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Did climate change make *Homo sapiens* innovative, and if yes, how? Debated perspectives on the African Pleistocene record

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ABSTRACT

Our enhanced capacity to innovate is a key feature that sets *Homo sapiens* apart as a species. The Middle Stone Age archaeological record of Pleistocene Africa documents the emergence and elaboration of this capacity, and its relationship to changes in past climate and environments. However, the models and interpretations developed to understand the relationship between early *Homo sapiens'* innovativeness and climate change are varied and often contradictory. Here, we review these contrasting interpretations. We contend that while climate change may have influenced early human innovation, it was in an inconsistent and multifaceted way.

1. Introduction

Homo sapiens evolved in Africa during the Middle Stone Age (MSA), and this is a critical period for understanding the nature of human-environment interaction and human sociality from a deep-time perspective. MSA innovations, such as complex technologies and the symbolic roots of art and language, set the foundation for the massive, technologically reliant, globally connected community that we are today. The enhanced human capacity for innovation is often considered a key trait that distinguishes us from other primates and hominins, and the concept of innovation is receiving increased attention across the many subfields of evolutionary research including archaeology, primatology, and developmental psychology.

The archaeological record reveals that human capacities for innovation have roots in the Middle and Late Pleistocene in Africa, based on evidence across the continent attesting to the first-time use of symbolic resources, new technologies, and new foraging strategies (McBrearty and Brooks, 2000; Scerri and Will, 2023). The first humans were foragers, getting all their needed resources from the natural landscape around them. To optimize their foraging efforts, early *Homo sapiens* moved around the landscape so that their families were close enough to valuable resources when they needed them (Ambrose and Lorenz, 1990; McCall and Thomas, 2012). To mediate the effects of changing resource availabilities, human foragers also create and maintain social networks that facilitate critical information exchange (Stewart et al., 2020; Wiessner, 1982; Yellen, 1986), and optimize technologies, which often requires extensive knowledge about multiple material types and complex manufacturing processes (Lombard and Haidle, 2012). Over the course of the MSA, *Homo sapiens* innovations accumulated. This includes, for example, the emergence of long-distance, high velocity projectiles like the bow-and-arrow to increase hunting success and survival over the use of hand-delivered weapons (Backwell et al., 2018; Lombard, 2011; Shea, 2006). In the Late Pleistocene, early humans also began recording information on material objects, which represents the origins of art and language (d'Errico et al., 2001; Henshilwood et al., 2009; Henshilwood et al., 2018), and making personal ornaments out of shells, which serve as a medium for communicating information about identity and group membership (Bouzouggar et al., 2007; d'Errico et al., 2005). In coastal contexts, Late Pleistocene foragers figured out and shared information about tidal timings so that they could harvest large amounts of high-quality, nutritious shellfish (Marean, 2011, 2016).

Recent emphasis has been placed on understanding the role of climate and environmental change on the emergence of these innovations, with conflicting results. For example, Ziegler et al. (2013) compared the timing of two Late Pleistocene technocomplexes in southern Africa, the Still Bay (SB) and the Howiesons Poort (HP), with the timing of humid pulses based on discharge data from a sediment core at the mouth of Great Kei River. The timing of the technocomplexes and humid phases roughly correlated, and thus it was argued that rapid cooling events in Marine Isotope Stage 4 (MIS 4, 71 - 59 ka) created selective pressure promoting new technologies (bifacial points and backed pieces, respectively) that characterize the Still Bay and

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Howiesons Poort technocomplexes (Ziegler et al., 2013). In contrast, Roberts et al. (2016b) examined several environmental proxies at the archaeological sites of Blombos Cave and Klipdrift Rockshelter, finding that significant changes in vegetation, aridity, rainfall seasonality, and sea temperature did not correlate with changes in technology and material culture (specifically shell beads, ochre, bone tools, lithic raw material). Thus, based on this lack of correlation they argued that climate change (e.g., MIS 4 cooling) was not implicated in the emergence of SB and HP innovations in the Late Pleistocene.

Here, we consider these conflicting conclusions and other views about the role of climate change in the emergence of human innovation and innovativeness. Through a review of existing studies and archaeological data, we consider how to archaeologically identify innovativeness and assess the relationship between climate change and human behavioral evolution. We start by discussing the definition of innovation, then provide background on the environmental context for human evolution in Africa, followed by an overview of the key hypotheses and models that propose climate-driven environmental stimuli for *Homo sapiens* evolution, and the key hypotheses and models that counter environmentalist approaches.

2. Identifying early innovation and innovativeness

Innovation is a commonly used term, but it is defined slightly differently between researchers and across different fields (Bandini and Harrison, 2020; Fogarty et al., 2015; Lew-Levy et al., 2020). The ethological definition of innovation is a new behavior that provides a solution to a problem (Kummer et al., 1985; Ramsey et al., 2007), and many different animal species innovate in this way (Bandini and Harrison, 2020; Ramsey et al., 2007; Reader and Laland, 2001). In archaeology, innovation is often considered distinct from invention, where invention is a new idea, method, or tool, and innovation is an invention that builds on previous ones, adding value to existing processes and adaptations, and spread across a population via social learning (Fogarty et al., 2015; Walsh et al., 2019). This latter characteristic of innovation means that innovations occur at high enough frequencies to be detectable in the archaeological record (Fogarty et al., 2015). With its emphasis on transmission and social learning, the archaeological definition of innovation includes the process of cumulative cultural evolution, which is the result of knowledge, behavior, and technologies accumulating over time across multiple generations (Boyd and Richerson, 2005). The capacity for cumulative cultural evolution is rare in the animal kingdom and unlike other species, humans rely intensively on it (Boesch and Tomasello, 1998; Boyd and Richerson, 2005; Tennie et al., 2009). Thus, the archaeological definition of innovation is most relevant to understanding the MSA record of changing *Homo sapiens*' behaviours from an evolutionary perspective.

Innovativeness can be thought of as the tendency to embrace innovation, to invent and adopt new things, techniques, and ways of life (Frieman, 2021). When considering the record of human evolution, this is about identifying new capacities for innovation, for introducing and spreading novel behaviours. Greater innovativeness is associated with more frequently adopting more new ways of doing things and recognized archaeologically through increased variability and/or increased rates of material culture change. Importantly, innovativeness is not equivalent to complexity – as innovation can lead to a new way of achieving a goal that may be less complex than previous methods.

One potential way to recognize innovativeness is via the evidence for new behaviors not previously recognized in the archaeological record. Along this vein, innovation in early *Homo sapiens* is often linked to the concept of 'modern human behavior'. The phrase 'modern human behavior' originated as a means of describing the whole suite of 'unique' behaviors that characterize *Homo sapiens* as a species (Henshilwood and Marean, 2003; McBrearty and Brooks, 2000). From an archaeological perspective, this was marked in the archaeological record by artefact types and technologies that were known to be associated with early hunter-gatherer *Homo sapiens* across Eurasia and Africa, including artefacts with symbolic relevance (i.e. ochre, beads, engraved pieces), artefacts on diverse raw materials like bone, shell, and antler, technologies with multiple components like high-velocity projectiles, and evidence for the exploitation of new resources and ecologies (i.e., fishing and shellfishing). The phrase, 'modern human behavior' is falling out of favor, in large part due to the inadequacy of the concept for explaining the high degree of variability seen in archaeological record (Shea, 2011), and increasing evidence for admixture, hybridization, and interaction between Pleistocene hominin populations that problematizes any kind of real boundary between 'modern' and 'not modern' (Ackermann et al., 2016). Nonetheless, evidence for many new kinds of behaviours appear first during the Pleistocene and there is consensus that these new behaviours signal new cognitive, social, and/or adaptive capacities in many cases. Effectively, these new behaviors reflect innovations in that they represent new ideas, methods, or tools that were valuable enough to be passed down multiple generations and thus have visibility in the archaeological record.

Another potential way to recognize innovativeness is via increased evidence for behavioral variability. Humans today exhibit extreme behavioral plasticity, mediated by culture and technology, which permits us to adapt rapidly to new environments and situations. The African archaeological records show that by the Middle Pleistocene (~200 ka) humans exhibited the same capacity for behavioral variability as *Homo sapiens* in the Late Pleistocene and early Holocene (Shea, 2011). This is based, in part, on the representation of Clark's various 'technological modes' in eastern African Middle Pleistocene lithic assemblages (Shea, 2011); assemblages variably contain core tools (Mode 1), large bifaces (Mode 2), prepared cores or points (Mode 3), and blades (Mode 4). This high degree of variability may indicate that early humans were adaptable, generating new innovations when needed.

Variability across geographic space may also attest to human innovativeness during the MSA. It has also been suggested that regional diversification, represented by the different lithic industries and point styles, reflects different 'cultures' and/or human adaptations across the African continent (Clark, 1959, 1970; Lahr et al., 2001; McBrearty and Brooks, 2000). This regionalization differs from earlier time periods; the Acheulean is considered to have been relatively homogenous across geographic space.

Evidence for the occupation of extreme environments may also be used to identify innovativeness in the archaeological record. The capacity for behavioral variability explains how humans have been able to occupy diverse and extreme environments. Humans have been described as "generalist-specialists", which means they have a broad capacity to thrive in various niches, through specialist adaptation to local conditions (Roberts and Stewart, 2018). This characteristic is what has enabled humans to occupy and thrive in environmental extremes such as deserts, high altitudes, the arctic circle, and dense tropical forests. By the MSA, humans were occupying the Central African rainforest (Mercader, 2003), the Sahara, Kalahari and Namib deserts (McCall et al., 2011; Scerri, 2017; Wilkins et al., 2021), and the Lesotho Highlands (Stewart et al., 2012). Innovations and innovativeness are likely to have helped facilitate this.

In sum, researchers have the potential to recognize innovativeness in the archaeological record of early humans in diverse ways; through evidence of new behaviors, increased behavioral variability, and habitation of new environments. The MSA record of Africa documents all these traits, especially in comparison to earlier time periods. It is important to note here that like everything, the evolution of innovativeness would not have been a linear process. Innovativeness is not optimal in all situations, nor would it have been universally valuable or valued (Frieman, 2021).

3. The environmental context

3.1. Pluvials and interpluvials

Researchers have long considered the relationship between palaeoenvironmental change and human evolution. From a historical perspective, however, views of African palaeoenvironments have been radically shifting over time. Largely influenced by research in Europe, early considerations attempted to establish named periods of contrasting wetter and drier hydroclimate conditions. For example, “East African Pluvials” refer to periods of enhanced precipitation and increased lake levels that occurred during the late Pleistocene and early Holocene (Davies, 1956; Leakey, 1931; Nilsson, 1949). Terms used to describe these pluvial periods included Kageran, Kamasian, Kanjeran, and Gamblian. Originally these period names were used as a climato-stratigraphic relative chronological system, but they are not used anymore. Increased evidence for human occupation was largely believed to have been tied to pluvials, with abandonment or smaller populations during interpluvials. In many ways this idea that humans thrived during wetter periods has persisted to the modern day. It was also originally believed that the pluvials correlated to glacial periods in Europe (the “pluvial hypothesis”), which is now a defunct idea due the advancement of dating techniques that enable precise cross-correlation of climate events and trends both regionally and globally. Rather, some have argued that during glacial periods, Regions in eastern Africa tend to be characterized by increased aridity (deMenocal, 1995; Kappelman, 1986).

The Green Sahara refers to periods (also referred to as “Africa Humid Periods”) when North Africa experienced a wetter climate and was characterized by vegetation cover and wetlands. The concept of a “Green Sahara” has deep roots and has been supported by a growing body of research. Paleolake deposits, pollen records, and paleontological and archaeological deposits provide evidence for this wetter period (Kuper and Kropelin, 2006; Tierney et al., 2017). The presence of humans within the Sahara Desert during this period is indicated by archaeological findings (Foley et al., 2013; Kuper and Kropelin, 2006; Manning and Timpson, 2014; Masojć et al., 2019; Scerri, 2017), suggesting that the Green Sahara was inhabited and utilized by human populations. The presence of interconnected lakes, rivers, and inland deltas in the Green Sahara facilitated dispersals, as evidenced by the movement of both animals and humans across the region (Drake et al., 2011). The Green Sahara eventually transitioned to a drier environment, as indicated by paleoclimate evidence (Kröpelin et al., 2008).

3.2. Marine isotope stages

The pluvial-interpluvial system, which once dominated the study of climatic variability across much of Africa, has been superseded by the Marine Isotope Stages (MIS) classification framework. MIS are defined by shifts in the isotopic composition of marine sediments, providing a globally applicable framework for understanding past climate changes. The LR04 stack is a compilation of marine oxygen isotope records from 57 deep-ocean sediment cores around the world, and MIS are defined based on these data (Lisiecki and Raymo, 2005). Changes in the ratio of oxygen isotopes δ18O to δ16O in benthic foraminifera (ocean-floor fossils) can be used to track shifts in global ice volume. This, in turn, is related to global temperature and sea levels. Each MIS is numbered, with warmer inter-glacial periods given odd numbers and cooler, glacial periods given even numbers. These data provide a near-continuous record of climate change over the last 2.6 million years and are invaluable for providing a framework of long-term environmental change and its relationship to archaeology. MIS at a global scale may not be great representations of climate for all regions (discussed further below), but they are frequently used by researchers to temporally structure the archaeological record, and in the development of models for early human behavioral change (e.g., Mackay et al., 2014; Stewart and Jones, 2016).

Along the south coast of South Africa, sea level changes have been modelled with respect to MIS (Fisher et al., 2010; Van Andel, 1989). The broad and wide Aghulus Plain, extends out from the south coast and its topography means that slight changes in sea level result in large changes in the landscape. Today, several MSA sites occur in sea caves along the modern-day coast, however, lower sea levels in the past would have resulted in the coastline being more distant from the sites. For example, in MIS 4, sea levels dropped by nearly 100 m, and the archaeological site of Pinnacle Point 5–6 was as much as 79 km away from the coast. During these times, the MSA sea cave sites were inland rather than coastal and this has very different implications for human foraging strategies and adaptations (Marean, 2010; Marean et al., 2014, 2015). The exposed Agulhas plain would have supported savanna vegetation and animals when sea levels were low (Klein, 1972). In contrast, when sea levels were high or equivalent to today, the environment is characterized by the Cape Floristic Kingdom and abundant marine resources are available (Compton, 2011). In coastal areas along the western and eastern coasts of South Africa where the continental shelf is steep, palaeoenvironmental changes would not have been as pronounced because sea level changes would not have resulted in as dramatic changes in the coastline location (Fisher et al., 2010, 2013).

Views on the impact of MIS on rainfall patterns in southern Africa have been changing over the last several decades. The region is divided into two main rainfall zones – the Summer Rainfall Zone (SRZ) which receives most of its rainfall during the summer months and the Winter Rainfall Zone (WRZ) which receives most of its rainfall during the winter months (Chase and Meadows, 2007). The SRZ extends across the interior of southern Africa and the eastern coast, and the WRZ has a more limited distribution across the western and southern coasts. Where the two zones meet is called the Year Round Zone (YRZ) and rainfall is distributed more equally across the year. It is predicted that the location of the boundary between the SRZ and WRZ changed in response to global temperatures and sea levels, but there have been contradicting perspectives on how. Palaeoenvironmental records at key archaeological sites were originally interpreted as indicating that the WRZ contracted during cooler MIS (MIS 2, 4, 6 etc) and resulted in drier conditions (Bar-Matthews et al., 2010; Deacon et al., 1984; Klein, 1972, 1980; Klein et al., 1983; Van Zinderen Bakker, 1983). Other studies indicate that the winter rainfall expanded during the cooler MIS, causing some regions to become wetter (Chase, 2010; Chase et al., 2018; Faith, 2013). Continued research is teasing out the complexities in this relationship between the rainfall zones and MIS, with a focus on the drivers behind some of these changes.

How glacial/interglacial periods and their relative changes in sea level affected the interior regions of southern Africa is less well-known than in the coastal and near-coastal areas. Historically, there has been a general consensus that glacial periods would have caused drying across much of the African continent, posing more challenges for early human hunter-gatherers (Ambrose and Lorenz, 1990; Barham and Mitchell, 2008; Foley and Lahr, 1997; Klein, 1999; Lahr and Foley, 1998; Mackay et al., 2014; Willoughby, 2007; Wurz, 2019). New evidence from the Kalahari and Karoo have been challenging this view. At Ga-Mohana Hill in the southern Kalahari Basin, tufa formations dated by U–Th show that much of MIS 4 was wetter than today (von der Meden et al., 2022). In the middle Kalahari, similar evidence shows wet periods during MIS 2, 4 and 6 (Burrough, 2016; Collins et al., 2014; Wiese et al., 2020). Furthermore, the Kalahari is not abandoned during glacial periods, with several archaeological deposits now dating to MIS 2, 4 and 6 (Chazan et al., 2020; Robbins et al., 2016; Wilkins, 2021). Large, now-dry palaeolakes existed through parts of MIS 2 in the interior Karoo region of South Africa (Carr et al., 2023).

In synthesizing these data, it becomes apparent that not all regions responded to MIS scale changes in the same way and/or different researchers have come to contrasting conclusions based on the specific evidence used. In a meta-analysis of African palaeoclimatic data from

~150 to 30 ka, Blome et al. (2012) aggregated multiple palaeoenvironmental and archaeological datasets across the African continent. In general, they found a poor fit between MIS and local environmental (Blome et al., 2012). Rather, periods of increased aridity were asynchronous and palaeoclimatic conditions throughout the continent were spatially and temporally varied. The variable responses to MIS are the likely result of complicated interactions of numerous local factors and atmospheric dynamics (Blome et al., 2012). This kind of work highlights the importance of identifying local paleoenvironmental changes wherever possible and not relying exclusively on MIS. While in many ways researchers have moved beyond the issues of the old pluvial scheme, in many ways they have not, instead using MIS as a replacement. But climate drivers can and do vary within MIS and can impact environments in spatially varying ways (e.g., Singarayer and Burrough, 2015; Thomas et al., 2012; Weij et al., 2024).

3.3. *Dry is bad, wet is good?*

The prevailing perception has long been that dry periods in Africa were detrimental for human populations, while wet periods were favorable. However, empirical evidence challenges this simplistic understanding in many contexts. Studies examining past climate and archaeological records have revealed that African populations have demonstrated remarkable resilience and adaptability to both wet and dry periods. Desiccation of the Green Sahara starting ~7 ka, for instance, has been associated with the spread of innovative strategies such as pastoralism across North Africa, which allowed communities to thrive in arid environments (Gatto and Zerboni, 2015; Kuper and Kropelin, 2006). Conversely, wet periods can have their own challenges, including increased disease prevalence (Trájer et al., 2020; Wadley, 2012).

During the Pleistocene, in the tropical regions of Africa, there is a pattern of increased site abundance during periods of amplified aridity, particularly between ~115–90 ka (Blome et al., 2012). This may be the result of forest fragmentation and the expansion of savannah grasslands. Support for this pattern is found in the faunal assemblages at sites in central Africa, where site occupation coincided with dryer intervals when open grassland habitats were more abundant. Faunal assemblages include fossils of species that favor open savanna grasslands such as zebra, ostrich and wildebeest at the sites of Kt9 at Katanda, dated to ~120–60 ka (Brooks et al., 1995) and Matupi Cave, dated to ~41–32 ka (Brook et al., 1990).

These findings underscore the need to move beyond the binary notion of “good” and “bad” periods and instead recognize the nuanced interactions between climate variability and cultural adaptations throughout Africa’s diverse landscapes. What is clear is that through the climatic variability of the Pleistocene, humans encountered varying lake and sea levels, fluctuations in rainfall patterns, and shifts between drier and wetter climates. These environmental changes had cascading impacts on resource availability, influencing the distribution of vegetation and wildlife and human occupation.

4. Hypotheses and models that propose environmental drivers for *Homo sapiens* evolution

4.1. *Refugia*

It has been proposed that certain isolated regions or habitats within Africa served as refuge areas during times of environmental change (Ambrose, 1998; Blinkhorn et al., 2022; Lahr and Foley, 1998; Marean, 2016). These refugia may have provided relatively stable and favorable conditions for human populations, allowing them to persist, innovate and pass down innovations across multiple generations, and potentially undergo unique evolutionary processes. The isolation within these refugia may have led to genetic differentiation and the development of distinct regional lineages. As the climate fluctuated, populations could expand or contract from these refugial areas, contributing to genetic diversity and influencing the overall trajectory of human evolution in Africa.

Specifically, Lahr and Foley (1998) suggested that glacial cycles led to the expansion of deserts and the fragmentation of savannas into isolated niches. This phenomenon has implications for human population sizes and distribution, and they cited evidence for genetic population bottlenecks (e.g., Harpending et al., 1993). Lahr and Foley (1998) propose two potential models for *Homo sapiens* origins, namely single refugium/single origins or multiple refugia/multiple origins, to explain the effects of savanna expansion and desertification on human populations. They cite simulations that provide stronger support for a single origin scenario.

The single origin model has been critiqued on genetic, archaeological, and theoretical grounds by Scerri et al. (2018). Instead, Scerri et al. (2018) argue for a ‘structured’ population model consisting of multiple nodes isolated in refugia, occasionally connected via genetic drift, noting that the North-South rainfall gradient across Africa is asynchronously affected by changes in the monsoonal ITCZ, the regions that are refugia under some conditions may be uninhabited in another. Using palaeoclimatic data, Blinkhorn et al. (2022) establish that persistent human occupation was possible for 28%–66% of the African continent throughout the Late Pleistocene, and that these potential refugia zones are in geographically diverse regions.

Ambrose (1998) suggested that a volcanic winter followed the Toba eruption, a supervolcanic eruption that occurred ~74 ka at Lake Toba, located in what is now Sumatra, Indonesia. It is considered one of the largest volcanic eruptions in recorded history and the environmental fallout from the eruption could have caused a significant population bottleneck in humans. Ambrose (1998) argues that there were fewer sites across Africa during MIS 4 and 3 compared to MIS 5. Additionally, Ambrose (1998) proposes that areas experiencing extremely high rainfall today, exceeding 2000 mm, may have served as refugia during the post-Toba volcanic winter. However, the extent of the eruption’s impact is still a subject of ongoing research and debate (Lane et al., 2013; Roberts et al., 2013; Smith et al., 2018), with archaeological evidence from Central India (Clarkson et al., 2020) suggesting population continuity, rather than abandonment, through the Toba eruption fallout.

4.2. *Coastal hypothesis*

Long-term and large-scale research projects have been studying the changes in resource availability and human responses to environmental changes on the south coast of South Africa (Marean, 2015, 2016; Marean et al., 2015). Based on this research, it has been argued that the Cape Floral Region (CFR) along the coast of South Africa, known for its unique flora, provided an exceptional environment for early human foragers. This region offered abundant coastal resources like shellfish, tubers, even during glacial periods, and possibly migrating large mammals when the Agulhas bank was exposed (Marean, 2010, 2014). While the Toba eruption has been hypothesized to have had a significant global climatic impact and potentially affected human populations (Ambrose, 1998; Williams, 2012), it appears that the eruption did not negatively impact human populations on the South Coast (Smith et al., 2018).

The coastal adaptation hypothesis, proposed by Marean (2014) as a specific instance of the refugia concept, suggests that human adaptation to the CFR and the rich coastline played a pivotal role in transforming human social behavior. This adaptation led to the development of cooperative behaviors and distinct prosocial characteristics that may have helped foster the spread of innovations. The predictable food sources found in the CFR, once effectively foraged by humans, stimulated territoriality, investment in boundary defence, inter-group conflict, and altruistic intra-group cooperative behaviors. Many of these new human behaviors are reflected in the first appearance of complex elements of material culture (Will et al., 2016, 2019).

Furthermore, some researchers have proposed a connection between human brain expansion, the origins of human social behavior, and increased accessibility to long-chain omega-3 fatty acids (Broadhurst et al., 2002; Parkington, 2010). These fatty acids are crucial for human brain development, and coastal resources, particularly shellfish, are abundant in this nutrient. The hypothesis suggests that regular and systematic foraging for shellfish by early humans along the west and south coasts of South Africa may have alleviated constraints on brain growth, leading to cascading effects on human life history and culture.

4.3. Variability selection

Variability selection is a concept that connects adaptive change with changing environments (Potts, 1998). It describes the process in which traits promoting adaptability across diverse environments outcompete traits that are advantageous only in specific conditions. This type of selection leads to the development of complex structures or behaviors that can respond to unpredictable and novel adaptive settings. Over the past 6 million years (Ma), there has been an observed increase in environmental variability. Potts (1998) summarizes that based on deep-sea core oxygen isotope data, that the greatest environmental variability occurred within the last 6 Ma out of the past 27 Ma, and within the last 2 Ma out of the last 6 Ma. Pollen analysis from the Tenaghi Philippon peat bog in Greece suggests even greater variability within the last approximately 700,000 years (ka) out of the last 2 Ma. Additionally, global climatic variability has gradually increased over time, with the delta 18O values spanning the entire range known for the last approximately 700 ka. Paleontological evidence demonstrates that variability selection influenced numerous faunal species in eastern Africa between 900–600 ka. Species that survived beyond this period exhibited broader dietary niches and smaller body sizes compared to those that went extinct, and thus experienced variability selection (Potts, 1998). Potts (1998) argues that variability selection provides an explanation for the mix of bipedal and arboreal adaptations observed in early hominins, who were adapted to both closed and wooded environments, and helps account for encephalization (i.e., increasing brain size) between ~600–150 ka, enabling innovation/innovativeness, and flexible *Homo sapiens'* responses to new environments. Furthermore, the replacement of Acheulean by Middle Stone Age technologies ~400 ka ago is contemporaneous with large-scale environmental fluctuations in eastern Africa (Brooks et al., 2018; Deino et al., 2018; Potts et al., 2018, 2020).

4.4. Generalized-specialist niche

Some researchers have highlighted humans' exceptional adaptability to diverse ecological conditions, including 'hard', 'marginal', or 'extreme' environments (e.g., Elton, 2008; Gamble, 1994; Roberts et al., 2016a; Roberts and Stewart, 2018; Stewart et al., 2012; Wilkins, 2021). Roberts and Stewart (2018) show that in comparisons to other members of the genus *Homo*, humans, because of our innovativeness, have a capacity to thrive in a wider range of environments while also specializing in adapting to extreme ecological conditions, which include deserts, high altitudes, and tropical rainforests. Based on this they assert that our species evolved a new ecological niche – the generalist-specialist niche. *While H. sapiens* are often highlighted as a classic example of a generalist species in that we can utilize various resources, local populations of our species are also able to specialize in the use of specific resources. For example, Pleistocene humans specialized to particular environments. In Africa, this includes the coasts of South Africa (Marean, 2016), the Kalahari (Robbins et al., 2016; Wilkins, 2021) and Namib (Dewar & Stewart, 2012, 2016; Vogelsang et al., 2010) deserts, the Lesotho Highlands (Stewart et al., 2012), and the Ethiopian Highlands (Brandt et al., 2017).

Both variability selection and the generalist-specialist niche share common ground as both models highlight the behavioral adaptability of humans. However, a significant distinction sets them apart. While variability selection is about humans' ability to adapt rapidly to temporal variation in environment, the generalized-specialist niche is about humans' ability to adapt to spatial variation in environment.

4.5. Mobility and settlement

Some researchers have focused on the impact of environmental change on mobility and settlement systems. Changes in mobility and settlement systems are related to innovation because they can reflect new foraging strategies, and/or new kinds of interaction. In a seminal study, Ambrose and Lorenz (1990) suggested that Pleistocene foragers in southern Africa generally had higher mobility during glacials than during the current interglacial. Building on this, McCall and Thomas (McCall & Thomas) argue that the unique technological characteristics of two MSA industries that date to MIS 4 the Still Bay (SB) and Howiesons Poort (HP) indicate changing mobility during a glacial period. They suggest that the SB reflects extreme mobility, and the HP reflects a logistical mobility system. Logistical mobility systems are characterized by longer occupations at residential camps and reduced residential mobility. Archaeological evidence for some sites on South Africa's southern coast supports the idea of reduced residential mobility during MIS 4. For example, Karkanas et al. (2015) found there is sedimentological evidence for increased site occupation intensity during the MIS 4 glacial compared to the MIS 5 interglacial at PP5-6. This find is further supported by the lithic technology (Wilkins et al., 2017). Similarly, Reynard et al. (2016) found increased faunal density and trampling evidence consistent with increased occupation intensity at Klipdrift Shelter during the MIS 4 H P occupation. The main conclusions drawn from this work in southern Africa is that Pleistocene humans appeared to adapt to the environmental conditions of MIS 4 by either increasing their mobility or transitioning towards a logistical mobility system, or both.

4.6. Connectedness and interaction

Regarding the response of early humans to Pleistocene climate change, some research has focused on changes in interaction and intergroup connectedness. For example, Mackay et al. (2014) propose that during MIS 4 (glacial), there was an upsurge in interconnectedness, or 'coalescence', in contrast to MIS 5 and 3 (interglacials), where human populations tended to be more fragmented and isolated (see also Pazan et al., 2022). This notion is in line with the model proposed by Ambrose and Lorenz (1990), who suggest that during MIS 2 and 4 (glacials), there was a heightened exchange of information compared to the current interglacial period. The lowering of sea levels during glacials, which exposed a continuous, flat, unobstructed coastal plain accessible to the interior, may have facilitated these increased interactions (Compton, 2011).

Furthermore, innovation and symbolism have also been linked to the glacial conditions of MIS 4. The altered distribution of resources during glacials might have favored risk reduction behaviors in humans, such as the development of reliable technologies (Bousman, 2005) and an increase in trade and exchange (Ambrose and Lorenz, 1990). Increased information exchange and interaction between groups occupying diverse environments could have buffered the effects of environmental degradation and scarce resources (Wiessner, 1982, 1983). This interaction was potentially facilitated by the use of symbolic items such as ochre, beads, and engraved objects, which can be used to help communicate group identity (Deacon, 1989; Henshilwood and Marean, 2003; McBrearty and Brooks, 2000; Wilkins, 2010, 2020; Wurz, 1999). Such enhanced interaction in early humans may have fuelled innovation by expanding the number and reach of social learning opportunities (Powell et al., 2009). Mellars (2006) posits that the emergence of new economic, social, and cognitive behaviors during MIS 4 led to a significant demographic expansion, ultimately facilitating the dispersal of modern humans into Eurasia and beyond.

On the contrary, some researchers argue that rather than supporting interconnectedness, strong glacial pulses during the Pleistocene isolated some early human populations (Lahr and Foley, 1998; Marean, 2010, 2011), particularly during MIS 6. Some genetic models suggest a bottleneck in the human lineage at about that time (Fagundes et al., 2007). Such isolated populations could have contributed to the diversification of cultures across the African continent, and the extinction of some localized, regional populations. This perspective is more aligned with the concept of refugia during glacial periods that was discussed above.

In sum, there have been many hypotheses put forth on how early humans responded to Pleistocene climate change, and how these dynamics likely shaped the cultural, technological, and demographic trajectories of early human populations. These responses include retreat and adaptation to isolated refugia, adaptation to coastal environments with trickle down effects on cooperation and sociality, enhanced behavioral flexibility, specialization to extreme conditions, changes in mobility, and increased interaction and connectedness. When consolidating these viewpoints, a significant contradiction comes to light. The question arises whether early human populations, confronted with environmental deterioration, constricted and adapted to particular environments, thereby fostering greater cultural and behavioral diversity on the continental scale (*sensu* the refugia and coastal hypotheses, for example)? Or, alternatively, did early human populations increase interaction and interconnectedness as a risk reduction strategy during this harder periods, facilitating the emergence and diffusion of novel behavioral innovations? This kind of paradox underscore not only the intricate nature of early human adaptations in the face of environmental challenges and their far-reaching implications, but also highlights the challenges researchers face in detecting, analysing, and modelling these complex adaptive processes.

5. Evidence to the contrary

5.1. A lack of correlation

Summarized above, considerable research has emphasized the role of climate driven environmental changes in shaping human origins and the evolution of *Homo sapiens*. The prevailing notion is that these changes contributed to the development of our characteristic traits such as behavioral plasticity, enhanced sociality, complex technologies, and innovativeness. Several studies support this view. For example, in their multisite meta-analysis of eastern African paleoenvironments and Stone Age site distributions, Timbrell et al. (2022) demonstrate that rainfall amount influenced lithic assemblage composition; as rainfall increased, the probability of backed microliths, borers, centripetal technology, platform cores, and scrapers decreased. In southern Africa, it's been argued that timing of the appearance of Still Bay (SB) and the Howiesons Poort (HP) correlated with the timing of humid phases (Ziegler et al., 2013). Nevertheless, there are other studies that challenge this correlation narrative.

For example, at some southern African sites with well-preserved and high-resolution archaeological and environmental data, environmental change is uncoordinated with major cultural or technological changes. At Blombos Cave and Klipdrift Shelter (South Africa), significant changes in vegetation, aridity, rainfall seasonality, and sea temperature do not correlate with changes in technology and material culture, specifically shell beads, ochre, bone tools, raw material, and the first appearances of Still Bay- and Howiesons Poort-designated assemblages (Roberts et al., 2016b). At Sibudu Cave, Wadley (2013) and Clark (2013) have indicated that there is a sharp disconnect between the timing of HP-designated assemblages and paleoenvironmental changes indicated in the archaeological record there.

Jacobs et al.'s (2008) large-scale dating program of SB- and HP-designated sites across South Africa showed that the timing of MSA industries are not consistently correlated or uniquely associated with any particular climatic attribute on the global temperature curve. In their macro-scale study of MSA variability, Kandel et al. (2016) also argue that the timing of Early MSA-, SB-, HP-, and Late MSA-designated assemblages are not associated with any particular environmental condition or conditions, and thus cultural change is not connected to environmental factors. Similarly, in their African-wide meta-analyses, Blome et al. (2012) show that changes in the frequency of archaeological sites is asynchronous with climate change.

5.2. The role of environmental stability

The premise behind the idea that climate change influenced the emergence of innovativeness in *Homo sapiens* stems from the idea that populations, groups, or lineages that lack traits to buffer environmental stress during challenging times will go extinct. In other words, only phenotypes with the capacity to withstand the more challenging periods will survive. However, an important alternate hypothesis is that some complex traits may only develop in stable environments with consistent, long-term conditions, because they permit energy-demanding traits to persist across multiple generations (see Will et al., 2021). In their meta-analysis of the fossils belonging to the genus *Homo* and environmental variation, Will et al. (2021) found a negative correlation between brain size and long-term rainfall variability. Larger brain size occurred in more stable environments, which presents a challenge to the concept of variability selection discussed above (Potts, 1998).

A key component of the coastal hypothesis is that the rich and predictable resources along the southern coast of South Africa uniquely supported *Homo sapiens* during periods of environmental stress elsewhere (Marean, 2010, 2014). The south coast exhibits a high diversity of edible underground storage organs (Singels et al., 2016) and rich and abundant shellfish communities (De Vynck et al., 2016). It's been suggested that these characteristics of the potential food supply may have facilitated the persistence of humans on the south coast during the cold glacials of the Pleistocene (Marean, 2014). Stability and persistence are actually the foundation of all the refugia hypotheses. Food supplies are not interrupted as much within the refugia, which is why people are drawn there. In this view, it is really stability within the refugia that promotes the emergence of human social and cognitive traits, rather than variability.

Humans require daily access to drinking water (Pontzer et al., 2021) and the location of dense archaeological sites tend to correlate with stable water sources (Schoville et al., 2022). Prior to the MSA, Earlier Stone Age (ESA) sites are frequently stated to be associated with permanent water sources. Perhaps one of the earliest references to Acheulean sites being located close to water was by Clark (1959) who noted that places favored by ESA foragers were "along the river banks, where ESA tools are found so frequently" (p.103). Few studies have examined the relationship between water availability and MSA occupation, but Sampson et al.'s (2015) work in the Seacow River Valley survey only found a small difference between the distance ESA sites are located from springs (3 km) compared to the MSA (bimodally around 2.5 and 4.5 km). Stable access to water is a key component in human occupation in a region, thus providing opportunities for innovation.

5.3. Other factors

If environment did not drive innovation, what did? Non-environmental factors could include population size and distribution (Powell et al., 2009), inter-group and even inter-species interaction (Ackermann et al., 2016), various cultural and social dynamics, and local historical trajectories. Demographic arguments for changes in cultural complexity posit that a population size threshold had to have been met in order for certain behavioral traits to appear (Powell et al., 2009); however the hypothesis has not stood up to testing (Fay et al., 2019; Vaesen et al., 2016). Inter-group and inter-species interactions can promote innovation by facilitating the sharing of ideas and increasing diversity (Ackermann et al., 2016). These interactions can lead to the development of new strategies, adaptations, and solutions that contribute to the survival and success of the groups or species involved.

That groups interacted across Africa during the MSA is evidenced by the long-distance transfer of stone, ochre, and ostrich eggshell raw materials and finished products (Brooks et al., 2018; Stewart et al., 2020; Wilkins, 2020). Inter-species interaction was a real possibility too, with multiple species probably inhabiting the African continent during the Pleistocene, including *H. naledi* (Berger et al., 2017) and *H. heidelbergensis/rhodesiensis* (Grün et al., 2020). Like the environmental hypotheses, an alternative non-environmental perspective makes intuitive sense because humans have complex social strategies that not only help them buffer the influence of external environments, but also give them all sorts of non-environmental reasons for doing things. It has been suggested that the variable nature of the MSA archaeological record across Africa is best explained by multiple causal factors, with demographic processes such as population structure, size, and connectivity playing a key role (Scerri and Will, 2023).

Niche Construction Theory (NCT) has been applied in archaeology as a way of explaining the feedback loop which exists between human innovation and their environment. According to NCT, organisms actively construct their environmental niche through daily activities. In other words, humans did not only adapt to their environment but also modified their surroundings, thereby changing the selective conditions. From this perspective, the environmental factors of human innovation are less important than the innovations which alter those environments and allowed our species to construct adaptive niche spaces across a range of environments. Landscape burning (Thompson et al., 2020), making hearth-centered residential camps (Stiner and Kuhn, 2016), and most drastically, domestication and agriculture (e.g., Zeder, 2016), are all proposed key niche construction behaviors. NCT has been criticized for a lack of testability (Spengler, 2021), but has gained considerable traction as a way of tracking increased human impact on the environment across time (Boivin et al., 2016).

6. Conclusions

In summary, there are contradictory perspectives on the role of environment on the origins and evolution of *Homo sapiens'* innovativeness. There are differing perspectives on how to recognize innovations and innovativeness, the context, the drivers and explanations, and the scale of environmental influence (Table 1).

What these disparate views might reveal, is a need to reevaluate our current models for understanding the relationship between human innovativeness and climate change. The differing perspectives underscore potential model inadequacies when considering African continent-wide data, emphasizing the need for a more nuanced understanding. Alternatively, these disparate views might reveal that climate exerted an influence on human behavior and innovation in the past, but in complex and varied ways across the African continent. In other words, the reason for this seemingly contradictory record may be that the relationship between climate and human innovation was highly context-dependent and region-specific. Human responses to climate change manifested differently in various parts of Africa, perhaps in part due to the continent's vast geographic and ecological diversity. In some contexts, shifts in climate seemed to have spurred innovations and innovativeness, whereas in other contexts the response was less pronounced or entirely different. This heterogeneity underscores the intricate ways in which humans adapted to their surroundings in the face of changing environmental conditions, and the multitude of factors, including cultural, social, and technological dynamics that influence human behavior.

We can be confident that it is not a straightforward narrative of dry periods being universally detrimental and wet periods being universally beneficial, nor is it solely reliant on the dynamics of glacials and interglacials or marine isotope stages. The impact of climate on human development cannot be attributed to a specific location or observed consistently across all regions. Moreover, while they did sometimes, behavioral shifts and innovations did not always occur simultaneously or in direct correlation with climatic changes.

Table 1
Summary of opposing viewpoints on environmental change and impacts on human innovativeness in Pleistocene Africa.

Environmental context		
Expansion/contraction of Winter Rainfall Zone (WRZ) in southern Africa	WRZ contracts during cooler MIS (MIS 2, 4, 6 etc) resulting in drier conditions e.g., Bar-Matthews et al. (2010); Deacon et al. (1984); Klein (1972), 1980; Klein et al. (1983); Van Zinderen Bakker (1983)	WRZ expands during cooler MIS, resulting in wetter conditions e.g., Chase (2010); Chase et al. (2018); Faith (2013)
Drier vs wetter in the interior of southern Africa	Interior regions are drier during cooler MIS e.g., Ambrose and Lorenz (1990); Barham and Mitchell (2008); Foley and Lahr (1997); Klein (1999); Lahr and Foley (1998); Mackay et al. (2014); Willoughby (2007); Wurz (2019)	Interior regions are at least sometimes wetter, or there are variable responses during cooler MIS e.g., Blome et al. (2012), Burrough (2016), Carr et al. (2023), Collins et al. (2014), Singarayer and Burrough (2015), Thomas et al. (2012), von der Meden et al. (2022)
"Dry is bad, wet is good"	Drier conditions are detrimental to human populations	Drier conditions are not always detrimental to human populations e.g., Blome et al. (2012), Gatto and Zerboni (2015), Kuper and Kropelin (2006)
Environmental drivers		
Single origin refugium vs. multiple origin	*Homo sapiens* originated in a single locale and spread from there e.g., Lahr and Foley (1998), Marean (2016)	The origin of *Homo sapiens* involved multiple locales with gene flow between semi-structured populations e.g., Scerri et al. (2018)
Influence of Toba ~74 ka	The eruption of Toba had a significant effect on African environments and human populations e.g., Ambrose (1998)	The eruption of Toba did not have a significant influence e.g., Lane et al. (2013); Roberts et al. (2013); Smith et al. (2018)
The role of coastal resources	The unique characteristics of coastal environments and resources influenced the emergence of complex *Homo sapiens* behaviours e.g., Broadhurst et al. (2002), Marean (2014), 2016, Parkington (2010), Will et al. (2019), Will et al. (2016)	Complex *Homo sapiens* behaviours simultaneously emerged in non-coastal contexts e.g., Wilkins et al. (2021)
Variable vs. stable environments	Humans developed complex behaviours as an adaptation to temporally variable environments e.g., Brooks et al. (2018); Deino et al. (2018); Potts (1998), Potts et al. (2018); Potts et al. (2020)	Humans developed complex behaviors in stable environments e.g., Will et al. (2021), Marean et al. (2014)
Interconnectedness vs. isolation during cooler conditions	Human populations were more interconnected during cooler MIS e.g., Ambrose and Lorenz (1990), Compton (2011),	Human populations were isolated during cooler MIS e.g., Lahr and Foley (1998); Marean (2010); Marean (2011)

(*continued on next page*)

Table 1 (*continued*)

Environmental context		
	Mackay et al. (2014), Pazan et al. (2022)	
Correlation vs. lack of correlation	There is correlation in the timing of environmental change and behavioral change e.g., Ambrose (1998), Potts (1998), Timbrell et al. (2022), Ziegler et al. (2013)	There is no correlation in the timing of environmental change and behavioral change e.g., Blome et al., 2013, Clark (2013), Jacob et al., 2008, Kandel et al. (2016), Roberts et al. (2016b), Wadley (2013)

Considering these factors, future research in the field of human-environment interaction across Africa could involve more contextualized studies that examine region-specific dynamics by conducting localized, fine-grained investigations within ecological and cultural contexts. Of particular value would be new investigations in regions that have historically been understudied or under-published. Additionally, researchers can conduct larger-scale comparative analyses across the African continent to identify both common patterns and unique adaptations in response to changing environments. Embracing multidisciplinary approaches that integrate expertise from archaeology, geology, and climatology, is essential for a thorough understanding of the relationships between climate and human behavior.

It is also essential to recognize that humans are not merely passive recipients of environmental pressures but active agents capable of shaping their surroundings. This capacity for innovation and adaptation remains relevant today, especially in the context of modern climate change. With the growing recognition of the impacts of climate change on ecosystems and human societies, individuals and communities have the power to decide to innovate in the face of these challenges.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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