic associations, both because the key factor in the *Homo* niche is topographic features rather than other variables, and also because complex topography typically creates mosaic ecological conditions that we would expect to see reflected in variable faunal and floral records at some of the sites studied.

Table 2 shows that early *Homo* sites are variously associated with grasslands, steppe, open and closed forests and mixed habitats, and with climatic conditions that range from relatively cold to subtropical, and from dry to humid and even monsoonal. There is no clear association with any particular vegetational or climatic context that might provide an alternative explanation for the pattern we have highlighted.

At one level, this demonstrates the wide range of environmental conditions in which early *Homo* was able to survive, an important indicator of the adaptability of the taxon. However, that wide range is itself a product of complex topography, which typically favours the close juxtaposition of different biomes, ecosystems and subsistence resources. This evidence, taken with the other evidence

discussed in the previous section, shows that the only factor that hominin sites share in common is complex topography. Moreover, in contrast to the evidence discussed in the previous section, the results of this test cannot be dismissed as the result of taphonomic bias, which can only selectively destroy evidence and thus cannot artificially inflate the range of conditions preserved at sites of a single taxon.

5.4. Removal of physical barriers to dispersal

Finally, we turn to the issue of physical barriers, and the possibility that dispersal occurred simply because of their removal by climatic or geological processes, rather than by new evolutionary adaptations. All the exit points out of Africa are short and relatively narrow transit corridors potentially vulnerable to blockage by physical or ecological variables: the terrestrial route through the Sinai Peninsula and into the Levant, and potential sea-crossings at the southern end of the Red Sea, the Gibraltar Strait, and the gap

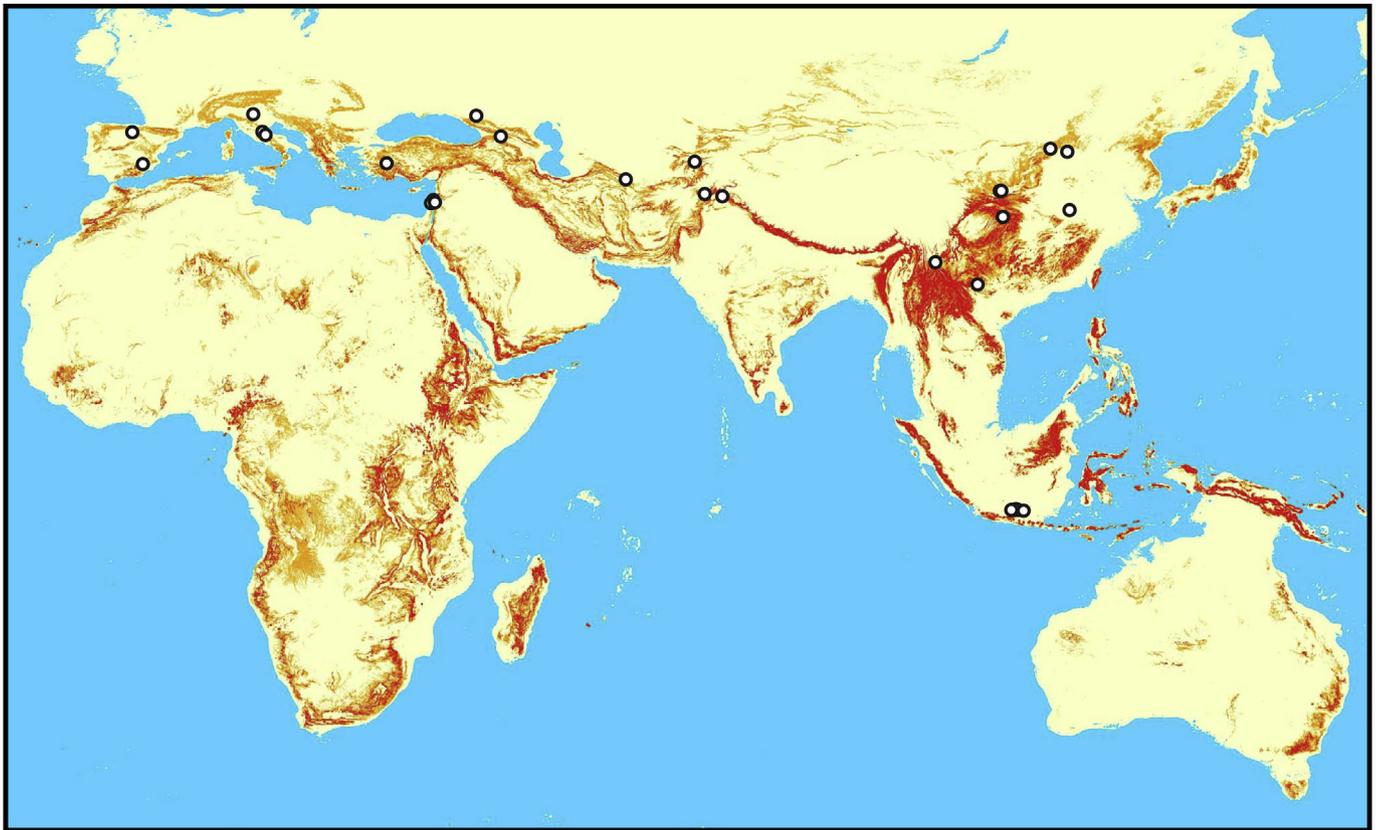


Figure 7. The sites described in Table 1 plotted on the map of landscape roughness of Figure 3, adjusted to remove high-altitude and high-latitude areas using an interglacial filter as shown in Figure 2(e).

between Tunisia and Sicily (Fig. 8; Flemming et al., 2003; Field and Lahr, 2005). Of the sea crossings, the most plausible is the southern Red Sea, where lowered sea level would have offered short (<4 km) sea crossings via the Hanish Islands for long periods of the glacial cycle throughout the Pleistocene (Lambeck et al., 2011). This route has been much discussed in relation to *H. sapiens* dispersal in the late Pleistocene in conjunction with the possibility of newly developed skills in seafaring and marine-resource exploitation (Lahr and Foley, 1994; Walter et al., 2000; Field et al., 2007; Bailey, 2009; Boivin et al., 2013; Mellars et al., 2013). If the hypothesis was correct that *H. sapiens* crossed the southern Red Sea because of newly developed maritime skills, then it could be argued that this route was closed off to earlier *Homo* populations lacking such skills. However, the evidence in favour of the maritime hypothesis is at best weak, and a proper test of it would require systematic investigation of the extensive submerged landscapes of the southern Red Sea and Arabian Peninsula where most of the relevant evidence is likely to be found, an investigation that has only just begun (see Fig. 4; Bailey et al., 2015). Crossings at low sea level would have been possible at many periods during the Pleistocene, both for *H. erectus* as well as *H. sapiens*, without requiring seafaring skills or implying dependence on marine resources, and in any case earlier hominin populations could have accessed the attractive landscapes in the southwest of the Arabian Peninsula by land from the north via the Sinai Peninsula.

Access to the Mediterranean crossing-points might have been possible either by a land-based dispersal along the coastline of North Africa, or from southern Europe. In any case, as in the Red Sea, so in the Mediterranean, there is no decisive evidence in favour of direct movement across sea gaps, as opposed to land-based

dispersal, despite much recent speculation about early Mediterranean seafaring (Derricourt, 2005; Broodbank, 2006; Strasser et al., 2011; Ammerman, 2014).

The possibility of a physical barrier between the Sinai Peninsula and the Jordan Valley associated with strike-slip motion and faulting of the Dead Sea transform can be ruled out (Devès et al., 2011), and it seems that this land route would have been generally passable as a dispersal pathway throughout the Quaternary. If there are physical features that created a potential barrier on this northward chain, they are to be found further north in the border region between Israel, Jordan and the Lebanon (Fig. 5), where the convergence of the Lebanon and anti-Lebanon Mountains, a steeply shelving offshore topography restricting movement to the west even at low sea level, and desert conditions to the east, would have seriously impeded easy passage except under intermittently favourable climatic conditions (Devès et al., 2014).

We conclude that, although the exit points from Africa into adjacent territory are very few and quite restricted, and may have become more or less severe according to changes in sea level, imposing bottlenecks that likely impeded dispersal, an absolute physical barrier seems most unlikely, and cannot be invoked by itself as a sufficient reason for the failure of hominin populations to expand out of Africa earlier than the evidence indicates.

6. Discussion

The key to the complex topography hypothesis as applied to early *Homo* dispersal lies in two factors. The first is the attractions afforded by complex topography in terms of tactical advantage, access to biomass-rich areas where large mammals could be

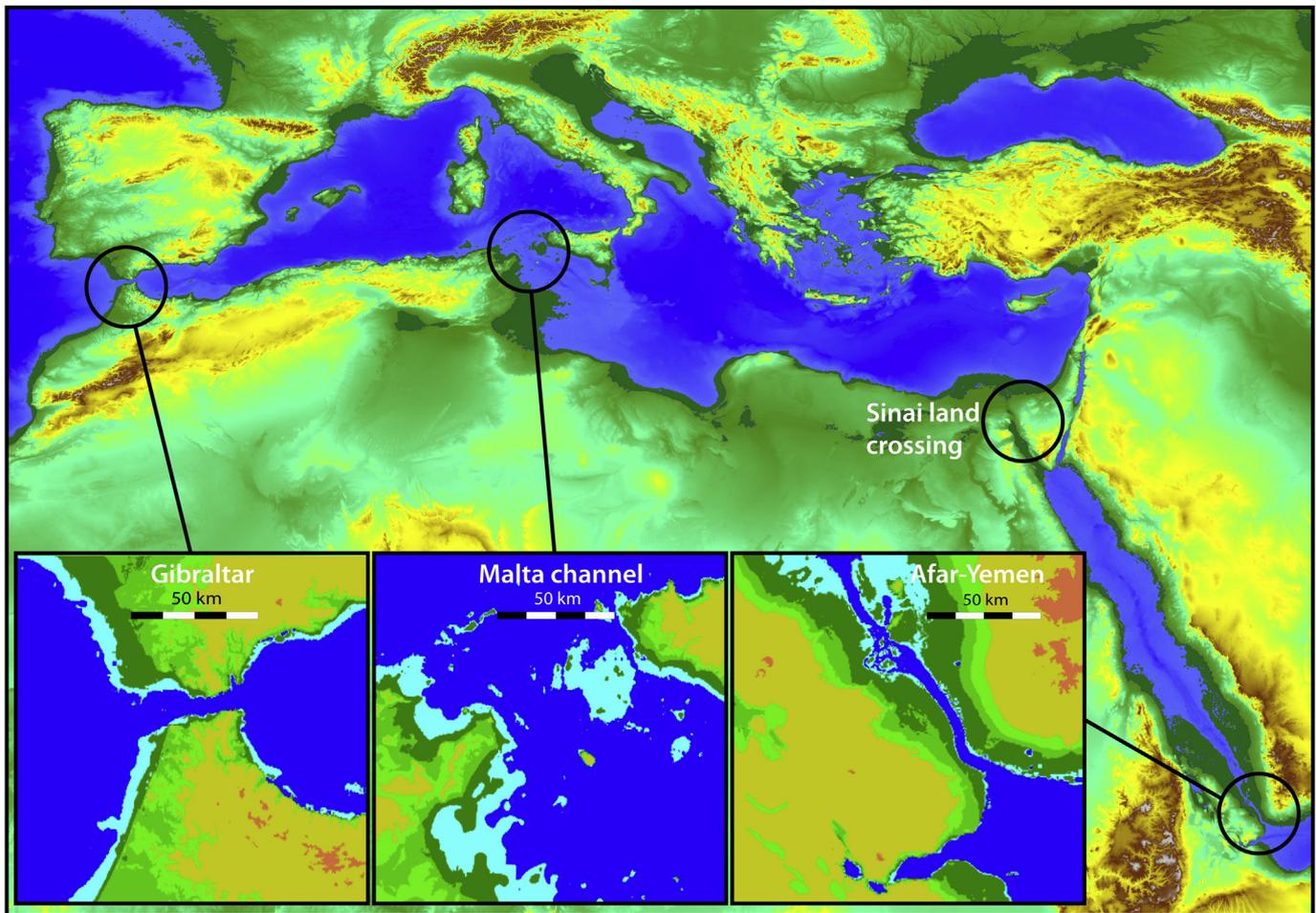


Figure 8. A map of North Africa, southern Eurasia and Arabia, showing the four possible exit routes for out-of-Africa dispersal. In the main image, the coastline is shown with sea levels set 100 m below present. In the inset maps, sea level is set at 50 m below present and the white shading (pale blue on the colour image) indicates water less than 50 m deep. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

targeted with relatively high chances of success, predictable water supplies and other resources. The second is the constraint imposed on dispersal, in confining the main pathways of dispersal to regions of complex topography with these advantages.

The implications of this hypothesis appear to stand up well to evaluation, at least at a first order of approximation. We have demonstrated that concentrations of complex topography with these landscape conditions form extensive and broad pathways that would have facilitated wide-ranging dispersal across varying ecological and climatic zones into many regions of Europe and Asia; that these corridors line up rather well with the distribution of known Eurasian sites with early *Homo* fossils; that collecting even simple palaeovegetation and palaeoclimate data on these sites shows that there is no simple model of the hominin niche based on these variables alone that provides an alternative explanation for the distribution pattern; and that physical barriers by themselves do not provide a sufficient explanation for the failure of earlier hominin populations to disperse outside Africa. At the same time our results raise some additional issues of method and problems in need of further investigation.

Regarding methodology, one issue is the relatively small size of our site sample, which compromises any attempt at more sophisticated quantitative and statistical analysis. Sample size could be expanded if we were to include more sites with stone tools but lacking associated human fossils (e.g., [Gamble, 1993](#); [Lycett and von](#)

[Cramon-Taubadel, 2008](#); [Bar-Yosef and Belfer-Cohen, 2013](#)). Published information is often lacking geographical coordinates or chronological information except within very large margins of uncertainty, but this would not compromise evaluation using large-scale, low-resolution maps, as we have done here. Better-quality archaeological and locational data would also make it possible to factor in variations in the frequency or intensity with which particular sub-regions or locations were used, and thus to undertake a more robust test of the complex topography hypothesis with more data points and at higher resolution (e.g., [Devès et al., 2014](#)). The prediction to be tested is that the largest sites should be associated with advantageous topographic conditions as defined here, and that areas lacking such topography should have fewer and smaller sites or none at all.

Another type of test would be to target regions with extensive areas of smooth topography and to evaluate their relative advantages for hominin occupation. Certainly, water supplies and large mammals are sometimes present in such topography, but important questions centre on security from predation and ease of access to such resources in competition with other carnivores. Also, these regions are more vulnerable to climatically induced fluctuations in available food and water, or their complete removal. All the indications are that extensive regions of smooth topography were not exploited until a very late stage in human evolution. Even so, comparative investigations of such regions using the methods

described here can reveal subtle variations in topographic conditions, which help to explain differences in the distributions of archaeological data (Holdaway et al., 2015). The changing distribution of large mammal faunal communities (e.g., Tchernov, 1992; Turner and O'Regan, 2007) offers another line of investigation to compare with our topographic mapping.

Regarding substantive issues, one problem is the discontinuities in the distribution of physical landscape features, with gaps between topographically attractive regions that appear to pose a challenge to population movement between them according to our hypothesis. These gaps occur both within Africa, particularly between East Africa and regions of complex topography in the west and northwest, and outside it. One possibility here is that the gaps are not so lacking in the necessary topographic conditions as appears to be the case from low resolution mapping, and that more detailed investigation will change the picture, revealing topographic complexity at a smaller spatial scale. Generally speaking, topographic roughness has a fractal dimension, meaning that roughness measured at larger scales should also be present at smaller scales. But this relationship does not always hold and will also depend on the mathematical treatment of slope functions, requiring closer examination of target areas at higher resolutions and more detailed investigation of the local tectonic history, ground observations of small-scale features, and dating of local landforms.

In addition, as our more detailed mapping of the southern Levant shows (Fig. 5), impediments to movement might also result not so much from absence of topography, but from excess, with steep and mountainous topography interacting with climate change to create nearly impassable physical barriers that would have severely impeded further dispersal if not wholly blocked it. As with the desert examples, interaction with climate change would have been a significant factor in accentuating or relaxing the effect of these physical barriers.

Another possibility is that the gaps between attractive regions were not easily bridged or only intermittently so. The complex topography hypothesis does not rule out the dispersal of early human populations into regions lacking the advantages of complex topography, but rather specifies that dispersal into such regions would have been more intermittent, sustaining populations at lower densities, for shorter intervals, or scarcely at all except for ephemeral passage. Where the distances involved are relatively small, this might not pose a problem to continued contact, but as they increase, so the risk of failure, local extinction and isolation would become higher. In North Africa, Arabia, and the Near East, these constraints on dispersal are typically associated with deserts or semi-arid climates, which would have varied with climate change. For example, 'green corridors' would have opened up at least intermittently across the desert regions of North Africa and Arabia (Lahr and Foley, 1998; Osborne et al., 2008; Garcea, 2012; Petraglia et al., 2012; Boivin et al., 2013; Dennell, 2013; Drake et al., 2013). These are usually discussed in relation to the dispersal of *H. sapiens* but might equally have been available to earlier *Homo* populations during periods of wetter climate. However, in the absence of topographic and tectonic factors concentrating food resources and water supplies, these regions would always have been more vulnerable to climate change, and may also have required additional social and cognitive adaptations to help to maintain social contacts over longer distances at low population densities and to track variable and unpredictable water supplies, adaptations that do not appear to have developed until the appearance of *H. sapiens* (Gamble, 1993; Balme et al., 2009; Dennell, 2013).

At higher latitudes, the limiting factor on dispersal would have been increased cold rather than increased aridity or smooth topography. If our corrections for altitude and latitude are broadly

correct (Figs. 2 and 3), they suggest that the climatically accessible regions of complex topography in Europe would have become compressed southwards and more isolated during glacial periods, or else would have required improved adaptations to cold climates. Regions of topographic complexity certainly occur at higher latitudes in many parts of central, northwestern and northern Europe, either resulting from active tectonics or from glacial activity. Although glacial landscapes are not as frequently rejuvenated as their tectonic analogues, they would have offered similar combinations of rougher and smoother terrain at the regional and local scale. Many glaciated areas are home to landforms like moraines, erratic boulders, 'u' shaped valleys with more-or-less sculpted sides, steep escarpments, and tunnel-valleys, which would have offered similar terrain to tectonically active zones. As early hominins became better adapted to living in colder climates, a process initiated by the time of *Homo heidelbergensis*, these more northerly regions would have become progressively more amenable to full colonization following the same pathways of complex topography as in more southerly latitudes.

Finally, we observe that barriers or bottlenecks in our broad-scale corridors of topographic complexity, even if they did not act as impermeable barriers to population movement and dispersal, may well have acted to restrict population contact and gene flow between the regions so separated. Here, we note that these bottlenecks, whether created by topographic factors alone, or topography interacting with climate change under extreme conditions at the margins of the *Homo* habitat, appear to have been more prevalent to the west and the north of our broad-scale map than to the east (Fig. 3). This may be why the European record of early *Homo* is so much less certain and complete than that of mainland Asia, and seemingly more prone to regional taxonomic variation in the *Homo* lineage, as witnessed in the extensive debates about the taxonomic status of the hominin finds at Dmanisi in the Caucasus or Sima del Elefante in Spain, and the validity of such European taxa as *Homo antecessor* or even *Homo neanderthalensis*. Such variation has been discussed in relation to climatic variation (notably by Dennell et al., 2011), but topographic factors interacting with climate change offer a further line of investigation. A more detailed examination of discontinuities and bottlenecks in topographic conditions, whether within Africa or beyond it, may prove fruitful in suggesting other times and places that created or accentuated genetic bottlenecks and the resulting opportunity for evolutionary change.

7. Conclusions

We have argued here that spatio-temporal variation in the physical landscapes in which hominins lived would have been a significant part of their environment and we have shown how simple techniques taking advantage of satellite data can be used to map these variables in relation to locations of fossil and archaeological evidence. An important outcome is the demonstration of how topographic and climatic variables can interact to accentuate constraints or opportunities for hominin settlement and dispersal.

The complex topography hypothesis proposes that the dynamic landscapes prevalent in many regions of Africa were a key factor in early hominin evolution, and we have expanded this hypothesis to propose a new model of the niches occupied by early *Homo* both within and beyond their original range. Dispersal, we suggest, followed broad pathways of complex topography associated with active tectonics, perhaps also in coastal regions where topography has been moulded and rejuvenated by sea level change, isostatic deformation and localized tectonics, and, in later periods, regions subjected to glaciation. All of these circumstances create the conditions of complex topography that we identify as important for early hominin settlement. Living in these environments would

allow for a compromise in our models of early *Homo* ecology, which helps to explain why members of this taxon show considerable flexibility in their tolerance for different vegetation types, habitats and climates, but also why their pattern of dispersal appears to be constrained to clearly delineated and non-random zones across continents.

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