Cultural inheritance is driving a transition in human evolution

Timothy M. Waring[1], Zachary T. Wood[2]

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[1]School of Economics, Mitchell Center for Sustainability Solutions, University of Maine, Orono, ME, USA. ORCID: 0000-0001-7364-1130, timothy.waring@maine.edu
[2]Ecology and Environmental Sciences, University of Maine, Orono, ME, USA. ORCID: 0000-0001-7369-9199

Abstract

Previous research on a transition in human evolution has been befuddled by the complexity of adaptive culture and made little effort toward empirical tests. We resolve these problems with a novel and testable theoretical mechanism. First, we explain how a differential in adaptive capacity between genetic and cultural inheritance could drive an special evolutionary event, an evolutionary transition in inheritance and individuality (ETII). We elaborate the ETII hypothesis, and show it can resolve the prior debates, such as why genetic group selection is not a necessary precondition to transition. Next, we develop quantitative metrics of evolutionary transition in both phenotype and fitness to measure movement along this transition. We evaluate available evidence and find that patterns in gene-culture coevolution lend credence to the possibility of an ongoing transition. Finally, we derive a set of testable predictions and outline an agenda for future research.

Keywords: culture; gene-culture coevolution; evolutionary transition; inheritance; human evolution

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I. Confusion over long-term human evolution

The possibility that human evolution might be shifting to a higher level of biological organization has fascinated scholars for decades (Maynard Smith and Szathmáry 1995, Stearns 2007, Gowdy and Krall 2014, Powers et al. 2016, Andersson and Törnberg 2018, Waring and Wood 2021, Carmel 2023). The emergence of a higher level of biological organization, such as the evolution of multicellularity, is termed an evolutionary transition in individuality (ETI) (Michod 2000, Queller and Strassmann 2009, McShea et al. 2011, Szathmáry 2015, West et al. 2015). ETIs are thought to proceed through a series of contingent stages, as follows: (i) initially free-living individuals organize into cooperative groups, then (ii) groups come to determine individual outcomes, leading to greater group-level selection pressures, and finally, (iii) sustained group selection drives the emergence of a highly integrated superorganism (Michod 2000, Okasha 2005). Such transitions include the emergence of new divisions of labor, the loss of individual reproduction, and the rise of new routes of information transmission (McShea et al. 2011, Szathmáry 2015, West et al. 2015). ETIs have been proposed to explain the evolution of prokaryotes (Szathmáry and Demeter 1987), eukaryotic cells (Margulis 1970), multicellular organisms (Michod 2007), and eusocial species (Anderson 1984).

Many suspect that an evolutionary transition in humans may be linked to the emergence of language, culture, and institutions (Szathmáry 2015, Powers et al. 2016, Andersson and Törnberg 2018). Homo sapiens exhibits many features characteristic of other superorganisms (e.g. cooperation with non-kin, complex division of labor, non-genetic information transmission). One common observation is that human psychological and social interactions share features with other superorganisms. For example, our species exhibits characteristics which appear to have facilitated the emergence of large, complex, cooperative societies, from well-developed mechanisms to achieve unity of action and resolve internal conflict (Kesebir, 2012) to the development of institutions that facilitate the division of labor (Powers et al., 2016).

However, there is significant disagreement about the possibility, nature and status of a human evolutionary transition. Scholars disagree on status of a human ETI. Powers et al. (2016) suggests that large complex societies constitute a completed evolutionary transition. Andersson and Törnberg (2018) argue that humans completed an ETI when human encephalization quotients began to rise ~2 million years ago. Alternatively, our species may have begun, but not completed, an ETI. Importantly, unlike in other lineages with and ETI, our species has not lost reproductive autonomy or developed physiological integration. Thus, Gowdy and Krall (2014) suggest humans are in a state of incomplete transition, with the emergence of agriculture representing a partial transition to 'ultrasociality' short of a fully eusocial state. Stearns (2007) argues that a human evolutionary transition is stalled since factors such as migration, which reduces genetic group differentiation, and trade, which increase interdependence between groups, undermine conditions for genetic group selection.

Others have suggested that the ETI theory does not apply to humans (e.g. McShea 2023). Szathmáry (2015) concludes that human evolution is not an ETI in the same sense that the emergence of multicellularity or eusocial insect societies were, because human "group structure is too transitory to allow for a major transition in evolution in a purely biological sense." Similarly, Kesebir (2012) argues that superorganism metaphor fails to describe the human case when our groups are fluid and individuals have multiple group identities. One important loose end concerns the evolving role of culture and society.

This biological debate echoes an older debate among anthropologists and sociologists on whether human society represents a source of group-level causation, or constitutes a new level of individual (i.e. a "superorganic" entity). As early as 1898, Spencer (Spencer 1896, Simon 1960) saw society as a superorganic, emergent property of interacting individuals. So did Kroeber (1917), who drew on Darwinian principles to explain a superorganic society. Others argued that the concept of superorganic culture is a misplaced biological analogy (Simon 1960), or a reification (Duncan 1980). More recently, Richerson and Boyd have argued that culture is rooted in human biology (Richerson and Boyd 2001), and propose that human society does constitute a 'crude superorganism' with group-level causation, structure and function

(Richerson and Boyd 1999). Anthropologists increasingly agree that human society and culture exhibit an group functionality and may even expresses agency above the level of the individual (Hanson 2004).

In summary, the theory on this topic is befuddled. Basic definitions are unsettled. Does the ETI framework apply properly to humans? What new level of individuality is implicated? What is the role of culture? More importantly, very little research has sought to develop novel empirical tests of the possibility of an evolutionary transition in humans.

In this paper, we develop a parsimonious description of human evolution that resolves the prior debates. Building on dual-inheritance theory (Campbell 1965, Richerson and Boyd 2005, Henrich and McElreath 2007), we argue that culture constitutes a second system of adaptive inheritance which could drive a special type of evolutionary transition. We develop empirical metrics to measure the progression of this transition and review the available evidence. Finally, we derive a series of testable predictions and outline a research agenda.

The human evolutionary transition, revisited

A dual-inheritance account of human evolution starts with two observations. First, groups such as societies or organizations provide humans countless evolutionary benefits (e.g. shelter, food provision, defense, health care, education) for humans. Second, in contrast to other animal societies the organization and operation of human groups is facilitated by cultural inherited information such as narratives, language, symbols, traditions and institutions (Moffett 2024). Human societies and organizations vary according to cultural differences (e.g. language, habits, norms, traditions, institutions of power, infrastructure), which are modified through cultural processes (e.g. creativity, tradition, legislative change), and inherited culturally (i.e. from ancestor groups, other groups). Variations in the structure and function of human groups can have dramatic impacts on human learning, survival and reproduction. Thus, human cultural inheritance can be said to "superintend" the structure of most human groups. But the implication that cultural inheritance may have guided human evolution through the design of society has been largely overlooked. Here, we develop the theory that the cultural evolution of human groups, from organizations to societies, can clarify outstanding questions on human evolution, explain a long-term transition in human evolution, and even yield testable predictions. Hereafter, we refer to human groups generally. The nature and features of groups that may become most important is a quantity we would care to derive from theory and data, precisely because we seek to develop a theory that concerns the emergence of a new level of evolutionary individual.

We have proposed that human evolution is uniquely and parsimoniously described by an evolutionary transition in inheritance and individuality (ETII), which would help explain long-term patterns in human evolution (Waring and Wood 2021, Waring et al. 2022). Here we develop this hypothesis for empirical use. An ETII would unfold via positive feedback (i.e. Crespi 2004) between the adaptive

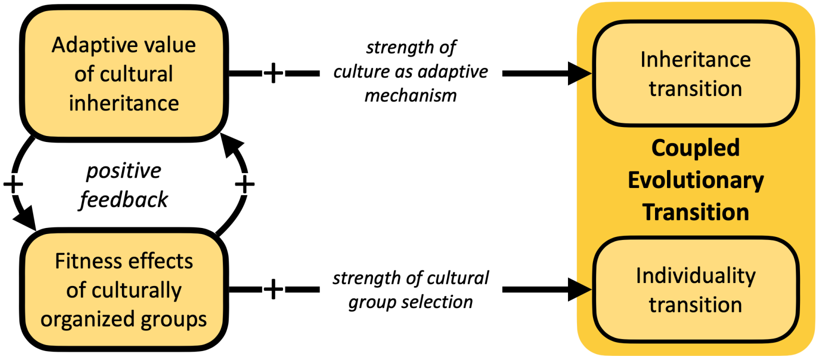

Figure 1. The evolutionary transition in inheritance and individuality (ETII) hypothesis proposes that long-term human evolution is driven by positive feedback between the fitness advantages of organized groups and the adaptive capacity of culture relative to genetic inheritance.

value of cultural inheritance and the fitness effects of culturally organized groups (Figure 1). This hypothesis helps to resolve many of the outstanding problems encountered when considering an evolutionary transition in humans. It reveals how the ETI framework may be applied to humans specifically, it clarifies the role of culture in human evolution, it elucidates the status of the transition, and it explains why a lack of genetic group selection need not be an impediment to a certain special type of evolutionary transition.

Each evolutionary transition has certain logical preconditions. *A transition in individuality requires that adaptive information must accumulate at the higher level, and selection at that level must overwhelm countervailing selection at the lower level.* Jablonka (1994) argued that epigenetic inheritance systems, including culture, play an important role in the evolution of new levels of individuality. The transition from RNA to DNA provides the best and most closely studied example of an inheritance transition. One theory suggests that the transition from RNA to DNA (Forterre 2005, Sterelny 2011) might have occurred because DNA is a more stable medium of information storage than RNA, with higher fidelity (Lazcano et al. 1988). Thus, the relative capability of inheritance systems should influence the likelihood of an inheritance transition. *Therefore, an inheritance transition requires that a novel system of inheritance provides a more effective means of accumulating adaptive traits than the original system, thereby circumventing adaptive evolution in the original.* A human ETII would therefore require that cultural evolution both (a) becomes more adaptive than genetic evolution, and (b) generate and accumulate group-level adaptations. We focus on the central causal role of cultural inheritance.

II. Interacting inheritance systems

The evolutionary interaction between genes and culture results from their differences as mechanisms of inheritance. The transmission of culture, commonly defined as socially transmitted information such as language, beliefs, norms, institutions, and technology, provides an alternative inheritance system for humans distinct from genetic inheritance (Boyd 2017). The two inheritance systems are neither parallel in the routes of transmission (Creanza et al. 2017) nor similar in mechanism (Figure 2). Genetic inheritance involves the physical replication of the storage medium (or genotype) and transfer from parent to offspring. By contrast, cultural inheritance involves the ability to copy the knowledge, behavior, skills, and norms of

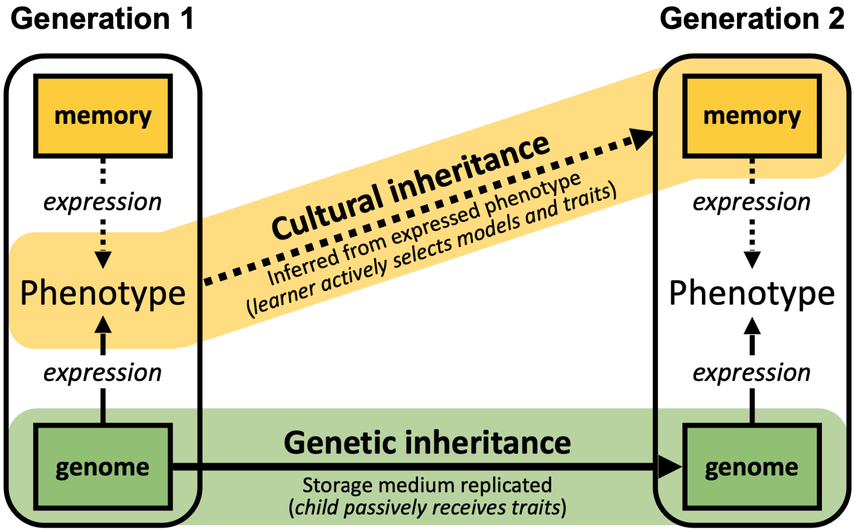

Figure 2. Cultural inheritance is neither parallel nor equivalent to genetic inheritance. While genetic material is physically replicated and directly transmitted, cultural memory is neither replicated nor passively received. Instead, cultural traits are transmitted via their influence on the observable phenotype (e.g. behavior), and active processes of inference and imitation on the part of the learner. Moreover, genetic traits are passively inherited by offspring, while cultural learners are active and often strategic agents in the selection and adoption of cultural traits.

others and to store the result in synaptic patterns in the brain. While our primate relatives are capable of innovation and cultural transmission (e.g. Whiten et al., 1999), they appear to lack the robust capacity to accumulate open-ended cultural variation that defines human culture (Tennie et al. 2009, Tomasello 2019, Townsend et al. 2023). For cultural transmission, underlying storage medium need not be physically transmitted between individuals. Instead, cultural learners actively reconstruct the cultural phenotypes of model individuals they select.

Consequently, cultural evolution is mechanistically distinct from genetic evolution in multiple ways (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Mesoudi 2011). For example, while genetic inheritance is primarily vertical and passive for the recipient, cultural inheritance often occurs through strategic social learning, includes many cultural models, and can occur in vertical, horizontal, or oblique directions relative to genetic lineages (Cavalli-Sforza and Feldman 1981, Mesoudi 2011). While genetic variation is largely random, cultural variation can be 'guided' by intentional innovation (Boyd and Richerson 1985). Overall, the differences between genetic and cultural evolution (Table 1) appear to explain why cultural evolution can solve adaptive problems more rapidly (Perreault 2012, Lambert et al. 2020).

	Human genetic evolution	Human cultural evolution
Variation	• Primarily random mutation • Mutation rates low μ=0.5×10^{-9}bp^{-1}year^{-1} (Scally 2016)	• Includes guided, intentional innovation (Boyd and Richerson 1985) • Mutation rates high, μ=11% (Adamic et al. 2016)
Inheritance	• vertical (parent → offspring) • 2-to-1 (sexual) or 1-to-1 (asexual) • non-strategic for recipient	• vertical, horizontal, oblique, etc. • many-to-one (frequency dependence) • strategic and selective adoption of cultural traits (Mesoudi 2011)
Selection	• Natural selection • Sexual selection	• Natural selection • Sexual selection • Cultural selection (Henrich 2015)
Structure	• Little evidence for genetic evolution of groups	• Cultural variation is more group structured than genetic variation (Bell et al. 2009)

Table 1. Human cultural evolution is distinguished from genetic evolution in mechanisms and sources of variation, the routes of inheritance, the mechanisms of selection, and consequently the speed of change, and resulting population structure.

There are, therefore, fundamental differences between genetic and cultural inheritance systems. However, Darwinian change, and adaptive evolution do not require the replication of discrete particles of inheritance (Henrich et al. 2008). These differences suggest three facts: human culture holds greater adaptive potential than genes, human culture acts as a type of heritable behavioral plasticity, and cultural adaptations accumulate for human groups as well as for individuals. Below we explore these possibilities.

Comparing the adaptive potential of culture and genes

The adaptive potential of genetic and cultural inheritance systems can be compared using breeder's equation (Kempthorne 1957). Our goal is only to compare adaptive capacity in a heuristic and evenhanded manner, not to calculate rates of change. The ability of an inheritance system to facilitate adaptation depends on the speed with which it can generate, store, and spread phenotypic variation with fidelity. The breeder's equation was developed to guide artificial selection programs, describing evolutionary change as the result of both selection and heritability. Our concern is to understand how change in a quantitative phenotype might differ if it were driven by cultural versus genetic evolution. Consider a phenotype, such as realized visual acuity, integrating both biological vision (e.g. eyes) and cultural vision supports (e.g. glasses). Change in phenotype, ΔZ, is given by the product of trait heritability (h^2) and the selection differential (S). To allow comparisons between genes and culture, we scale phenotypic change by the generation time (G), following Hendry and Kinnison (1999):

$$\Delta Z = \frac{h^2 S}{G} \quad (1)$$

Equation (1) shows us that cultural evolution will cause more phenotypic change than genetic evolution if, relative to genetic change, the section differential is greater, heritability is higher, the generation time is shorter, or some combination thereof. Evidence and theory suggest that culture often fulfills all three of these conditions:

Generation time (G)

Generation time, G, is influenced by different constraints in genetic and cultural transmission. In the genetic case, the 'generation time' G is the average time between the birth of parents and the birth of their offspring, a number constrained by the slow processes of human reproduction and maturation (1-2 decades). In the cultural case, G reflects the average time between learning a piece of information and transmitting it. Cultural generation time is therefore constrained only by the rate of social learning, and the frequency of social interaction, which can be very rapid in many social environments (seconds). Thus, both the lower bounds and averages of cultural G can be orders of magnitude shorter than those of genetic G (Lambert et al. 2020). Indeed, humans reproduce culturally well before reaching sexual maturity.

Heritability (h^2)

Heritability, h^2, is a measure of the amenability of a trait to multi-generational change by selection and is defined as the proportion of total phenotypic variation that can be attributed to additive genetic variation. In the case of cultural traits, this can be generalized to ‘the amount of phenotypic variation that is attributable to inherited variation’ (Wagner and Danchin 2010). Typically, an increased genetic mutation rate decreases trait heritability (Falconer 1960). While genetic fidelity is very high. For example, rate of nucleotide polymerization errors is estimated between $1:10^8$ - $1:10^{10}$ (Bębenek and Ziuzia-Graczyk 2018). However, genetic heritability in animals is typically low, with large environmental influences. Meanwhile, cultural transmission fidelity may have been initially very low in early human evolution. The rate of mutation in cultural traits is likely higher than in genetic traits (Baer et al. 2007, Adamic et al. 2016, Scally 2016). However, phenotypic differences between cultural learners and models are often corrected through instruction, teaching, and error checking (Kline 2015, Kempe et al. 2018) allowing the phenotypic behavior of the learner to be iteratively refined to better match the model. Error checking, multiple model learning, linguistic communication may also reduce the environmental influence on phenotype, allowing culture to reach even higher levels of heritability. Theoretical models suggest the fidelity of cultural transmission has likely increased during human evolution (Lewis and Laland 2012), providing ever greater scope for adaptation. Thus, generalized cultural heritability may vary considerably and depend on domain and social learning mechanisms, but digital communication suggests that cultural heritability may be quite high in many circumstances.

Selection differential (S)

The selection differential (S) is the intergenerational change in the distribution of a trait. In a cultural system, a learner may have many cultural parents, which would tend to decrease S from the 2-parent genetic case. However, cultural learners also actively select models to imitate, which might increase S by restricting the pool of cultural parents to high performing individuals. In addition, intentional instruction and formal education systems may further refine the pool of cultural models, making it both smaller and more specialized. The result is that in many domains, cultural S will be much higher than is possible in natural genetic systems.

Empirical comparisons of genetic and cultural variation and change remain a major methodological challenge (Perreault 2012, Lambert et al. 2020, Ramsey and DeBlock 2017). And, although the breeder’s equation is useful in conceptualizing evolution at a theoretical level it since it assumes that correlated traits have essentially no fitness effects. For empirical research outside of laboratory conditions, the Robertson–Price identity provides a better starting point (Morrissey et al., 2010).

Nonetheless, even small average differences in S, h^2 and G could make cultural evolution more rapid than genetic evolution when compounded geometrically over the long term (Perreault 2012, Mathew and Perreault 2015, Boyd 2017, Lambert et al. 2020).

Human culture generates group-level adaptations

Although group selection is thought to be involved in ETIs, it remains rare in animal societies. However, evidence suggests that group selection on culture is common in our species (Richerson and Henrich 2012, Richerson et al. 2016, Francois et al. 2018, Handley and Mathew 2020). Quantitative estimates show that human culture is exhibits greater between-group variation than human genes (Bell 2010). Theory and experiments show that group selection on cultural variation is facilitated by mechanisms that have no genetic parallel, such as conformity (Coultas 2004, Whiten et al. 2005, Claidière and Whiten 2012, Morgan and Laland 2012) and social marking (Boyd and Richerson 1987, Nettle and Dunbar 1997, McElreath et al. 2003) as well as emergent processes within groups such as selection on institutions (Bowles et al. 2003). The accumulation of group-level adaptations may occur via two types of multilevel selection (MLS). MLS1 concerns group selection on characteristics of the individuals that make up the group, while MLS2 selects on the characteristics of the groups themselves (Okasha 2005). For example, MLS1 might have operated on the human capacity for cooperation and linguistic coordination, while MLS2 may operate on human institutional structure. Four factors enhance the importance of culturally organized groups for evolution of both genes and culture.

First, *culturally organized groups are more powerful than individuals*. If humans compete, organized groups of humans will tend to win in direct competition with unorganized populations and proliferate at their expense. For example, the advent of agriculture is known to have accelerated the development of complex, organized and hierarchical societies, enabling their subsequent proliferation and the displacement hunter-gatherer populations despite evidence shows that sedentary agriculture reduced human health and nutrition relative to a hunter-gatherer lifestyle (Larsen 2006, Fields et al. 2009, Latham 2013). Thus, the agricultural transition likely required a difficult life history tradeoff in which the increased disease and childhood mortality caused by sedentary agriculture was compensated for by women having more children (Page et al. 2016).

Second, *group competition facilitates cooperation and organization within groups*. The operation of group-level selection is mathematical fact that holds for any system or species (Traulsen and Nowak 2006). In humans, group competition appears to suppress non-cooperative individual behaviors, and facilitate the expansion of cooperation and prosocial tendencies (Chudek and Henrich 2011). Theoretical models of cultural evolution show that group competition can drive the evolution group-level competitive traits, such as within-group altruism and out-group hostility, via both warfare (Choi and Bowles 2007) and resource use (Waring et al. 2017). This pattern is supported by cross-cultural evidence through human history (Richerson et al. 2016) and in economic competition across geographic regions (Francois et al. 2018), and by quantitative evidence from violent group conflict in pastoral societies (Zefferman and Mathew 2015, Handley and Mathew 2020).

Third, *culturally organized groups solve adaptive problems more readily than individuals.* When humans form groups we learn from each other more rapidly, accelerating the accumulation of adaptive cultural traits relative to isolation. The accelerated accumulation of advantageous traits may allow our species to exploit resources and bolster the survival and reproduction more efficiently than in insolation (Muthukrishna and Henrich 2016). Theory suggests that cultural adaptation should increase with greater interconnectedness, cultural diversity, and transmission fidelity (Schimmelpfennig et al. 2020). This is supported by behavioral experiments showing that people learn skills more accurately when they can observe more cultural models (Muthukrishna et al. 2014). Simulations show that rapid group-based cultural adaptation could have driven the correlated evolution of human sociality, brain size and life history traits as human groups themselves grew (Muthukrishna et al. 2018). Accelerated group-level cultural adaptation also functions in modern economies (Brahm and Poblete 2021). And economists have repeatedly shown that larger and more interconnected groups are robustly more creative and innovative. For example, cities with greater population density generate patents more rapidly *per capita* (Carlino et al. 2007).

Fourth, *larger groups may make cultural adaptation more efficient*. Larger groups with shared culture may further achieve group-level cultural adaptations more even rapidly than smaller groups. For example, in Oceania population size predicts technological complexity in the absence of environmental variability (Kline and Boyd 2010). Languages with more speakers are more efficient from an information theoretic perspective (Muthukrishna and Henrich 2016), likely because the rate of language evolution increases with population size (Bromham et al. 2015).

Long-term gene-culture coevolution

Stearns (2007) argued that an evolutionary transition in individuality because humans lack strong genetic group structure. But this argument misses the adaptive importance and group structure of cultural variation. The mechanisms outlined above create culturally organized human groups that can influence genetic outcomes (Henrich and Boyd 1998, Henrich 2004, Boyd and Richerson 2010, Richerson et al. 2016, Boyd 2017). So, while human groups reliably interbreed, group-level cultural differences can be maintained by conformity and social pressure to adopt group behavior. Genetic evidence has shown that distinct genetic groups may dissolve through population mixing even while members continue to belong to distinct cultural groups (Dorp et al. 2018). The implication is that cultural group selection may have driven genetic selection for human sociality and cultural capacity (i.e. the ability to work effectively in groups), without causing strong group-selection on genes. In this way, the accumulation of adaptive group-level cultural variation could drive a human ETII despite increasing genetic mixture. The long-term interactions between cultural and genetic evolution can be organized into the effects on selection and reproduction of both individuals and groups. In the long term, cumulative cultural evolution tends to strengthen group reproduction and group selection while weakening individual selection and reproduction (see Table A1).

In summary, evidence suggests that cultural inheritance exhibits three pertinent characteristics in relation to genetic inheritance. Culture (a) holds greater adaptive potential than genes, (b) exhibits a strong plastic effect, and (c) generates more heritable group-level structures and adaptations than genes. We propose that these characteristics are sufficient to enable an evolutionary transition in both inheritance and individuality. Below, we develop a simple conceptual model of the transition.

III. An evolutionary transition in inheritance and individuality

Consider an evolutionary transition that begins with a species evolving primarily via genetic inheritance and competition among individuals and concludes with a very different species evolving primarily via cultural inheritance and competition among culturally integrated groups (Figure 3). The transition is driven by the long-term accumulation of adaptive group-level cultural variation, such as via cultural group selection. Cultural group selection causes changes in both inheritance and group organization (Henrich 2004, Smith 2020), and is considered a primary explanation for the emergence of human collective culture (e.g. Richerson et al. 2016). However, while formal models demonstrate the possible role of selection on group culture in social evolution (Turchin and Gavrilets 2009, Waring et al. 2017), it remains difficult to measure empirically (e.g. Turchin and Currie 2016, Waring and Acheson 2018, Waring et al. 2021).

As the inheritance transition proceeds, culture replaces genes as the primary determinant of phenotype. Note that cultural inheritance need not make genetic systems disappear or render them irrelevant. Instead, culture would only supplant their role as primary driver of human phenotypes, starting with behavior, and extending to physical capacities (e.g. flying, extended underwater swimming), and eventually including biological traits (e.g. enhanced immunity to pathogens). Phenotypic traits which are currently partly genetic and partly cultural in origin help us reason about this transition. Take human cooperative tendencies for example. It seems likely that we have evolved a genetic capacity for cooperation but that the forms that cooperation or moral norms take vary significantly between human cultural groups (e.g. Boyd and Richerson 2009). How much cooperation is genetically determined and how much is cultural is, of course, difficult to determine but serves as a helpful thought experiment. For example, early in human evolution genetic traits for cooperation may have been selected via MLS1 on genes through their influence on collective success at big game hunting. Since that time, social structures such as paying jobs, incentives, and jail have evolved via MLS2 on culture. These further align individual self-interest with that of the group, even without the need for cooperative inclinations. If the relative contributions of genes and culture to cooperative behavior were to change, so would the importance of genetic and cultural selection in determining the evolutionary trajectory of the trait.

In parallel, as the individuality transition continues, group outcomes become a primary determinant of individual fitness. The unit of selection shifts from individual humans to groups of humans and their cultural systems, infrastructure and technology, which we may loosely call 'societies.' In the beginning the health and reproduction of individual humans drives evolutionary change (in both genes and culture). At the end, the health and reproduction of societies (includes and involves that of individuals, but not in any simple way) becomes most important (for changes in both genes and culture). For example, city drinking water systems provide easy access to drinking water for large populations of people. The water is typically purified and of a high and uniform quality, and the system allows for better drinking water in a dense city than is possible when individuals handle their own water collection and sanitation. Naturally, city dwellers become dependent on city water. If the water stopped flowing or were contaminated, the all city residents would suffer. Thus, differences between cities come to determine how water quality influences individual health and fitness, and city-level efficacy. Here, the city is the unit of cultural selection. But cities do not evolve biologically, and rarely undergo natural selection by extinction. This is where purely biological accounts of a human transition often run aground. Instead, cities, like human groups in general, evolve culturally via imitating useful practices and systems from peers.

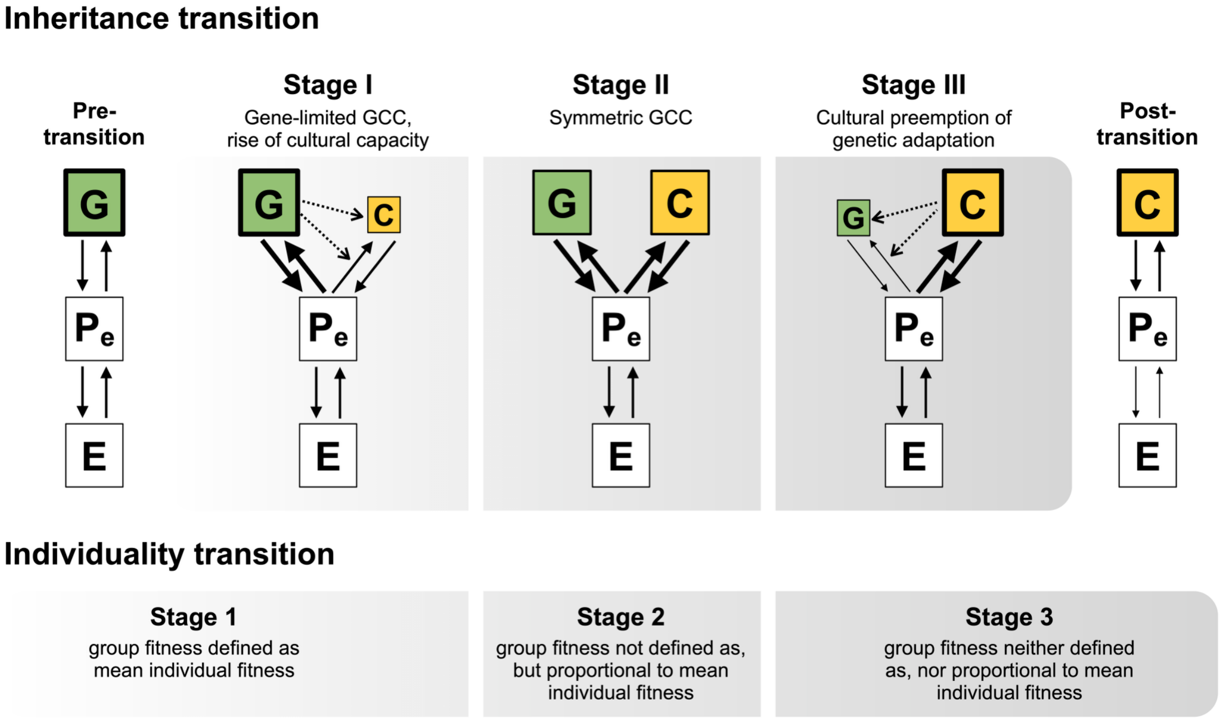

Figure 3. An evolutionary transition in inheritance and individuality unfolds through a series of contingent stages. The inheritance transition passes through three stages, (1) the initial selection for cultural capacity (e.g. via MLS1 on genes), (2) a period in which the adaptive capacities of two systems are roughly equivalent, and finally (3) the preemption of genetics by culture as primary inheritance mechanism (e.g. via MLS2 on culture). Arrows represent long-term evolutionary influences between genotypes (G), extended phenotypes (P_e), culture (C), and the environment (E). Simultaneously, the transition in individuality proceeds by multilevel selection as Okasha described. Note that RNA is not depicted in this figure.

Group-level cultural adaptation occurs when the differences between cities (e.g. the prevalence of water borne diseases) drives the transmission of cultural traits to design, build, operate and maintain city water systems. As the process of group-level cultural adaptation continues, we expect an increase in the proportion of individual fitness variation due to the group (Okasha 2005).

In summary, the human ETII begins with a change in the dominant mode of phenotypically relevant information transmission. One crucial effect of such a transition is a change in the dominant mode of selection.

Stages of transition

Okasha (2005) argues that ETIs can be understood through the changing relationship between collective and individual fitness and broken into three stages. In stage 1, collective fitness is defined as average individual fitness. In stage 2, collective fitness is not defined as average individual fitness but is proportional to it. And in stage 3, collective fitness is neither defined as average individual fitness nor proportional to it. An inheritance transition could be understood through the relationship between the original and novel inheritance systems. We propose that the gene-culture inheritance transition is likely to proceed through stages which roughly parallel the level of selection stages described by Okasha. These stages are: (1) the genetic evolution of cultural capacity, (2) symmetric gene-culture coevolution, and (3) cultural preemption of genetic adaptation. Figure 3 shows the interaction between the transitions in inheritance and individuality.

Prior to the transition, human evolution is dominated by natural selection and genetic niche construction, in which genotypes, phenotypes, and the environment interact in the absence of culture (Odling-Smee et al. 2013, Hendry 2016).

Stage I: Emergence of culture

A gene-culture inheritance transition begins with an initial cultural breakout phase, in which cultural capacity is limited but selected for. Over time, human ancestors would have transitioned from ape-like culture to human-like culture (Tennie et al. 2009) and become capable of extensive open-ended cultural refinement. In this phase, adaptive cultural evolution is dependent directly on genetic capacity for cultural storage and transmission. At first, individual-level genetic variation in cultural capacity should be much greater than variation in cultural traits themselves, and any fitness gains from cultural evolution will mostly be realized at the individual level. This is the only stage in which Lumsden and Wilson's (1981) statement that "genes hold culture on a leash" is accurate.

Stage II: Symmetric gene-culture coevolution

Once genetic capacity for social learning can support the inheritance and accumulation of adaptive culture (Henrich et al. 2016), cultural adaptation accelerates. Culture contributes to the extended phenotype (Dawkins 1982). For example, culturally adapted technologies (e.g. the plough), can increase absolute or relative fitness. Michod and Herron (2006) describe 'fitness export' the evolutionary process by which cooperation and specialization among individuals causes fitness to accumulate at the group level. Humans export fitness to our societies when we cooperate and specialize to create group level benefits with culturally defined roles such as armies for collective defense, farmers to feed cities, and doctors keep the population healthy. Thus, in human evolution, fitness is exported from the individual to the group through a greater reliance on adaptive information accumulated and stored in the cultural inheritance system. As culture plays a larger role in increasing fitness, there is strong selection for genetic traits that increase cultural capacity further. This feedback, or ratchet, allows culture to rapidly increase its phenotypic footprint in a process known as runaway cultural niche construction (Rendell et al. 2011). Specialization further allows for adaptive cultural information stored to multiply with the number of roles in a society.

Stage III: Cultural preemption of genetic adaptation

As the size and capability of human groups increases the pace of group-level cultural adaptation accelerates further. More minds working together can solve larger and more complex problems, accelerating collective learning and the accumulation of adaptive cultural traits for group-level benefits. In this stage, cultural evolution outpaces genetic evolution on a rapidly growing set of fronts from food and shelter to health and medicine. Culture, acting as an extreme form of behavioral plasticity, reduces the efficacy of natural selection on genes. And, through the emergence of group-level technological adaptations, culture supports even more concrete phenotypic plasticity. For example, culturally adapted vision technologies (e.g. eyeglasses, binoculars, telescopes, microscopes) may increase relative and absolute fitness but require a complex society with a specialized economy to invent, refine and maintain. However, eyeglasses and other cultural phenotypic enhancements will tend to idle selection on genes. Rapid cultural evolution can also cause conflicts between new adaptive cultural traits and existing genetic adaptations. And as cultural adaptation is more rapid, such conflicts tend to be resolved by further cultural adaptation, rather than genetic adaptation, leading to a runaway process in the inheritance transition (See Table 4).

The speed of a level of selection transition in stage III would depend on the fraction of cultural adaptations that are group-level. While that proportion is unknown, a positive feedback may dominate the transition whereby greater reliance on cultural adaptations favors greater group-level competitiveness, and greater competition between cultural groups drives faster group-level cultural adaptation. For example, we might ask how much of human fitness is determined by one's belonging to a nation with a robust health care system (group-level cultural adaptation) versus the adoption of effective personal health practices (individual-level cultural adaptation).

A completed transition

Following a complete ETII, human phenotypes would be culturally determined by the societal environment, which evolves via group-level processes of cultural evolution. In this post-transition stage, individual phenotypes are dominated by group-derived culture and there is extremely low or zero genetic heredity of many phenotypes, resulting in little-to-no genetic selection on the individual. In the hypothetical RNA-to-DNA transition, RNA transitioned from the primary medium of inheritance to a functional and intermediary system for expressing adaptive information stored in DNA. Similarly, the genetic components of human biology, might come to serve as a helper system for culturally encoded biological traits. For example, if humans take to genetic engineering and selecting biological traits of our offspring.

Finally, in a process akin to the multicellular ETI in which soma and germline cells become distinguished, individual reproduction becomes controlled by group-level cultural structures (for example reliance on medical facilities, fertility technology, regulation and family size or birth spacing norms) and gives rise to group-level reproduction, completing the transition. From the perspective of natural selection, the genetically determined individual has been replaced by the culturally determined group.

Metrics of transition

To understand the transition in detail it is useful to follow changes in phenotype and fitness. We propose two indices to measure the transition. The fraction of a phenotype determined by culture rather than genes: T_P, and the fraction of fitness determined by groups rather than individuals: T_ω. The transition indices detailed in Table 2 help to define the stages of transition.

Index measure	Metric	Description
Cultural determination of phenotype	$T_P = \frac{\eta_C^2}{\eta_C^2 + \eta_G^2}$	The proportion of individual phenotype explained by culture (η_C^2) relative to that explained by both genotype (η_G^2) and culture (η_C^2) together. If interaction between culture and genes in phenotypic expression matter, see formulation in Appendix 2.
Group determination of fitness	$T_\omega = \frac{\sigma_{\omega_{Group}}^2}{\sigma_{\omega_{Total}}^2}$	The proportion of individual fitness variation due to the group ($\sigma_{\omega_{Group}}^2$) relative to the total variation in fitness ($\sigma_{\omega_{Total}}^2$). T_ω is equivalent to F_{ST} calculated on variation in fitness, ω, rather than trait variance.

Table 2. Two indices measure shifts in inheritance and individuality during a long-term evolutionary transition.

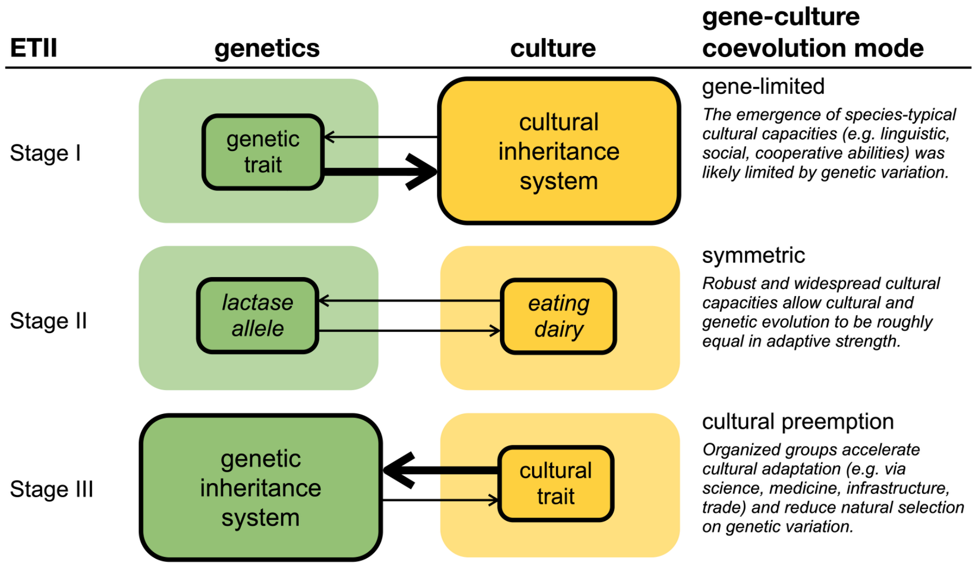

Figure 4. The dominant mode of gene-culture coevolution is expected to change as the ETII unfolds and cultural evolution outpaces genetic evolution as a driver of adaptive change in humans. In Stage I, MLS1 on genetic variation gives rise to our capacity for culture, while in Stage III, MLS2 on cultural variation integrates individuals within a functional society or group, preempting genetic adaptation.

Stage I: Emergence of culture

As genetic capacity for culture is inherited from parents, most heritable phenotypic variation (even that in cultural traits) will be explained by genotype (η_G remains high) though the proportion of phenotypic variation explained by culture (η_C) will start to increase. Therefore, T_P and T_ω will be close to zero. In addition, the correlation between genes and culture—which other authors have used as a metric for an ETI in humans (Stearns 2007) —will be close to zero due to limited cultural variation.

Stage II: Symmetric gene-culture coevolution

Strong correlations emerge between genotype, phenotype, and culture. As phenotypes begin to reflect a combination of correlated cultural and genetic influences, the proportion of phenotypic variation explained by genotype (η_G) will decrease, the proportion of phenotypic variation explained by culture (η_C) will increase for many traits. Furthermore, once the genetic basis for culture becomes widespread, cultural groups should begin to play a stronger role in individual fitness. Thus, we expect a sharp increase in both T_P and T_ω. At this stage, since most cultural traits still have some genetic basis, gene-culture correlation will peak, and start to decline.

Stage III: Cultural preemption of genetic adaptation

Both indices approach 1, nearly all heritable phenotypic variation is explained by culture, nearly all individual fitness is determined by its cultural groups, and the genotype-culture correlation declines toward 0. The gene-culture correlation should decrease in stage three due to the weakening of the genotype-phenotype link, rather than increasing as others have implied.

IV. Evidence

Our hypothesis can be compared against evidence of the influence of culture on human evolution. The evidence that culture is a major adaptive force in the evolution of many animal species is strong, and the strongest evidence for the greatest impacts of gene-culture coevolution appear in humans (Whitehead et al. 2019). Human culture is the by far most complex and extensive form of culture, and its impact on human genetics is profound (Laland et al. 2010, Stearns et al. 2010). Extensive evidence exists for gene-culture coevolution throughout human history (Richerson and Boyd 2020). Humans are thought to have acquired significant genetic changes as a result of long-term gene-culture coevolution, including dramatic digestive changes, the emergence of docility and reduced aggression (Gibbons 2014), modified vocal tracts (Hunley 2015), the cognitive apparatus for social learning (Boyd and Richerson 1985, Henrich and McElreath 2003), and altruism and norm internalization (Gintis 2003). A review of theory and evidence on patterns in human gene-culture coevolution shows general support of the ETII hypothesis (Waring and Wood 2021). Here, we categorize potential cases of human gene-culture coevolution into stages according to the ETII hypothesis: Stage 1 (gene-limited), Stage II (symmetric), and Stage III (preemptive cultural adaptation) (Figure 4).

Gene-limited gene-culture coevolution – Stage I

Early in human evolution the capacity for culture was limited by genetic variation, and change was slow. The emergence of the core set of cognitive, social, and linguistic competencies which became species-typical traits appear to have entailed dramatic evolutionary changes to brain size (i.e. to facilitate the production, storage and sharing of cultural traits) and life history (i.e. to provide time to learn complex skills as a juvenile). Table 3 provides examples of the species-typical genetic traits which likely emerged from early gene-limited gene-culture coevolution. These traits may have emerged via MLS1 on genetic alleles that supported effective group coordination and integration.

Symmetric gene-culture coevolution – Stage II

With species-typical cognitive abilities in place to support cumulative cultural evolution, the importance of culture as a mechanism of inheritance grew rapidly. We reason that for a time cultural and genetic adaptation must have been roughly equal in strength. This would allow symmetric coevolution between genes and culture, in which a cultural trait might spread about as fast as its genetic counterpart. However, despite classic theory suggesting that cultural and genetic traits might evolve at the same rate in gene-culture coevolution (Feldman et al. 1985), we few examples in the literature, the best case being the coevolution of lactase persistence and dairying (Gerbault et al., 2011a; Ingram et al., 2009; Itan et al., 2009; Liebert et al., 2017; Tishkoff et al., 2007). We surmise that this period of equivalence did not last long.

Preemptive cultural adaptation – Stage III

In the third stage of the hypothetical human ETII, gene-culture coevolution shifts into a different mode in which cultural adaptation preempts genetic adaptation and natural selection on genes. In this stage rapid cultural evolution facilitated by groups of millions work to solve collective problems. Here, MLS2, operating on cultural variation generates an

Genetic traits	Cultural traits	References
Brain size	Ability to innovate, infer and remember complex skills and language	Muthukrishna et al., 2018; Navarrete et al., 2011; Rendell et al., 2011
Longevity and life history	Extra learning opportunities to acquire complex skills	Caspari and Lee, 2004; Finch, 2010a; Gurven and Kaplan, 2007a; Kaplan and Robson, 2002a; Richerson and Boyd, 2020
Menopause	Opportunities to teach complex skills	Hawkes, 2003; Lahdenperä et al., 2004; Peccei, 1995
Docility and reduced agression	Collective and cooperative social structures	Gibbons, 2014; Leach, 2003; Theofanopoulou et al., 2017; Wilson, 1991; Wrangham, 2019
Linguistic ability	Expressive human languages	Blasi et al., 2019; DeMille et al., 2018; Hunley, 2015
Shortened foregut, vestigial appendix	Cooking, food processing	Carmody and Wrangham, 2009; Wrangham and Conklin-Brittain, 2003; Wrangham et al., 1999

Table 3. Examples of gene-limited gene-culture coevolution, which predominate in Stage I of the ETII, and generate species-typical traits.

expansion of sophisticated group-level systems, infrastructure and services to support for the needs of individual humans. This process entrains individuals within the group, and utterly redefined the environment in which genetic evolution unfolds. In this mode, new cultural adaptations often arise to resolve adaptive challenges before genetic selection can respond, forestalling both genetic evolution by natural selection (Odling-Smee et al. 2003). In this way, group-level cultural change preempts genetic adaptation. As cultural preemption proceeds, it works to reduce the fraction of adaptive information stored in and tied to genes and to increase that fraction in culture, T_P.

Many of the most salient examples of cultural preemption are medical and reproductive. Scientific medical practice is a preemptive cultural adaptation because it obviates natural selection and weakens the genetic determination of phenotype and fitness. It is intended to do so. One example is the development of cesarean section, a cultural adaptation to treat dangerous and deadly birth complications. The success and spread of the cesarean procedure have changed (and relaxed) genetic selection in humans, increasing the likelihood that a daughter borne by cesarean will herself require one (Mitteroecker et al. 2017a). A second example is that of gestational surrogacy, in which couples who cannot conceive elect to have another woman gestate and birth their child through the implantation of an egg fertilized in vitro (Brinsden 2003). Gestational surrogacy constitutes a preemptive cultural adaptation for reproduction where it would otherwise be impossible. Both solutions require major group-level support in the form of organizations (hospitals), investment, and technology. Indeed, most preemptive cultural adaptations are group-level cultural traits (Table 4). As Mitteroecker (2019) points out, gene-culture coevolution operates differently now that human bodies are evolving exclusively within modern societies.

Adaptive challenge	Cultural adaptation	References
Individual inability to reproduce (G).	Cesarean section, gestational surrogacy, reproductive medicine	Brinsden, 2003; Källén et al., 2010; Kumar and Singh, 2015; Mitteroecker et al., 2017b; Walker et al., 2004; Walsh, 2008
Modern agriculture creates surplus calories (C), leading to unbalanced diets, nutrient deficiencies, obesity.	Nutrient supplements, dieticians, food regulations	Bellisari, 2008; Breslin, 2013; Cordain et al., 2005; Pinhasi and Stock, 2011
Medicine, technology, and improved nutrition (C) extend human lifespan, causing emergence of age-related diseases.	Further medical technology, assisted living	Finch, 2010; Gurven and Kaplan, 2007; Kaplan and Robson, 2002a; Robson and Kaplan, 2003
Large societies (C) conflict with instincts for tribal size social groups (G), hampering social efficacy.	The “work-arounds” hypothesis: small and segmented social groupings within complex society.	Richerson and Boyd, 1999
Dental hygiene (C) lengthens tooth life, causing impaction of third molar.	Wisdom tooth removal	Carter, 2016; Dean et al., 2001; Dodson and Susarla, 2014; Friedman, 2007; Hillson, 2014; Mann et al., 1990
Industrial dairy production and increased consumption (C) outstrips lactase persistence (G), causes indigestion.	Non-dairy foods, lactase pills	Gerbault et al., 2011a; Vesa et al., 2000; Zeder, 2016
Industrial wheat production and consumption (C) outpaces gluten digestion (G), causing indigestion.	Gluten-free foods	Hall et al., 2009; Pasquali et al., 2017; Zeder, 2016

Adaptive challenge	Cultural adaptation	References
Time-saving devices and communication technology (C) reduced need for collective work (G) leading to isolation, depression.	Therapy, antidepressants	Ambrose, 2010; Berland, 2009; Carter, 2014; Hidaka, 2012; Richerson and Christiansen, 2013; Stout et al., 2011
Artificial light and longer workdays (C) conflict with sleep requirements (G), disrupting sleep schedules.	Sleeping drugs, shades, sleeping masks	Nunn et al., 2016; Samson and Nunn, 2015; Wright et al., 2012
Work saving devices reduce labor (C) conflicting with need for exercise (G), decreasing general health.	Exercise culture, equipment, sports, drugs	Abarca-Gómez et al., 2017; Baldwin and Haddad, 2002; Egan and Zierath, 2013; Flück and Hoppeler, 2003; Janssen et al., 2002; Stenholm et al., 2008

Table 4. Examples of the cultural preemption. Cultural preemption is a mode of gene-culture coevolution in which rapid group-level cultural adaptation preempts natural selection on genetic variation. This occurs commonly in domains in which prior genetic (G) and cultural (C) traits are in conflict.

V. Status

Taking the preceding evidence into account, our species appears to be in a period of preemptive cultural adaptation. While prior human evolution is replete with evidence for the gene-limited gene-culture coevolution (e.g. food preparation and digestion, culture and brain size, language and vocal morphology, human development, and social organization), there is increasing evidence of the cultural preemption that defines Stage III (e.g. altering phenotypes after birth via surgery, education, medicine, social structure, and technology). We use the empirical transition metrics to help evaluate our status.

1) Cultural determination of phenotype, T_P

Human phenotypes are increasingly determined by culture. Cultural adaptations in food supply, nutrition, shelter, clothing, education, coordinating organizations of complex society, technology determine the human extended phenotype in ways that make individual humans in modern society healthier and more capable than humans without those cultural traits (Henrich 2015). Furthermore, rapid group-level cultural adaptation is increasingly disrupting the genotype-phenotype link, as the examples of cesarian section and gestational surrogacy demonstrate. We note that to measure T_P new methods are needed to compare cultural and genetic contributions to phenotype in an unbiased manner.

However, the transition is far from complete. The genetic component of phenotypic variation is still strong relative to the cultural component. Genotype still plays an overwhelmingly large role in shaping human traits (Guo et al. 2018), while humans currently only employ small a set of cultural mechanisms to select the genotype of their offspring, including amniocentesis or sex-selective abortion (Sahni et al. 2008). More invasive genetic germline intervention techniques such as pre-implantation genetic diagnosis (Greely 2016) and human gene editing (Joseph 2019) are rare. Despite significant ethical concerns with these techniques, their increasing technical sophistication and decreasing costs make them likely to become more common.

2) Group determination of fitness, T_ω

Human evolutionary history is replete with group-level events which had substantial effects on genes and culture. For example, the genetic study of the descendants of the Kuba kingdom in southern Africa showed that the onset of statehood increased genetic mixture among pre-existing groups (Dorp et al. 2018). The same pattern can be observed in other "melting pot" societies which generally break down genetically distinct groups through genetic admixture, dissolve old cultures through acculturation, conformity, and coercion, and facilitate the growth of new group cultures. Importantly, this type of cultural group selection can occur without conquest or the loss of human lives.

Today, the majority of improvements in human health, reproduction and survival comes from highly centralized and specialized group-level cultural systems and infrastructure for food production, defense, education and health care. Thus, while there is still variation in human fitness within societies, societal factors play an important role in determining individual health and fitness (UN 2019). Overall, we estimate the human species to have recently entered Stage III with the onset of the industrial era.

VI. Predictions

Unlike prior descriptions of a human evolutionary transition, the ETII is amenable to empirical tests. Without a formal model, we derive qualitative predictions concerning long-term average trends in human evolution. Some relate to the evolutionary past, some concern patterns observable in human evolution and society today, others only pertain to various alternative possible futures for our species.

Inheritance predictions

Various predictions emerge from the proposition that culture will continue to replace genes as the primary inheritance system.

1. *Relaxed selection and accumulation of culturally dependent genetic traits*. By relaxing selection on genetic variation, cultural adaptations in medicine will allow genetic traits that would previously have been maladaptive to accumulate. This would have a ratcheting effect of driving increased dependency on cultural systems. Evidence of this pattern exists today in human fertilization and birth (Brinsden 2003, Walker et al. 2004, Walsh 2008, Källén et al. 2010, Kumar and Singh 2015, Mitteroecker et al. 2017b).
2. *Reduced selection for individual genetic reproduction*. Despite clear evidence of positive selection for fertility in some populations (Stearns et al. 2010), we expect a long-term average relaxation of selection against non-biologically reproducing individuals, as the evolutionary advantage to groups of culturally inherited skills overtakes that of more individuals at the margin.
3. *Increased group control of and support for reproduction, child-rearing, and education*. Cultural groups play currently determine individual reproduction via a variety of cultural mechanisms including norms and laws that support and prescribe reproduction, childcare and education, reproductive technology, and investment of non-relatives in raising children (Booth and Crouter 2001, Hesketh et al. 2005, Hotz and Xiao 2011, Wells et al. 2014). This trend is expected to continue.
4. *Increased importance of cultural groups and group identity*. Human social identities are a culturally inherited trait, influencing how people behave in the context of a defined group. As cultural inheritance grows in importance relative to genetic inheritance, human identities are likely to become less linked to genetic family and more linked to cultural group identity, as happens when people move away from kin.

Individuality predictions

A second set of predictions emerges from proposition that group capacities, traits and successes tend over time to become more influential than those of individuals. We not that because an individuality transition involves emergent changes in the levels of social organization over time, the type of cultural group which comes to matter most cannot be easily predicted.

1. *Individuals outsource increasing degrees of their extended phenotypes (and fitness) to their cultural groups*. When people invest resources in and accept support from communities or organizations, they couple their future success to group-level features. Examples include connecting a home to municipal utilities for water, gas or electricity or investing money in a business venture. This trend is expected to grow.
2. *Increasingly integrated, efficient, and effective cultural groups*. We expect continued evolution in factors known to enhance group efficacy such as strengthened group boundaries for both information and resources, mechanisms to reduce within-group conflict (e.g. punishment, policing), individual functional specialization, and more robust communication and integration within groups (Richerson and Boyd 2005, Fay and Ellison 2013, Norenzayan et al. 2016).
3. *Increasing group differentiation*. Group-level variation in cultural marking should increase generally. Group identities may become self-reinforcing, in a manner roughly parallel to ecological speciation (Nosil 2012). Group differentiation can also exacerbate group polarization (Gorard 2000, Musick and Mare 2004, Baldassarri and Gelman 2008),

competition, and conflict (e.g. wars, identity politics, economic competition, social strife) (Roscoe 2013) when resources are limited.

These qualitative predictions may be difficult to test. Our purpose here is to demonstrate that the ETII hypothesis is testable in principle. More precise and unique predictions derived from formal models and tested against large and reliable datasets will help to draw these mechanisms into better light. There is even some possibility that a well calibrated theory of a human evolutionary transition could be of use for future societies in avoiding undesirable paths in social evolution.

VII. Causation in human evolution

Social scientists often explain behavior and society as the consequence of factors such as costs, institutions, power or wealth distributions, or cultural diversity. Evolutionary studies seek to explain those phenomena as a consequence of uniquely human traits, such as our cooperative ability and capacity for cumulative culture. But explaining human uniqueness itself has remained out of reach. These proximal explanations of societal phenomena can themselves be ordered and explained, at least in part, by the motion of the human species along the evolutionary transition we describe above. For example, why have educational institutions spread and grown in scale and complexity so dramatically in the last half millennium? From the perspective of the ETII, institutionalized education is a group-structured cultural inheritance system which can improve the adaptive capacity of a society by increasing the likelihood that human innovation and creativity is deployed on the frontier of cultural knowledge rather than being wasted on reinvention. The amount of knowledge and length of schooling must increase for societies to master more complex technology. Thus, as societies grow in complexity, educational institutions must also grow.

The ETII hypothesis may also help explain the ongoing decline in the human fertility across societies. The demographic transition is well studied, but an ultimate explanation has proven vexing for social scientists and evolutionists alike (Borgerhoff Mulder 1998). Why would human fertility decline when individuals are on average more comfortable and healthier than ever? The correlates and proximate causes are broadly understood: the total fertility rate declines across societies with increasing education and economic development (Götmark and Andersson 2020).

One evolutionary theory suggests that the demographic transition is a result of the increasing transfer of wealth (extra-somatic capital) from one generation to the next (Kaplan and Robson 2002b, Kaplan et al. 2003). The ability to transfer and inherit material wealth, in combination with a negative correlation between wealth and genetic reproduction could have selected for strategies to acquire status and wealth even at a short-term cost to biological reproductive success (Harpending and Rogers 1990, Boone and Kessler 1999, Aarssen 2005, Mulder et al. 2009, Wodarz et al. 2020). Another evolutionary theory suggests the demographic transition occurs when social networks expand to include more non-kin (Newson et al. 2005), causing a decline in social pressure for reproduction (Newson and Richerson 2009). But both evolutionary explanations rest on unexplained aspects of human uniqueness; they explain how a change is unfolding but not why.

The possibility of a social or cultural factors causing reduced reproduction has vexed scientists for decades (Wispe and Thompson 1976, Vining 1986). But from the perspective of an ETII, a decline in human fertility is not so perplexing. If human adaptation is shifting from genetic to cultural systems of inheritance, then cultural reproduction will tend to be favored over genetic reproduction. Although humans are necessary for society, their production, development, education and distribution may be evolutionarily optimized to meet the needs of society in various ways. For example, human reproduction may become a specialized task carried out by a subset of the population, as has been observed in the transitions that gave rise to eusocial insects and multicellular life. Evaluate such possibilities logically is important if we care to avoid them.

Nonetheless, the historical decline in the fertility across societies is perhaps the strongest evidence of the cultural preemption of genetic inheritance. The same logic would present the ETII as the ultimate cause of the human demographic transition.

VIII. Conclusion

Building on dual-inheritance theory (Boyd and Richerson 1985), we have suggested that cumulative group-level cultural evolution is more adaptive and more rapid than human genetic evolution. This difference has caused an increasing fraction of human life to be mediated by culturally evolved group-level practices and technology, and a decreasing fraction by genetic traits. Available evidence suggests that this trend is ongoing and accelerating. Both cultural and environmental change are far from equilibrium, which we suspect is the result of changes in the human niche due to the ETII (Waring et al. 2023). We speculate that, in the long term, culture will continue to grow in influence over human evolution, until genes become secondary structures that encode human biological design blueprints but are ultimately governed by culture.

Contrary to suggestions that a human evolutionary transition has stalled because the correlation between genes and culture is decreasing (Stearns 2007, Kesebir 2012), the decoupling of genes and culture is a primary indicator that the transition is going strong because humans are undergoing a transition in inheritance alongside a transition in individuality. Gazing further afield, the ETII hypothesis also highlights the incompleteness of popular conceptions of a 'technological singularity' (Kurzweil 2005) in which all of humanity might become subsumed into a single digital society and may further contribute to more dispassionate research on human 'post-biological' evolution (Dick 2003).

The ETII hypothesis opens new doors in research on human evolution and suggests a set of research priorities. First, theoretical models of long-term gene-culture coevolution are needed to explore the features of a coupled inheritance-and-individuality transition. These should be compared with other models of human evolutionary transition (e.g. Andersson and Czárán 2023). Second, an empirical system for estimating transition metrics, whereby systematic measures can be taken with some frequency would help to estimate the rate of fitness export from genes to culture. For example, Carmel (2023) compiled the first empirical measures of the human ETI. Third, better historical and modern estimates of the strength of culture-driven group selection on human genes are needed. For example, Andersson and Tennie (2023) propose that human culture evolved to be group-oriented and group-selected *before* it became significantly cumulative. They call this 'Trajectory B,' in comparison to the standard explanation in which cumulative culture emerges first, and group structure second (Trajectory A). What are the implications of this difference for the ETII?

Finally, studying the future of human evolution raises deep ethical challenges. We do not ascribe any moral valence to the evolutionary mechanisms and conceptual model we have delineated. We mean only to describe a novel type of evolutionary process and provide means to measure it. For example, we do not suggest that nation states are "more evolved" than other forms of society, or that a hypothetical cultural superorganism would be superior in any moral sense to our current form of society or any other form. So, we also propose that ethics research and development to accompany these scientific endeavors.

When will the human evolutionary transition in individuality be complete, if ever? Addressing such questions is far beyond current scientific ability. Nothing about human evolution is inevitable. Evolutionary processes are always contingent on their environment, and so too must be the human evolutionary transition we describe. Nevertheless, the coupled evolutionary transition provides a uniquely parsimonious explanation for both social and biological aspects of human change, past, present, and future. Given the available evidence, we estimate that a coupled transition in human evolution is underway and accelerating.

Author contribution statement

TW and ZW developed the theory, researched, wrote and revised the article. TW submitted and revised the article for publication.

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Author biographical

Timothy M. Waring is an associate professor of applied cultural evolution in the Mitchell Center for Sustainability Solutions and the School of Economics at the University of Maine, in Orono, Maine, in the United States, where he leads the applied cultural evolution laboratory. Zachary T. Wood is an independent researcher living in Winslow, Maine, in the United States.

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Appendix

Culture weakens:	Culture strengthens:
…individual selection because: ● culture weakens genotype-phenotype link. ● culture causes reduction of genetic heritability. ● culture "fixes" maladaptive phenotypes.	…group selection because: ● culture generates and maintains group level variation. ● group-structured cultural inheritance is sometimes faster than individual genetic inheritance. ● group-structured cultural inheritance can be more flexible (institutions tailored to context).
… individual reproduction because: ● culture supports individual reproduction. ● culture relaxes selection against non-reproducing individuals.	… group reproduction because: ● cultural groups support and equalize reproductive opportunities. ● variation between cultural groups increasingly impacts individual reproductive success relative to genetic inheritance. ● culture facilitates group growth. ● culture facilitates group differentiation via social identity, and cultural group markers.

Table A1. Long term interactions between cultural and genetic evolution. Long term gene-culture coevolution as influenced by group-structured cultural selection will generate predictable effects on individual and group level characteristics in both genes and culture.

The metric of phenotypic determination

We can divide phenotypic variation into several sources:

$$\sigma_P^2 = \sigma_G^2 + \sigma_C^2 + \sigma_E^2 \tag{1}$$

Where $\sigma^2{}_P$ = phenotypic variation; $\sigma^2{}_G$ = genetic variation (additive + dominance + epigenetic); and $\sigma^2{}_E$ = environmental variation (plasticity). Converting Equation 1 into a regression model and calculating partial R^2 (η^2) gives us:

$$1 = \eta_G^2 + \eta_C^2 + \varepsilon^2 \tag{2}$$

Where $\eta^2{}_G$ is the proportion of phenotypic variation explained by genes, $\eta^2{}_C$ is the proportion of phenotypic variation explained by culture, and ε^2 is the residual (which we can assume to be environmental variation).

η^2_G and η^2_C are the *heritable* drivers of phenotype (i.e. genetically and culturally heritable). So, we could construct a transition metric that is the proportion of heritable phenotypic variation that is driven by culture:

$$T_P = \frac{\eta_C^2}{\eta_C^2 + \eta_G^2} \qquad (3)$$

If there is a meaningful interaction between culture and genes in expressing an individual's phenotype, we can expand this metric:

$$T_P = \frac{\eta_C^2 + {}^{1}/{}_{2}\,\eta_{C\times G}^2}{\eta_C^2 + \eta_G^2 + \eta_{C\times G}^2} \qquad (4)$$