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The Extended Evolutionary Synthesis and Distributed Adaptation in the Genus *Homo*: Phenotypic Plasticity and Behavioral Adaptability

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ABSTRACT

It has been argued that enhanced phenotypic plasticity and life-history variability, in addition to a greater adaptive dependence on social learning, behavioral flexibility, and niche construction, are characteristics of the hominin lineage that accommodated both environmental variation and the colonization of new environments. The extended evolutionary synthesis (EES) integrates these and other mechanisms of adaptability, incorporating development and intergenerational effects, inclusive inheritance, and niche construction. Over the past decade we have gained considerable resolution in our understanding of spatio-temporal variation in fossil hominin phenotypic variation, material culture and behavior, and a refined understanding of the intergenerational and developmental mechanisms driving phenotypic diversity within our species. This paper reviews evidence for phenotypic and behavioral diversity within the genus *Homo* to evaluate the hypothesis that our evolution was characterized by a shifting distribution of adaptation across different systems described by the EES. We define and apply a model that we term 'distributed' adaptation, where mechanisms of both plasticity and culture serve to accommodate environmental variability in ways that are more rapid than genetic adaptation, thus distributing selection across a range of adaptive systems. Adaptation that is distributed towards physiological and cultural mechanisms allows for more rapid adaptability in stochastic environments and buffers the genome against selective sweeps that generally involve a reduction in genetic diversity and potential future adaptability. Predictions of distributed adaptation throughout hominin evolution are proposed in relation to: (a) biology and morphology, (b) habitual behavior, and (c) feedback between behavioral change and biology. To evaluate these predictions in relation to (a) we consider evidence for shifts in phenotypic plasticity and morphological variation, including the emergence of body and brain size variation, limb proportions, skeletal robusticity, regional variation in plasticity and canalization within the body, and how these relate to environmental factors and dispersals. Predictions of behavioral change (b) are considered in light of the emergence of markedly increased spatial and environmental variation in archaeological assemblages in the late Middle and Late Pleistocene as indicators of local adaptability, cognition, and niche construction. Finally, we consider the relationships between dispersals, material culture, and morphological plasticity in response to cultural change in relation to (c). Current evidence suggests a mosaic pattern of the

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evolution of distributed adaptation and selection within our genus. In early *Homo* there is evidence of phenotypic diversification and increasing plasticity that precedes evidence of increased cognitive, behavioral, and cultural variation among Middle and Later Pleistocene *Homo*. This can be interpreted as representing a shift towards the distribution of adaptation, first onto mechanisms based on phenotypic plasticity, and later onto cognition, cultural buffering of environmental stress, and enhanced niche construction.

THE EXTENDED EVOLUTIONARY SYNTHESIS

The extended evolutionary synthesis (EES) grew out of a gradual acknowledgement that strict gene-centered neo-Darwinian evolution did not solely account for the full pattern and process of evolutionary change or, at the proximate level, the markers of phenotypic variability that are used to characterize evolutionary change. The EES emphasizes integrative approaches to understanding evolution and adaptability by incorporating a diverse range of mechanisms such as epigenetics, growth and development, cultural evolution, niche construction, and inclusive inheritance. While the general scope and importance of the EES has been recently articulated (Laland et al. 2014; 2015; Pigliucci and Müller 2010), it can now be considered to encompass a range of approaches that have enhanced our understanding of evolutionary processes over the past century (Pigliucci and Müller 2010). These approaches build upon early research on the importance of ontogeny to evolution (Thompson 1942) and epigenetic aspects of developmental plasticity (Waddington 1959). Within the framework of modern genetics, recent research in evolution and development (evo-devo) has enhanced our understanding of constraint and evolvability of phenotypic variation (Rolian 2020). A thorough review of the EES is beyond the scope of this paper, but several broad components are of particular importance to paleoanthropology.

Developmental Systems Theory (DST) coalesced in the 1990s, building on Conrad Waddington's concept of the developmental system (Waddington 1941; 1959), and Susan Oyama's (1985) emphasis on the central role of information in the interaction of environments and genes during the developmental process. The approach emphasizes the role of environmental dynamics in driving developmental outcomes through integration of physiological systems and the construction of life cycles (Ford and Lerner 1992; Griffiths and Tabery 2013; Oyama et al. 2001). DST is associated with an increasing acknowledgement that genetic regulation and epigenetic factors are important in mediating the relationship between the environment and observable variation at the level of the organism and individual (Jablonka and Lamb 1995) and an understanding that growth and development are crucial components of evolutionary change. While DST importantly broke down the simple and false nature:nurture dichotomy, challenges lay in the transition from theory to testable hypotheses as our understanding of epigenetics was poorly resolved at the time. In the late 20th century, there was an increasing appreciation of morphological integration (Olson and Miller 1957) and the importance of neutral evolutionary mechanisms (Kimura 1983). While not formally seen as part of the EES, these theoretical developments further challenged strict adaptationism by emphasizing the fact that much observable variation may not be directly adaptive, and, conversely, that components of variation may be adaptive but not strictly genetic in origin. These insights have helped to frame evolutionary theory in a broader and more critical perspective.

A key development in the extension of evolutionary theory was the idea that the phenotype is not limited to the body and physiology of the organism, but extended to include the effects of evolution on the organism's interaction with the environment (Dawkins 1982). Building upon and expanding this general idea—and concurrent with the development of DST in the 1990s—Niche Construction Theory (NCT) characterized the active modification of environments by organisms as an evolutionary process in its own right (Odling-Smee et al. 1996; 2003; 2013). NCT emphasizes that the behavior of an organism and its modification of the environment has a direct influence on genetic evolution on intergenerational timescales. A crucial contribution of NCT is the acknowledgement that all organisms, to a certain extent, modify, regulate, construct, and select biotic and abiotic components of their local environments through their metabolism and behavior, and thus influence their own and even other species' biological evolution. The acknowledgement that our species may be particularly disposed towards adaptively modifying our environments or niche constructing has been a long-standing theme within anthropology (Boivin et al. 2016; Childe 1936; Frisancho 1983; Laland et al. 2001; Odling-Smee 1994; Odling-Smee et al. 2013).

While evolutionary theorists have emphasized the importance of heredity and replication systems beyond DNA (Dawkins 1976; Jablonka and Lamb 2005; Richerson and Boyd 2005) there is, of course, a deep history of the application of evolutionary theory to culture. Herbert Spencer's application of Darwinian ideas to culture, as well as 20th century attempts to develop a science of culture viewed it as a 'superorganic' form of inheritance (Kroeber 1957), to which evolutionary mechanisms applied (White 1949) were inherently 'progressionist' (implying evolutionary progress and innate directionality). Subsequent research developed quantitative approaches to the understanding of cultural evolution as a consequence of modes and mechanisms of transmission that determined the frequency of cultural traits (Boyd and Richerson 1988; Cavalli-Sforza and Feldman 1981). This can be seen as a shift towards a more 'kinetic' theory, a term applied to approaches (Lewens 2019) that focus on cultural transmission rather than selection, and which consider culture as a component of a gene-culture dual inheritance system (Richerson and Boyd 2005). These approaches emphasize that, in addition to the intergenerational transmission of genetic variation in biological evolution, social information can be transmitted horizontally, obliquely, or vertically, but similarly act as an evolutionary system of cultural inheritance. This may or may not be 'adaptive' in the Darwinian sense (Wells and Strickland 2006) and might even include maladaptive traits—the differential adoption and transmission of a cultural trait may be due to a difference in content (intrinsic attractiveness such as ease of imitation or functional superiority), prestige or success bias (preferential adoption of a trait due to social status or skill of the user), or situational context such as its sheer abundance in the group (frequency-dependent, such as in conformist behavior or novelty bias) (Creanza et al. 2017; Eerkens et al. 2007; McElreath et al. 2008; Mesoudi 2011). The study of gene-culture coevolution in the age of genomics has led to an increased appreciation of the role of culture in driving biological evolution (Laland et al. 2010), demonstrating one of the key predictions of gene-culture coevolutionary theory.

Darwinian theory is centered around the acknowledgement that evolution will occur when there is a) naturally occurring variation in a trait, that is b) heritable / transmitted between individuals, and c) there is differential fitness, different copy numbers based on variation in reproduction or survivorship. A key component of the development of EES is the acknowledgement that there are multiple systems of transmission (of genes, culture, environment, for example) that we might consider 'inheritance systems' that form distinct legacies or adaptive systems. Just what constitutes such a system of inheritance is poorly resolved. In addition to genes, some have identified culture as a second system of inheritance (Richerson and Boyd 2005; Richerson et al. 2010), others have added epigenetics and divided culture into symbolic and behavioral components (Jablonka and Lamb 2005), or included ecological inheritance (when organisms inhabit an environment that has been modified by previous generations) on the basis of niche construction (Odling-Smee 2015; Odling-Smee et al. 2003). An implication of the existence of multiple inheritance systems relevant to evolution is that they may not be subject to the same transmission processes and rules, they may apply on different timescales, and their interaction may lead to novel evolutionary dynamics. In some ways, each system of 'inheritance' may be better understood as a mechanism of transmission. Inheritance implies intergenerational effects, which each system may engender, but it obscures cultural transmission within the lifespan, epigenetic regulation of genes within cell lines, and adaptability within the lifespan through non-heritable mechanisms such as phenotypic plasticity (Fusco and Minelli 2010; Schlichting and Pigliucci 1998; West-Eberhard 2003).

While the point of the above review has been to demonstrate that there has been a long history of revision to our understanding of the complexity of the evolutionary process, many issues remain unresolved. In many ways the full scope of the EES is still dynamic and being developed and reframed. For the purposes of this review, we consider the EES to include a range of mechanisms that can be considered 'cultural' within the human lineage, including niche construction; and those that relate broadly to physiology and development, which include general plasticity and physiological flexibility, as well as epigenetic mechanisms that may or may not propagate effects to the next generation. Figure 1 represents the broadening of some of the areas of theory associated with the EES, with emphasis on the integration of cultural evolution and phenotypic plasticity. The discussion below considers some specific aspects of the EES that have appeared in the paleoanthropological literature.

THE EXTENDED EVOLUTIONARY SYNTHESIS AND HUMAN EVOLUTION

There have been several attempts to integrate the EES more formally into paleoanthropology (Antón and Kuzawa 2017; Antón et al. 2014; Fuentes 2016; Kissel and Fuentes 2021; Wells and Stock 2007; Zeder 2018), with a particular emphasis on the genus *Homo* in general, and *Homo sapiens* more specifically (Roberts and Stewart 2018). Increased variability in African terrestrial environments has long been seen as a likely driver of Plio-Pleistocene hominin evolution (Maslin et al. 2014; Potts 1996; 1998; Shultz and Maslin 2013) and may have been central to the emergence of the genus *Homo*. In a previous review paper, two of us argued that enhanced developmental plasticity, dietary flexibility, variation in life history strategies, niche construction, and the transmission of cultural information were general biological characteristics of hominin species that predisposed members of our genus to the colonization of novel and more extreme natural environments (Wells and Stock 2007). We further argued that the constant exposure to new niches associated with dispersal provided its own selective pressure favoring plasticity, causing these characteristics to gain prominence in the adaptive capacity of *Homo* taxa, and particularly within *H. sapiens.* The role of plasticity and variation in life history characteristics such as growth rates, maturation, and reproductive scheduling with reference to the speciation of the genus *Homo* was explored by Kuzawa and Bragg (2012), who argued that plasticity may have accelerated phenotypic change and genetic adaptation within our lineage. Specific aspects of an extended view of human adaptability were applied by Antón and colleagues (2014; Antón and Kuzawa 2017) with reference to the emergence of our genus. They demonstrated that early *Homo* were associated with a broader range of paleoenvironments than australopithecines (Antón et al. 2014). Antón et al. (2014) suggested that this environmental variation was accommodated by early *Homo*'s dietary flexibility, increased carnivory, reduced sexual dimorphism, cooperative breeding, and flexibility in their development. This paper was built upon by Antón and Kuzawa (2017) who more explicitly tied developmental plasticity and epigenetic mechanisms

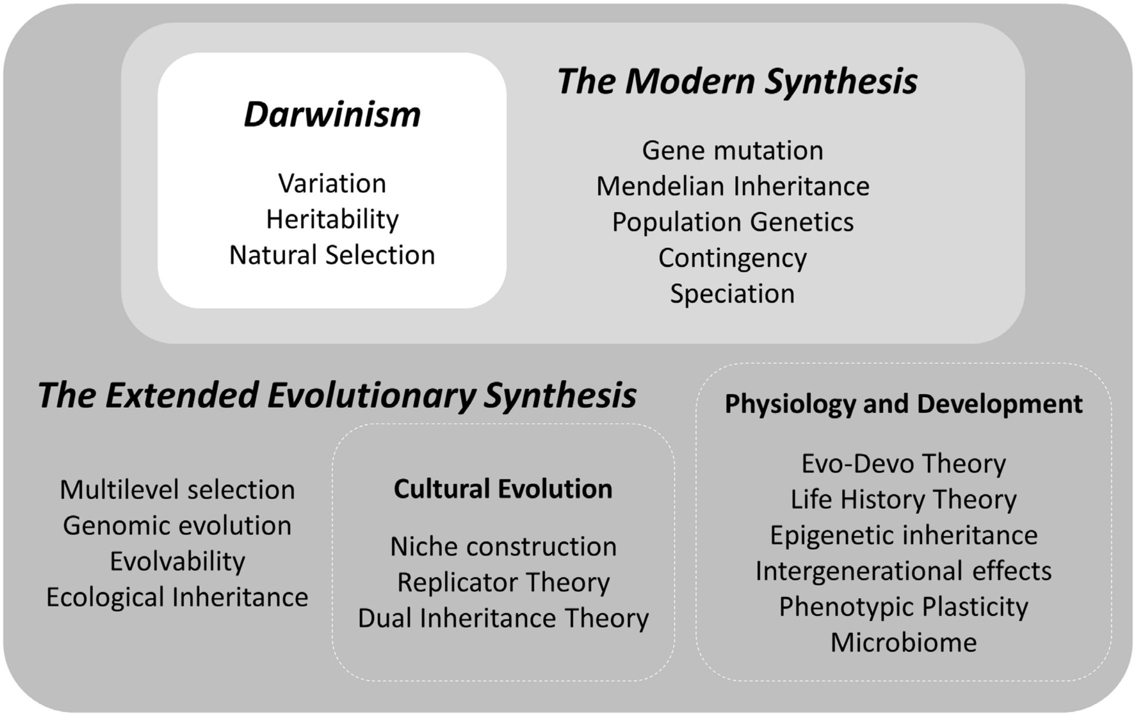

Figure 1. The expanding scope of the evolutionary synthesis, with emphasis on two components of particular relevance to paleoanthropology, physiology and development, and cultural evolution (adapted from Pigliucci and Muller 2010).

of phenotypic variation in living humans to plausible mechanisms driving phenotypic variation in the fossil record (Antón and Kuzawa 2017). These approaches may be linked, if we appreciate that the hominin tendency to colonize inherently exposed each generation to new selective pressures over short timescales, favoring the evolution of greater physiological and biological plasticity (Wells and Stock 2007).

The human propensity to culturally mediate environmental stress and modify the environments around us is well understood as an important component of our adaptive niche (Childe 1936; Laland et al. 2001; Wells and Stock 2007). The application of the EES and its elements to (Paleolithic) archaeology is still relatively novel and mostly consists of case studies instead of a full-blown research program. Examples include the use of niche construction theory to understand large-scale behavioral patterns in the Pleistocene archaeological record (Braun et al. 2021; Bush et al. 2022; Iovita et al. 2021; Riel-Salvatore 2010; Riede 2011), as it integrates human influences on the environment in our understanding of cultural and biological evolution (Murray et al. 2021). Compared to other animals, pervasive material culture and a stronger reliance on cultural inheritance as rapid means of information transmission have transformed the capacity of niche construction and ecological inheritance in modern humans and likely other species of *Homo*. While no direct transmission from individual to individual occurs in ecological inheritance, all members of a group are affected by growing up in niches changed by other species, or modified by human agency and material culture (Odling-Smee 2015; Odling-Smee et al. 2003). Ecological inheritance in the genus *Homo* thus resulted in the intergenerational transfer of environments enriched by material culture or transformed by the side-effects of human activities: Consequently, new generations are born, raised, and socialized in materially modified worlds, and this has an additive effect on future descendants. In recent years, archaeologists have primarily applied NCT within the context of major cultural changes of the terminal Pleistocene and Holocene, such as the origins of agriculture (Boivin et al. 2016; O'Brien and Laland 2015; Smith 2007). There is also a growing interest in the application of these ideas to Pleistocene archaeology and hunter-gatherer communities (Braun et al. 2021; Haas and Kuhn 2019; Iovita et al. 2021; Riel-Salvatore and Negrino 2018; Thompson et al. 2021). A final focus has been on the unique behavioral variability evidenced by our genus and species, with an emphasis on the relationship between environmental change and behavioral variability (Lombard 2012; Shea 2015), behavioral flexibility (Kandel et al. 2015) or concepts of plasticity borrowed more directly from biology (Grove 2015; Roberts and Amano 2019; Roberts and Stewart 2018).

Epigenetics, growth and development, and phenotypic plasticity are generally seen as key components of the EES. However, the role of phenotypic plasticity in human evolution and its contribution to fossil hominin morphology is poorly understood. This is due, in part, to a paradox in our knowledge of the mechanisms influencing the human phenotype. Many aspects of human phenotypic variation are assumed as being highly heritable based on twin or sibling studies, although many of the most 'heritable' traits are also highly plastic during growth and development (Wells and Stock 2011). Common environmental conditions (ecological inheritance, within NCT), such as those experienced by most twins, can constrain developmental plasticity in a way that inflates heritability estimates and would give the illusion of strong genetic influences on phenotype. The systematic inflation of estimates of the heritable component of phenotypic variation in such studies, if taken at face value, could lead to the overestimation of the genetic basis of variation in the fossil record. The majority of past research in human paleontology has assumed that morphological variation reflects the underlying process of natural selection, although recent research has begun to integrate quantitative genetics and non-adaptive models to explain morphological variation (Schroeder and Ackermann 2023). It is important to acknowledge that adaptationist models make the *a priori* assumption that phenotypic differences are the result of natural selection and are rooted in underlying genetic differences. An integrated understanding of phenotypic plasticity within living humans and an acknowledgement of the distributed nature of adaptation can serve to enlighten patterns of variation observed in the fossil record.

While the role of plasticity has been explored with respect to the fossil record (Antón and Kuzawa 2017; Kuzawa and Bragg 2012; Wells and Stock 2007), it is important to note that there is a considerable body of evidence emerging from studies of recent and living humans relevant to our understanding of the role of plasticity in the generation of phenotypic variation. An exhaustive review of the relevant literature is beyond the scope of the current article, however, recent research questions assumptions of the underlying genetic basis of some aspects of human phenotypic variation. A case in point is the classic example of human adaptation known as Allen's Rule (Allen 1877), which predicts that members of homeothermic species living in colder environments will have shorter limb lengths, reducing surface area to volume and heat loss from thermal exchange at the body surface. Humans have long been observed to fit the predictions of Allen's rule by exhibiting shorter tibiae in colder environments and low crural indices (the ratio of the length of the lower leg to the thigh) (Auerbach 2012; Holliday 1999; Trinkaus 1981). While it has often been assumed that the biogeography of human limb proportions represents adaptation via natural selection, experimental research demonstrates that shortening of limb bones in mice exposed to cold temperatures during development is due to variation in blood flow to the peripheries, and thus a result of phenotypic plasticity (Serrat et al. 2008). Subsequent studies of variation in limb segment growth among living humans demonstrates that exposures to multi-stress childhood environments result in foreshortening of distal segments of the upper and lower limbs to the exclusion of hand and foot variation, indicating both that the body prioritizes resources to specific tissues, but also that lower crural indices are likely a plastic response to generic stress exposure during childhood (Payne et al. 2018; Pomeroy et al. 2012b; Ríos et al. 2020). While these studies illustrate plasticity in human limb proportions, broader phenotypic plasticity in response to thermal stress has been illustrated by classic experimental studies in pigs (Fuller 1965) and macaques (Paterson 1996). Collectively, these results suggest that phenotypic variation observed in the fossil record and commonly interpreted as representative of long-term genetic adaptation may be strongly influenced by plastic response to environmental stress during growth and development. For example, adult stature (a trait that is often the target in archaeology) is more heritable than the developmental trajectory through which it is reached, where limb segment and trunk proportions appear to reflect considerable plasticity in response to environmental stress.

ACCOMMODATION OF ENVIRONMENTAL VARIABILITY THROUGH DISTRIBUTED ADAPTATION

This brief review of the literature has focused attention on the roles of cultural evolution and plasticity in the determination of intraspecific phenotypic variation. Building upon this, we now explicitly operationalize the roles of phenotypic plasticity and cultural variation in adaptation with respect to the paleoanthropological record. To do so, we define and apply a model of 'distributed' adaptation, where mechanisms of both plasticity and culture serve to accommodate environmental variability in ways that are more rapid than genetic adaptation, thus distributing selection across a range of adaptive systems. Phenotypic plasticity can accommodate environmental stress on time scales ranging from immediate physiological responses to stress that maintain homeostasis, to intergenerational patterns of epigenetic inheritance that are distributed over decades. Culture, similarly, can buffer our physiology and genes through the creation of microenvironments that alleviate stresses of the macroenvironment (Frisancho 1983). Cultural adaptation can occur across similar time scales to plasticity, from intergenerational to instantaneous, but it can also extend into the future. Social transmission and cognition within our species provide the capacity to predict the timing, duration, and severity of environmental stress and culturally mediate stresses before they occur, thus extending adaptability into the future. Accumulated knowledge of past environmental events and its transmission within and between groups via learning is a crucial component of human adaptability. The process of natural selection poses risks to survivorship and reproduction which require considerable physical and social investment throughout the lifespan. In contrast, knowledge of the past and prediction of the future allow our species to conduct thought experiments, predict outcomes, and risk ideas that are both low cost and immediate compared to long-term risks of mortality. Physiological mechanisms, in contrast, are primarily responsive to environmental stimuli on whatever timescale they operate. Developmental plasticity in reaction norms that allow flexibility in physiological outcomes depending on environmental variation encountered during development (Schlichting and Pigliucci 1998) provide a passive rather than active extension of human adaptability to ac-

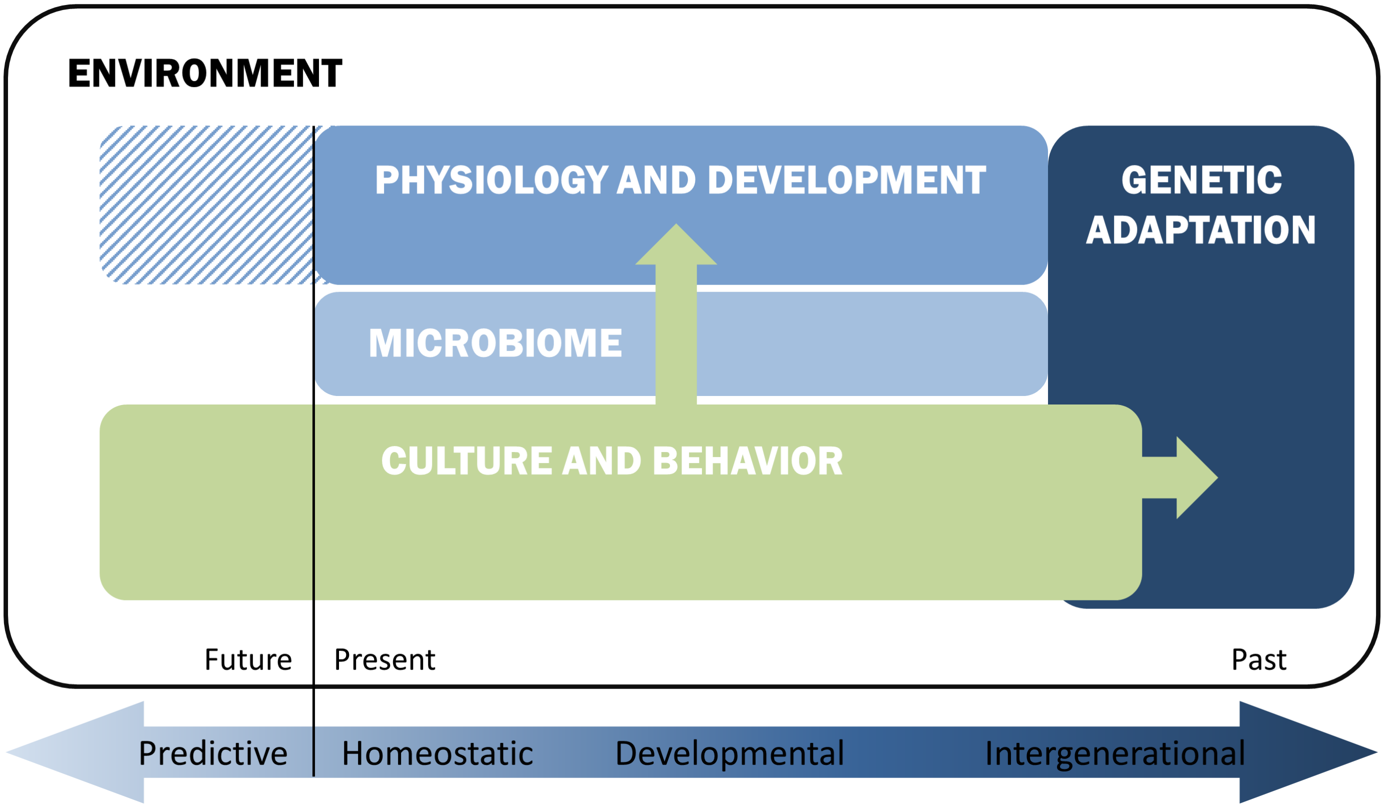

Figure 2. A visual representation of 'Distributed' Adaptation. The range of human adaptability can be expressed as a combination of genetic adaptation, physiology and plasticity, and culture, which operate on different timescales. Genetic adaptation is a long-term process of intergenerational adaptation to environmental stress. Mechanisms of physiological adaptation and plasticity can act on scales from intergenerational to immediate homeostatic responses, as can interactions with our microbiome, which provides access to millions of 'extrasomatic' genes which mediate our interaction with the environment. Cultural adaptation can act across all timescales but is the only adaptive mechanism that can be predictive rather than responsive, on the basis of advanced cognition and communication. It also may directly alter environmental stress, influencing physiology and development, the microbiome, and genetic adaptation. While physiological responses may not be truly 'predictive' in the sense of actively preparing for future stress, a more plastic organism is better able to accommodate stresses encountered in the future, and in this way has greater 'future' adaptability.

commodate future stresses (Figure 2). A shift in emphasis towards adaptability that is distributed away from genetic adaptation towards physiological and cultural mechanisms has two key benefits: a) it allows for more rapid adaptability in stochastic environments, and b) protects the genome from adaptive 'costs' of selective sweeps that trade off current adaptation against future adaptability by reducing genetic diversity.

We consider the evolution and variation of the human microbiome to be of further relevance to the evolution of distributed adaptability. All primate microbiomes are, to some extent, phylogenetically constrained but also show plasticity (Gomez et al. 2019) and coadaptation with diet (Fellows Yates et al. 2021). This makes the human microbiome particularly variable and sensitive to cultural variation. The microbiome provides a means of extending genetic adaptation beyond the body, to produce a 'meta-organism' through a symbiotic relationship with other organisms that enhance our flexibility in response to environmental variation (Bang et al. 2018). Within the context of human adaptation, variation in the microbiome allows for a form of extrasomatic extension of genetic adaptation to other species that provide a multitude of additional genes through which the relationship of our bodies to the environment is mediated, which in turn preserves our own genetic stability (Rook et al. 2017).

The re-evaluation of the genetic basis of variability in the fossil record is analogous to changes in biomedical understanding that emerged through the 20th century. Following discovery of the structure of DNA in the 1950s, and the possibility of investigating gene structure and function, biomedical research increasingly emphasized the direct interaction of genotype and environment. This perspective shifted radically in the 1980s, however, through a new wave of research emphasiszing the importance of developmental experience for adult phenotype, function, and fitness. The 'developmental origins of adult health and disease' (DOHaD) hypothesis is now central to mechanistic understanding of variability in health. Despite increasing interest in the past decades, this central insight of the importance of developmental experience has yet to be adequately integrated in paleoanthropological analyses.

THE EES AND CHARACTERISTICS OF OUR SPECIES

Our species, *H. sapiens*, is characterized by a number of unique features that include, but are not limited to: (a) a broad environmental range relative to other species, and the accommodation of rapidly changing environmental conditions (Groucutt et al. 2015); (b) a low level of genetic diversity relative to non-human primates (Kaessmann et al. 2001; Premo and Hublin 2009) and low somatic mutation rates (Cagan et al. 2022) accompanied by a high degree of phenotypic variation (Buck et al. 2010; Stock and Buck 2010); (c) extended life history characterized by an extended pattern of growth and neural development (Bogin and Smith 1996; Dean et al. 2001); (d) relatively high levels of phenotypic plasticity (Bogin and Varela-Silva 2011; Kuzawa and Quinn 2009; Kuzawa and Thayer 2011; Stock and Buck 2010; von Cramon-Taubadel 2009; Wells 2017; Wells and Johnstone 2017; Wells and Stock 2011); (e) intergenerational buffering of offspring in early life that limits natural selection to stress experienced across multiple generations (Thayer et al. 2020; Wells 2003; 2012a); and, (f) advanced cognition and cognitive plasticity (Coolidge and Wynn 2009) that is likely driven by culture (Thompson et al. 2016).

The question of the relative evolutionary timing of the emergence of these traits, and thus the distribution of adaptation across different adaptive systems, is an important one. The variable roles of evolution of these systems are difficult to tease apart, and specific outcomes (such as phenotypic variation) may have different underlying mechanisms. Here, we argue that since variation may have emerged from a range of plastic responses based on physiology, development, and life history, an approach incorporating the EES must make no assumptions about the genetic contribution to variation until those links are demonstrated. A contemporary example would be that the average height of someone in the Netherlands today is 20cm greater than in 1800, a phenotypic change attributed to cultural change rather than underlying genetic differences or natural selection (Fredriks et al. 2000).

While the mechanisms underlying similar variation in paleoanthropological data remain difficult to determine, the application of an EES perspective in paleoanthropology allows for some general predictions for future research to be generated based on observations both within and outside of the discipline of paleoanthropology. In the remainder of this paper, we propose a series of predictions that researchers might make of the fossil and archaeological records that would provide evidence of a shift towards 'distributed adaptation,' which would involve greater phenotypic plasticity and reliance on culture as an environmental buffer in our genus. We briefly evaluate the state of current evidence in support of each prediction. Predictions are presented in relation to: (A) biology and morphological variation; (B) material culture and the archaeological record; and (C) adaptive feedback between cultural and biological change. These predictions are by no means exhaustive but are meant to be illustrative of the application of the EES to paleoanthropological questions, and to provide preliminary evidence of the timing of shifts in distributed adaptation within our lineage.

HYPOTHESIS TESTING AND KNOWLEDGE IN PALEOANTHROPOLOGY AND THE INDUCTIVE SCIENCES

Before considering specific predictions of an EES model on the fossil and archaeological record, it is worth noting several issues relating to inference, prediction, hypothesis testing, and causation in evolutionary biology. A valid critique of the application of the EES to the paleoanthropological record is that it is often not possible to differentiate adaptive mechanisms to directly test whether long-term genetic adaptation or developmental and physiological plasticity underlie the observable variation in the fossil record. However, if multiple mechanisms may generate phenotypic variation that appears 'adaptive' in the broad sense, the default assumption that observed differences rest on underlying genetic adaptation may not be supported (Gould and Lewontin 1979). The lack of controlled experimental testing of hypotheses in fields such as paleoanthropology has led to the critique that Darwinian hypotheses are often not falsifiable (*sensu* Popper 1974). However, such fields leave hypotheses open to check by generating predictions or retrodictions (Popper 1978). William Whewell (1847) theorized that in such 'Inductive Sciences,' the rejection or acceptance of hypotheses is made through consilience of inductions from different lines of evidence, and that new discoveries constantly test predictions made from previous observations. More recently the process of hypothesis testing and knowledge generation in inductive sciences has been developed through the theoretical framework of Inference to the Best Explanation (IBE), where inference is used to arrive at the best explanation among multiple competing working hypotheses (Chamberlin 1965; Harman 1965; Lipton 2004). This approach is commonly applied in archaeology without explicit acknowledgement and can be seen as a part of the creative process of science that allows for the development of explanations and predictions that are subject to further scientific inquiry (Campanaro 2021; Fogelin 2007). In standard hypothetico-deductive studies, hypotheses can only be rejected or confirmed, whereas in inferential research, explanations are proposed, and may become more or less compelling in the face of new analyses and evidence. In such a probabilistic framework, archaeological explanations are based upon observable characteristics of the material record, but are responsive and can be challenged or modified in the face of new evidence or analyses (Campanaro 2021).

In the remainder of this paper, we apply theory associated with the EES and the concept of distributed adaptation to generate a series of predictions that require further testing and evaluation on the basis of the paleoanthropological record, using the approach of IBE. In some cases, predictions are derived from emerging research in adjacent fields such as human biology or primatology, in others they are derived directly from current observations of the archaeological record. In all cases, we consider 'predictions' to be consilient explanations of the paleoanthropological evidence as it stands, to be evaluated, rejected, or revised in the face of new analyses. This process is analogous to Heidegger's or Gadamer's 'hermeneutic circle,' which, when applied within archaeology, aims to arrive at more coherent explanations of phenomena over time in an iterative manner (Campanaro 2021). This is a process where explanations are (re-)evaluated by the amount of data that are accounted for by one hypothesis relative to another at a given time (Hodder 1999), a core tenet of inductive sciences that extends back to Whewell's 'Consilience.' Our predictions provide illustrative examples of the application of EES theory to our understanding of the paleoanthropological record. In many cases, the specific timing of such shifts towards distributed selection remains an open question, so we cautiously discuss individual species or time periods only when there is compelling evidence to do so.

With regards to the status of the EES and the emergence of the genus *Homo*, in our opinion we are not yet able to determine what specific characteristics of early *Homo* may be the result of distributed selection and mechanisms of adaptability that lie beyond natural selection acting upon underlying genetic variation. We are, however, in a position to highlight aspects of biology and behavior that are consistent with the EES and generate hypotheses from existing evidence in human biology, primatology, and paleoanthropology, that can be evaluated in future research. Our purpose in generating these predictions is not to deny the relevance of natural selection and underlying genetic variation in human evolution, but to highlight areas where the role of natural selection remains an open question. Paleogenomics and new research in paleo-epigenetics are certainly making significant contributions in our understanding of evolutionary mechanisms. Nevertheless, we argue that until direct genetic evidence for traits can be demonstrated, explanatory models should be *a priori* neutral as to the underlying cause of phenotypic variation in the fossil and archaeological records and draw upon a broader range of physiological, cognitive, and cultural evidence to interpret the mechanisms of change in the past to make inferences of causation.

A. PREDICTIONS OF THE EES ON MORPHOLOGY AND BIOLOGY

Biological implications of the EES are those that primarily reflect a shifting emphasis towards plasticity and physiological accommodation of stress, away from long-term genetic adaptation and evolution. While a variety of aspects of human physiology, like mutations related to the developmental enhancement of eccrine sweat glands and thermoregulatory capacity (Aldea et al. 2021) are difficult to test directly against the fossil record, below we outline several predictions that could be tested in some circumstances. Some of the changes described below may be rooted in the Darwinian evolution of underlying genetic variation, but the results may be seen to shift adaptive variation onto more rapidly deployed mechanisms of adaptability via plasticity.

Prediction 1: Life history shifts towards an extended period of growth and development

The extended period of growth and development of modern humans relative to non-human primates is well documented. It confers upon our species a long period of post-weaning development with slow somatic growth (Bogin and Smith 1996), characterized by social learning, neural maturation, and plasticity (Bjorklund and Ellis 2014), and an adolescent growth acceleration to achieve a large adult body size during a period of increased neural maturation and connectivity (van Duijvenvoorde et al. 2019). The extended period of growth allows for considerable neural and cognitive plasticity throughout development (Buttelmann and Karbach 2017). A recent broadscale comparative study demonstrates that patterns of activity among hunter-gatherers and mixed subsistence foragers serve to enhance the acquisition of social knowledge and cooperation in relation to ecological variation (Lew-Levy et al. 2022). In addition to social learning, there is also considerable plasticity in phenotypic variation and growth outcomes afforded by extended development (Hochberg 2011; Wells 2012b).

The primary evidence for human uniqueness in extended growth and development comes from human and comparative primate biology, and psychology, however, patterns of cranio-dental development provide a means for paleoanthropologists to interpret developmental timing from the fossil record. The evolutionary origins and developmental timing of the unique pattern of human growth have been of long-standing research interest. The most significant body of evidence for a shift towards an extended pattern of life history comes from the studies of dental formation through daily incremental growth markers (Guatelli-Steinberg 2023; Smith et al. 2010). Tooth morphology is generally considered to be highly canalized and correlated with underlying intraspecific genetic variation (Rathmann and Reyes-Centeno 2020). There is strong evidence for faster dental development among *Australopithecus*, *Paranthropus* (Kelley and Schwartz 2012) and the early members of the genus *Homo* including *Homo erectus* (Dean et al. 2001), suggesting that the extension of life history occurred later within our lineage. Studies of crown formation identified dental development similar to modern humans among some of the earliest fossil representative of our species, but the results are suggestive of faster periods of growth and development among most Neandertals (Smith et al. 2010). However, a recent study of the Neandertal child from El Sidrón reveals a pattern of dental and skeletal maturation similar to modern humans (Rosas et al. 2017). While these results hint at developmental variability among Neandertals, recent research has identified a range of enamel microstructural variation among Middle Pleistocene hominin fossils of the Atapuerca sites that are generally indicative of faster development but show some similarities to the delayed pattern of human dental development (Modesto-Mata et al. 2020). Both Neandertals and modern humans are born with an elongated braincase, but the ontogenetic trajectory of *H. sapiens* diverges within the first year to become more 'globular' (Gunz et al. 2012). Although all later

Pleistocene hominins are relatively large brained, their distinct ontogenetic trajectories have been linked to variation in life history, energetics, and cognition (Hublin et al. 2015). Overall, our current understanding of the evolution of human life history demonstrates that a unique pattern of extended growth, in comparison to the faster life history of the earliest hominins, is specific to *H. sapiens*. Middle Pleistocene hominins, in contrast, appear to show regional and temporal variation with some indications of extended development in specific individuals. Within the context of the EES, the unique pattern of growth and development of modern humans also extends to neural development, which underpins social, language, and behavioral learning, and ultimately cultural adaptability, in turn enhancing the distribution of adaptation away from the genome. Future research will be required to resolve the biogeographic and temporal variation in hominin life history.

Prediction 2: Emergence of regional variation in phenotypes and body size

Modern humans have high levels of variation in phenotypic measures such as body size and limb proportions (Ruff 2003). The evolutionary increases in hominin body size from the Pliocene to the present are well documented (Jungers et al. 2016; McHenry 1992; Pilbeam and Gould 1974; Ruff et al. 1997; Will and Stock 2015; Will et al. 2017). Modern humans are highly variable in body size, variation that is achieved through a combination of genetic variation and developmental plasticity in response to environmental stimuli. While early studies of the genetic contribution to human body size illustrated that known genetic variation accounted for only a small proportion of observable variation (Maher 2008), it was assumed that the remainder, the so-called 'hidden heritability' was coded in undetectable pleiotropic effects and regulatory genes. A significant proportion of this variation has been found to correspond to small additive effects of many genes that were previously undetected (Yang et al. 2010; Yengo et al. 2022) and while heritability estimates for height remain high, known genetic variants now account for about 40% of observed variation (Lello et al. 2018). Despite this, it remains likely that heritability estimates overestimate the proportion of variation influenced by specific genes, due to strong environmental influences on growth and the common environments of development that bias twin studies (Wells and Stock 2011). The fact that there are significant and near universal secular trends in human stature (Cole 2003) and catch-up growth following niche-change, such as through international adoption (Van Ijzendoorn et al. 2007), underscores the significant plasticity in body size within our species. Early life developmental context, however, is important to growth trajectories, as birthweight correlates with patterns of variation adult phenotype (Kuzawa et al. 2012; Wells et al. 2007). Birthweight variation is shaped, in part, by variation in maternal energetics that can be expressed as intergenerational increases or decreases in body size (Wells 2010) and these maternal influences may in turn contribute to long term trends in body size observed in the fossil record (Pomeroy et al. 2019).

The prediction of more significant variation in body size and regional variation in phenotypes is driven by emerging perspectives in human biology. When applied within paleoanthropology, the mechanisms underlying phenotypic diversity may remain unknown, but researchers can investigate spatiotemporal patterns that may illustrate the emergence of greater regional phenotypic variation. From an evolutionary perspective, there is no reason to believe that plasticity in human growth is necessarily a recent phenomenon, so the question becomes what specific scenarios would be suggestive of elevated plasticity in somatic growth in the past? As human size variation is environmentally sensitive and regionally variable, we might consider the rapid emergence of regional phenotypic variation within a species as suggestive of developmental plasticity. Cranial morphology is generally considered to be highly canalized (Mitteroecker and Stansfield 2021) and to reflect at least neutral genetic variation (Betti et al. 2010), and there is both a high degree of intraspecific variation within the Dmanisi hominins at ~1.8 Mya (Rightmire et al. 2019) and strong evidence for the emergence of regional variation in cranial morphology in *Homo habilis* (Spoor et al. 2015). Neutral genetic variation may underpin much cranial diversity in the fossil record as it does in humans (Betti et al. 2010), however, postcranial variation is likely to be more plastic (Stock and Buck 2010). The emergence of regional variation in body size is established among the earliest members of the genus *Homo*. While body size increase is generally attributed to the evolution of *Homo erectus*, and the earliest members of the genus *Homo* were smaller and more variable (Plavcan 2012), the variation among early *Homo* is spatiotemporally patterned on comparatively small geographic scales, with larger body mass and statures only being observed in the Koobi Fora region (Figure 3; Will and Stock 2015). The emergence of small phenotypes among modern humans attests to an interaction of genetic adaptation, plasticity, and life history shifts (Cameron et al. 2021; Migliano et al. 2007; Perry and Dominy 2009; Pfeiffer 2012; Stock and Migliano 2009), so it is a reasonable inference that a similar range of mechanisms may be involved in the initial diversification of phenotypic variation within our genus. Given that the body size range of healthy modern humans encompasses the entire range of variation observed in the fossil record (with the exception of *Homo floresiensis*) (Will et al. 2017) and that much of this variation is likely due to plasticity in growth and development, the observation of similar patterns of variation in the fossil record would be suggestive of the distribution of adaptation onto phenotypic plasticity without underlying genetic adaptation.

Prediction 3: Greater skeletal variation in areas of the body known to be more highly plastic

There is considerable variation in the relative plasticity of different regions of the skeleton (Buck et al. 2010). In general, craniofacial and articular regions of the skeleton are more canalized in development, while diaphyseal regions of bones are more plastic throughout the lifespan (Stock

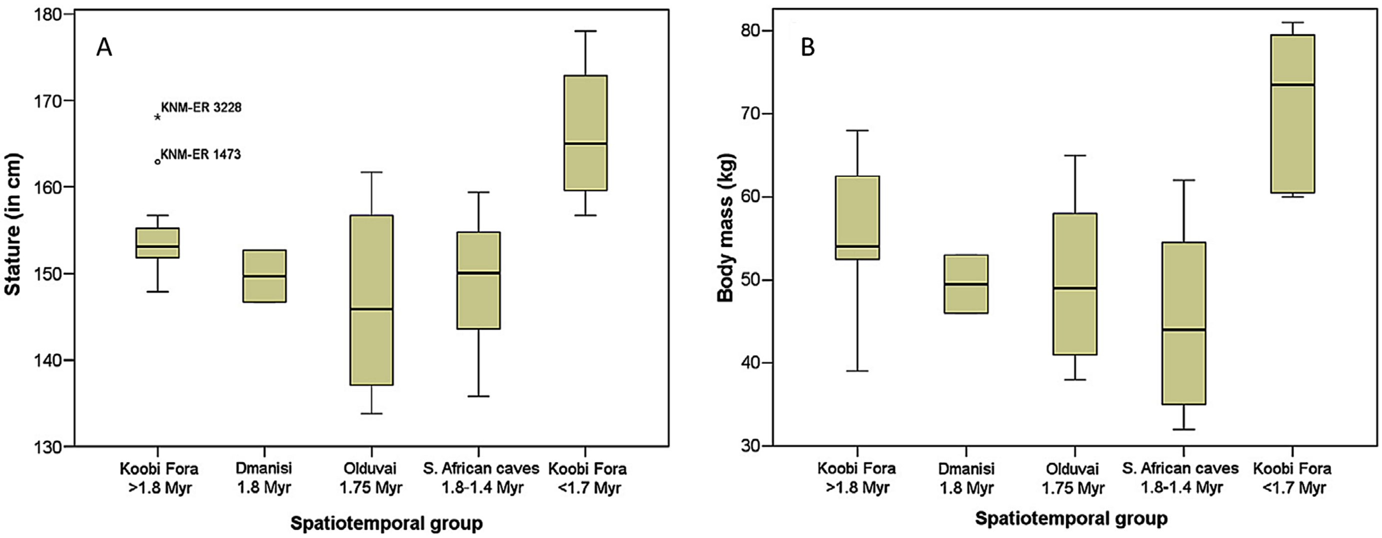

Figure 3. Spatiotemporal variation in estimates of: a) stature, and b) body mass among the earliest fossils attributed to the genus Homo, *illustrating the emergence of regional variation in phenotypes and increasing stature and body mass among the hominins from Koobi Fora (adapted from Will and Stock 2015).*

and Buck 2010). However, there is also clear evidence of mechanical influences on the growth of regions of the skeleton generally considered to be canalized, like the mandible (Von Cramon-Taubadel 2011) and growth plates of long bones and vertebrae (Stokes 2002). While plastic effects of mechanical loading will be considered in another section, here we consider linear aspects of limb growth that are often considered adaptive, expanding on our earlier example of crural indices. Earlier in this paper, we argued that crural indices are an example of a phenotypic trait often thought to reflect underlying genetic adaptation, but where the preponderance of evidence in human biology suggests that crural indices reflect phenotypic plasticity. Variation in the crural index, the length of the tibia relative to the femur, is well known and the low crural index of Neandertals and peri-arctic modern humans is seen as a key example of adaptation to climatic variation in human evolution (Holliday 1997; Trinkaus 1981). Such variation in crural indices is widely considered a textbook example of adaptation in human evolutionary adaptation, but there is reason to question the underlying mechanisms that produce this variation. Studies have demonstrated that tibial length varies highly in response to environmental and/or nutritional stress in populations of Peru (Pomeroy et al. 2012), the Himalayas (Payne et al. 2018), and Guatemala (Ríos et al. 2020), and elegant experimental research has revealed that developmental plasticity may underpin variation in the crural index (Serrat et al. 2008). These studies raise important questions about the physiological mechanisms that regulate variation in limb segment growth among humans and suggest that increases in underlying variation in the human tibia may be reflective of greater phenotypic plasticity in limb growth. Moreover, limb proportions appear to have implications for other components of phenotype that have especial relevance to understanding human adaptability, such as the size of energy-expensive organs (Shirley et al. 2022).

At present, the evidence for developmental plasticity of lower limb growth is derived from human and experimental animal biology. The evidence for ontogenetic variation in limb bone growth in the past, as interpreted by the skeletal and fossil record, is at present inconclusive. Analyses of Upper Paleolithic and Mesolithic humans demonstrate that there is a higher level of variation in the tibia than the femur, and that correlations between limb proportions and climate are primarily driven by higher levels of tibial variation (Holliday 1999; Holliday and Ruff 2001). A comparison of limb growth using widely available anthropometric data (Eveleth and Tanner 1991) shows that limb proportions among recent living populations are relatively consistent through growth (Cowgill et al. 2012), however, the Eveleth and Tanner dataset does not include the high latitude populations that are known to drive the observed ecogeographic patterns. As ecogeographic patterns in human phenotypic variation are known to be sensitive to secular trends and cultural change (Katzmarzyk and Leonard 1998), it is important to gain a better understanding of the ontogeny of limb proportions in the past.

The comparisons we provide below illustrate developmental variation in crural indices among Holocene hunter-gatherers that range between equatorial Africa, Siberia, and the high Arctic (Table 1). While the data are patchy, when they are grouped into age cohorts and crural index is plotted against latitude, two general trends emerge: (1) there is considerable variation in crural index between groups and throughout ontogeny, and (2) high latitude populations of Siberia and the Canadian Artic have relatively high crural indices at birth (similar to those of low-latitude populations) that decrease throughout development to reach the low crural indices typical of adults in cold cli-

TABLE 1. SUBADULT SKELETAL SAMPLES USED IN THE COMPARISON OF THE ONTOGENY OF CRURAL INDICES.

Population	Latitude	Date	n
Later Stone Age, Tanzania	3°S	5700 BP	4
Andaman Islanders	11 °N	100 BP	3
Jebel Sahaba, Sudan	23°N	13,700 BP	2
Natufian, Levant	32°N	12,500–9500 BP	8
Iron Gates Mesolithic	45 °N	8500–7500 BP	2
Kitoi, Siberia	53°N	8800–6900 BP	23
Sadlermiut	64°N	150 BP	41

mates (Figure 4). These results are suggestive of considerable developmental plasticity in the growth of the tibia, but require further research to accept or reject this hypothesis. Ontogenetic changes in crural index during development have also been found among children in Egypt (Bleuze et al. 2014), but consistent patterns of limb proportions were found during development in Jomon period Japan (Temple et al. 2011). While there are likely to be genetic influences on limb segment growth, considering the evidence for plasticity in tibial growth among living humans we suggest that a significant amount of observed variation in the fossil record may represent plasticity of growth in distal limb segments in response to environmental stress, which could include thermal or nutritional stress. Documentation of greater variation in skeletal regions known to be more plastic within our species would provide supportive evidence for enhanced plasticity among fossil taxa.

Prediction 4: Greater adaptive cognitive flexibility

Arguably the most obvious and often discussed component of the extended evolutionary synthesis as it applies to the evolution of the genus *Homo* is the extension of cognitive and behavioral flexibility. This factor alone accounts for a number of predictions of the archaeological and fos-

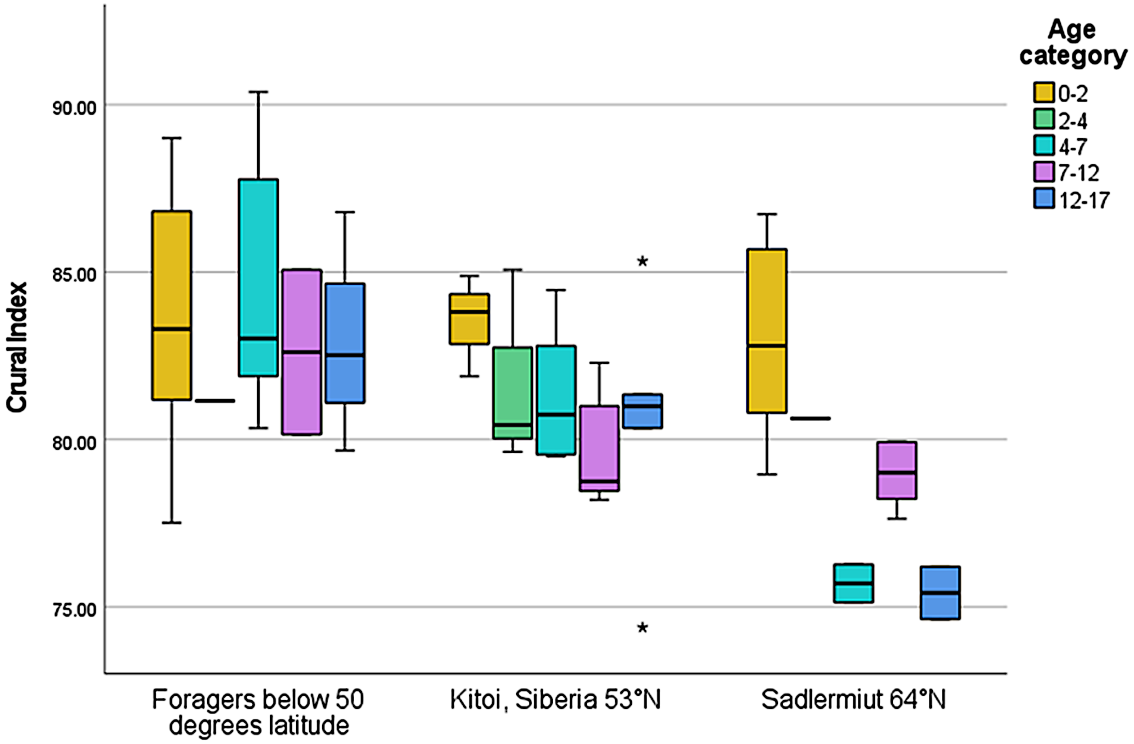

Figure 4. Boxplot of crural indices of subadult foragers by latitude and age category, illustrating the high level of variation in intra-limb indices throughout development. Among foragers living below 50 degrees latitude, crural indices remain relatively stable during development, among populations at high latitude (above 50 degrees) children are born with high crural indices, typical of lower latitude populations, but the relative length of the tibia decreases throughout the period of growth.

sil records which stem from the EES. We consider aspects of cognition reflected through material culture in Section B, below, but consider morphological correlates here. The three-fold increase in cranial capacity throughout hominin evolution (Elton et al. 2001; Rightmire 2004; Ruff et al. 1997), its energetic implications (Foley and Lee 1991; Snodgrass et al. 2009), and its developmental timing (Leigh 2012; Vinicius 2005) are well documented and have been longstanding areas of research interest. Human encephalization is broadly considered to be driven by directional natural selection in response to either the cognitive requirements of maintaining complex social interaction (Dunbar 1998) or cultural intelligence and related social learning and transmission (van Schaik et al. 2012). The increased energetic demands of a large brain are thought to be fueled through dietary shifts towards more energy rich food that reflects associated shifts in behavior and morphology (Aiello and Wheeler 1995). This shift may have also driven selection for genes associated with increased life expectancy, meat consumption, and resistance to hypercholesterolemia (Finch and Stanford 2004).

Most of the key observations of interspecific variation and human uniqueness in cognition come from comparative primatology or psychology, but there are of course crucial limitations to how these differences can be interpreted in paleoanthropology. A key issue of relevance to the EES is the timing and evolutionary context of increases in brain size. The broad comparison of endocranial volumes across the past 3.5 million years (Figure 5a) of hominin evolution illustrates three periods of marked increase in absolute brain size with intervening periods of relative stasis. The first increase occurs among early *Homo* between 1.9 and 1.5 MYA, the second in the Middle Pleistocene (Du et al. 2018) roughly between 600–350 kya, followed by a diversification of brain size and some further increase in endocranial volumes after 200 kya. In a recent paper we analyzed Middle and Late Pleistocene body brain sizes in the context of global climatic models to determine whether there are specific environmental predictors for encephalization (Will et al. 2021). Our results demonstrated that while hominin body sizes are strongly correlated to temperature, a significant proportion of brain size variation in the fossil record corresponds inversely with net-primary productivity (rate of accumulation of biomass in a system) and the expansion of hominins into more marginal and variable environments. A reasonable inference from this trend is that cognitive flexibility was a selective pressure on brain size increases, at least in the Middle Pleistocene period of increase in endocranial volumes.

Data relevant to these questions can also be drawn from human biology. Plasticity in somatic growth and body composition allow for the growing body to accommodate ecological stress while sparing brain development, thus providing a more stable energy supply to the brain (Wells 2012b). In this respect, encephalization and the stability of neural development is linked to plasticity in hominin body size (Figure 5b). The genus *Homo* can only afford to commit to the energetically demanding large brain, a genetically conserved trait, by embedding a capacity for plastic responses of phenotype that spare the brain from environmental stress during development. There is evidence for such brain sparing on several levels: a) the relatively low investment in muscular strength relative to brain size in humans compared to chimpanzees (O'Neill et al. 2017); b) brain sparing during development via the thrifty mechanisms of phenotypic allocation (Giussani 2011; Hales and Barker 1992; Pomeroy et al. 2012a; Wells 2007); and c) acute short-term trade-offs between muscular activity and cognition (Longman et al. 2018).

We have considered morphological evidence for cranial capacity as a proxy for cognition in this section, however, stronger evidence for cognitive flexibility as a component of distributed adaptation would involve correspondence between such morphological evolution and the timing of archaeological evidence for changes in habitual behavior. The relationship between cognition, habitual behavior, and human adaptability is a key component of the EES, which we explore in more detail in the following sections.

B. PREDICTIONS OF HABITUAL BEHAVIOR

Prediction 1: The emergence of spatio-temporal diversity and patterning in material culture

As an ongoing result of increasing diversity of behavioral responses to environmental change, one may expect both a stronger reliance on cultural transmission and heightened feedback between different modes of inheritance. Cultural variation is widespread in non-human species (Whiten 2021) and would be expected to be characteristic of all hominin species (Whiten 2005), although cumulative cultural evolution is relatively rare and thought to be a central characteristic of our species (Derex and Mesoudi 2020). Humans adapt not only to their ecological surroundings but also to the environments enriched or transformed by material culture and modified by behavioral choices, i.e., materially furnished worlds. The resulting archaeological record is expected to be marked by an increased diversity of material culture in form and material (lithic, organic etc.) alongside an increasing resource space, meaning the number, types, and origins of natural substances incorporated into habitual behaviors (Hussain and Will 2021). As an inheritance system, culture is historical and path-dependent and can thereby create different adaptive or maladaptive trajectories for different groups, even when they live in comparable environments (Fuentes 2016; Mathew and Perreault 2015). Assuming ancient population sub-structure and historically contingent cultural change, the distribution of adaptation onto cultural variation would be detectable through increased regionalization such as clearly definable spatio-temporal patterns of archaeological artifacts.

Based on the record of stone tools, patterns of regional typo-technological differentiation are not readily visible during the beginning of the Early Stone Age (ESA) or Lower Paleolithic (i.e., Oldowan), though some localized spatial structure has been claimed at times for the Acheulean (Hosfield et al. 2018). The reduced morphological range of

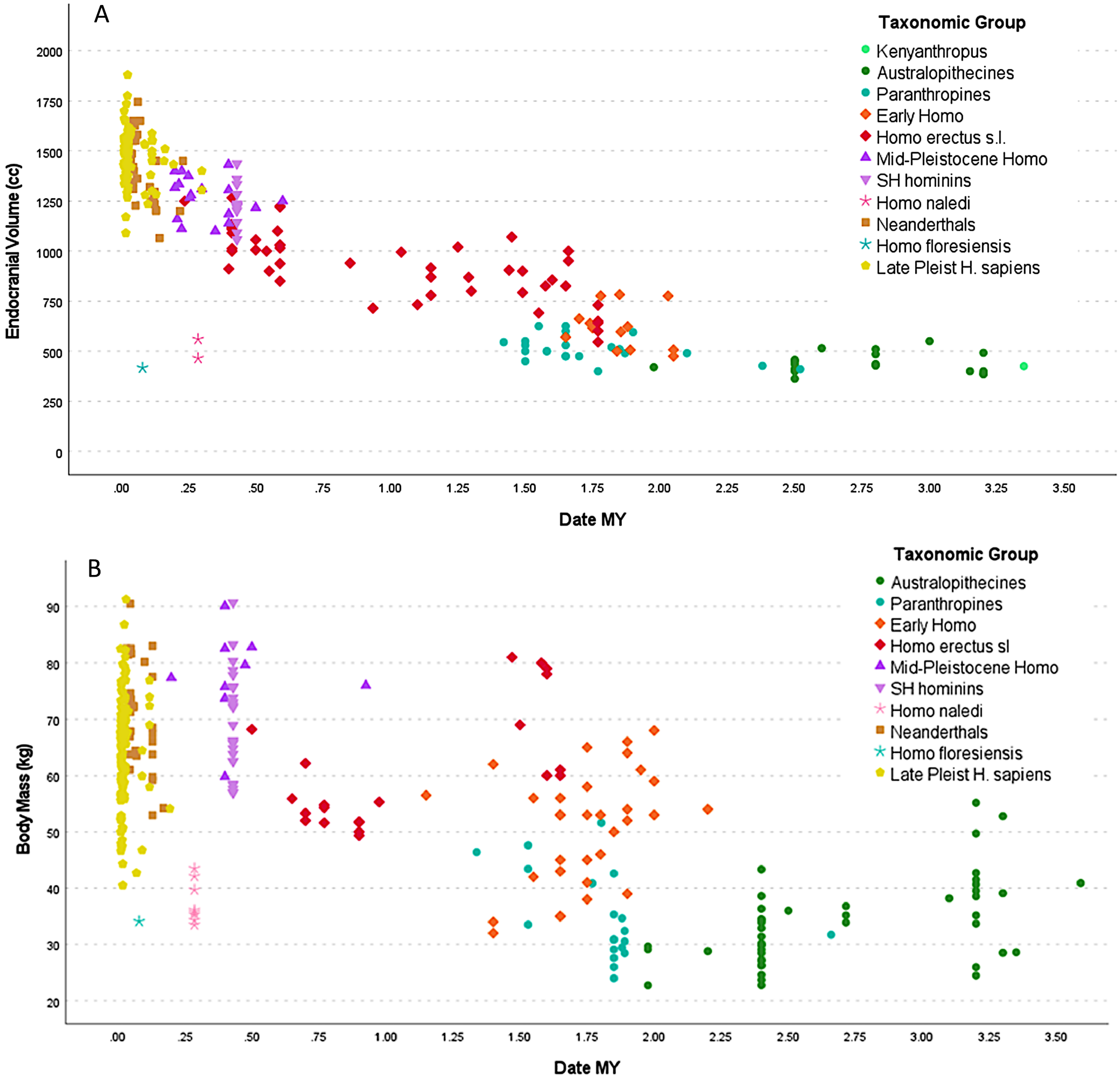

Figure 5. Temporal variation in: a) endocranial volume illustrating periods of increased endocranial volume associated with early Homo *between 1.9 and 1.5 MYA, the Middle Pleistocene between 600–350 kya, and the terminal Pleistocene Neandertals and modern humans, and b) body mass, illustrating the rapid increase in body size and phenotypic variation associated with early members of the genus* Homo *and* Homo erectus (sensu lato)*. The high level of spatiotemporal variation in phenotypes is a general characteristic of the genus* Homo *but is most pronounced among* Homo sapiens*. Increases in body size generally preceded increases in endocranial volume, and thus plasticity in body size may be an essential physiological mechanism to buffer brain development from environmental stress during growth (data from Will et al. 2017; 2021).*

these early stone tools, coupled with the comparatively low number and coarse spatio-temporal resolution of sites, hinders a clearer assessment at present. The transition between ESA and Middle Stone Age (MSA) industries appears to be regionally structured and develops with different timing and form throughout the African continent (Herries 2011; Tryon and McBrearty 2002). Stronger evidence for idiosyncratic variation of material culture, restricted in both space and time and associated with a higher tempo of technological change, comes from the MSA of Africa. This is reflected in the increase of named technocomplexes particularly from 200 ka onward (Clark 1988; Lombard et al. 2012; Scerri 2017), the distribution of specific forms of pointed tools or other 'diagnostic' lithics (McBrearty and Brooks 2000), and the considerable increase in new innovations from a variety of materials in different regions and at different times (Scerri and Will 2023; Wadley 2015; Will et al. 2019b). An important observation is that many of these technocomplexes cross ecological zones. In the Late Pleistocene, some regional variants may persist only for a couple of thousands of years—such as the Howiesons Poort of South Africa—and some are quite locally specific with high internal variability such as the Sibudan in South Africa (Bader et al. 2015; Will and Conard 2018; Will et al. 2014). We also see evidence for localized innovation and limited spread of specific technologies on new materials. Examples include the engraving of similar motifs on ostrich eggshell that occur at two South Africa MSA sites 400km distant from one another (Henshilwood et al. 2014; Texier et al. 2013) or the manufacture of shell beads from the marine gastropod *Nassarius* both in northern (MIS 5) and southern Africa (MIS 4) that come and go at different times (Steele et al. 2019; Will et al. 2019a), forming distinct legacies.

Recent reviews of the MSA record found that different regions of the African continent are characterized by distinct, historically contingent spatio-temporal trajectories from 200 ka onward, reflected in both material culture and behavioral repertoires (Scerri and Will 2023; Will et al. 2019b). These observations fit with the prediction of a greater reliance on culturally transmitted information as part of a Late Pleistocene shift towards more distributed adaptation. While the evidence is less clear for the Middle Paleolithic of Europe, Neanderthal lithic technology also forms more discrete patterns in space and time compared to the Lower Paleolithic, particularly in the form of geographical patterning in its bifacial component (Ruebens 2013) and specific technocomplexes such as the 'Blattspitzengruppe' (Conard and Fischer 2000) or potentially the Chatelperronian (Zilhão 2006). Recent evidence for specialization in the production of birch tar provides a compelling example of localized cumulative cultural change among Neandertals (Schmidt et al. 2023). From at least 40 kya onward, Upper Paleolithic and Later Stone Age industries of Africa and Eurasia show a multitude and higher-turnover of technocomplexes of even lower temporal duration and spatial expansion with a wide range of variable material culture made from diverse materials. Further archaeological evidence for greater regional and chronological diversity in cultural repertoires would provide supportive evidence for enhanced distribution of adaptation onto cultural mechanisms associated with the EES.

Prediction 2: Greater dissociation between behavioral and environmental change

In addition to the greater range of cultural and technological innovation noted above, we would expect to observe a greater range of behavioral options employed within a given ecological circumstance rather than a single 'optimal' solution, signifying a degree of autonomy from the natural surroundings and selective pressures. Testing such predictions requires matching well-resolved archaeological and paleoenvironmental data (see e.g., Marean et al. 2015), ideally in a diachronic framework to assess association or detachment between behavioral and environmental change. Over time we expect there to have been an increased emphasis on cultural and other extrasomatic means of environmental mediation that ultimately allowed modern humans to react in a plethora of different social, economic, and technological ways to a given environmental context. When such shifts are associated with longer lifespans of hominins there may be additional pressure on the requirement of behavioral flexibility as genetic adaptations become a less agile form of adaptability in dynamic environments. A close integration between culture and neural development is expected, whereby encephalization is driven by behavioral change, and behavioral plasticity and niche construction are themselves ways to buffer the expensive brain from ecological stresses.

Much work in Paleolithic archaeology has focused on demonstrating direct links between specific periods of environmental change or ecologies and human behavior, but these have met with varying degrees of success (Foley and Lahr 2003; Goñi 2020; Maslin et al. 2014; Vrba 1995; Ziegler et al. 2013). A different perspective has focused on the role that rapidly changing and fluctuating environments had on human behavior, predicting that periods of climatic instability that characterize the paleoenvironment from 1.0 Mya onward would select for behavioral traits of increased cognitive capacities such as forward planning and heightened levels of behavioral flexibility (Potts 1998). A recent application of this variability selection hypothesis on the crucial transition period between the ESA and MSA in the Olorgesailie Basin found that significant behavioral changes found here were associated with higher levels of climatic and ecological variability between ~500–300 ka (Potts et al. 2018; 2020). This fits predictions of an increasing detachment from direct external selection pressures by current environmental states, instead redistributing them to other systems, such as culture, that predictively buffer against a range of potential environments encountered.

In recent years, there has been particularly strong and growing evidence from the MSA that early modern humans showed major changes in their material culture and behavioral repertoire independent of environmental change, with periods of environmental stability associated with drastic changes in hunting behavior and lithic technology at several South African sites (Clark 2011; Conard and Will 2015; Douze et al. 2018; Porraz et al. 2013). In these cases, behavioral change appears to be driven by demographic or other socio-cultural factors. A large meta-analysis of the MSA in southern Africa found climate was not the main factor driving human activities, with increasing behavioral flexibility itself being the key observable change over time (Kandel et al. 2015). These few examples attest to high levels of behavioral flexibility and a certain degree of autonomy from direct environmental pressures among early members of our species in the late Middle and Late Pleistocene. Despite this, there is also evidence that Neandertals, at least in the Late Pleistocene, adapted to changing and often challenging environments through behavioral flexibility and the construction of their own stable niche (Banks et al. 2021). In any case, more studies of the ESA and Lower Paleolithic are required to probe the time depth of the ongoing dissociation of behaviors from strict climate determination in human evolution, as are methodological advances to better link paleoclimatic and behavioral data on the appropriate scales (Blome et al. 2012; Chase and Meadows 2007; Marean et al. 2015). The accumulation of new archaeological evidence for cultural variation that varies independently of environment context would illustrate independent 'kinetic' change in cultural systems that are not constrained by Darwinian mechanisms.

Prediction 3: Human impact on the geological and ecological surroundings becomes visible on inter-generational and supra-local scales

As behavioral responses to environmental variation become more diverse and prominent, so does the output of material culture, which could result in large-scale niche construction in space and time that can be observed in a well-resolved, diachronic, archaeological record (Hussain and Will 2021). This pattern could be distinguished from the niche construction behaviors of earlier hominins and other animals by its magnitude, duration, and scale. In constructing their niche, hominins increasingly homogenize their environments alleviating or buffering against external stress. With its mostly coarse-grained resolution on the level of populations and multiple generations, the Paleolithic record is ideally equipped to detect these instances of large-scale niche construction as opposed to smaller-scale changes to environments within an individual's life-span and on local scales (e.g., site-scale). Evidence of hominin impact on the environment can already be seen by the origins of stone tool manufacture and the concomitant redistribution of lithic material on the landscape through manufacture and transport (Pope 2017), representing early components of human niche construction. However, a more significant question is when do we first see human impact on even larger temporal and spatial scales? Arguments can be made that we see glimpses of this in the Middle and Late Pleistocene archaeological record already in at least two different ways, though likely many more:

a. Large-scale re-distribution of (lithic) resources, reconfiguration of landscapes, and re-use of constructed locales. At several Stone Age localities in Africa and Eurasia, researchers have observed substantial accumulations of anthropogenic material, consisting of millions of stone tools, over long time scales through recurrent hominin activities at specific locales. These novel landscapes are the result of long-term procurement, knapping, and transport of lithic material (Hiscock 2014; Pope 2017; Hussain and Will 2021; Pope et al. 2006). At the Messak Settafe in Libya, the accumulation of Acheulean and MSA material over the last ~500,000 years, and subsequent deflation of deposits, has generated a 'lithic-strewn pavement' that averages about 75 artifacts per square meter, and stretches to over 350km in length (Foley and Lahr 2015). Such modified landscapes acted as an external raw material reservoir for mobile hominin populations, but also served as 'attractors,' entrenching their own position in the wider land-use system through repeated hominin visits and material input over time. Activities at such places favor embedded procurement strategies and further impact on human mobility, and subsistence strategies thus depended more on previous hominin behavior rather than natural lithologies (Haas and Kuhn 2019; Hussain and Will 2021). Systematic mining activities are known by at least 100 ka for chert in Egypt (van Peer et al. 2010) and by >30 ka for ochre in southern Africa (Bader et al. 2021). These further attest to the capabilities of Pleistocene hominins to enact permanent to semi-permanent changes in landscape forms. The subsequent impact of these activities on erosion and vegetation patterns likely influenced subsistence and mobility patterns of their own and other populations.

b. Inter-generational modification of ecosystems. Broad-scale human modification of ecosystems is ubiquitous in the Holocene and the hallmark of the Anthropocene (Fox et al. 2017), but the earliest archaeological traces of ecosystem engineering require subtle interdisciplinary analyses to detect. While fire is commonly discussed in the context of thermal adaptation, there are broader impacts of the use of fire on both humans and their environments (Gowlett 2006). In a recent example, fire use in the MSA has been linked to shifting patterns of vegetation and erosion, and an increasingly anthropogenic influences on ecosystems that led to more uniform use of fire between seasons, a process that began and intensified after 92 kya (Thompson et al. 2021). Similar evidence, also including transformations to plant communities due to fire use, have been documented during the Late Pleistocene expansions to Asia, Australia, and the Americas (Boivin et al. 2016). Interglacial Neanderthals at the German site of Neumark Nord shaped vegetation structure and succession by the various activities performed over ~2000 years in this landscape, including the use of fire (Roebroeks et al. 2021). Translocation and displacement of species as well as reconfiguration of food webs are also known from Late Pleistocene contexts, including instances of overhunting and other overexploitation of resources, often leading to a depletion and other negative long-term effects on the structure and viability of ecosystems (Boivin et al. 2016; Stephens et al. 2019; Stiner et al. 1999). While the extent of the early direct anthropogenic influence is often difficult to demonstrate, examples include the anthropogenic impact of modern humans on the extinction of megafauna during their expansions to Australia and the Americas at the end of the Pleistocene (Sandom et al. 2014; Van Der Kaars et al. 2017) and intense shellfish exploitation in the LSA of South Africa (Klein and Steele 2013) and the Upper Paleolithic of Europe (Turrero et al. 2012). In the latter case, continuous collection led to a decline in mollusc populations, as well as a reduction in the size of individuals and their genetic diversity. Similar evidence for the intensification of shellfish exploitation is also found in the southern African MSA (Langejans et al. 2012). While much of the current evidence is quite recent, new archaeological and paleoecological analyses that illustrate long-term cultural impacts on the environment would be illustrative of more systematic niche construction and 'ecological inheritance' in the past.

C. PREDICTIONS OF FEEDBACK BETWEEN BEHAVIORAL CHANGE AND BIOLOGY

Human culture can affect ecological and biological change but can also itself be the outcome of changes in these spheres, via co-evolution between genes and culture (see e.g., Gintis 2007; Richerson and Boyd 2005; Tomlinson 2018). In the framework of EES, a ratchet effect in this relationship would be most strongly expressed during the later phases of hominin evolution with an increase in the repertoire of behavioral innovations and material culture transmitted across generations. Pervasive material culture in the human lineage transforms the magnitude of ecological inheritance as predicted by niche construction theory. Such a pattern can buffer some selective pressures but also accelerate evolutionary change by producing new selective regimes and allowing for directional changes (Boivin et al. 2016; Laland et al. 1999; Odling-Smee et al. 2003). Heightened levels of interaction across different inheritance systems and associated feedback loops can have exponential and unexpected effects with cascading outcomes (Hamilton et al. 2020; Richerson and Boyd 2005; Tomlinson 2018), such as in the hypothesized positive co-evolutionary relationship between tool use, meat eating, brain size, dependence on social learning and teaching, and ultimately language (Aiello and Wheeler 1995; Antón et al. 2014). Among the different channels of information transmission, culture becomes a more frequent driver of phenotype and genotype by setting the environmental context of growth and development. From this, we can predict a close association between cultural change and phenotypic variation acting on short intergenerational timescales or within the lifespan. Here we propose several macro-evolutionary predictions testable within the Pleistocene fossil and archaeological record.

Prediction 1: Dispersals into novel environments clearly associated with material culture

There is a clear impact of cultural innovations on the effective occupation of unfamiliar territories. Improved technologies generated through innovation and transmitted through social learning can facilitate dispersal into environments that were previously uninhabitable. The initial colonization of extreme environments by modern humans was associated with the accumulation and transmission of local environmental knowledge, including material culture based upon locally available resources, and a combination of physiological adaptability and natural selection. The importance of social learning, cultural transmission, and material culture to human environmental adaptability is illustrated by the colonization of the Artic (Pavlov et al. 2001), and the Pacific (Couper 2009), and both are regions that show correspondence between phenotypic variation and environmental conditions (Daanen and Van Marken Lichtenbelt 2016; Houghton 1996; Steegmann 2007). Despite the reliance on technology for survival in both environments, there is evidence of environmentally driven natural selection associated with adaptation to local environmental stresses (Fan et al. 2016; Fumagalli et al. 2015; Raghavan et al. 2014). The best current evidence for the earliest dispersal of modern humans highlights the interaction between cultural and genetic adaptability as a crucial component of the process (Groucutt et al. 2015).

The environmental context of the emergence of the genus *Homo* is characterized by microhabitat variability (Patalano et al. 2021). The earliest widespread dispersal of members of our genus, often referred to as 'Out of Africa 1,' led to the broad geographic distribution of *H. erectus (sensu lato)* between Africa, Georgia, and Java, and the emergence of regional phenotypic variation (Antón 2003). Regardless of the point of origin of this species, which is generally agreed to fall within Africa, the dispersal was across a region broadly characterized as a savannah environment (Dennell 2011; Dennell and Roebroeks 2005). This suggests that this migration was not necessarily associated with material culture 'opening' new environments for colonization but that hominins instead migrated within familiar ecozones. The distinction between dispersals of early *Homo* into regions of relatively low climatic variability, and the Middle Pleistocene migrations adaptability to a wider range of habitats is supported by recent climatic modelling (Timmermann et al. 2022). The migration of Neanderthals into colder environments of glacial and interglacial Europe is well understood to be associated with a range of behavioral and morphological adaptations to the cold (Churchill 1998). Key components of this adaptability relate to material culture, such as the use of shelter and clothing, and aspects of behavior relating to dietary ecology, including physical activity levels and a protein heavy diet (Ocobock et al. 2021). While Neandertals occupied many temperate regions within Eurasia, they encountered considerable seasonable variation throughout their range. Recent evidence from Lichtenberg (Germany) demonstrates that Neandertal material culture appears to respond to cooling conditions, and a shift from temperate forest to cold steppe/tundra environmental conditions at the beginning of the last glaciation (Weiss et al. 2022). The use of fire does not appear to be associated with the earliest dispersals of *Homo*, or with the colonization of Europe or Northern Europe, but there is evidence for fairly regular controlled use of fire in the region during OIS 11 (after 424 kya) (Gowlett 2006; Roebroeks and Villa 2011; Rosell and Blasco 2019), although it is contested whether Neandertals were obligate fire users (Dibble et al. 2017). Clothing is an essential component of cold adaptation within our species. An analysis using ethnographic data to model the environmental circumstances under which clothing would be required, suggests that Neandertals required clothing that, even if not tailored, provided significant coverage during the winter (Wales 2012). Neanderthal lithic assemblages have high frequencies of scrapers, many of which were likely used for hide preparation, and there is evidence that hide preparation may have driven the noted bilateral asymmetry in Neandertal humeri (Shaw et al. 2012). Species commonly used to produce cold weather clothing are found in Neandertal and early modern human faunal assemblages (Collard et al. 2016). In combination, the evidence suggests that specific components of material culture and technology were essential for survival in Mid-Pleistocene Europe. The associations between material culture and dispersal into new environments is a clear example of distributed adaptation within the EES.

Prediction 2: Skeletal plasticity in response to cultural variation

Functional adaptation of the skeleton in response to mechanical stress is well documented and fairly well understood (Ruff et al. 2006; Stock 2018). Much of the evidence for plasticity in skeletal robusticity is drawn from variation in modern humans, which helps to generate hypotheses that can be tested against the fossil record. However, the relationship between material culture and the mechanical performance of the human body is complex. Specific technologies may open up new adaptive niches, but may require greater physical effort to use or may reduce physical demands on the human body. Such changes in habitual behavior may influence the patterns of skeletal robusticity, both positively and negatively. In this respect, we would predict that evidence for plasticity should involve significant changes in the pattern of hominin robusticity in response to technological or behavioral change. In the very broadest terms, there has been a clear and consistent decline in postcranial robusticity associated with origin of the genus *Homo* and continuing change within the lineage (Ruff et al. 1993). This trend is interpreted as evidence of a reduction in mechanical loading that may be reflective of shifts in cognition and habitual behavior, although brain size increases in early hominins do not coincide directly with the timing of change in robusticity, suggesting a complex relationship between cognitive, behavioral, and biomechanical change among early *Homo*. A key characteristic of modern human skeletal morphology is the comparitively low level of upper limb relative to lower limb robusticity. This pattern appears to be established within *H. erectus* but not *H. habilis* (Ruff 2009). The emergence of distinct patterns of bilateral asymmetry within the genus *Homo*, and particularly among Neandertals and Upper Paleolithic humans, is a clear indicator of plasticity in response to mechanical loading and cultural influences on the human phenotype (Trinkaus et al. 1994). Bilateral asymmetry of up to 70% in diaphyseal rigidity demonstrates extreme phenotypic expression in limb morphology with the same underlying genetic influences.

Within this timeframe we also see evidence of the emergence of regional variation in skeletal robusticity in response to locally contingent patterns of mobility and subsistence behavior (Shackelford 2007). Differences in the pattern of plastic response among Neandertals and modern humans have been interpreted as evidence for distinct hunting technology, specifically the use of close-quarter versus projectile weapons respectively (Churchill and Rhodes 2009; Schmitt et al. 2003). Similar evidence has also demonstrated that variation in lower limb morphology can be directly linked to differences in terrestrial mobility (Shaw and Stock 2013; Stock 2006; Stock and Pfeiffer 2001) and the use of specialized technology such as watercraft among modern human foragers (Stock and Pfeiffer 2001; Stock et al. 2018).

The pattern of evidence for the diversification of morphology in response to loading is clear among Middle Pleistocene hominins. While the general mechanism of functional adaptation is similar among all species with a skeletal system, the specific feedback between emergent cultural variation and skeletal plasticity is particularly relevant to our consideration of the extended evolutionary synthesis and the genus *Homo*, and will be important for future research in this area. Within a framework of distributed adaptation, cultural influences on plastic regions of the skeleton provide a secondary reflection of shifting patterns of cultural diversity within our lineage, and should be linked with the regionalization of behavioral strategies outlined in section B.

DISCUSSION AND FUTURE DIRECTIONS

In this review we have highlighted a series of both generalized and specific predictions that stem from the EES and what we have termed distributed adaptation and selection, where diversity and adaptability are distributed across multiple adaptive systems and mechanisms that serve to buffer the genome from the relative costs of natural selection. While there are many routes through which environmental accommodation can be achieved, we broadly grouped these into categories relating to cultural evolution, or physiology and phenotypic plasticity. We additionally considered the interaction between culture and biology.

For each prediction we have briefly considered the current evidence for our understanding of distributed adaptability within the genus *Homo*. From this review, it appears that key components of distributed adaptability arose in different times and contexts within the genus *Homo*. Our species, throughout our full contemporary range, fulfills all predictions of distributed adaptation generated on the basis of the EES, however, the relative timing of the origins of these characteristics is variable.

The emergence of regional variation in phenotypes in *H. erectus* may be an important component of the evolution of distributed adaptability. It is not unreasonable to suggest that the mechanisms that influence living human growth in response to environmental stimuli may have also characterized earlier members of our genus, and regional variation in crural indices that emerge in the Middle Pleistocene can be parsimoniously interpreted as plastic responses to thermal or other environmental stress. Such plasticity may still be considered adaptive, either to thermal stress (Serrat et al. 2008) or as a mechanism of protecting the development of the brain in response to stress (Pomeroy et al. 2012). Overall, the morphological evidence suggests a mosaic pattern of distributed adaptation with evidence for various traits emerging among early *Homo*, Middle Pleistocene *Homo*, and within *H. sapiens*.

There is already strong archaeological evidence for distributed adaptation in our species having deep roots in the Pleistocene, supporting key predictions from the EES with a stronger emphasis on adaptability via cultural means. Many of these traits are not exclusive to modern humans and their archaeological record, however, and some evidence for increased cultural mediation of the environment, and phenotypic and cognitive plasticity are also found among Early and Middle Pleistocene *Homo*. For larger-scale and long-term niche construction, the earliest persuasive cases derive from the late Middle and Late Pleistocene and are associated with our species or Neandertals. In sum, our predictions for macro-scale patterns in the archaeological record identified some support dating to the ESA and Lower Paleolithic, however, the most convincing evidence comes from the MSA/Middle Paleolithic and beginning in the late Middle Pleistocene.

While we have tried to separate and identify discrete predictions and evolutionary trajectories where possible, it should be noted that a key prediction of the EES is the increasing cultural influence on physiology and genetic variation. There is strong evidence that culture enabled or enhanced hominin dispersal capacity and colonization of extreme environments by the Middle Pleistocene and subsequently. There is also clear evidence for skeletal plasticity in response to cultural variation on the same timescale.

Overall, we have illustrated what we suggest represents a mosaic pattern of the evolution of distributed adaptation and selection within our genus. In early *Homo* there is evidence of phenotypic diversification that precedes cognitive, behavioral, and cultural variation of Middle Pleistocene *Homo*. This can be interpreted as representing a shift within the distribution of adaptation between systems, first onto mechanisms based on physiological plasticity, and later onto cognition, cultural buffering of environmental stress, and enhanced niche construction. There are two fundamental ways that humans may have developed these traits. The first can be considered as an 'it happened to us' hypothesis, where these trends are a passive response to increasing volatility of climate through human evolution that accelerated the rate of local ecosystem change (Lisiecki and Raymo 2005). The second can be considered as a 'we did it to ourselves' hypothesis, where our lineage increasingly colonized, encountered, and constructed new niches and selective pressures on rapid timescales (Wells and Stock 2007). The latter would include a ratchet effect, where populations that can cope with ecosystem change through distributed adaptation experience demographic expansion, but also have greater capacity to probe more ecosystems, colonize new environments, and eventually create and engineer their own. One might predict that reaching a certain level of climate variability pushes hominin adaptability and demography over a threshold whereby colonization suddenly became much more achievable (see also Scerri and Will 2023). Most of these observations relate to long-standing topics of consideration within paleoanthropology, however, the EES provides a detailed and unified theoretical framework within which to consider their integration and generating predictions for the interdisciplinary research required to disentangle the unique and complex evolutionary trajectory of our genus.

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DATA AVAILABILITY

Data used in this study are available at the PAVELab Borealis Dataverse: https://borealisdata.ca/dataverse/pavelab.

STATEMENT ON USE OF AI

No artificial intelligence (AI) technologies were used in the research, analysis, or writing of this paper.

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