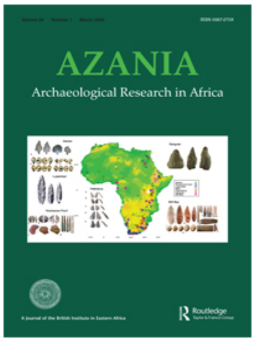

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Ecology and demography of early *Homo sapiens*: a synthesis of archaeological and climatic data from eastern Africa

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ABSTRACT

Eastern Africa maintains a key position in debates surrounding the emergence of *Homo sapiens* across Africa. Extensive research in the region has revealed a rich fossil record in association with a 'generic' but variable Middle Stone Age (MSA) material culture, providing an important laboratory for testing hypotheses about the behavioural evolution of our species. For example, multiple archaeological studies of the eastern African MSA note a link between the distribution and density of sites, archaeological diversity and environmental conditions, with ecology and demography often cited as key drivers of cultural evolution. This article formulates new hypotheses using theoretical models of complex fitness landscapes of evolution and reviews the archaeological and climatic records of Middle-late Pleistocene eastern Africa in the light of these ideas. It proposes that evidence from eastern Africa implicates much of the region as a refugial zone within Pleistocene Africa, providing consistently suitable conditions for survival that were characterised by high and changing biodiversity, facilitating population growth and interconnectivity as well as material culture diversification. Interactions between different evolutionary processes likely resulted in the complex cultural mosaic observed across Africa, including the appearance of 'specific' innovations against a backdrop of more 'generic' MSA elements.

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Modern human evolution; Middle Stone Age; ecological refugia; lithic technology; palaeoenvironmental change; complex fitness landscape

RÉSUMÉ

L'Afrique de l'Est occupe une position clé dans les débats autour de l'émergence de l'*Homo sapiens* en Afrique. Les recherches approfondies dans la région ont révélé de riches archives fossiles en association avec une culture matérielle 'générique' mais variable de l'Âge de Pierre Moyen (MSA), fournissant un laboratoire important pour tester les hypothèses sur l'évolution comportementale de notre espèce. Par exemple, de multiples études archéologiques sur le MSA d'Afrique de l'Est ont relevé un lien entre la répartition et la densité des sites, la diversité archéologique, et les conditions environnementales. L'écologie et la démographie sont souvent citées comme moteurs clés de l'évolution culturelle. Cet article

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formule de nouvelles hypothèses en utilisant des modèles théoriques de ‘fitness landscapes’ évolutionnaires complexes, passant en revue les archives archéologiques et climatiques de l’Afrique de l’Est du Pléistocène moyen-tardif à la lumière de ces idées. Nous proposons que les données provenant d’Afrique de l’Est impliquent une grande partie de la région comme zone refuge au sein de l’Afrique au Pléistocène, offrant des conditions de survie qui restèrent appropriées de façon durable, caractérisées par une biodiversité élevée et changeante, facilitant la croissance et l’interconnectivité de la population ainsi que la diversification de la culture matérielle. Les interactions entre différents processus évolutionnaires ont probablement abouti à la mosaïque culturelle complexe que l’on observe à travers l’Afrique, y compris l’apparition d’innovations ‘spécifiques’ sur fond d’éléments MSA plus ‘génériques’.

Introduction

Our species, *Homo sapiens* (*H. sapiens*), evolved in Africa around 300,000 years ago (kya) (McBrearty and Brooks 2000; Scerri *et al.* 2018; Scerri and Will 2023). Historically, eastern Africa has yielded some of the earliest evidence of this emergence, although more recent research from across the continent has led to the rejection of theories implicating this region as the single area of endemism (Hublin *et al.* 2017; Scerri *et al.* 2018, 2019; Scerri and Will 2023). That said, eastern Africa maintains a key position within these debates surrounding the evolution of human behaviour and anatomy. This is because extensive research in the region has revealed a rich behavioural record, particularly at Middle Stone Age (MSA) sites (Clark 1988; Basell 2008; Tryon and Faith 2013; Blinkhorn and Grove 2018, 2021), now known to be the first and longest-lasting cultural phase associated with our species. Additionally, the MSA fossil record of the region has yielded some of the earliest individuals deemed to be part of the *H. sapiens* lineage, with variable constellations of morphological traits (Brauer *et al.* 1997; White *et al.* 2003; McDougall *et al.* 2005; Mussi *et al.* 2014; Tryon *et al.* 2015; Vidal *et al.* 2022).

Eastern Africa, defined here as the modern-day countries of Tanzania, Kenya, Uganda, Ethiopia, Somalia, Djibouti and Eritrea (Tryon and Faith 2013), also has a diverse and unique geography, hydrology, geology and environment, lying at the conjunction of the Arabian, Nubian and Somalian tectonic plates (Schlüter 1997). Tectonic movements have created its distinctive volcanic landscapes and rift valleys, with high topographic relief and heterogenous habitats suitable for hominins. Determining how MSA populations interacted with such diverse landscapes is vital for understanding the emergence and subsequent proliferation of our species; eastern Africa can therefore provide important insights into the links between demography, ecology and archaeological diversity of early *H. sapiens* populations. In this review, the eastern African MSA archaeological and climatic records are considered together within the context of the wider MSA, offering new perspectives into the causal mechanisms behind the evolution of *H. sapiens* in this key region and beyond.

Understanding the African Middle Stone Age

The status of the African MSA has been debated since its inception nearly a century ago (Goodwin and van Riet Lowe 1929). This review is not intended to go through that history (see Clark 1993; McBrearty and Brooks 2000; Scerri and Will 2023), but rather to assess the current position of the MSA and recent theoretical developments that have moved the subject forwards. The MSA has received much attention because it is commonly thought to represent the first material culture produced by *H. sapiens* in Africa. Starting from around ~300 kya across most of Africa (Barham *et al.* 2015; Grün 2016; Hublin *et al.* 2017; Richter *et al.* 2017; Potts *et al.* 2018, 2020), large cutting tools like hand axes were abandoned in favour of prepared core technology and the hafting of pointed pieces to form projectile weapons (McBrearty and Brooks 2000). This marked a major technological shift seemingly associated with the earliest manifestations of *H. sapiens* morphology (Grün 2016; Hublin *et al.* 2017). As well as a reconfiguration of lithic (stone tool) technology, the MSA saw the proliferation of other behaviours typically associated with 'complex culture', such as pigment use and intentionally perforated shells, probably used for personal ornamentation, and an increase in ecological niche and dietary breadth (Scerri and Will 2023), marking the evolution of behavioural flexibility and plasticity crucial for the 'generalist specialist niche' specific to humans (Roberts and Stewart 2018).

The MSA also marks the first widespread evidence of regionally distinctive material culture styles in hominin evolution (Clark 1982, 1993; Figure 1). The sporadic appearance of these 'specific' regional innovations occurs alongside more 'generic' elements, such as Levallois reduction and scrapers, that seem to represent the baseline of technology present across large areas throughout much of the MSA. This pattern of regionalisation has historically been linked with the punctuated appearance of 'modern' cognition during the MSA, i.e. with the appearance of 'specific' behaviours thought to represent distinct periods of cultural efflorescence in cognitively diverse populations. More recently, it has been suggested that it may reflect the interaction between demographic and ecological variables, as well as the evolutionary trajectories of individual sub-populations through deep time (Will *et al.* 2019; Scerri and Will 2023). For example, climatic amelioration and the expansion of grasslands in the Upper Pleistocene led to human occupation of the Sahara and northern Africa (Drake *et al.* 2011). Specific cultural features, such as 'Aterian' tanged tools, bone technology and marine shell beads, are observed in certain North African assemblages (Bouzouggar *et al.* 2007, 2018; d'Errico *et al.* 2009; Iovita 2011; Figure 1), with differences in lithic assemblages not articulating with archaeologists' interpretations but rather with the palaeoecology of the region (Scerri *et al.* 2014).

In Central Africa, the Lupemban could be considered to be a 'specific' variant of the early MSA. Lupemban assemblages have been thought to indicate adaptations to rainforest and woodland environments, including heavy-duty axes, bifacial worked lanceolate points, backed flakes and blades, picks and segments (McBrearty 1998; Barham 2001; Taylor 2011, 2016, 2022; Figure 1). The Sangoan industry, which similarly exhibits large heavy-duty core-tools characteristic of earlier periods (Shea 2020; Douze *et al.* 2021; Figure 1), has also historically been thought to represent a Central African forest adaptation. Yet more recently Sangoan-like tools have been suggested from sites across Africa, including in open habitats, both questioning the association between the industry and forest ecosystems and implying that they may have a much wider geographic distribution than initially assumed (Taylor 2022; Figure 1). Few occurrences have been securely dated, so it is difficult to ascertain the behavioural significance of

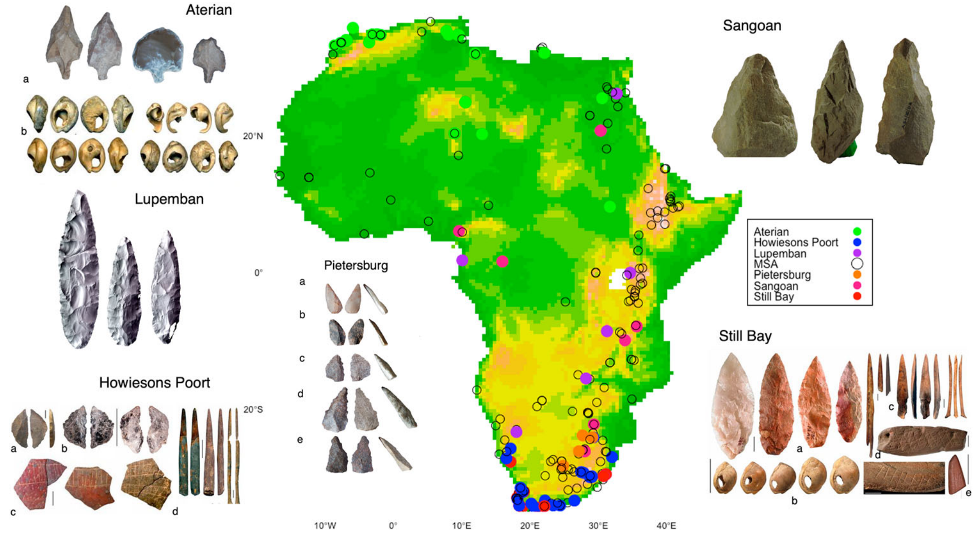

Figure 1. Map illustrating the distribution of 'generic' (black hollow circles) and 'specific' (coloured circles) Middle Stone Age (MSA) sites from the 'ROCEEH – Out of Africa database' (www.roceeh.net) (Kandel *et al.* 2023). Note that other terms are also used in Africa to describe region-specific lithic industries that are not included here and that many stratified sites have a combination of 'specific' and 'generic' MSA assemblages. Images highlighting some of these 'specific' cultural innovations have been included with permission: a) Aterian tanged tools from Oued Djouf, Algeria Iovita 2011: Figure 1, courtesy of R. Iovita) and b) marine shells from Grotte des Pigeons, Morocco (d'Errico *et al.* 2009: Figure 2, courtesy of F. d'Errico); Pietersberg retouched lithic artefacts from new excavations of Mwulu's Cave, South Africa (de la Peña *et al.* 2019: Figure 15, images by and courtesy of Paloma de la Peña) a–b) unifacial points, c) triangular blank and d–e) denticulated points; Howiesons Poort artefacts a) segment made of hornfels and b) segments made of quartz from Sibhudu Cave, South Africa (original images by P. de la Peña), d) bone point and awls from Sibhudu Cave and I) engraved ostrich eggshell from Diepkloof Shelter (d'Errico *et al.* 2017: Figure 2, courtesy of F. d'Errico); 'Lupemban' lanceolate points (flint replica tools created, imaged and courtesy of C. Scott); Sangoan core axes from Kalambo Falls, Zambia (images by and courtesy of L.S. Barham); Still Bay artefacts from Blombos Cave, South Africa (d'Errico *et al.* 2017: Figure 2, courtesy of F. d'Errico) a) bifacial points made of quartz and silcrete, b) perforated shell beads, c) bone points and an awl, d) engraved ochre fragments and e) an ochre fragment shaped by grinding.

the Sangoan, although some suggest that it may be better understood as a variant of the Acheulean rather than as a 'specific' MSA industry (McBrearty 1998; Taylor 2022).

In South Africa, the MSA record is routinely divided into chrono-cultural stages based on the appearance of 'specific' periods of innovation, most commonly the Still Bay and Howiesons Poort, among others (Wurz 2013; Wadley 2015; Figure 1). Similarities in aspects of spatially disparate Still Bay and Howiesons Poort assemblages, such as the style of projectile points, have been proposed to reflect extensive intergroup interactions (Villa *et al.* 2009; Mackay *et al.* 2014), with shared behaviours proposed to map the geographic spread of behaviourally distinct populations across the region (Jacobs *et al.* 2008). Others have argued that these similarities reflect shared ecological conditions are opposed to deriving from group contact (Ziegler *et al.* 2013; Archer *et al.* 2016). Eco-cultural niche modelling by d'Errico *et al.* (2017) proposed that the Still Bay represents a particular coastal adaptation during mild conditions, whereas populations during the Howiesons Poort had a much broader niche, incorporating more arid and high-altitude environments, and thus developed a cohesive adaptive system with flexible technologies.

Theoretical expectations for cultural variability in the MSA

The MSA as a cultural phase can be described as demonstrating both widespread features of persisting material culture and a fluctuating presence of region-specific technologies. A series of recent reviews, summarised in Table 1, highlight how there does not appear to be a pan-African trajectory for cultural evolution, with different regions each having their unique expression of the MSA through both space and time (Conard 2013; Scerri *et al.* 2018, 2019; Will *et al.* 2019; Scerri and Will 2023). Scerri *et al.* (2018, 2019) propose that multiple, periodically interacting, sub-populations across the continent likely permitted the divergence of some, but not all, cultural and genetic variants within the overall *H. sapiens* metapopulation (Harding and McVean 2004). To explain such patterns a dynamic demographic model invoking both population size and structure has been proposed (Scerri *et al.* 2019). For example, it is thought that larger populations maintain both more cultural complexity and greater genetic variability (Powell *et al.* 2009). However, at the local level, population sub-structure and fragmentation lead to a decrease in cultural complexity and genetic diversity, while at the metapopulation level more genetic and cultural diversity is expected. This is because isolated groups follow different evolutionary trajectories causing global heterogeneity, yet cultural knowledge becomes more deteriorated, improvements to existing cultural traits are less frequent and cultural trait diversity becomes difficult to maintain over long timeframes, often leading to the maladaptive loss of skills (Derez *et al.* 2013; Henrich *et al.* 2016). During population coalescence, or under continuous low-level interconnectivity, any beneficial mutations and innovations originating in local populations spread throughout the metapopulation, leading to global decreases in cultural diversity but overall increases in cultural complexity (Wright 1982). Shifts in demography through time and at different spatial scales may thus explain the fluctuating appearance of seemingly 'sophisticated' behaviours that tend to be linked to 'specific' MSA industries, as well as 'generic' lithic elements of the MSA that remain largely unchanged in the metapopulation throughout the period (Scerri and Will 2023).

However, other empirical studies have cast doubt on the link between population size and cultural innovation (Powell *et al.* 2009; Collard *et al.* 2011, 2013; Grove 2016). Mobility among a set of sub-populations, for example, has been found to have the same effect on cultural change as increasing the size of a single population (Powell *et al.* 2009). Grove (2016) demonstrated that population size has little influence over rates of cultural transmission except in very small populations and that it is population density and mobility that affect cultural evolution through their influence over the encounter rate between populations. Alternative models invoke ecological risk as an extrinsic explanation for cultural variability, proposing that innovations in technology will tend to increase as resources become less abundant and/or more unevenly distributed in time and space. For example, Collard *et al.* (2011) argued that foragers tend to make more complex and diverse tools in areas of decreased net primary productivity and increased temperature seasonality with shorter growing seasons, while Torrence (2001) highlighted how the

Table 1. Key traits thought to reflect the spectrum of innovative behaviour across the African Middle Stone Age, following Conard (2003), Will *et al.* (2019) and Scerri and Will (2023).

	Overall behavioural signature	'Specific' MSA	Bifacial technology	Backed technology	Bone tools	Beads	Engraving	Ochre	Coastal aquatic	Hafting	Long distance transport
East	Mosaic with stable components	Not present	Early and enduring	Late	Late	Ostrich eggshell and marine shell (mainly MIS 3)	Late	Enduring	Rare	Early and enduring	Early and enduring
West	Mosaic with stable components	Not present	Late and enduring	Rare	Unknown	Unknown	Unknown	Unknown	Unknown	Late	Unknown
Central	Mosaic with stable components	Present	Early and punctuated	Early and punctuated	Sporadic and early	Unknown	Unknown	Sporadic	Unknown	Early	Rare
South	Mix of discontinuous and continuous traits	Present	Early and punctuated	Enduring	Frequent and enduring	Marine shell (mainly MIS 4)	Rare	Enduring	Widespread during MIS 5 and MIS 3	Late	MIS 5 onwards
North	Mix of discontinuous and continuous traits	Present	Early then disappears	Rare	Frequent and enduring	Ostrich eggshell (mainly MIS 3) and marine shell (mainly MIS 5)	MIS 4	Early then disappears	Widespread during MIS 5 and MIS 3	Early and enduring	MIS 5 onwards

risk of resource failure leads hunter-gatherers to produce more complex tools that improve the speed and success of subsistence capture.

Traditional demographic and ecological risk models have thus been thought to have contradictory expectations in relation to the expected patterning of cultural variability; increases in population sizes should occur in regions with lowest ecological risk and highest net primary productivity (Porter and Marlow 2007), yet the former expects increases in cultural complexity, and the latter expects cultural stasis (Thompson *et al.* 2018). However, ecology and demography do not act on cultural evolution in the same way and thus are not strict alternatives; ecological risk elicits selection for (and thus causes) more specialised technologies, whereas population density merely provides greater rates of innovation and the ability to better maintain and improve upon existing technologies. Increases in cultural complexity should therefore emerge only when both the cause (risk) and the capability (provided by greater population density and/or mobility) are present. Developing theoretical and computational models that emphasise this interaction between ecological variability and hominin demography, including their dual effects on technological change and innovation in the MSA record, are thus required.

Wright's (1932) concept of 'complex landscapes of evolution' from the field of genetics may provide a useful framework (Figure 2). Within the context of cultural rather than biological evolution, this idea proposes that early humans were likely confronted with various local fitness states, which varied dynamically between regions and through time (Kuhn 2006; Lombard and Parsons 2011; Will *et al.* 2019; Scerri and Will 2023). In a rugged adaptive landscape (Figure 2b–c), populations will tend to adapt to the local fitness 'peak' within the overall 'space' of possible behaviours that is closest to their starting point (which may or may not be the highest peak across the landscape). Once a population has begun to adapt, it may be difficult to shift to another 'peak' even if it provides greater fitness as moving between peaks would first involve a reduction

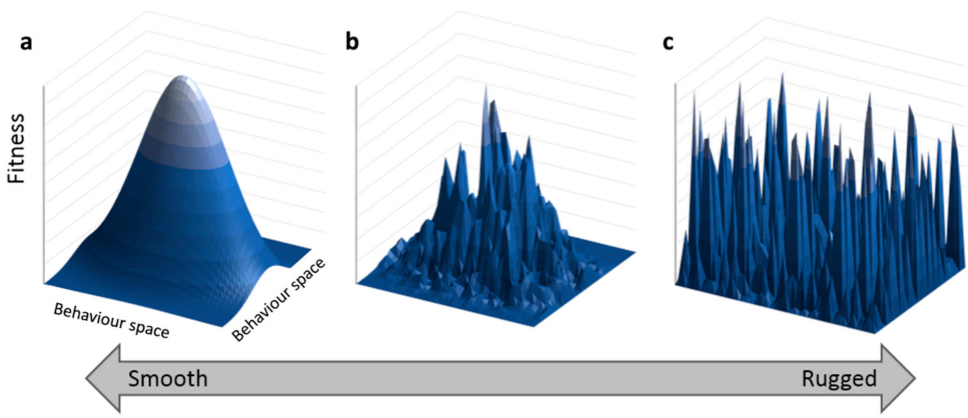

Figure 2. Idealised model for the theoretical cultural fitness landscapes that display increasingly more adaptive solutions within the 'space' of possible behaviours. A smooth fitness landscape (a) leads to a single adaptive peak within behaviour space. As more adaptive responses become possible within behaviour space (b), the fitness landscape becomes more rugged (c). Figure modified after Will *et al.* (2019: Figure 4), original by T. Shafee (CC-BY-SA 3.0).

in fitness — something that is rarely promoted by evolutionary processes. Environmental or demographic change may cause fitness displacements of a population leading to adaptative shifts towards new 'peaks' that arise within behaviour space. When extrinsic (i.e. ecology) and/or intrinsic (i.e. demographic) factors act in a similar way to shape behaviour, comparable adaptive peaks may occur in diverse geographic locations. Nubian technology found in the northern and southern African MSA records could be a potential example of this, probably linked to engagement with arid environments (Will *et al.* 2015; Groucutt 2020). Timbrell *et al.* (2024) discuss how the appearance of 'specific' MSA points may reflect adaptation to specific ecological zones but may also be linked to increased social pressure in order to facilitate trade across the hunting landscape within particular environments. In this sense, information transmission between interacting populations can also serve as attractors to similar peaks, creating homogeneous signals *within* a region and leading to divergence *between* regions.

Interactions between demographic and ecological variables lead to different cultural phenomena in the archaeological record by conditioning behaviour space. For example, when resources are low, increased ecological stress on hunter-gatherer populations leads to the maintenance of a wider range of contacts across greater distances to act as a 'safety net' in order to pool risk (Whallon 2006; Grove 2009, 2018). This is seen ethnographically in the '*hxaro*' system within the Kalahari, where the exchange of arrows among some San communities leads to similarities in form between often disparate groups (Wiessner 1977, 1982, 1983). Analyses of language diversity indicate that when climate variability is greater increased social networks are required to maintain adequate subsistence and therefore communication systems become more geographically widespread (Nettle 1998). Instead, Gamble (1982) proposed a similar hypothesis to explain the extensive distribution of similarly designed 'Venus' figurines across Europe during the Upper Palaeolithic. Moreover, habitat quality influences the carrying capacity of an area, which in turn affects population density. Archer (2021), in an analysis of MSA backed pieces, found that regions with stable resources tend to support larger populations, which in turn means that they tend to have more complex technologies. Increases in resource pressure through increases in demographic pressure on carrying capacity then act to maintain effective technologies that minimise risk (Archer 2021). Technological change can therefore be shaped social pressures, which exerts a selective force on behaviour that is unrelated to subsistence function, as well as, or in response to, ecological pressure, which together influence the range of adaptive solutions reflected in the archaeological record.

Developing new hypotheses about the MSA

Four potential scenarios can be envisaged when considering demography and ecology within the context of complex landscapes of evolution (Table 2). These hypotheses consider both effective population size, i.e. the number of individuals present who contribute offspring to the next generation, and resource availability. Growth in effective population can be achieved by either increasing population density or by extending interconnectivity, with differences between the two related to the level of migratory activity and sociality between sub-populations, subsequently determining the spatial structuring of cultural innovations (Powell *et al.* 2009). Scenario A suggests that when effective population

Table 2. Hypothesised scenarios considering demographic and ecological factors and their predicted effects on social and cultural patterning in the MSA record.

Ecological and demographic scenario	Prediction	Archaeological pattern expected
A) Large (effective) population and high resource availability	Large populations maintain high rates of innovation. Weak selection pressures due to lack of resource risk Multiple adaptive peaks and rugged adaptive landscape	High variability between sites and through time.
B) Large (effective) population and low resource availability	Large populations maintain high rates of innovation. Selective pressures imposed by resource risk. Increased mobility and information sharing across wider networks to mitigate resource risk. Smoother fitness landscape with fewer adaptive peaks.	Innovations that maximise fitness become widespread. Increased standardisation in certain artefacts that facilitate interaction between neighbours.
C) Small (effective) population and high resource availability	Small populations struggle to maintain new innovations. Decreased mobility and less extensive social networks. Multiple adaptive peaks due to lack of resource risk and rugged adaptive landscape.	Increased experimentation to find new adaptive peaks. More differentiation between coeval sites.
D) Small (effective) population and low resource availability	Small populations struggle to maintain new innovations that would enable them to move towards new adaptive peak. Increased information sharing across wider networks, dispersal or extinction.	Lack of archaeological sites.

size and resource availability increases, the rate of innovation should also increase (Powell *et al.* 2009). Adaptive peaks, however, should remain moderate to low in height due to a lack of resource risk imposing strong selective pressures. They should also form a rugged fitness landscape with high cultural variability between sites that adopt different technological solutions within that setting. Scenario B proposes that when effective population size is high, but resource availability is low, the capacity for innovation should also be high due to increased population density and/or increases in mobility between sub-populations pooling risk (Powell *et al.* 2009; Grove 2016, 2018). However, unlike the previous scenario, strong selective pressures imposed by the environment would lead to high adaptive peaks forming in an otherwise smooth fitness landscape, resulting in the adoption of innovations that maximise fitness within specific conditions. Increases in information sharing between sub-populations under increased ecological risk may also lead to increased appearance and/or standardisation of certain artefacts that facilitate interaction between neighbours, increasing spatial structuring of overall cultural variability. Small effective population size in areas of high resources is hypothesised in Scenario C to lead to increased cultural experimentation as populations find new adaptive solutions within resource rich landscapes. More differentiation between coeval sites would be expected as mobility decreases and interaction networks between sub-populations break down. Population density should however increase over time, facilitated by increases in the carrying capacity of the landscape. Finally, in Scenario D, small effective population size and low resource density may result in an inability to maintain new innovations that would otherwise enable populations to move up new fitness peaks; increased mobility and information sharing may occur initially to increase effective population size, although ultimately dispersal to more suitable areas would be required to avoid population extinction. In this article, I apply these hypotheses to the eastern African MSA to evaluate the archaeological record of the region in relation to the biogeographical patterning of the MSA across Africa (Table 1).

Archaeological data from eastern Africa

Chronological change through the eastern African MSA sequence

Following Tryon and Faith (2013) and McBrearty and Tryon (2006), the eastern African MSA can roughly be split into 'early' and 'late' phases, with the earlier phase of the MSA referring to sites predating the Last Interglacial (~120 kya) and the later MSA to those within or after the Last Interglacial (Figure 3). Early and late MSA assemblages overlap in multivariate space and show many similarities, although some later MSA assemblages appear more distinctive (Tryon and Faith 2013). Blinkhorn and Grove (2018) demonstrated, however, via a suite of quantitative approaches that, rather than a transition from early to late MSA behaviour, a tripartite split of the eastern African MSA record may be more appropriate (Figure 3). Marine Isotope Stage (MIS) 5 was highlighted as a distinct phase in which earlier MSA behaviours continue to occur but are significantly augmented with new combinations of stone tools (Blinkhorn and Grove 2018).

The eastern African Middle to Upper Pleistocene archaeological record was likely made by morphologically diverse populations of our species, *Homo sapiens* (Brauer *et al.* 1997; White *et al.* 2003; McDougall *et al.* 2005; Mussi *et al.* 2014; Tryon *et al.* 2015; Martinón-Torres *et al.* 2021; Figure 3). As with fossils found across the African continent (Gunz *et al.* 2009), populations in this region seem to demonstrate a diverse mix of anatomical traits that have been historically (and rather subjectively) labelled as being either 'modern' or 'primitive' based on the morphological characteristics of recent and extant *H. sapiens.* To avoid the social and political baggage associated with such terms, Stringer and Crété (2022) recently proposed that fossils should instead be classified as 'basal', those with traits close to the ancestral position on the phylogenetic tree, and 'derived', who have specialised, non-ancestral morphological traits. Considering the time depth of the eastern African MSA record, such frameworks may be important for understanding the diversity of the early human populations that produced it. For example, Omo Kibish II has been suggested to be a 'basal' *H. sapiens*, while Omo Kibish I may belong to a 'derived' population (Stringer and Crété 2022), although both are assumed to be of a similar age at around 200 kya (McDougall *et al.* 2005; Vidal *et al.* 2022, although see Sahle *et al.* 2019a, 2019b for further discussion). This highlights how evolution may have transpired independently in different groups inhabiting small areas.

However, dichotomising the fossil record in such a way still struggles to account for that fact that Middle/Upper Pleistocene *H. sapiens* fossils tend to exhibit different combinations of 'basal' and 'derived' traits (Scerri *et al.* 2018). The cranium discovered at Herto in Ethiopia, dated to ~160 kya (Clark *et al.* 2003; White *et al.* 2003), possesses a

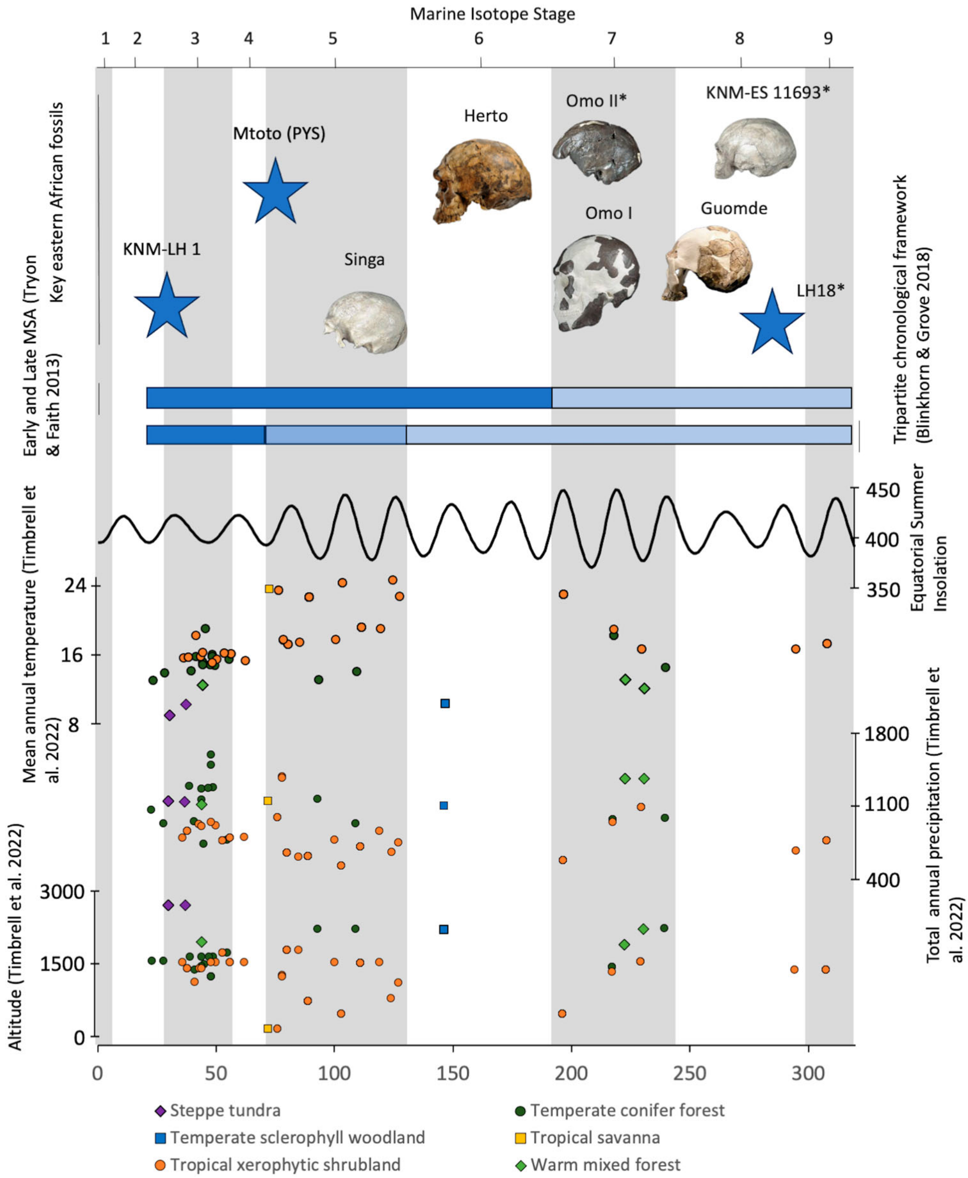

Figure 3. Timeline of eastern African MSA showing the broad chronological placement of key eastern African MSA fossils (image of Herto by and courtesy of T. White, all others courtesy of C. Stringer), with those that have not been directly dated highlighted with an asterisk (*), as well as chronological divisions of the MSA by Tryon and Faith (2013) and Blinkhorn and Grove (2018), mean Equatorial summer (Jun-Aug) insolation (W/m2), modelled mean annual temperature (°C) and total annual precipitation (mm) and (k) altitude (metres above sea level) within a 50 km radius of eastern African MSA assemblages, illustrated at the mid-age point for each occupation and symbolised according to its biome classification (Timbrell *et al.* 2022a). Grey vertical bars indicate odd-numbered Marine Isotope Stages.

relatively globular braincase (a 'derived' characteristic) with a robust occipital and large facial skeleton (traits associated with earlier Middle Pleistocene hominins). The Eliye Springs crania (KNM-ES 11693), estimated to be between 200 and 300 kya, exhibits another different combination of cranial characteristics, sharing affinities with Omo II in some features (e.g. cranial vault shape), whereas in others (e.g. cranial capacity) it appears more similar to the LH18 fossil from Laetoli in Tanzania. The recent discovery of a child burial at Panga Ya Saidi, Kenya, (nicknamed Mtoto) demonstrates the late retention of archaic features to around 78 kya (Martinón-Torres *et al.* 2021). This review of the eastern African MSA does not intend to focus on the anatomical evolution of *H. sapiens*, nor the potential link between morphological and archaeological change in eastern Africa, however the fossil record suggests that current approaches to interpreting morphological diversity likely somewhat underappreciate the complexity of population dynamics in the Middle/Upper Pleistocene.

MIS 6 and older

The earliest appearance of MSA artefacts in eastern Africa appears around ~320–305 kya at Olorgesailie in Kenya (Deino *et al.* 2018). Olorgesailie documents stone technology, fauna and environmental conditions from the Earlier Stone Age (ESA) to the MSA, with MSA layers being distinctive from those of the ESA due to a hiatus in the record from 499 to 320 kya (Brooks *et al.* 2018; Deino *et al.* 2018; Potts *et al.* 2018). Raw material sourcing of obsidian MSA artefacts revealed that around 78% of the samples were attributed to sources located from 25–50 km in five directions from the sites, with a small number of artefacts made from raw material deriving from more distant sources, indicating the formation of interaction networks or procurement over longer distances than seen previously (Brooks *et al.* 2018). The Kapthurin Formation also yields early examples of MSA assemblages, showing no clear unidirectional succession from the ESA to the MSA (Tryon and McBrearty 2002; Blegen *et al.* 2018). This suggests that the ESA and MSA in eastern Africa could have overlapped both in space and time, do not conform to discrete typological packages and do not seem to be related to appearance or disappearance of any specific hominin species (Blegen *et al.* 2018). Sites at Gademotta in the central Ethiopian Rift represent some of the earliest MSA occupations in higher latitude areas, dating from 280–100 kya (Sahle *et al.* 2014). Douze and Delagnes (2016) suggest that there were two diachronic changes in convergent tool production at the site, the development of Levallois core reduction methods to produce point technologies and the shift from unifacial and bifacial shaping of convergent tools to localised slight retouch of predetermined points. Earlier MSA assemblages at Gademotta are thus thought to be embedded within an ESA-concept of tool production, whereas the later industries demonstrate the emergence of a new constellation of cultural behaviours indicative of a 'fully MSA' tradition (Douze and Delagnes 2016). A similar phenomenon is also seen at ESA sites like Kilombe Caldera and Olduvai Gorge in the Kenyan Rift Valley, where small bifaces appear to fall along the same technological continuum as large flake points in later layers (Gowlett *et al.* 2017).

MIS 5

MIS 5 assemblages are found in highly diverse ecological contexts across the region (Figure 3). Panga ya Saidi in coastal Kenya documents a 78,000-year archaeological record, notably revealing an early phase of the MSA transitioning to the Later Stone Age (LSA) (Shipton *et al.* 2018; d'Errico *et al.* 2020). Iron-rich fragments from the MSA layers suggest that red pigment was transported and perhaps processed at the site between 76 and 67 kya, although the first definitive use of ochre appears at 48.5 kya (d'Errico *et al.* 2020). Puka shells (i.e. the beach-worn apices of cone shells belonging to the family Conidae) may have been worn as personal ornaments by MSA populations as early as 67 kya, although there is only more concrete evidence for this behaviour between 33 kya and 25 kya, potentially around the same time as ostrich eggshell beads are first found (d'Errico *et al.* 2020). MSA finds at Aduma in the Middle Awash Valley in Ethiopia, likely dating to ~100–80 kya have been thought to represent a regional variant characterised by distinctive point, scraper and core types, notably their small 'microlithic' size, which becomes more emphasised through time (Yellen *et al.* 2005). Analysis of the faunal evidence from Aduma found in association with hominin remains, which meet the morphological definition of *H. sapiens*, indicates how multiple habitat-types were occupied with a strong reliance on riverine resources (Yellen *et al.* 2005). Within the Lake Victoria Basin, ~250 km to the west of the Central Rift, assemblages from Rusinga Island, Mfangano Island and Karungu consist of flakes and blades removed from a variety of reduction methods; retouched pieces are rare (Tryon *et al.* 2010, 2012). Small point and Levallois based assemblages from the Lake Victoria Basin are quite distinct from similarly dated deposits to the west (Tryon *et al.* 2019), such as at the ~60–70,000-year-old Katanda sites on the Congo/Uganda border, which yield distinctive barbed bone harpoons (Brooks *et al.* 1995).

At Prospect Farm in the Central Rift, assemblages representing at least seven occupation phases have been proposed to date to between 45.7 and 120 kya (van Baelen *et al.* 2019). MSA levels at this site also yielded a high density of artefacts, indicating that foraging groups likely repeatedly reoccupied the area over many thousands of years, possibly for the harvesting of obsidian sources on the slopes of Mount Eburru for use and exchange (van Baelen *et al.* 2019). Obsidian sourcing has shown that groups in the area were moving around and perhaps beyond the Nakuru-Naivasha Basin to either bring in a limited amount of exotic obsidian or obtaining it via exchange networks (van Baelen *et al.* 2019).

MIS 4 and younger

The MSA/LSA transition occurs at Prospect Farm between ~53.5 and 46.7 kya, although MSA artefacts were still manufactured until ~40 kya to 35 kya (van Baelen *et al.* 2019). In Tanzania, Mumba rock shelter contains one of the richest continuous sequences from the MSA to the Iron Age in eastern Africa, with transitional assemblages between the MSA and LSA yielding LSA-like geometric microliths and knives, ostrich eggshell beads and MSA-like stone points, dating to between ~49.4 and 40 kya (Gliganic *et al.* 2012). *H. sapiens* fossils have been discovered at nearby Lake Eyasi (Domínguez-Rodrigo *et al.* 2008). To the north of Lake Eyasi, Nasera also documents the MSA/LSA transition, marking a gradual shift from Levallois and bipolar reduction strategies, the replacement of points by backed microliths and the decrease in artefact size (Tryon and Faith 2016). Obsidian is rare at the site but was acquired from sources approximately 250 km away. MSA layers at Porc-Epic Cave in Ethiopia, dating to ~40 kya, yield a large amount of ochre and ochre processing tools, discovered in an area specifically devoted to the activity (Rosso *et al.* 2016). Perforated opercula shells have been also discovered dating from 33–43 kya, with evidence of polishing suggesting that they were used as beads (Assefa *et al.* 2008).

Further features of the eastern African MSA record

Eastern Africa does not appear to have formally defined temporally or regionally specific MSA 'diagnostic tools' as seen in other regions (Table 1). Archaeologists have either proposed MSA industries or variants for eastern Africa to characterise patterns of variability that are nevertheless usually limited to individual sites, with only a few appearing at more than one site located over 50 km apart, and/or borrowed nomenclature from other regions, such as 'Still Bay'. In a recent synthesis Shea (2020) described the current situation as 'lithic systems anarchy', requiring the development of a novel region-specific 'mode' system to describe assemblage diversity rather than 'industries' as used elsewhere. This demonstrates that eastern Africa's MSA record can indeed be emphasised as being highly variable, although long periods of relative homogeneity are also apparent, for example in the manufacture of bifacial pieces, long-distance trade and hafting (Shea 2008; Tryon and Faith 2013; Mirazón Lahr and Foley 2016; Blinkhorn and Grove 2018). Sites with long sequences, such as Gademotta, Mumba, Nasera and Porc-Epic, do not appear to show consistent trends through time, yet when comparing across the region sites in the Lake Victoria Basin, Ethiopia and the coastal area seem to have their own distinct 'variants' that somewhat distinguish them from other MSA assemblages (Clark 1988). For example, exploitation of primarily local raw materials, as well as a clear absence of obsidian, is a regional character of Ethiopian MSA sites, such as at Gotera (Fusco *et al.* 2021), Melka Kunture (Mussi *et al.* 2014), Gademotta (Douze and Delagnes 2016) and Mochena Borago (Brandt *et al.* 2012). Clark (1988) proposed that regional lithic traditions are likely reflective of local style, as well as strategic and technological innovations, driven by the diverse topological environments and climatic conditions of the region. This hypothesis has proven to be robust since increased chronological resolution has improved our understanding of eastern African population dynamics (Basell 2008; Blinkhorn and Grove 2018, 2021; Timbrell *et al.* 2022a).

Eastern Africa is also unique in that the MSA to LSA transition may have begun here by around 71 kya (Shipton *et al.* 2018), which is well within the timeframe of the MSA of other regions (Scerri and Will 2023). For example, Panga ya Saidi reveals an early phase of the MSA where typical Levallois cores appear alongside LSA backed artefacts and blades, as well as the first putative evidence of ostrich eggshell beads in the region (Shipton *et al.* 2018; d'Errico *et al.* 2020). The MSA/LSA transition is more frequently observed around 50–40 kya in other areas of eastern Africa (Ambrose 1998; Miller and Willoughby 2014; Tryon *et al.* 2018). In the Central Rift, Enkapune ya Muto possesses layers that may mark it at ~46 kya (Ambrose 1998), with a technological shift towards blade-based assemblages (Leplongeon 2016). Tryon and Faith (2013) when reviewing eastern African MSA technology highlight a distinctive subset of late MSA assemblages, which Marks and Conard (2008) label 'transitional', including those dated to <75 kya from Mumba, Nasera, Porc-Epic, Mochena Borago and undated assemblages from Mtongwe. These assemblages yield more beads, ochre, backed pieces, bipolar cores, blades, grindstones and anvils (Tryon and Faith 2013). At Mochena Borago in Ethiopia there is a longstanding persistence of core reduction strategies through time, despite dramatic climatic fluctuations and possibly catastrophic volcanic events, suggesting that early human technological strategies were highly flexible (Brandt *et al.* 2017). Reconciling technological change with the 'MSA/LSA transition' has been deemed challenging, given that backed pieces appear in assemblages showing technological continuity with prevailing reduction methods (Brandt *et al.* 2012). MSA technological characteristics appear with LSA components well into the mid-Holocene at Goda Buticha (Tribolo *et al.* 2017; Leplongeon *et al.* 2017). At this site, there is a hiatus in the sequence (from ~25–7.5 kya) coinciding with the arid conditions of MIS 2. It has been proposed that this gap, as well as potentially resulting from research bias, could represent the reintroduction of cultural traits or convergence resulting from regional-scale population movements from refugial areas or localised persistence in technological traditions (Pleurdeau *et al.* 2014; Leplongeon *et al.* 2017; Tribolo *et al.* 2017).

The transition to the LSA was expressed variably throughout eastern Africa (Tryon 2019), although broad shifts towards increased site occupation intensity (Shipton *et al.* 2018), a more regular use of beads as social communicators (Shipton *et al.* 2018; d'Erricco *et al.* 2020) and a broadened diet to include lower ranked resources (Mehlman 1989) suggest that it may be linked to a widespread increase in population density. Ambrose (1998, 2002) alternatively suggests that the transition in eastern Africa may represent a combination of ecological and social changes to accommodate increases in resource risk during cooler, drier, and more variable conditions during the Upper Pleistocene. However, several proxies indicate decreased mobility at Nasera that appears unrelated to environmental shifts, suggesting increased population density among local forager populations at the onset of the LSA (Tryon and Faith 2016). Increased manufacture of backed microliths, ceramics and domesticates associated with the LSA may thus reflect new strategies at this site to reduce the costs of resource failure in an increasingly packed landscape. Understanding the processes that caused such changes in population size and structure is likely critical to interpreting different scales of technological change across the region, particularly considering genetic, fossil and climatic evidence from across Africa (Scerri *et al.* 2018).

Environmental context of the eastern African MSA

Eastern Africa has a unique environmental setting, with its central position at the Equator acting as a 'hinge' with all the major regions of Africa: deserts in the north, tropical forests to the west, and southern Africa through the central Rift Valley (Mirazón Lahr and Foley 2016). Unlike these other regions that tend to only a have a few habitat types (in most places just one), eastern Africa exhibits a mosaic of woodlands, shrublands, rainforests, grasslands and deserts. It has thus been deemed one of the world's biodiversity hot spots (Jenkins *et al.* 2013). Moreover, the Rift Valley system has created a series of variable localised landscapes and lake basins, providing both a source of water for MSA populations and fluvial habitats with high biomass that attracts large mammals. This combination of high relief and habitat heterogeneity creates conditions for biological and cultural adaptation on a micro-scale (Mirazón Lahr 2012; Mirazón Lahr and Foley 2016). Figures 3 and 4 highlight some of this heterogeneity in relation to eastern African MSA sites using modelled data.

Palaeoenvironmental proxies

Ecological change in eastern Africa has been studied extensively because Rift Valley lake basins preserve paleoenvironmental proxies, and therefore record diachronic climatic

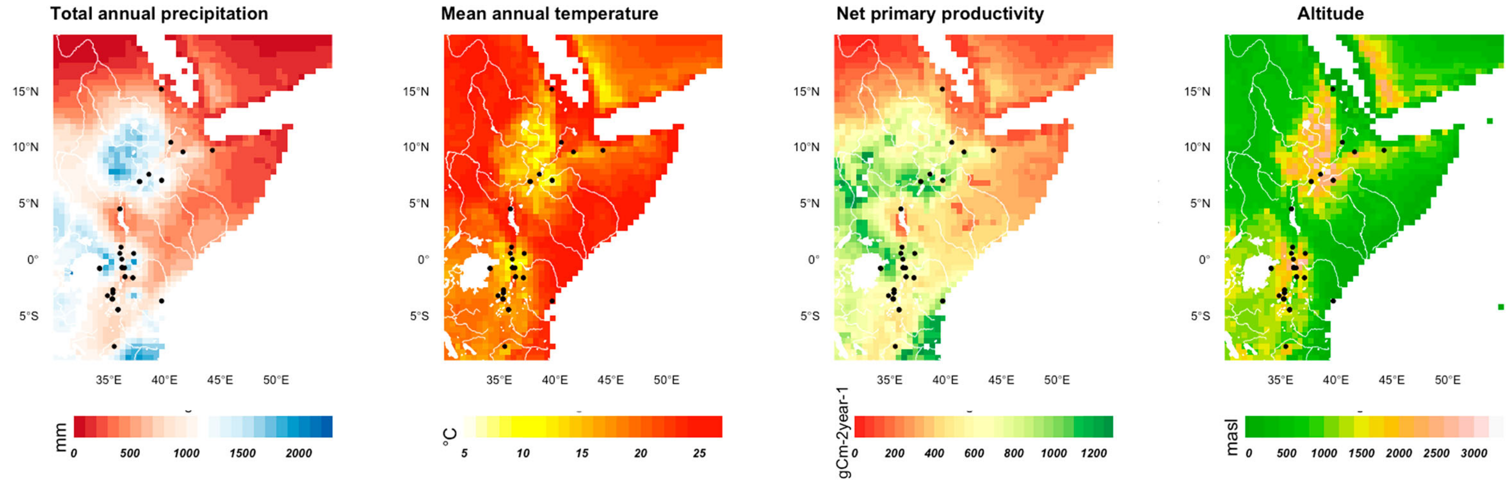

Figure 4. Maps of eastern Africa demonstrating average total annual precipitation (bio12, millimetres), mean annual temperature (bio1, degrees Celsius) and net primary productivity (NPP) across the Middle-Late Pleistocene (21–320,000 years ago) using climate simulations from pastclim (Krapp *et al.* 2021; Leonardi *et al.* 2023), as well as altitude (EPOTO2020, metres above sea level). Major rivers and lakes have been mapped in white (Natural Earth, 2020) as well as the distribution of dated Middle Stone Age sites in black from Blinkhorn and Grove (2021).

shifts, exceptionally well. When in direct association with archaeological strata, these records have provided a vital link between cultural and environmental change. For example, long sequences at the Olorgesailie Basin, southern Kenya, have revealed rich ESA layers associated with relatively stable environments, with MSA phases linked to highly dynamic and fluctuating arid-moist climate variability (Owens *et al.* 2018; Potts *et al.* 2018, 2020). It has therefore been suggested that the emergence of the MSA and its replacement of the ESA in the Kenya Rift by ~320 kya could represent an evolutionary response to resource landscapes that were less predictable in time and heterogeneous in space, as well as dramatic faunal turnover (Potts *et al.* 2020). Acquiring resources in increasingly variable environments may have required the development of a more flexible and mobile toolkit, as demonstrated by the shift from a few multi-purpose tools to a wider array of task-specific tools during the MSA. These adaptable 'generalist' behaviours become distinctive of later *H. sapiens* (Potts 1998; Roberts and Stewart 2018). Behavioural plasticity was likely vital to the occupation of new previously unexplored areas of the region. For example, Panga ya Saidi yielded multiple proxies indicating its position at a tropical forest-grassland ecotone, such as terrestrial molluscs, which require humid shady conditions, the presence of open and bush/forest adapted mammalian species and woody, grass and palm phytoliths surrounding the site (Shipton *et al.* 2018; Roberts *et al.* 2020; Faulkner *et al.* 2021). A shift towards drier conditions around ~78–73 kya corresponds with isotope data that suggest an increase in C_4 plants found in grasslands in the diets of the fauna being exploited at the site (Shipton *et al.* 2018).

Diverse biomarkers have provided crucial information about the environmental context of recent human evolution in eastern Africa. Leaf waxes from Lake Malawi reveal an amelioration of conditions after the Middle Pleistocene, with warmer and wetter conditions than seen previously, especially during interglacial periods (Johnson *et al.* 2016). Lake levels decreased multiple times between 600 and 100 kya when lakes in the Kenyan Rift expanded (Trauth *et al.* 2007; Ivory *et al.* 2018). Numerous vegetation shifts from tropical forests to desert or semi-arid bushlands are reported at Lake Malawi, with a megadrought resulting in a shallow saline lake surrounded by semi-desert during late MIS 5 and MIS 6 when higher-latitude areas experienced wetter conditions (Johnson *et al.* 2016; Foerster *et al.* 2022). Pollen-based reconstructions at Lake Bosumtwi in Ghana indicate oscillations between forested biomes during La Niña-like conditions and open savanna coinciding with El Niño-like conditions (Miller and Gosling 2014), with the reverse at Lake Magadi in eastern Africa (Owen *et al.* 2018), highlighting the asynchrony of low latitude climatic change (Kaboth-Bahr *et al.* 2021). Lake-level variations may have been key mediators of human mobility and interaction within eastern Africa; for example, occupations of the Lake Victoria Basin tracked fluctuations in the shoreline that were resource-rich and coupled with the expansion and contraction of grasslands with grazing herbivores (Tryon *et al.* 2019). Further north, in Ethiopia's Awash Valley wadi palaeochannels likely formed natural corridors for MSA populations to ephemeral ponds and marshes, and thus to more reliable water and other resources of the larger Awash River further east (Niespolo *et al.* 2021).

Volcanism and tectonic activity have created a unique and evolutionarily significant suite of topographic conditions specific to the region (Trauth *et al.* 2007). They have, for example, raised the Ethiopian Plateau and Central Rift Valley high above those adjacent areas of Africa of similar latitude (King and Bailey 2006; Bailey *et al.* 2011) so that cyclonic storms tracking eastward across equatorial Africa irrigate the Plateau and the westward-facing slopes of the Rift Valley, while eastward-facing slopes receive precipitate from monsoons travelling up the coastline of the Indian Ocean (Trauth *et al.* 2009). Periods of increased aridity were somewhat offset in eastern Africa by the steep gradients in altitudinal relief and rainfall that allowed movements upwards to cooler and wetter altitudes, as well as by the expansion of forest populations when the canopy was more open and fragmented (Ambrose 1998; Basell 2008; Blome *et al.* 2012). Evidence from Fincha Habera in the Bale Mountains of Ethiopia suggests that this high-altitude region saw recurrent occupation from 47 to 31 kya, coinciding with a phase of glaciation and extreme cold temperatures (Groos *et al.* 2021). Ossendorf *et al.* (2019) concur that mountains would have provided humid refugia during periods when the lowlands were arid. Moreover, different ecotones are preserved in eastern Africa as a result of high topographic relief, bringing forest, woodland and grassland communities closer together than would normally be the case in less topographically complex landscapes (Foley 1995).

In a pan-African synthesis of palaeoclimatic reconstructions from offshore marine sites, lake cores and terrestrial sedimentary archives, Blome *et al.* (2012) propose that populations in tropical and eastern Africa show a relatively muted demographic response to climatic change due to the relative stability of site densities through time. Blinkhorn and Grove (2018) in an extended analysis of eastern African MSA sites conversely found fluctuating levels of occupation across interglacial-glacial cycles (Figure 3). However, smaller-scale variations, such as El Niño Southern Ocean oscillations and the position of the Intertropical Convergence Zone, caused different basins to exhibit different patterns of climatic change at a finer-scale than captured by successive MIS cycles (Kaboth-Bahr *et al.* 2021). Environmental fluctuations, and the demographic shifts that likely accompanied them, were thus asynchronous, occurring under varied regimes of climate forcing and creating alternating opportunities for migration into and interaction with adjacent regions (Blome *et al.* 2012; Scerri *et al.* 2018; Kaboth-Bahr *et al.* 2021).

Palaeoenvironmental models

Proxy records remain the most accurate method for capturing the environmental context of site occupations, yet the resolution and nature of such data are highly variable and often not reconcilable at the regional scale. Model data have helped to 'fill the gaps', with a suite of recent quantitative analyses offering insights into the relationship between environmental and cultural change across eastern Africa. Basell (2008) found that the placement of MSA sites was limited to ecotonal settings where access to wooded ecologies was available, with lake margins and highland areas offering habitat stability during periods of aridity; coastal areas were also occupied. This interpretation has since been supported by Timbrell *et al.* (2022a) and Blinkhorn *et al.* (2022) using new higher-resolution simulations (Beyer *et al.* 2020; Krapp *et al.* 2021). These data are explored further in Figure 5 to demonstrate the spatiotemporal variability of different biomes in eastern Africa throughout the Middle to Late Pleistocene. Figures 3 and 5 demonstrate that tropical xerophytic shrubland was the most dominant biome type in the region, thus representing a core habitat for early human populations that

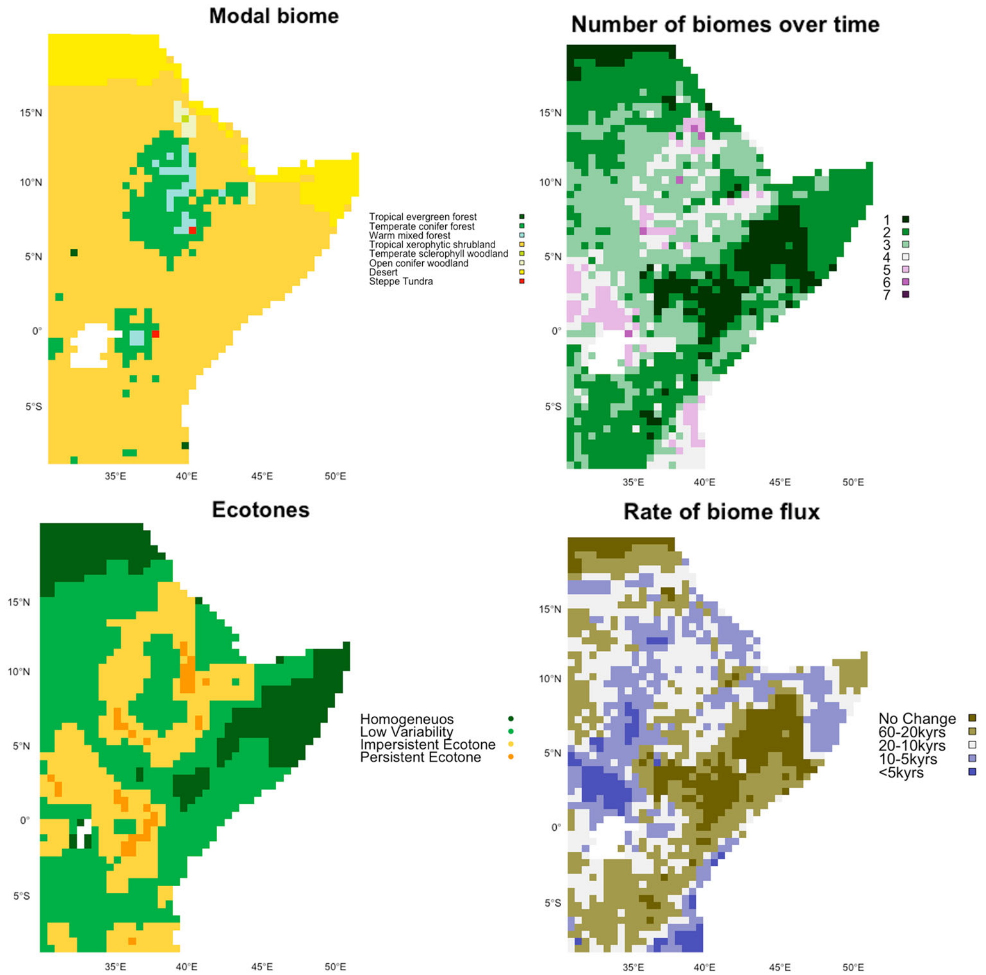

Figure 5. Changing biome distributions during the eastern African Middle Stone Age (21–320,000 years ago following Blinkhorn and Grove [2021]), including modal biome (top left), number of biomes present (top right), the presence of ecotones between open and forested landscapes (bottom left) and rate of biome flux (bottom right). Data from Krapp *et al.* (2021) is employed in pastclim (Leonardi *et al.* 2022), extending the work of Blinkhorn *et al.* (2022).

was likely rooted much earlier in hominin evolution (Timmerman *et al.* 2022). Yet Figure 5 also demonstrates that ecologies within the region fluctuate asynchronously and at different rates in different areas; for example, coastal Kenya is found to change rapidly (every 5–10,000 years or less) whereas the Ethiopian highlands fluctuate at a slower rate (every 10–20,000 years; Figure 5). This supports trends highlighted by diverse proxy and lake records across eastern Africa of asynchronous ecological change.

MSA occupations have been found to be more prevalent during interglacial phases (MIS 3, 5 and 7; Figure 3), with the occupation of more diverse and widely distributed environments during these periods (Blinkhorn and Grove 2018, 2021; Timbrell *et al.* 2022a). Ecotones between open and forested biomes are suggested to have been a core environment for human populations (Blinkhorn *et al.* 2022; Timbrell *et al.* 2022a), supported by the distribution of sites tending to fall in areas implicated as either persistent or impersistent ecotones (Figure 5). Improving climatic conditions during MIS 5 are hypothesised to have facilitated the movement of populations out of lake margins and highland areas and into new environments (Basell 2008), eliciting new behavioural adaptations (Blinkhorn and Grove 2018). This corresponds with evidence from Chew Bahir where the development of humid conditions coincides broadly with the earliest *H. sapiens* fossils in the region (Schaebitz *et al.* 2021). During MIS 3, populations occupied cooler landscapes than seen previously during the MSA, specifically within mountainous settings, likely as a response to the extreme temperatures experienced during this phase (Timbrell *et al.* 2022a; Figure 3). It appears that more suitable habitats were a 'pull' factor for population expansion during the MSA, with volcanic and tectonic activity acting as a 'push' factor and both stimulating migrations within and out of eastern Africa (Basell 2008).

The complex landscape of cultural evolution in the Middle Stone Age

Understanding the role of eastern Africa in the evolution of Homo sapiens

This review has highlighted that eastern Africa possesses a mosaic of MSA lithic technology with few spatiotemporal trends, a blurring of strict boundaries with both the ESA and LSA and an absence of regionally diagnostic artefacts (Table 1). It also has a diverse ecological patchwork, with low seasonality due to its equatorial position, high topographic relief and habitat heterogeneity as result of tectonics and the existence of the Rift Valley. MSA sites tend to be found in areas characterised by high rainfall, low temperature, high net primary productivity and high altitude, as well as having variable and fluctuating biomes rather than any single habitat type (Figures 3–5). Such rich and diverse landscapes were likely key for human survival, offering assorted resources within the foraging range of increasingly mobile populations (Basell 2008). In view of this, I propose that Scenario A in Table 2 could most accurately capture the long-term evolutionary dynamics reflected in the eastern Africa MSA record. Archaeological and climatic evidence converge to implicate both a spatially and temporally fluctuating physical and social landscape. Shifting selective pressures in the region would have led to a series of small adaptive peaks within behaviour space and a dynamic fitness landscape. Populations could potentially have adapted to move between these small peaks without detrimental effects on fitness through the development of a flexible and 'generic' MSA material culture, a process captured in the archaeological record at Olorgesailie (Potts *et al.* 2018, 2020). This may explain the lack of 'specific' innovations in the region, as these should only arise when the reward of time invested in traversing a steep adaptive peak exceeds the risk of not having done so.

Eastern Africa occupies a central position within the continent, with climatic shifts facilitating the formation of migration corridors between different areas of Africa at varying times (Blome *et al.* 2012; Mirazón Lahr and Foley 2016; Miller and Wang 2022). Variability in the eastern African MSA may therefore also be linked to interaction with other regions. For example, Miller and Wang (2022) have claimed that evidence from ostrich eggshell beads suggests regional connections between eastern and southern Africa that were periodically broken down during periods of climatic deterioration.

Within eastern Africa, the archaeological record at Olorgesailie highlights how MSA populations increased mobility and moved over greater geographic distances in order to grapple with increasingly varied environments, leading to the maintenance of long-distance regional networks (Brooks *et al.* 2018; Potts *et al.* 2018). Refugia modelling has suggested that, whilst the ecosystem was variable, eastern Africa exhibited consistently suitable conditions for habitation within Pleistocene Africa (Blinkhorn *et al.* 2022; Niang *et al.* 2023), with clear potential for promoting demographic growth and interconnectivity (Mirazón Lahr 2012). Archaeological evidence concedes that eastern Africa supported increasingly dense populations throughout the Middle and Upper Pleistocene (Shipton *et al.* 2018; Ambrose 1998; Tryon and Faith 2016), reinforced tentatively by genetic estimates of effective population sizes (Lipson *et al.* 2022). Theoretically, high rates of cultural innovation are expected in large effective populations (Powell *et al.* 2009) and this is supported by the observed technological diversity between eastern African MSA sites (Blinkhorn and Grove 2018, 2021; Shea 2020). Whilst the region has been suggested to be too large and diverse to be treated as a single homogenous refugium (Mirazón Lahr 2012; Blinkhorn *et al.* 2022), something also highlighted here in Figures 3–5, large areas were likely able to maintain populations whose migratory behaviour changed through time and space, with dynamic mosaic habitats helping to mediate the distribution, density and interaction of social networks at a local and regional scale.

Archaeological evidence suggests that novel innovations may have enabled the occupation of new environments within eastern Africa. For example, MSA lithic assemblages dated to MIS 5 have been found to coincide with an increase in habitat variability, reflecting a shift towards the occupation of previously uninhabited ecologies associated with new constellations of technological behaviours (Blinkhorn and Grove 2018; Timbrell *et al.* 2022a). Data from Panga Ya Saidi, however, suggest that beads were in use in coastal regions of eastern Africa before inland areas (d'Errico *et al.* 2020), implying that innovations did not just occur within core landscapes but also at the peripheries. Stone tools play an active role in subsistence procurement, and thus new technologies help facilitate expansion into previously unknown ecologies by offering access to diverse food resources. Movement away from these core zones may have been particularly important when faced with an increasingly packed landscape, that provided increased capacity for technological innovation (Tryon 2019). Beads, on the other hand, as well as ochre and other symbolic behaviours, were likely manufactured to signal group identity and aid social cohesion, which would have become particularly important for foraging groups in newly occupied areas of increased ecological risk (Whallon 2006).

Poor chronological resolution of the eastern African MSA currently precludes any further assessment of more localised dynamics, even though fluctuations at smaller spatial scales are almost certainly reflected in the archaeological diversity discussed here. Nevertheless, the current data do show that eastern Africa afforded early *H. sapiens* populations a rich variety of resources; the signal of cultural variability from the region thus likely reflects a fluid rugged landscape of multiple adaptative peaks. Aspects of cultural consistency in eastern Africa (Groucutt *et al.* 2015; Miller and Wang 2022) may reflect its role as a core refugial zone (Blinkhorn *et al.* 2022; Mirazón Lahr 2012), with strong inter- and intra-regional social connections across wide areas. This combination of low resource risk, high resource variability and increasing population density and mobility could explain why there are few clear signs of regionalisation in this region of Africa, as well as the persistence of a highly variable but 'generic' MSA material culture.

Eastern Africa within the context of continental-wide cultural change

Evidence from across Africa helps to shed led light on drivers of cultural change during the MSA. Strong evaluation of the West African record is hindered by the current paucity of data from this region; even so, notable similarities and differences with eastern Africa can be observed. For example, some well-studied sites in Senegal demonstrate high temporal variability in core reduction and tool assemblages (Robert *et al.* 2003; Scerri 2017; Chevrier *et al.* 2018), yet other areas of West Africa demonstrate longer-term stability (Niang *et al.* 2020, 2023). For example, Tiémassas is located in a broadly similar ecological context to that of Panga ya Saidi in Kenya, occupying a coastal location at close proximity to mangroves in ecotonal grassland and potential woodland settings (Roberts *et al.* 2020; Faulkner *et al.* 2021). However, considerable cultural dynamism is apparent at Panga Ya Saidi with an early onset of the MSA/LSA transition (Shipton *et al.* 2018), when compared to the consistency of technology at Tiémassas (Niang *et al.* 2020). Ndiayène Pendao in northern Senegal also features a late persistence of classic MSA core axes, basally thinned flakes, Levallois points and denticulates, right up until the transition to the Holocene (Scerri *et al.* 2017). In a regional synthesis, Niang *et al.* (2023) demonstrated that stable and enduring lithic reduction practices persisted across West Africa between 150 and 10 kya.

Western Africa appears slightly chronologically offset compared with other African regions, although with comparable 'generic' patterns of cultural change to eastern Africa. Such similarities may relate to both areas being highlighted as equatorial refugia by Blinkhorn *et al.* (2022) and Niang *et al.* (2023). At low latitudes, small scale climatic fluctuations have been found to drive longitudinal fragmentation of African forests during alternate wet-dry phases, leading to periodic appearances of resource-rich ecotones that were key refugia for hominins and thus encouraging population growth within these regions (Kaboth-Bahr *et al.* 2021). However, western Africa is relatively isolated from other regions of the continent, forming a discrete evolutionary realm within a persistent forest 'island' that was supported by a remote river basin network (Cerasoni *et al.* 2023). It could be hypothesised that the late persistence of MSA technology in western Africa, and overall cultural consistency across extended timeframes, was linked to an overall low rate of ecological flux (Blinkhorn *et al.* 2022; Niang *et al.* 2023), as well as to potentially limited inter-regional interaction with other areas of Africa. Enduring, low-risk and stable resources have similarly been suggested to underpin the persistence of ESA technological systems in the southwestern Cape of South Africa (Archer *et al.* 2023). Cultural change requires shifting to a different adaptive peak, which would be maladaptive in an otherwise smooth fitness landscape, except in the face of significant social or environmental disruption. Cultural consistency should therefore be expected within more stable ecologies and demographies. In this vein, the early onset of the LSA in coastal regions of eastern Africa may conversely relate to dramatic environmental flux, requiring behavioural flexibility to enable shifting between changing peaks to facilitate engagement with varied ecologies within relatively short evolutionary timescales.

In contrast to equatorial regions, the MSA records of southern and northern Africa demonstrate signals of punctuated change (Table 1). These areas exhibit both continuous and discontinuous elements that have been characterised as a series of 'specific' MSA industries against the backdrop of the 'generic' MSA (Will *et al.* 2019; Scerri and Will 2023). Due to their more extreme latitudinal positioning, populations in these areas of Africa were likely more exposed to climatic and demographic shifts compared to equatorial regions (Blome *et al.* 2012), with modelling suggesting smaller and more isolated pockets of stable precipitation refugia around the southern African and Maghreb coasts compared to those at lower latitudes (Blinkhorn *et al.* 2022). Climatic-forced habitat perturbation would have had a profound impact on population density and connectivity through time in these areas; for example, the expansion of the Sahara Desert ~130 and 75 kya likely limited populations to habitats close to fresh water sources, leading to similarities in certain aspects of lithic technology along hydrological networks (Scerri *et al.* 2014). Major innovations across diverse biomes within southern Africa have been linked to climate change towards more humid conditions (Ziegler *et al.* 2018; Wilkins *et al.* 2021; Mackay *et al.* 2022). Southern and northern regions of Africa may therefore have seen historically contingent variations on Scenarios A–D (Table 2), resulting in structured patterns of cultural efflorescence and the sporadic appearance and loss of cultural traits.

Scenario B (Table 2) may be particularly important for understanding the appearance of MSA innovations, due to both the cause (risk) and capacity (population size) for increases in cultural complexity being present. For example, in areas experiencing climatic change populations may have innovated new technological solutions to respond effectively to shifts in resource predictability and distribution (d'Errico *et al.* 2017). This is seen in well studied regions of South Africa, like the southern Cape coastal plains (d'Errico *et al.* 2017), as well as in the more arid Succulent Karoo Biome, where innovation appears to have been responsive to environmental conditions (Mackay *et al.* 2022). Additionally, or instead, populations may have increased mobility and extended their social networks to mitigate against risk, therefore maintaining large effective population sizes and the capacity to innovate (Powell *et al.* 2009). This could also explain the widespread appearance of new 'specific' innovations, as has been proposed for the Still Bay and the Howiesons Poort (Ambrose and Lorenz 1990; McCall and Thomas 2007; Powell *et al.* 2009). Shared traditions likely benefitted early human co-operation in the face of climatic stress, promoting sociality between neighbours and increasing information sharing throughout a broader network. Mackay *et al.* (2014) suggest that population interaction, mediated by climatic change that facilitated coalescence, was a significant driver of the increased appearance of symbolic artefacts in southern Africa. In this study, population interaction appears to breakdown during periods of habitat fragmentation, due to the interrupted transmission of cultural information (Mackay *et al.* 2014). Population size likely was key for maintaining social networks across wide areas; analyses of Khoe-San genomes predict a period of decreased effective population size from 100,000 years ago (Schlebusch *et al.* 2020).

Simulation studies have shown that dramatic environmental change can also lead to a rapid loss of traits that are not useful in a new environment (Kolodny *et al.* 2015), resulting in either population migration and/or extinction (Scenario D; Table 2) or cultural change through shifting to a new adaptive peak (Scenario B–C; Table 2). Figure 6 captures how evolution in alternating conditions could theoretically lead to the appearance and subsequent disappearance of 'specific' MSA adaptations and also the consistent readoption of the 'generic' MSA. In this model, changes in climate and demography abruptly alter the fitness landscape, leading to the redundancy of 'specific' adaptations in new conditions and evolution towards the global optimum, in this case the 'generic' MSA (Scenarios C–D; Table 2; Figure 6). This process is most notably observed in southern regions of South Africa (see also Mackay *et al.* 2022). For example, the period following the Howiesons Poort sees the loss of Howiesons Poort-like traits, such as bow-and-arrow technology (Lombard and Pearson 2011), as well as an increase in experimentation, decrease in investment in tool manufacture and higher variability between coeval sites as populations dealt with new challenges and regained momentum for attaining new fitness levels (Lombard and Parsons 2011; Conard *et al.* 2012; Timbrell *et al.* 2022b; Figure 6).

Finally, it is worth noting that distinguishing the 'specific' MSA from the 'generic' MSA has typically been based on historical qualitative interpretations of the African data established early in the study of human evolution (Goodwin and van Riet Lowe 1929). Some scholars have since rejected the distinction of these assemblages, suggesting that dividing the MSA record into industries is neither necessary nor useful, as many industries are not archaeologically meaningful units of analysis (e.g. Shea 2020; Wilkins 2020). Some historic definitions of 'specific' MSA industries are increasingly being recognised as problematic, such as the Pietersburg (de la Pena *et al.* 2019) and the Sangoan (Taylor 2022). Regional and inter-regional data-led synthetic analyses will ultimately determine the validity of dividing the MSA record using such frameworks, although further work should also aim to establish whether the 'specific' MSA should, in fact, be considered more innovative or culturally complex than the baseline of the 'generic' MSA, particularly in the light of complex landscapes of cultural evolution. This review applies this body of theory to elucidate the mechanisms driving differences in regional expressions of the MSA (Table 1; Figures 2–6), regardless of whether these are ultimately labelled as belonging to pre-defined industries, like the Aterian, Lupemban or Still Bay.

Conclusion

This article proposes that variability in eastern African MSA toolkits may reflect 'generic' but flexible adaptative strategies that facilitated the procurement of a wide range of resources across mosaic habitats. Different constellations of tools and behaviours were likely deployed from a baseline repertoire of cultural and technological knowledge that was variably expressed through both time and space in response to distinct social or environmental settings at a local level. Future modelling and empirical work can use and build upon the hypotheses within this review to explore the role of demography and ecology, and the interaction between the two, in generating different aspects of behavioural diversity in human populations. This includes the interplay between

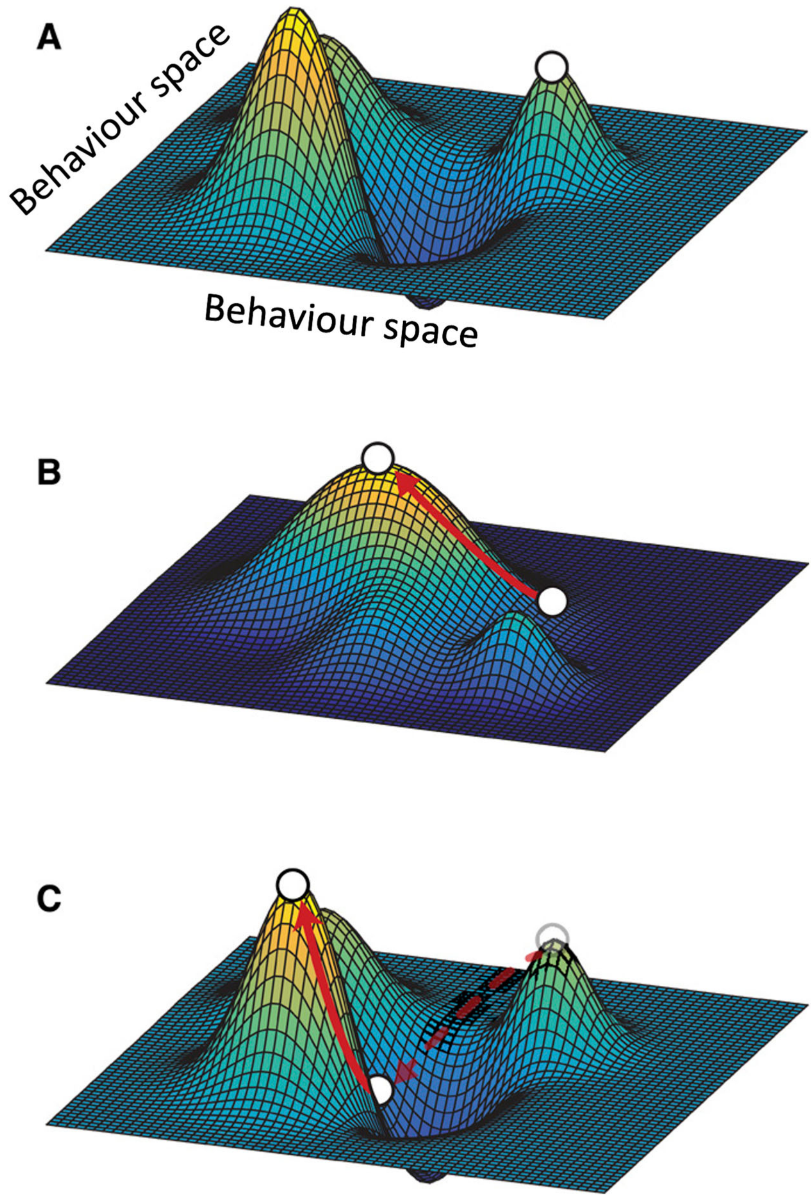

Figure 6. Simplified model representation of how evolution in alternating environments that help modulate the fitness landscape can lead to the crossing of fitness valleys within 'behaviour space' and the adoption and loss of different behavioural solutions. The solid red arrow indicates an evolutionary pathway following increasing positive selection pressure. (A) A population with a 'specific' cultural adaption (circle) sits at an optimum separated from the global optima by a fitness valley; (B) A change in the social and/or physical environment alters the fitness landscape such that the population adopts a new cultural response that previously resided in the valley within behavioural space; (C) Upon return to the original environment, that cultural adaptation now resides in the fitness valley, but the population can now evolve to the global optimum, which lies uphill. Figure modified after Steinberg and Ostermeier (2016; CC BY-NC 4.0).

population density, innovation and adaptation that likely led to the 'generalist specialist' niche specific to humans (Roberts and Stewart 2018) and their eventual colonisation of all environments across the world.

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Data availability statement

Data and code to reproduce Figures 1, 4 and 5 in this article can be found here: https://github.com/lucytimbrell/ecodemo

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