Human dispersal across diverse environments of Asia during the Upper Pleistocene

Nicole Boivina, Dorian Q. Fuller, Robin Dennell, Robin Allaby, Michael D. Petraglia

1. Introduction

Archaeological discoveries in the Levant have long played a critical role in debates about human evolution. Situated at the western edge of the Asian landmass, the small region has, since the late 1920s, yielded key fossil finds of both Homo sapiens and Homo neanderthalensis (Shea, 2003, 2008). Interpretation of the Levantine sites has never been straightforward, however, with problems of chronology and a shared Mousterian technology, for example, generating numerous opportunities for controversy. While findings in the region were initially taken to support a gradual transition between H. neanderthalensis and H. sapiens, improved chronologies have indicated significant overlap between the two types of human, on the order of 25–50,000 years. This recognition has seen the Levantine fossil remains come to be drawn upon as a major strand of evidence in support of a replacement model for modern human origins, with the Levantine H. sapiens fossils now widely interpreted as representing a first foray of modern humans out of Africa, at a time of improved climatic conditions in Marine Isotope Stage 5 (MIS 5) (Frumkin et al., 2011). In the absence of early fossil finds further afield and in light of certain primitive morphological features, the Levantine MIS 5 exit has generally been seen as a failed dispersal (Mellars, 2006a, 2006b; Shea, 2008; Oppenheimer, 2009, 2012). This notion is offered support by recent molecular analyses of mitochondrial DNA (mtDNA), which suggest a successful expansion of H. sapiens out of Africa only at around 60 thousand years ago (ka) (e.g. Macaulay et al., 2005; see below).

The apparent agreement of archaeological and genetic findings has led to the emergence of a consensus view regarding the dispersal of modern humans out of Africa. This view holds that H. sapiens left Africa in MIS 4 or early MIS 3, and colonized Australia within perhaps as little as several thousand years by rapidly skirting the coasts of the Indian Ocean. While this may be a reasonable hypothesis, its uncritical and increasingly widespread multidisciplinary acceptance suggests the need for more careful appraisal. Here we will first examine current fossil, archaeological and genetic findings concerning the dispersal of H. sapiens from Africa, critically appraising these sources of evidence. We then consider how this evidence sits in relation to palaeoenvironmental evidence and a hypothesized dispersal of modern humans across
southern Asia. As we discuss below, a number of sites in the Arabian Peninsula and South Asia have begun to yield Middle Palaeolithic assemblages dating to MIS 5, suggesting that *H. sapiens* may have moved into these geographic zones during climatic ameliorations. The archaeological and palaeoenvironmental evidence is supported by new genetic findings that challenge the orthodox view that *H. sapiens* replaced archaic species of *Homo* in Asia. While there seems little need to invoke a multiregional model for the evolution of *H. sapiens* to explain these new genetic findings, more nuanced models of population structure and a degree of assimilation are required to explain a suite of recent autosomal and ancient DNA studies (to which we return to below). Overall, the picture of modern human origins, which seemed at one point to be crystallising into a fairly comfortable orthodoxy, is now looking decidedly more complex (Dennell and Petraglia, 2012). The time is ripe for consideration of alternatives to a straightforward MIS 4 or 3 exit of, and complete replacement by, modern humans, and in particular to examine the plausibility of earlier exits across southern Asia during MIS 5.

### 2. Absence of fossils and artefacts

Evidence for the late dispersal of modern humans out of Africa, and replacement of local archaic species of *Homo*, is by no means straightforward to interpret. Outside the sphere of molecular genetics, the story rests entirely on evidence from fossils and artefacts. Each class of evidence has its own problems, but both suffer in particular from regional biases in archaeological research. While industrialised regions with long histories of archaeological research like Europe and the Levant have seen more comprehensive study, equally if not more critical regions like the Arabian Peninsula, South Asia, East Asia and Southeast Asia have received relatively uneven coverage, and in some cases, minimal investigation.

The earliest well-dated fossils of modern humans outside of Africa, excluding the Levant, are in Laos (c. 46 ka) (Demeter et al., 2012), Sunda (c. 46 ka) (Barker et al., 2007), Australia (c. 40 ka) (Bowler et al., 2003), Sri Lanka (c. 38 ka) (Deraniyagala, 1992; Perera et al., 2011) and India (c. 20 ka) (Kennedy, 2000). In Arabia, modern human fossils have not been dated to earlier than the Holocene (Martin, 2007). Taken at face value, these dates might be interpreted to indicate a dispersal of modern humans from east to west rather than from out of Africa. The paucity of well dated fossils has not, however, prevented palaeoanthropologists from drawing meaning from the observed patterns. The earliest dated fossils from Sunda and Sahul are frequently taken to suggest not a minimal date for the exit of modern humans out of Africa, but an approximate date for Out of Africa. Since all the other dates for intervening regions in the west are younger, and thus clearly unreliable as indicators of initial dispersal, the dates from Sunda and Australia, in particular, have come to assume significance in attaching a chronology to the narrative of Out of Africa. It needs to be emphasised, however, that the earliest fossils do not necessarily date Asia’s first modern human colonization, let alone reflect a date for the exit of *H. sapiens* from Africa, contrary to some influential models that have been proposed.

Artefact assemblages also present their own challenges. Archaeological sites are subject to alterations and transformations in depositional contexts, and these play out exceptionally harshly in the hyper-arid and tropical environments that today dominate some of the most plausible out of Africa dispersal routes. Even the most well-preserved objects, stone tools, are often difficult to find in well stratified, datable contexts — the Arabian Peninsula, for example, has yielded a wealth of Palaeolithic surface finds (Petraglia and Alsharekh, 2003), but until recently, very few stratified assemblages (Groucutt and Petraglia, 2012).

Most pressing of all, however, is the problem of identifying straightforward signatures of modern human behaviour. In accordance with traditional European-derived models, the arrival of modern humans in a particular region was once seen to be traced relatively easily, through the appearance in the archaeological record of evidence for art, symbolism, and complex Upper Palaeolithic technologies, as seen in Europe around 45–40 ka. Recent years have, however, seen a thorough deconstruction of the notion of a straightforward ‘modern human revolution’. It has been recognised that so-called modern human behaviours, as traced through their apparent archaeological manifestations: 1) do not necessarily arrive as part of a package; 2) do not necessarily exhibit continuity through time; and, most significantly, 3) are not always present in modern human populations. There is nothing in terms of material culture attributes that is unique to *H. sapiens* and also universal among modern humans in Africa, Eurasia and Australasia. It is thus the case that with material culture as with fossils, absence of evidence need not necessarily indicate absence of absence.

Contrary to the notion of the sudden revolutionary appearance of a new behavioural package with the emergence of modern humans, a major synthesis of behavioural indices for Middle Stone Age Africa contradicted the gradual and non-contiguous emergence of modern traits (McBrearty and Brooks, 2000). Other parallel syntheses for South Asia (James and Petraglia, 2005) and Sahul (Brumm and Moore, 2005; O’Connell and Allen, 2007; Habgood and Franklin, 2008) have revealed a similar trend. The Australian evidence is particularly interesting in that *H. sapiens* appears to have arrived without an African ‘package’ of innovations, and to have acquired these independently and piecemeal. Examination of the South-East Asian record has also demonstrated the inadequacy of traditional markers of modern human behaviour, such as refined blade and bladelet technology, body ornamentation and mobiliary and parietal art (Barker et al., 2007; Moore and Brumm, 2007), and has focused instead on the appearance of, for example, new subsistence strategies and modes of engagement with the landscape with the arrival of *H. sapiens* (Summerhayes et al., 2010). Such studies have demonstrated the Eurocentric biases of models of behavioural modernity, which created a set of global expectations from a regional record. In reality, there is no single material trait that is inevitable in modern human assemblages.

What this means for Out of Africa models is that cognitive modernity may have emerged simultaneously or even before (Kingdon, 1993; Foley and Lahr, 1997) morphological modernity, and the appearance of traditional indicators of behavioural modernity in the archaeological record may mark demographic or social changes (Shennan, 2001; Petraglia et al., 2009; Powell et al., 2009), rather than cognitive ones. These new ideas about modern human behaviour suggest the possibility that *H. sapiens* may have been fully modern back to 200 ka or more, and exited Africa prior to the appearance of, or without bringing along, more complex technologies or archaeologically-attested symbolic practices. We cannot therefore rely on these forms of material evidence to trace dispersals any more than we can rely on fossils as indicators of the first anatomically modern humans to leave Africa. New understandings of behavioural modernity furthermore open up the possibility that the *H. sapiens* populations that exited Africa and are documented in the Levant in MIS 5 may have been fully cognitively and behaviourally modern (contra Mellars, 2006b).

### 3. Coastal route out of Africa?

Another problem with the current consensus view for Out of Africa is its increasing focus on a coastal route of dispersal. Part of the problem is that two related but separate hypotheses have
frequently been conflated. One argues that, along with a northern exit towards Europe and Siberia around 45 ka, *H. sapiens* also followed a more southerly route out of Africa at an earlier date, dispersing through southern Asia (Lahr and Foley, 1994, 1998). The other suggests that modern humans ‘coasted’ out of Africa (Stringer, 2000; Bulbeck, 2007), travelling along coastal corridors around the Indian Ocean rim to reach Australia by 45 ka. The latter idea has a long history, appearing in various manifestations since Sauer (1962) suggested the potential role of coastlines as corridors of dispersal for early humans. Subsequent discussions by Kingdon (1993), and by Field and colleagues (Field and Lahr, 2005; Field et al., 2007), explored the possibilities of a southern, coastally-focused dispersal route for modern humans out of Africa, all or part of the way along the Indian Ocean rim. The idea of a coastal route has been embraced by a number of geneticists, who have drawn upon it to explain certain patterns in the genetic record of human diversity (Macaulay et al., 2005; Thangaraj et al., 2005; Oppenheimer, 2009).

The gist of the coastal dispersal hypothesis (which should be distinguished from the more generic southern dispersal hypothesis) is that maritime environments offered particularly favourable environments for human occupation, and provided a dispersal corridor that enabled rapid movement along the coastal margin of initial colonising populations. This single dispersal event corresponded with the arid conditions of MIS 4 (Lahr and Foley, 1994; Stringer, 2000; Forster and Matsumura, 2005; Mellars, 2006a; Bulbeck, 2007; Oppenheimer, 2009), when desert dominated in northern Africa, the Arabian Peninsula, and the northwestern part of the Indian subcontinent. Such a model argues that humans were able to draw upon the rich resources of coastal environments, manifesting a maritime adaptation that led them to rapidly skirt continents (Oppenheimer, 2009), and to develop the seafaring technology that eventually enabled colonisation of Sahul (Forster and Matsumura, 2005). Research on the Red Sea coast of Eritrea and in coastal South Africa has suggested human adaptation to a coastal marine environment by MIS 5, and indicated to some that the emergence of modern human behaviour may be linked to a more intense and complex exploitation of marine resources (Deacon, 1989; Walter et al., 2000; Marean, 2010). Several recent genetic studies of mtDNA diversity, meanwhile, have suggested a single exit of modern humans out of Africa, as well as a rapid dispersal to Australia (Forster, 2004; Forster and Matsumura, 2005; Macaulay et al., 2005; Oppenheimer, 2009). These features have been seen as consonant with a coastal route, both because coasts are increasingly viewed as a kind of ‘highway’, enabling rapid dispersal, but also because desert expansion in many inland regions during the relevant time period would have created barriers to dispersal, forcing populations to move along coasts.

Despite the popularity of the coastal dispersal hypothesis, there are numerous reasons why the idea should be approached with a greater degree of caution. One is that archaeological evidence indicative of a maritime adaptation in early humans is extremely limited. At present, relatively secure evidence for use of marine resources by early *H. sapiens* appears in South Africa (Marean, 2010). Shell beads found in North Africa (d’Errico et al., 2009) indicate visitation to the coast and not coastal adaptation necessarily. The claim for an association between marine resources and archaeological sites in Eritrea (Walter et al., 2000) also include lag deposits and natural death assemblages (Bruggemann et al., 2004), which do not necessarily demonstrate human subsistence activities (Bailey, 2009). Even if we accept that a maritime adaptation is plausible, however, problems remain with the model. Bailey (2009) has noted the implausibility of the idea that the emergence of modern human cognition ushered in a sudden awareness of the richness of coastal resources, whose consumption was subsequently of an intensity sufficient to lead to local over-exploitation and to ultimately spur dispersal. Not only is exploitation of marine resources sufficiently simple to have been competently undertaken by archaic humans (Cortés-Sánchez et al., 2011) and even non-human primates (Malavijitnond et al., 2007), the probability that humans were at this early stage marine specialists is, based on ethnographic and archaeological parallels, extremely low (Bailey, 2009). The many inland Upper Pleistocene sites in Arabia, South Asia, East Asia and Southeast Asia argue much more for a more flexible subsistence approach in which terrestrial plant and animal resources continued to play a major role in human lifestyles. Even early modern human sites that are described as ‘coastal’ may furthermore demonstrate a terrestrial focus. Despite being one of the Upper Pleistocene human occupation sites closest to the coast, for example, Niah Cave in Borneo possesses a faunal assemblage dominated by terrestrial and freshwater taxa, and lacks evidence for the use of marine resources (Barker et al., 2007). Coastal sites may indeed be lacking from the record due to submergence along shallow continental shelves in many areas, although surveys in areas with tectonically raised reef formations and former shorelines have not produced evidence for marine-oriented archaeological sites either (Korisettar, 2007; Bailey, 2009). Even if we grant that most sites are submerged, the presence of many inland sites stresses the importance of terrestrial foraging adaptations over the marine specialization that is implicit in coastal dispersal models, particularly those that imply a rapid dispersal where repeated overexploitation of resources led to movements further down the coast.

Equally problematic is the idea that coasts were particularly rich and attractive environments for early humans. While certain coastal environments are favourable habitats, other coastal areas are effectively ‘deserts’ lacking entirely in critical freshwater resources. The notion of a ‘coastal oasis’ — the idea that freshwater springs appeared on emerged continental shelves at times of low sea level (Faure et al., 2002) — is central, often implicitly, to most models of coastal dispersal, yet lacks empirical support (Bailey, 2009). Even if valid, the coastal oasis model does not postulate the kind of uniformly equable coastline that such a dispersal necessitates (Sauer, 1962; Stringer, 2000). Instead, it suggests the probability of rather dispersed and non-interconnected wetland environments in places where underground springs exist. There are also many coastal regions wholly devoid of shellfish or any obvious marine sources that could be easily gathered or otherwise obtained. Furthermore, the idea that coasts were, in contrast to inland areas, particularly stable environments is open to question. Westley and Dix (2006) summarise evidence for coastal instability during the Upper Pleistocene, and emphasise that present day coastlines, and our ideas about coasts, are the product of relatively unique environmental circumstances during the exceptionally stable Holocene interglacial.

In sum, while coastal regions may have been used as dispersal routes in prehistory, both for *H. sapiens* and earlier hominid exits out of Africa, the notion of a coastal superhighway between Africa and Australia that enabled unexpectedly fast dispersal is simplistic and derives little if any support from empirical data. While probably a key necessary corollary of the currently popular notions of an MIS 4 exit for Out of Africa, and a rapid dispersal to Australia, it may be argued that the coastal dispersal model has a number of significant deficits and unproven assumptions.

4. The genetics of Out of Africa

If fossil and archaeological evidence offer little support for a rapid coastal dispersal of *H. sapiens* out of Africa at c. 60 ka, genetic data is equally problematic. While a consensus date of c. 60 ka
is often cited for the mtDNA data, recent literature actually offers a range of dates for human expansion out of Africa, anywhere between 85 and 45 ka (Oppenheimer, 2003, 2009, 2012; Macaulay et al., 2005; Kivisild et al., 2006; Cabrera et al., 2009; Endicott et al., 2009; Soares et al., 2009; Rasmussen et al., 2011). Variation is due, in part, to the values used to calibrate the mtDNA clock (e.g., Scally and Durbin, 2012). The problems associated with calibrating the mtDNA clock have been noted, including in particular the reliance on problematic assumptions about the timing of the divergence between humans and chimpanzees, as well as the constancy of the molecular clock (Ho and Larson, 2006; Endicott et al., 2009). Further research is required to improve confidence in molecular estimates of human evolutionary timescales.

Another under-appreciated issue is the anomalous nature of the genetic evidence for a rapid spread of modern humans from Africa to Asia. Echoing the fossil date anomaly, the mtDNA branch lengths for sampled populations are longest for those which are farthest east, in Near Oceania, and shortest in the Asian areas that would have been encountered first (Merriwether et al., 2005; Oppenheimer, 2009). The real problem, however, is that the variation in branch lengths suggests that a single genotype engaged in the expansion actually existed for 30 ka, which does not support a rapid expansion that was anomalously explained without it being an ‘M buffer’ effect (see Supplementary material A) which implies that the branch ages we observe are considerable underestimates of the time of arrival of the genotype to these areas. Such anomalously long-lived genotypes have been directly observed through ancient DNA in species such as the Iberian lynx (Rodríguez et al., 2011).

Much more problematic, however, is the challenge posed by new genomic studies that offer perspectives on evolutionary history that sometimes contrast markedly with those of mitochondrial and Y-chromosome-based investigations. Recent analysis of the frequency of alleles of SNPs (single nucleotide polymorphisms) from the International HAPMAP Project, for example, suggests that the out of Africa expansion may actually need to be modeled as two or more bottlenecks, rather than the single bottleneck suggested by the mtDNA clock (Ho and Larson, 2006; Endicott et al., 2009). The authors or more bottlenecks, rather than the single bottleneck suggested by the out of Africa expansion may actually need to be modeled as two or more bottlenecks, rather than the single bottleneck suggested by the mtDNA clock (Ho and Larson, 2006; Endicott et al., 2009). Further research is required to improve confidence in molecular estimates of human evolutionary timescales.

Archaic admixture in the modern human genome in Eurasia is now clear. While studies of mtDNA (Richards et al., 1996; Kriens et al., 1997; Handt et al., 1998; Serre et al., 2004; Green et al., 2008) and the Y-chromosome (Jobling and Tyler-Smith, 2003) have not indicated admixture, for example, it was widely recognized that autosomal DNA might tell a different story. Indeed this has proven to be the case, with evidence of archaic ancestry surfacing for the microcephalin gene (Evans et al., 2006), the tau (MAPT) locus (Hardy et al., 2005), the β-globin gene (Harding et al., 1997), the hematopoietic stem cell marker CD34 and CD133 (Barreiro et al., 2005), the dystrophin gene (Labuda et al., 2000) and others (Wall et al., 2009). Direct contact between archaic and modern humans is also supported by autosomal data for modern human head lice, Pediculus humanus (Reed et al., 2004). More recently, a draft sequence of the Neanderthal genome has been published that indicates gene flow from Neanderthals into the ancestors of non-Africans (Green et al., 2010). The study also demonstrated that Neanderthals shared more genetic variants with present-day humans in Eurasia than with present-day humans in sub-Saharan Africa, suggesting that the gene flow occurred before the divergence of Eurasian groups from one another. The main known region in which H. sapiens and H. neanderthalensis co-existed prior to the separation of European and Asian lineages of human is the Levant (but see Shea, 2008). Given that the overlap between these species in the Levant may have lasted only until c. 75 ka, this might be seen as supporting an exit in MIS 5. However, as our distribution map for Neanderthals (Fig. 1; Supplementary material B) suggests, a broad swath of western and central Eurasia may have been home to Neanderthals from MIS 5 until MIS 3, suggesting a range of possible regions of co-occupation. Subsequent regionally specific admixture is suggested by the presence of ancient alleles that are found only or predominantly in certain regions — for example, certain Europe-localised alleles for microcephalin in Europe (Evans et al., 2006), and Asia-localised alleles for β-globin dating to >200 ka (Harding et al., 1997) — and by the presence of basal clades composed entirely of Asian sequences, as for the RRM2P4 region (Cox et al., 2008). The Neanderthal findings were soon accompanied by a second hominin draft genome, that of the Denisovans of Siberia (Krause et al., 2010; Meyer et al., 2012). The finding of gene flow from Denisovans into some modern human populations of Melanesia suggest that admixture occurred after the dispersal of H. sapiens into Asia, and probably somewhere in South or Southeast Asia (Stewart and Stringer, 2012).

Recent revision of the human genomic mutation rate provides another line of nuclear DNA evidence that problematizes mtDNA-based Out of Africa estimates, while at the same time offering a chronology that supports evidence for modern human and archaic admixture. Direct measurements of the nuclear genomic mutation rate in contemporary humans using next generation sequencing technology have indicated a value that is approximately half of that previously estimated from fossil calibration (Scally and Durbin, 2012). When applied to the analysis of the time of...
separation of African and non-African populations, the revised rate yields an Out of Africa chronology in the range of 130–90 ka, suggesting that the Levantine MIS 5 artefactual evidence represents either permanent or repeated temporary occupation by modern humans (Scally and Durbin, 2012: 748). Younger estimates of Out of Africa on the basis of mtDNA data may, it is argued, derive from processes of later gene flow and drift/selection and/or complex demographic factors including bottlenecks (Scally and Durbin, 2012: 751).

5. Evaluating Out of Africa

The earliest fossils of H. sapiens are identified in East Africa at c. 195–160 ka (White et al., 2003; McDougall et al., 2005), though craniometric studies of African forms described as our species show considerable phenotypic diversity (Gunz et al., 2009). Fossil evidence thus suggests that the emergence of H. sapiens occurred towards the end of MIS 7, just prior to the onset of the colder and drier conditions of MIS 6. The return to these conditions led to an expansion of deserts, likely creating barriers to dispersal out of Africa of this new species. If speciation estimates are correct, this therefore means that other than a brief window at the end of MIS 7, there may have been no real opportunity for modern humans to leave Africa until MIS 5 (though see below; Dennell, 2009: 469). At this time, territorial ranges in Africa appear to have expanded in association with environmental amelioration, and Middle Stone Age sites seem to be relatively abundant and well distributed in East Africa (Basell, 2008) and the Saharan belt in MIS 5 (Smith et al., 2007; Hill, 2009), providing the basis for a dispersal both within and out of Africa (Osborne et al., 2008; Drake et al., 2011). As indicated, it is indeed in MIS 5 that we find the first evidence for anatomically modern humans outside of Africa. Fossil evidence at Skhul and Qafzeh indicates their presence in the Levant from perhaps as early as 130–120 ka (Grun et al., 2005; Shea, 2008), i.e., the early part of MIS 5 (5e).

The implications of the Levantine evidence are hotly debated. On the one hand, certain researchers describe the Levantine occupation by H. sapiens in MIS 5 as localized and temporary, and argue that these humans were not entirely cognitively modern. Though citing occupation dates that span approximately 40–20,000 years, Mellars (2006b) describes the Levantine occupation as a ‘short-lived event’. The Levantine Mousterian, often characterized by centripetal Levallois reduction methods and a variety of tools (e.g. points, scrapers, notches, burins), is viewed as archaic technology, and inadequate to the task of adaptive competition with Neanderthals, who are perceived to have replaced modern humans in this region (Shea, 2003, 2008; Mellars, 2006b). Others, however, note the likelihood that Neanderthals and modern humans overlapped for a significant time period in MIS 5 in the Levant, and argue for elements of modern human behavior in spite of the apparently ‘limited’ technology (Grun et al., 2005). The recent Neanderthal genome findings (Green et al., 2010) may support the notion of an overlap. Furthermore, the suggestion that use of Middle Palaeolithic technologies reflects a less competitive H. sapiens, which had to await full cognitive modernity and the related development of prismatic blades and more advanced projectile weaponry to outcompete Neanderthals, would seem to reflect a traditional bias in the interpretation of the material record. The variable appearance of advanced lithic technologies among Asian populations of H. sapiens indicates the strong likelihood that
stone tool technologies rather reflect particular adaptive responses to environmental circumstances and demographic parameters. The shift to Early Upper Palaeolithic technology in the Levant appears to have been associated with a reduction in prey size (Shea, 2008), suggesting that either demographic pressure (Stiner et al., 1999, 2000) or environmental change, rather than cognitive development, drove the appearance of new technologies. A demographic argument has recently been put forward for the appearance of Upper Palaeolithic technology and other elements of material culture in western Eurasia, in this case based around the idea that population needs to be of a certain density to retain cultural innovations (Powell et al., 2009). Available evidence suggests that parallels to Upper Palaeolithic technology do not emerge in South Asia until c. 35 ka, which is much too late to reflect an initial expansion of modern humans, and here as well, demographic arguments have been forwarded for the appearance of more advanced technologies (Petraglia et al., 2009).

The first out of Africa exit by H. sapiens is seen as part of a limited range expansion of North African human and faunal populations (Thernov, 1952; Lahr and Foley, 1994; Rabinovich and Thernov, 1995; Thernov, 1996). Mellars (2006b) and other scholars assume that this is a localized human expansion based on the absence of similar fossils further afield. Yet, as discussed earlier, the fossil record is clearly biased; the absence of modern human fossils in Arabia for MIS 5 is meaningless given that fossils of Homo do not appear in the regional record until the Holocene. Meanwhile, a recent multivariate analysis of cranial morphometric data suggests affinity between early modern humans from the Levant and terminal Pleistocene/early Holocene human populations from Australasia that is potentially reflective of a successful MIS 5 exit (Schillaci, 2008). From a palaeoenvironmental perspective, it is difficult to identify factors that might have prevented dispersals further afield. Dispersal barriers both into and within the Arabian Peninsula are at a minimum during MIS 5, especially in MIS 5e and MIS 5a, when humidity and rainfall were higher (Vaks et al., 2007; Fleitmann and Matter, 2009; Preusser, 2009) and when terrestrial environments are marked by lakes and river systems (Parker, 2009; Petit-Maire et al., 2010; Rosenberg et al., 2011). Genetic (mtDNA) data suggest that the dispersal from Africa to Arabia of at least one other primate, the Hamadryas baboon, in MIS 5 (Fernandez, 2009), though we would approach this chronology with caution in light of calibration and other issues. Glacial/stadial episodes, like MIS 4 and most of MIS 6, would have been characterized by reduced monsoon rainfall and greatly expanded deserts (the Sahara, Arabia and Thar deserts), with the desert barriers much more extensive and uninviting than those of the present day. By contrast the interstadials, especially the more pronounced upswings of MIS 5e and MIS 5a would have seen reduced deserts, which would furthermore have been significantly impinged upon by richer vegetation zones.

6. Modeling environments and movements

Despite the popularity in recent years of an Out of Africa model featuring a single exit, a date of c. 60 ka for a rapid dispersal, and the complete replacement of archaic species, it is clear that this model is in need of revision given new datasets from genetics, archaeology, and palaeoanthropology. This parallels conceptual developments in domestication studies, where genetics and archaeology initially supported a rapid, localized model for agricultural origins, but gradually came to recognise more complex and protracted processes involving multiple domestication events for many crops (Brown et al., 2009). Ancient DNA studies, both of domesticated plants and animals, and humans, have also begun to reveal the importance of recent demographic processes, and their ability to mask earlier genetic patterns (Haak et al., 2005; Larson et al., 2007, 2010; Ozkan et al., 2010). So it is not necessarily surprising to find that as further research is conducted, the picture of Out of Africa has become more complex. Continued research supports an origin of modern humans in Africa, and both expansion out of Africa and replacement of local populations. However, the apparent simplicity of this model is tempered by plausible evidence for a structured African population, multiple exits, archaic admixture and the existence of an increasing number of late archaic survivals in Asia. These considerations, together with data suggesting that archaeological sites in southern Asia correspond with modern humans extending back earlier than appreciated, suggest the need to explore other models for Out of Africa. Below we present arguments for an earlier and more complex dispersal pattern for modern humans, drawing in particular on relevant palaeoclimatic, vegetation, faunal and genetic data and a set of maps that reconstruct vegetation patterns across Eurasia in MIS 4 and MIS 5 (see Figs. 2–5, Table 1, Supplementary material).

Table 1

<table>
<thead>
<tr>
<th>Vegetation zone</th>
<th>Resource expectations</th>
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<tbody>
<tr>
<td>1. Mediterranean vegetation.</td>
<td>Abundant fruits and nuts, seeds, including wild almonds, acorns, Pistacia.</td>
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<tr>
<td>2. Mediterranean steppe-steppe, the classic ‘Fertile Crescent’ vegetation</td>
<td>Many edible grain resources, some nuts and fruits as above. Large herbivore herds.</td>
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<tr>
<td>3. The dry steppe of the Middle East and southern Central Asia.</td>
<td>Some edible seeds, but generally lower value and higher effort than above, and some tubers. Herbivore herds smaller than above.</td>
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<tr>
<td>4. Desert</td>
<td>Minimal edible plant and animal resources. No/low human populations expected.</td>
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<tr>
<td>5. Sub-Desert-Sahel vegetation, generally of the Sudano-Sindhan floristic province</td>
<td>Small seeded grasses and forbs occur, while seeds and fruit of many trees and shrubs are available. Herd of herbivores occur but these are often of smaller herd size and/or body size than for zones 2 or 7.</td>
</tr>
<tr>
<td>6. Riverine corridors: marshes and gallery forests.</td>
<td>Wild grains of grasses, sedges, and other aquatics as well as tubers are frequent. Small game, birds and fish are readily available, with some larger game, especially in dry season.</td>
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<tr>
<td>7. Tropical savannah/woodland-grass mosaic, including the tropical evergreen zones of India.</td>
<td>Wild grass grains and other seeds are numerous, including wild progenitors of most tropical cereals; some tubers are available and numerous edible seasonal fruits. Large herbivore herds. Numerous fruits, nuts and tubers.</td>
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<tr>
<td>8. Dry tropical woodland, including dry deciduous zones of India.</td>
<td>Edible seeds of herbaceous plants include wild pulses. Large herbivores are frequent but in small groups. Smaller game present but may be hard to catch.</td>
</tr>
<tr>
<td>9. Moist tropical woodland and grassland mosaic, in particular that of eastern India and Ganges plain in which Dipterocarpaceae including Shorea are frequent; this zone extends to Southeast Asia.</td>
<td>Wild grass grains and other seeds are numerous, including seasonal wild rice in local wetland; some tubers are available and numerous edible seasonal fruits. Large herbivore herds. Smaller game present but may be hard to catch.</td>
</tr>
<tr>
<td>10. Moist tropical woodlands, including both moist deciduous zones like those in India and true tropical rainforests.</td>
<td>Wild seeds are sparse in time and space; tree-nuts and fruits may be locally and seasonally abundant but are likely to be unpredictable in time and space. Larger game is rare and smaller game is harder to catch. Very low human population densities expected.</td>
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Vegetation reconstructions have been made at the macro-scale, based on examining broad patterns of modern vegetation maps and relating these to available paleobotanical and palaeoclimatic evidence sources. Synoptic vegetation descriptions, even in the modern day, are idealized simplifications, although of heuristic value in recognizing that vegetation structure and composition are strongly associated with climatic parameters of temperature and rainfall (Huggett, 1995). Climatic parameters are regionally and locally affected by topography and geographical coordinates, as detailed maps of modern vegetation make clear (e.g., Wang, 1961; Meher-Homji, 2001). Despite this, many quantitative models of past vegetation essentially flatten the earth and focus on temperature and rainfall in relation to latitude and longitude (e.g., Adams and Faure, 1997; Prentice et al., 2000). For such quantitative models, the diversity of vegetation zones is greatly simplified even for modern baseline maps. We have avoided this here through a less quantitative, if admittedly more subjective approach, drawing vegetation maps that take into account regional and topographic variations evidenced in modern maps. In addition, we have taken into account modern disjunct distributions of species or sister species, since such disjunction imply past periods of more or less continuous distributions between two regions, such as between northeast of India and Sri Lanka or the savannas of Africa and India (Asouti and Fuller, 2008:72–73). Such disjunctions have long been recognized in plant geography classifications, such as the “Nubo-Sindian” and the “Eritreo-Arabian” floristic territories (e.g., Zohary, 1973) or recognition of the “Indo-African element” in the flora of India (e.g., Legris, 1963; Awasthi, 1995). The maps provided here must therefore be regarded as initial hypotheses that require systematic testing, through both more palaeoenvironmental proxy records and quantitative modeling. To our knowledge, such reconstructions have not been previously attempted for these periods and geographical scales.

6.1. Taking steps eastwards

Entry into the Arabian Peninsula from Africa was possible by two main routes (see Fig. 2). The Sahelian vegetation of grasses and shrubs would have extended far northwards into the Sahara and across much of Arabia. Such environments can be expected to have extended across the regions bordering the Red Sea, from Sudan’s Jebel Elba through Egypt’s Jebel Abu Harba to the higher ground in the Sinai, providing both a corridor into the Mediterranean environments of the Levant and a potential land route around the Red Sea (see also Fig. 3 in Petraglia et al., 2010). A Bab el Mandab route at

<table>
<thead>
<tr>
<th>Vegetation zone</th>
<th>Resource expectations</th>
</tr>
</thead>
<tbody>
<tr>
<td>11. Tropical montane vegetation.</td>
<td>Some edible fruits, seeds and tubers, but generally only localized and seasonal. Few large game, and hard to catch small game. Low human population densities expected.</td>
</tr>
<tr>
<td>12. Warm temperate hill and sub-montane vegetation, including the vegetation of the Himalaya foothills, and the evergreen broadleaf forests of southern China.</td>
<td>Many seasonal edible fruits and nuts, including acorns. Tubers occur and some edible grains and seeds. Large herbivores are frequent but in small groups; smaller game present but may be hard to catch. Few seasonal nuts and fruits. Minimal seed or tuber resources. Sparse smaller game. Low human population density expected.</td>
</tr>
<tr>
<td>13. High elevation coniferous forests and desert/the Tibetan plateau.</td>
<td>Many seasonal edible fruits and nuts, including acorns. Some edible seeds, but tubers rarer than in zone 12. Large herbivores are frequent but in small groups; smaller game present but may be hard to catch.</td>
</tr>
<tr>
<td>14. Mixed evergreen-deciduous (mesophytic) forests.</td>
<td>Seasonal edible fruits and nuts, but fewer than in zone 14, and with higher toxicity. Edible seeds, seasonal and localized. Large herbivores frequent, as well as well to catch small game.</td>
</tr>
<tr>
<td>15. Mixed conifer and temperate deciduous</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 2. Vegetation reconstruction for western Eurasia in MIS 5. See Table 1 for details of vegetation zones. Labelled sites are: (A) Qafzeh; (B) Es-Skhu; (C) Jubbah Palaeolake; (D) Shi’bat Dibya 1 (MIS 3); (E) Jebel Faya; (F) Aybut; (G) 16R Dune; (H) Jwalapuram; (I) Site 50.
the southern end of the Red Sea was possible, with parallel vegetation zones existing on either side of this strait. Palaeoshoreline reconstructions over the past 150 ka indicate that there were a number of periods when short sea crossings (ranging from <5 km to <15 km) across the Red Sea were possible, thus suggesting there is no reason to invoke seaworthy boats or seafaring technology and skills (Lambeck et al., 2012). Moreover, potential short sea crossings correspond with favourable environmental conditions on the Arabian Peninsula, such as at the transition between MIS 6 and 5e (e.g., Armitage et al., 2011). Once outside Africa, movement beyond the Levant or southern Arabian Peninsula was likely to have been relatively straightforward in MIS 5. The disjunct distribution of a number of tree and shrub species including many food species that humans might have relied upon across Africa, the Yemeni

![Diagram of vegetation reconstruction for eastern Eurasia in MIS 5. See Table 1 for details of vegetation zones.](image)

![Diagram of vegetation reconstruction for western Eurasia in MIS 4. See Table 1 for details of vegetation zones. Site labels are as for Fig. 2.](image)

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highlands and South Asia suggests the likelihood that their ranges have contracted and that they would have occurred in much more frequent patches in MIS 5. This would have included taxa with edible fruits, such as drumstick trees (*Moringa* spp.), desert dates (*Balanites aegyptiaca*), sebesten plums (*Cordia* spp.), karira (*Capparis decidua*), and tamarind (*Tamarindus indica*) (see Asouti and Fuller, 2008). In addition, a similar range of edible wild millet-grasses, wild legumes and, on forest margins, yams (especially *Dioscorea bulbifera*) and other tubers (e.g., *Arisaema* spp.) are shared across such distributions. Attractive fauna for hunting, such as gazelles and ostriches, would also have occurred through these savannah-Sahelian corridors. Thus humans adapted to the northern savannah woodlands and the Sahel in Africa would have been able to expand through familiar environments out of Africa and across Arabia to the similar environments that framed a reduced Thar Desert. Riverine systems would furthermore have flowed east across much of Arabia, providing additional dispersal corridors (Edgell, 2006; Petraglia, 2007, 2011; Petraglia et al., 2012a). Lakes and rivers in such humid stages as MIS 5 were present in areas now characterized as desert in Arabia (Parker, 2009; Petit-Maire et al., 2010; Rosenberg et al., 2011) and India (Achuthan et al., 2007).

Archaeologically, such MIS 5 dispersal routes are not yet clearly supported by artefactual evidence. Though Middle Palaeolithic sites are abundant in Arabia, the majority have been identified from surface contexts and remain undated (Petraglia and Alsharekh, 2003; Groucutt and Petraglia, 2012). New information from stratified archaeological sites, however, is beginning to emerge. Jebel Faya rockshelter, situated about 55 km from the Persian Gulf, has been dated to c. 125 ka (MIS 5c) (Armitage et al., 2011). The recovery of cordiform handaxes, foliates, Levallois and discoidal cores and retouched tools is argued to be reminiscent of East African industries, implying the early movement of *H. sapiens* into Arabia. The most convincing case for a movement from Africa comes with the recovery of abundant ‘Nubian’ sites situated along riverine drainages in the Dhofar region of Oman (Rose et al., 2011). Here, a Nubian assemblage was dated to 106 ka (MIS 5c), suggesting connection with *H. sapiens* in northeast Africa. Middle Palaeolithic industries situated in northern Arabia, on the shores of the Jubbah Palaeolake, date to MIS 5 and MIS 7 (Petraglia et al., 2011, 2012a). The Jubbah Palaeolake occurs in the Nefud Desert (Fig. 2), indicating that hominins penetrated this marginal environment in an ameliorated period, where phytolith studies have demonstrated the presence of a grassland with some trees.

The existence of two potential routes from Africa to Arabia, and the presence of several main dispersal corridors through the Arabian Peninsula, suggest the possibility for multiple exits and more complex dispersal scenarios. Favourable conditions in the Arabian Peninsula, especially in the north, may have increased the range overlap between Neanderthal and modern human populations, presenting opportunities for interbreeding (Fig. 1). The potential range of Neanderthals in MIS 5 likely extended well into present-day Iran, Afghanistan and Pakistan, and possibly south into the Arabian Peninsula as well (Supplementary material B).

In contrast, MIS 4 saw widespread expansion of the desert in northern Africa and the Arabian Peninsula (Fig. 3). This would have impeded exit out of Africa other than via the Bab el Mandab, where coastal environments of unknown but potentially quite variable quality would have been encountered. Attractive grassland environments would have been located considerably inland from the coasts, and probably at high elevations, such as in the Yemeni highlands and the hills of southwest and eastern Oman peninsula. Relict populations appear to be present at Jebel Faya and Shi’bat Dihya across MIS 4 and extending into MIS 3, in both the Persian Gulf region and in the Yemeni uplands (Armitage et al., 2011; Delagnes et al., 2012). Pollen data furthermore suggest that in drier periods like MIS 4, there was a reduction in the mangrove environments that often support rich coastal resources. Thus, although the lowered sea levels of MIS 4 would have made crossing the Bab el Mandab (and Arabian/Persian Gulf) easier, the coastal deserts on either side are likely to have presented few attractions to hunter–gatherers. This is not to say that exit was not possible out of Africa in MIS 4 (see Field and Lahr, 2005; Field et al., 2007), only that it...
seems far less likely, and dependent on a number of coastal environmental parameters whose existence is debatable.

6.2. Passage to India

Subsequent to dispersal out of Africa and across Arabia, palaeoenvironmental data suggest a number of potential routes that H. sapiens may have followed into the Indian subcontinent (Fig. 2). These can be simplified into three broad routes, recognizing that both hybrid and multiple routes are also possible and indeed likely. Perhaps the most feasible route is the Sahel (marked as 5 on Fig. 2) vegetation corridor, a route through environments that would have featured many seasonal seed foods and recurrent medium-sized game like gazelle and ostrich. The many disjoint tree species between the dry tropical woodlands of India and Africa imply that these vegetation zones were connected through intervening Arabia in wetter periods in the past. These disjuncts include important food sources that could have contributed to subsistence (e.g., desert dates: Balanites, drumstick trees: Moringa, tamarind: Tamarindus).

The Sahel corridor route may have necessitated a sea crossing at the Strait of Hormuz to present-day southern Iran, although a route across or around the Persian Gulf is also feasible (Rose, 2010). A second possibility is that there was an expansion of H. sapiens from the Levant, via the Tigris/Euphrates riverine corridor that would eventually become a major trade conduit in the region. Such riverine corridors are always rich in small game, seeds foods and tubers, although they might require rather different adaptations than the Sahelian corridor. A third, perhaps less likely route is via the Indoranian plateau. This would have necessitated following the Mediterranean park-steppe (classic Fertile Crescent vegetation) into the Zagros Mountains (see Nasab et al., in press). This vegetation possibly extended across parts of the Iranian plateau or down to coast, then onto India. This is perhaps the least likely route for various reasons involving: 1) topographic complexity; 2) the need to adapt to significantly different environments and novel flora; and 3) the high potential that Neanderthals dominated this region (see Fig. 1, Supplementary material B). The range overlap with Neanderthals is potentially important in light of the evidence for Neanderthal gene flow into H. sapiens. Both of the latter two routes, and possibly also the first, would likely have entailed ecological overlap with Neanderthals. So it is possible that regions east and perhaps even south of the Levant would have provided opportunities for admixture between modern humans and Neanderthals.

With a greatly reduced Thar Desert throughout MIS 5, entering the Indian subcontinent would have been relatively straightforward compared to an entry in MIS 4 (Petraglia et al., 2012b). The Sahel corridor that originated in North Africa and extended along the southern Arabian Peninsula, subsequently skirting the Iranian and Makran coasts, also likely framed a reduced Thar desert, interfacing into the lusher savanna woodlands of the Deccan plateau. This Sahel corridor thus provides a key potential and previously unrecognized dispersal route between Africa and South Asia. The Thar Desert itself need not necessarily have been a barrier in MIS 5; palaeoenvironmental evidence from the desert in MIS 5 indicates a high percentage of C4 plants, increased summer rains and a strong monsoon (Achuthyan et al., 2007). And, indeed, the region can be expected to have had numerous rivers, and perhaps playa lakes at this time. Based on Early Holocene parallels, we expect that while many playas were quite saline, a few lakes would have been freshwater recharged by subsurface drainage to the east that was increased under stronger monsoons.

Is there fossil or archaeological evidence to support the presence of modern humans in South Asia in MIS 5? As indicated, fossils are lacking and skeletal remains of modern humans for India and Sri Lanka are relatively young, and almost certainly tell us nothing about the date of arrival of H. sapiens to the subcontinent. Archaeological evidence is more suggestive, particularly in light of recent findings. The recovery of numerous Middle Palaeolithic sites in many basins of peninsular India, together with stratified occurrences post-dating Late Acheulean assemblages (Misra, 2001), indicate that hominins were present in the region for a considerable period of time. Archaeological excavations at Jwalapuram, in the Jurreru Valley of southern India demonstrate that Middle Palaeolithic hominins were present by c. 78 ka (Petraglia et al., 2007, 2012c). Analysis of cores from the Jwalapuram localities indicates affinities with sub-Saharan African MSA assemblages produced by H. sapiens (Clarkson et al., 2012). The morphology and technology of the Jwalapuram cores may be distinguished from technologies manufactured by Neanderthals in Southwest Asia and Europe. Though the technology remains poorly described, the potential presence of Middle Palaeolithic assemblages dated 130–109 ka in the 16R Dune in the Thar Desert (Achuthyan et al., 2007; Singhvi et al., 2010) and c. 125–75 ka in the Iranamadu Formation of Sri Lanka (Deraniyagala, 1992; Abeyratne, 1996) also suggest MIS 5 occupations that may represent H. sapiens, although of course an archaic species cannot be ruled out (Petraglia et al., 2010). While lithic technology does not provide a straightforward or definitive signature of modern human presence, in this case it does appear to necessitate that we consider the possibility that H. sapiens was present in South Asia by MIS 5a, if not earlier.

Palaeoenvironmentally, India appears to have been amenable to human habitation in MIS 5 and into MIS 4 (Fig. 2). India had favourable environments, such as broad areas of savannah (7) and dry tropical woodlands (8), along with moist tropical woodland and grassland mosaic (9) vegetation in the Ganges region. All of these environments support a diversity of bovids and cervids, larger herbivores (e.g., elephant, rhino), and numerous food plants. They may also be regarded as quite well-buffered, in the sense that climatic oscillations would have opened woodlands and shifted but not removed resources. While climatic fluctuation might have extirpated local populations across much of more marginal environments like Arabia, populations in India may have been able to persist through such oscillations. The inherent ‘habitability’ of India, combined with a possible long-term modern human presence in the region, may go some way towards explaining the evidence for higher-long term population size in India than in neighbouring regions (Atkinson et al., 2008; Petraglia et al., 2009).

If there was indeed an entry of H. sapiens into India in MIS 5, it is possible, indeed probable, that modern humans encountered archaic species in the region. A cranial fossil find from the Narmada River valley supports the presence of an archaic human species (initially identified as Homo erectus or Homo heidelbergensis, now viewed as an indeterminate species of Homo) in the region sometime in MIS 6 or 5 (Athreya, 2007; Patnaik et al., 2009). Acheulean sites are certainly present in the early to middle stages of the Middle Pleistocene, indicating the long-term presence in the region of one or more archaic species (Petraglia, 2010). Recent dating of Late Acheulean sites to c. 140–130 ka in the Son valley of northern India (Haslam et al., 2011) demonstrates that at least one archaic species of Homo continued to inhabit India at the MIS 6/5 transition. The coincidence with the earliest potential dates for Middle Palaeolithic sites in the Thar Desert at 130–109 ka is obviously suggestive of an early human presence. It is possible that new competition from recently arrived anatomically modern humans led or contributed to archaic extinctions at this time. Admixture with H. sapiens prior to the extinction of archaic hominins cannot be ruled out.

6.3. Expansion into East and Southeast Asia

In many ways, the Indian subcontinent demonstrates significant ecological similarity in comparison with the environments of...
Africa. India is dominated by savannah and Sahel type vegetation, as well as vegetation zones whose differences from these are not radical, and similar food resources are attested to by disjunct taxa. The region just east of India, however, features significantly different environments that may have posed new challenges to dispersing humans (Fig. 4). The northeast Indian region of Assam and adjacent areas are characterized by high hills with dense tropical forests, and seasonally flooded and swampy river valleys. Tropical rainforests generally support low human population densities (cf. *Bailey and Headland*, 1991) and necessitate specific rainforest adaptations (e.g., techniques for hunting hard to catch arboreal game such as monkey, see *Piper et al.*, 2008; *Perera et al.*, 2011). Swamps may have supported lower populations due to higher disease loads (cf. *Sattenspiel*, 2000), and if not true barriers would nonetheless have reduced local populations. The impression of a major barrier between the regions of India and Indochina is reinforced by biogeographical and genetic studies suggesting that a wide range of animals are differentiated or speciated across this region. A number of species have their range limits at the Brahmaputra River, including various species of mongoose (*Herpestes edwardsii*, and the crab-eating mongoose, *Herpestes urva*), the small-toothed palm civet, the large Indian civet, the hog-badger, the Bengal fox, the Asian elephant, the pygmy hog, the Inpichad (or wild pig), the jungle cat (*Felis chaus*), the golden langur, the hoolock gibbon, and the stump-tailed macaque (e.g., *Corbet and Hill*, 1992; *Vidya et al.*, 2005; *Veron et al.*, 2007). The Brahmaputra also corresponds to four bird sister-species pairs boundaries (*Ripley and Beehler*, 1990). The Brahmaputra itself, however, is probably less as a physical barrier to gene flow than a marker between two significantly distinct ecozones that are the true barriers to genetic exchange (*Tosi*, 2007). Other species differences correlate to a region east of the Brahmaputra, in present-day Myanmar, suggesting that biogeographic barriers in this region are multiple. Examples of species separated by a Burmese biogeographic barrier include the mongoose species *Herpestes javanicus* and *Herpestes auropunctatus*, and three bird sister-species pairs (*Ripley and Beehler*, 1990). Other examples are the larger mammals that are restricted to Southeast Asia, such as orangutans, gibbons, sun bears and tapis (and also the pandas of South China); none of these ever entered South Asia, just as horses, camels and giraffes never entered Southeast Asia from South Asia. This pattern of barriers, along with a range of important human genetic (*Metspalu et al.*, 2004), cultural (e.g., milk drinking, *Simoons*, 1970), technological (e.g., the Movius Line, *Movius*, 1948) and domestic crop/animal traits (*Londo et al.*, 2006; *Fuller*, 2007; *Larson et al.*, 2010) that are or have also been differentiated across the Brahmaputra/Burma boundary, suggests that it has long constituted one of the most significant terrestrial biogeographic barriers of the Old World.

Accordingly, while it is not beyond the realm of possibility that East and Southeast Asia will prove to have been colonized prior to MIS 4, it would not be surprising to find that modern human colonization east of the Brahmaputra/Burma region is delayed, perhaps even until vegetation patterns change significantly in MIS 4. While *H. sapiens* obviously displays significant behavioural flexibility and complexity, novel, more densely forested tropical landscapes of the type encountered in Burma likely would have required significant new behavioural adaptations and toolkits. Factors such as these may have discouraged expansion eastwards unless population pressure arose or environments changed. Archaeological evidence to date seems to support this hypothesis. Technological differences between India and Indochina/Southwest Asia are significant throughout the Pleistocene. The colonization of Australia does not appear, on current evidence, to date to earlier than 60 ka. Perhaps also significant is the fact that an increasing number of archaic species of *Homo* appear to have survived until relatively late in East and Southeast Asia. These include *Homo floresiensis*, which survived on Flores until perhaps 17 ka (*Westaway et al.*, 2009), a possible Upper Pleistocene archaic population in South China (*Curnoe et al.*, 2012) and an as yet unknown new hominin species from southern Siberia, which existed as late as 50–30 ka (*Krause et al.*, 2010).

If expansion east from India was significantly slowed by ecotone change, then the opening up of this landscape in MIS 4 (Fig. 5) may have had a significant impact on *H. sapiens* dispersal patterns. *Bird et al.* (2004) note that in the tropics, glacial periods (and periods of transition between interglacial and glacial periods) may have been times of radiation, while interglacial periods were times of consolidation. Palaeoenvironmental data provide evidence that a corridor from east India through to insular Southeast Asia effectively opened up at the beginning of MIS 4, as the moist tropical woodlands of western Indochina transitioned into a moist tropical woodland and grassland mosaic landscape. Further east, this corridor would likely have opened onto a broad tropical savannah/woodland-grass mosaic stretching across much of mainland Southeast Asia. This has already been referred to as a ‘savana corridor’ and has been suggested to have constituted a key dispersal route into the region for modern humans (*O’Connor and Veth*, 2000; *O’Connor et al.*, 2001; *Bird et al.*, 2004, 2005; *O’Connor*, 2007; *Wurster et al.*, 2010). The presence of *H. sapiens* in Laos by MIS 3 is secure (*Demeter et al.*, 2012), and although dating is a problem, populations may be present in MIS 4. More open environments may therefore have enabled rapid colonization of the region down to the end of the Sunda plate. Effective dispersal beyond this point may have had to await the evolution of an appropriate maritime adaptation. On the other hand, though entry into Sahul is often taken to have occurred no earlier than 45 ka (*O’Connell and Allen*, 2004), occupations on the Huon peninsula and in northern Australia (e.g., Malakunana, Nauwalabila) may be as old as 60–50 ka (*Roberts et al.*, 1994), and in the Philippines as early as 67 ka (*Mijares et al.*, 2010). Patterns of archaeological, palaeoenvironmental and other data for China are complex and are beyond the scope of this article. We would only note that the development of the Upper Palaeolithic is young (35–30 ka) (*Qu et al.*, 2012) and the earliest unambiguous presence of *H. sapiens* in China appears to be no older than c. 40 ka based on existing fossil and archaeological evidence (*Shang et al.*, 2010; *Norton and Jin*, 2009), though there are potential hints of an earlier presence of *H. sapiens* fossils at sites such as Huanglong Cave (*Liu et al.*, 2010a), Liujiang (*Shen et al.*, 2002; *Wu*, 2004) and Zhirandong (*Liu et al.*, 2010b). Much of China is dominated by broadleaf woodlands, rich in tree nuts and some tubers, many of which resource extend into the Himalayan foothills. While acorns and other nuts are potentially rich resources, they would have necessitated the development of cultural techniques of processing, which could have contributed to a delay in the colonization of East Asia. Genetically, a degree of Asia-based interbreeding between newly arriving modern humans and archaic species is, as we have seen, suggested by data from certain genes in the nuclear genome of contemporary humans (*Harding et al.*, 1997; *Cox et al.*, 2008; *Wall et al.*, 2009).

7. Discussion and conclusion

The question of whether the earliest *H. sapiens* fossils found in the Levant reflect a failed dispersal of modern humans, or just the first step in a journey that brought them as far as India by the end of MIS 5, remains an open one. While mtDNA coalescence ages of 70–50 ka are typically cited for the timing of modern human movement out of Africa, the evidence in support of such a model, along with such linked elements as the notion of a single exit and rapid coastal dispersal, is actually minimal. Patterns in the fossil,
archaeological and genetic data do not conclusively support a c. 60 ka date for Out of Africa, and other readings of the evidence, as well as other models, are possible. Here we have presented a new analysis of the available evidence, together with a novel attempt to model Pleistocene environments on the basis of botanical vegetation reconstruction techniques. These demonstrate that an MIS 5 exit is equally if not more plausible than the MIS 3 or 4 exit that is currently widely advocated for Out of Africa (see also Hetherington and Reid, 2010). In addition, our analysis suggests that more complex scenarios for the dispersal of modern humans should be favoured. These potentially involved a structured African population of H. sapiens, multiple exits, multiple routes of dispersal, and a degree of interbreeding with archaic species of Homo as anatomically modern humans moved eastwards. Given the current ambiguity of much of the evidence for modern human dispersals out of Africa, it is critical that researchers remain open to alternative readings of the available data. We have focused here on the possibility that the modern human exit recorded by fossil evidence in the Levant in MIS 5 does not represent a failed dispersal, and that in fact our species was not only in the Levant but also the Arabian Peninsula during this marine isotope stage, and spread to India before the Toba eruption at 74 ka (Petraglia et al., 2007). Another valid hypothesis we do not explore here is that H. sapiens was able to leave Africa in MIS 6 via a grassland corridor (Frumkin et al., 2011; see also Scally and Durbin, 2012). Yet another is that our species dispersed out of Africa shortly after its first appearance c. 195 ka, in MIS 7 (Dennell and Roebrooks, 2005: 1102). One other possibility is that there were several, separate dispersals of our species out of Africa (Dennell and Petraglia, 2012). At the same time, we acknowledge that major demographic changes occurred in MIS 4 and MIS 3, perhaps explaining the relatively young mtDNA coalescence age in living populations. The increasing evidence for complexity as well as the clear patterns of bias for all records, whether archaeological, fossil or genetic, suggests the need for an open mind to multiple scenarios for Out of Africa, as well as for more rather than less complex models of H. sapiens dispersal across Eurasia.

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Appendix A. Supplementary materials

Supplementary material associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.quaint.2013.01.008.

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