Cultural inheritance is driving a major transition in human evolution

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Abstract

An evolutionary transition in individuality (ETI) is the emergence of a new level of biological complexity, such as multicellular life or eusocial insects. There is disagreement on the degree to which the human species is undergoing such a transition. Here, we advance a theory of long-term human evolution in which a transition in individuality is driven by an underlying transition in inheritance from DNA to cultural signals. We argue that such a transition could be driven by three features of human culture. First, human cultural inheritance provides greater capacity for rapid adaptation than genetic inheritance. Second, culture constitutes a mechanism of extreme heritable behavioral plasticity. These two features are sufficient to drive an evolutionary transition in inheritance. Third, cultural evolution generates and favors group-level adaptations. Therefore, we argue that an inheritance transition from genes to culture will cause a simultaneous transition in individuality from individual to group. We present a conceptual model of a coupled evolutionary transition in inheritance and individuality and review available evidence. The coupled transition hypothesis has major implications for causation in human evolution and the social sciences. We suggest a set of testable predictions and outline a research agenda on the culture-driven transition in human evolution.

I. Introduction

Evolutionary transitions in individuality (ETIs) are defined by the emergence of higher levels of biological organization through the formation of cooperative groups (1–5). ETIs proceed through a series of contingent stages. Initially, individuals become organized into cooperative groups, which can then become highly integrated superorganisms through changes in the dominant level of selection toward group selection (2, 6). Transitions in individuality typically include the emergence of new forms of divisions of labor, the loss or cooption of individual reproduction, and the rise of new routes of communication and information transmission (1, 4, 5). ETIs have been proposed to explain the evolution of prokaryotes, via group selection among competing replicators (7), the emergence of eukaryotic cells from prokaryotic ancestors (8), the emergence of multicellular organisms from eukaryotic cells (9), and of eusocial organisms from multicellular organisms (10).

There has been a general agreement that human evolution is somehow characterized by an ETI (4, 11–15). This is evidenced by the depth and scale of our cooperation with non-kin, our complex, full-time division of labor, and the advent of language and other forms of non-genetic information transmission. But scholars disagree about how best to apply evolutionary transitions theory to humans.

One view is that the emergence of language, culture, and institutions represent a completed evolutionary transition in humans (4, 11, 14). Powers et al. (14) argue that humans have experienced an evolutionary transition in the emergence of large, complex, cooperative societies through the key human ability to create institutions, which make cooperation individually beneficial and facilitate division of labor. Similarly, Kesebir (16) notes that human society shares some fundamental features of superorganisms, for example, human groups possess well-developed mechanisms to achieve unity of action or resolve conflict within a group. Anderson and Törnberg (11) suggest that humans completed an evolutionary transition in individuality when human encephalization quotients began to rise ~2 million years ago.

A more common view is that humans have begun, but not completed, an ETI (4, 12, 15), having evolved some characteristics of superorganisms but not others. For example, while humans remain autonomous, and capable of individual reproduction, humans are also highly interdependent, sharing culture, behavior, language and resources in large coordinated groups. Thus, Gowdy and Krall (12) suggest humans are in a state of incomplete transition, with the emergence of agriculture representing a major transition to an 'ultrasocial', rather than fully eusocial state. Stearns (15) further reasons that human evolution might be stalled amidst an evolutionary transition. Stearns points out that factors such as human migration, which reduces genetic group differentiation, and trade which increases interdependence between groups, undermine conditions for strong genetic group selection. Szathmáry (4) concludes that the human evolutionary transition 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 (16) suggests that the superorganism metaphor is imperfect because human groups are fluid and human individuals have multiple group identities.

One important loose end concerns the role of culture. Culture may facilitate the evolution of human groups as an emergent level of individuality (4, 11, 12, 14, 16). Anthropologists and sociologists have debated whether human culture and society themselves represent a new level of individual organization (i.e. a "superorganic" entity), and whether to consider culture as a source of group-level causation for more than a century. As early as 1898, Spencer (17, 18) saw society as a superorganic, emergent property of interacting individuals, as did Kroeber (19), who drew on Darwinian principles to explain a superorganic society. Others have argued that the concept of superorganic culture is a misplaced biological analogy (17), or a reification of human culture (20). Cultural evolutionists suggest instead that the concept of culture as 'superorganic' is a red herring because culture remains rooted in human biology (21), and that human society itself constitutes only a 'crude superorganism' in the traditional biological sense (22). Anthropologists increasingly agree that human cultural organization exhibits an important group functionality and even expresses agency above the level of the individual (23).

In summary, there is general agreement that humans exhibit signs of being involved in an evolutionary transition in individuality, but significant disagreement about the definitions, details, and status of a human ETI. Moreover, there is a vague consensus that human cultural capacities and structures, such as language and institutions, are somehow implicated in an evolutionary transition. Yet, there is disagreement about the relationship of the cultural and 'biological' aspects of human evolution, and role of culture in long-term of human evolution remains unclear. Major questions remain unanswered. How can the ETI framework apply to humans? What is the status of a human evolutionary transition? What new level of individuality is implicated? And what is the role of culture? Building on dual inheritance theory (24) we introduce a new theoretical framework to resolve these issues.

The human evolutionary transition, revisited

We propose a *coupled* human evolutionary transition in inheritance and individuality instigated by the central role of culture in human evolution. This coupled evolutionary transition would be characterized by positive feedback between the adaptive capacity of cultural inheritance and the power of culturally organized groups (Figure 1). Such positive feedback systems are likely a common feature of evolutionary transitions (25). A coupled transition resolves many outstanding problems in explaining the human ETI. It reveals how the ETI framework applies to humans specifically, clarifies the role of culture in the transition, elucidates the status of the transition, and explains why a lack of genetic group selection need not be an impediment to evolutionary transition.

Both types of evolutionary transition have 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 (26) 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. Many theories suggest routes by which the transition from RNA to

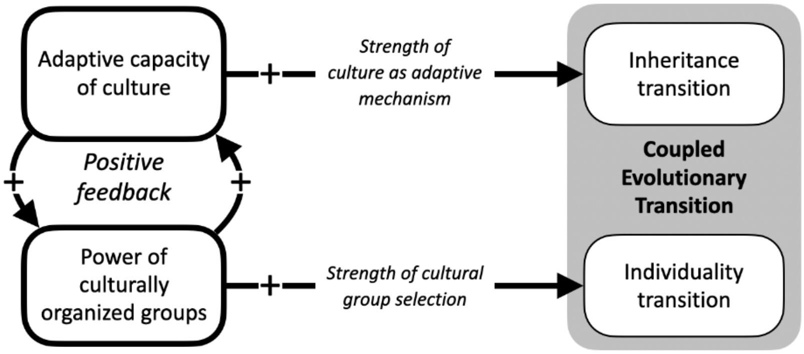

Figure 1. A coupled evolutionary transition in inheritance and individuality caused by the role of culture in long-term human evolution is characterized by a positive feedback between the power of culturally organized groups and the adaptive capacity of culture relative to genetic evolution.

DNA might have occurred (27, 28). But the transition was most likely made permanent because DNA is a more stable—and therefore more adaptive—medium of information storage than RNA (29). Thus, the relative qualities of inheritance media facilitate the transition. *Therefore, an inheritance transition from genes to culture requires that culture provides a more adaptive inheritance system, circumventing adaptive genetic evolution.*

Therefore, the coupled transition in inheritance and individuality we propose requires that cultural evolution both (a) becomes more adaptive that genetic evolution, and (b) generates and accumulates group-level adaptations.

II. Interacting inheritance systems

The long-term evolutionary interaction between genes and culture ultimately stems 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 (30). Where genetic inheritance involves the direct copying of the storage medium (or genotype) and transfer from parent to offspring, cultural inheritance involves memory, skill and norms, stored in synaptic patterns which need not be duplicated or physically transmitted between individuals. Instead cultural learners actively reconstruct the cultural phenotypes of model individuals they select (Figure 2).

Consequently, cultural evolution is mechanistically distinct from genetic evolution in multiple ways (24, 31, 32). For example, while genetic inheritance is primarily vertical and non-strategic 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 (31, 32). While genetic variation is largely random, cultural variation can be 'guided' by intentional innovation (24). Overall, the differences between genetic and cultural evolution (Table 1) appear to explain why cultural evolution can solve adaptive problems more rapidly (33, 34).

These basic differences already hint that culture might hold greater adaptive potential than genes in certain scenarios (and possibly generally), that culture acts as a type of heritable behavioral plasticity, and that cultural adaptations accumulate for human groups as well as for individuals.

Comparing the adaptive potential of culture and genes

The ability of an inheritance system to facilitate adaptation depends on the speed with which that system can generate, store, and spread phenotypic variation. The amount of change in a quantitative phenotype driven by cultural or genetic evolution can be understood heuristically with the breeder's equation. Here, 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 (39):

(1)

$$\Delta Z = \frac{h^2 S}{G}$$

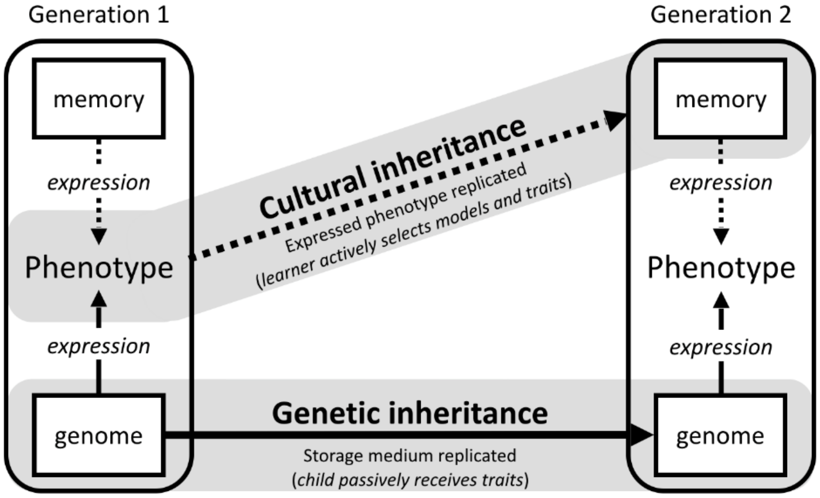

Figure 2. Cultural inheritance is not parallel or analogous to genetic inheritance. While genetic material is physically replicated and directly transmitted, cultural memory is neither replicated nor transmitted. Instead cultural traits are transmitted via their influence on the observable phenotype (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.

	Genetic evolution	**Cultural evolution**
Variation	- Primarily random mutation - Mutation rates low $\mu=0.5\times10^{-9}\text{bp}^{-1}\text{year}^{-1}$ (35)	- Includes guided, intentional innovation (24) - Mutation rates high, $\mu=11\%$ (36)
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 adoption of cultural traits (32)
Selection	- Natural selection - Sexual selection	- Natural selection - Sexual selection - Cultural selection (37)
Structure	- Little evidence for genetic evolution of groups	- Cultural variation is more group structured than genetic variation (38)

Table 1. 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.

Equation (1) shows us that cultural evolution will cause more phenotypic change than genetic evolution in a given trait 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 can fulfil 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* (33). 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' (40). Typically, an increased genetic mutation rate decreases trait heritability (41). Genetic heritability in animals is typically low, with large environmental influences. While the rate of mutation in cultural traits is likely higher than in genetic traits (35, 36, 42), phenotypic differences between cultural learners and models are often corrected through instruction, teaching and error checking (43, 44) allowing the phenotypic behavior of the learner to be iteratively refined to better match the model. Such error checking may also reduce the environmental influence on phenotype, allowing culture to reach even higher levels of heritability. Thus, generalized cultural heritability may vary considerably and depend on domain and social learning mechanism, with the potential to be quite high in certain 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.

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 (30, 33, 34, 45).

Culture generates group-level adaptations

Group selection is rare in genetic systems, but cultural group selection appears common in human history (46–49). Human culture is more group structured than human genes (50) and group selection on cultural variation is facilitated by mechanisms that have no genetic parallel, including conformity (51–54) and social marking (55–57) as well as emergent processes within groups such as equilibrium selection on institutions (58). Many factors enhance the evolutionary importance of culturally organized groups.

First, *culturally organized groups are often more powerful than individuals.* This means that if humans do compete, groups will tend to win and proliferate, even at the expense of average individual fitness. For example, the advent of agriculture is known to have accelerated the development of complex and hierarchical societies but decreased human health and nutrition in the early generations of the first agricultural societies (59–61). Yet organized, well-armed, and well-defended agricultural states spread around most of the world (62).

Second, *competition between culturally organized groups facilitates the evolution of cooperation* within groups (63) in part by suppressing non-cooperative individual behaviors, leading to the expansion of human cooperation and prosocial tendencies with a genetic basis (64). This pattern is supported by cross-cultural evidence through human history (48) and across geographic regions (46), and by quantitative evidence from violent group conflict in pastoral societies (47, 65).

Third, *culturally organized groups can solve adaptive problems more readily than individuals,* through the compounding value of social learning and cultural transmission in groups (66, 67). The cost of cultural adaptation for a group is equal to the cost of a single invention plus the transmission cost for teachers and social learners. This means that the average cost of solving a particular problem can be lower for a group capable of learning than for the same number of individual learners if the cost of transmission within the group is lower than the cost of invention. Moreover, shared culture, such as language and values, are likely to increase the efficacy and efficiency of within-group problem solving. And indeed, societies may operate to make each of their members more innovative than they would otherwise be individually (68).

Fourth, *larger groups may make cultural adaptation more efficient*. Larger groups with shared culture may achieve group-level cultural adaptations more rapidly than smaller groups. For example, in Oceania population size predicts technological complexity in the absence of environmental variability (69). Languages with more speakers are more efficient from an information theoretic perspective (68), likely because the rate of language evolution increases with population size (70).

Long-term gene-culture coevolution

The mechanisms outlined above create cultural groups that can influence genetic and, of course, cultural fitness outcomes (30, 48, 63, 71, 72). Consequently, cultural groups can compete even as genetic groups homogenize (73). In other words, distinct genetic groups can dissolve through population mixing even while members continue to belong to distinct cultural groups (74), making a culture-driven human ETI possible 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, cultural evolution exhibits three pertinent characteristics relative to genetic evolution - greater adaptive potential, a strong plastic effect, and the generation of group-level adaptations. These are sufficient to facilitate a coupled transition in inheritance and individuality. We develop a simple conceptual model of the transition process below.

III. A coupled evolutionary transition in inheritance and individuality

Consider a hypothetical evolutionary transition beginning with a species evolving primarily via genetic inheritance and competition among individuals and concluding with evolution occurring primarily via cultural inheritance and competition among groups of individuals. Two quantities assist us in reasoning about how the transition might proceed: T_P : the fraction of a phenotype determined by culture, rather than genes, and T_ω : the fraction of fitness determined by groups rather than individuals. Transition indices are detailed in (Table 2).

Index measure	Description	Metric
Cultural determination of phenotype	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.	$T_P = \frac{\eta_C^2}{\eta_C^2 + \eta_G^2}$
Group determination of fitness	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.	$T_\omega = \frac{\sigma_{\omega Group}^2}{\sigma_{\omega Total}^2}$

Table 2. Indices to measure the coupled inheritance and individuality evolutionary transition in humans.

As the transition proceeds, culture should replace genes as the primary determinant of phenotype. 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 vastly between human cultural groups (75). How much cooperation is genetically determined and how much is cultural is, of course, difficult (if not impossible) to actually determine but serves as a helpful thought experiment. As the relative contributions of genes and culture to cooperative behavior changes, so does the importance of genetic and cultural selection in determining the evolutionary trajectory of the trait. Secondly, as the transition proceeds and cultural group selection becomes the primary driver of individual fitness, we expect an increase in the proportion of individual fitness variation due to the group, T_ω (6).

In summary, the human coupled evolutionary transition begins with a change in the dominant mode of phenotypically relevant information transmission. One crucial knock-on 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 three stages which roughly parallel the level of selection stages described by Okasha. These stages are: (1) the genetic evolution of cultural capacity, (2) mutualistic 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 (76, 77).

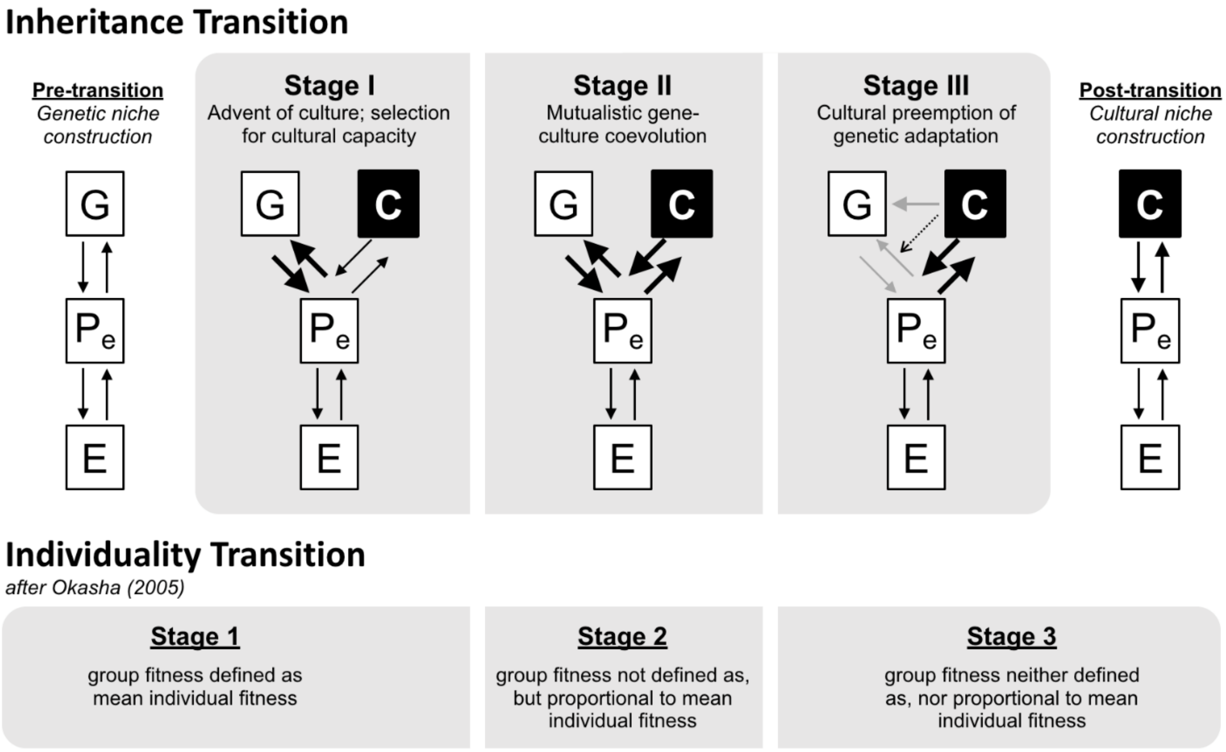

Figure 3. A coupled evolutionary transition links an inheritance transition with a transition in individuality. The inheritance transition passes through three stages, (1) initial selection for phenotypic flexibility via cultural capacity, (2) mutualistic gene-culture coevolution, and (3) preemption of genetics as primary inheritance mechanism. Arrows represent long-term evolutionary influences between genotypes (G), extended phenotypes (P_e), culture (C), and the environment (E). The stages of the inheritance transition can be aligned with Okasha's stages in a transition in individuality by multilevel selection.

Stage I: Advent of culture

A gene-culture inheritance transition begins with an initial cultural breakout phase, in which cultural capacity is limited but selected for. 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 (78) statement that "genes hold culture on a leash" is accurate. 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 (15)—will be close to zero due to limited cultural variation.

Stage II: Mutualistic gene-culture coevolution

Once genetic capacity for culture is sufficient to support the accumulation of adaptive culture (79), cultural evolution accelerates. 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 (80). Culture contributes to the extended phenotype (81) via, for example, technology as humans begin to accumulate traits that increase absolute fitness. This process has also been described as fitness exporting (11).

During Stage II 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.

Stage III: Cultural preemption of genetic adaptation

As the transition proceeds, the pace of cultural evolution accelerates further due increased group size and the accumulation of cultural adaptations. Cultural evolution outpaces genetic evolution. The faster rate of cultural evolution dictates that any conflicts between new cultural adaptations and existing genetic adaptations are more likely to be resolved by additional cultural adaptations, rather than genetic changes, leading to a runaway process in the inheritance transition.

In stage III, both indices approach 1, nearly all heritable phenotypic variation is explained by culture, nearly all of individual fitness is determined by its cultural groups, and the genotype-culture correlation returns to 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 suggested.

The speed of a level of selection transition here would depend on the fraction of cultural adaptations that are group-level. While that proportion is unknown, a positive feedback system 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 adaptation) versus the adoption of cost-effective personal health practices (individual-level adaptation).

The completed transition

A post-transition stage is a type of extreme cultural niche construction (80, 82), in which human phenotypes are culturally evolving in and determined by a societal environment, which is itself driven by 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. 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 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.

IV. Evidence

This conceptual model can be compared with available evidence on the influence of culture on 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 (83). Human culture is the by far most complex and extensive form of culture, and its impact on human genetics is correspondingly profound (84, 85). 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

(86), modified vocal tracts (87), the cognitive apparatus for social learning (24, 88), and altruism and norm internalization (89). Examples of gene-culture coevolution can be separated into two categories: mutualistic coevolution and preemptive cultural adaptation, which bear on our model of the human ETI.

Mutualistic coevolution – Stages I and II

In stages I and II of the transition, gene-culture coevolution is dominated by a pattern in which favorable combinations of cultural and genetic traits coevolve. Extensive evidence exists for mutualistic gene-culture coevolution throughout human history (90).

For example, theoretical models (80, 91) suggest that the tripling of human brain size over the course of human evolution could be the result of the fitness benefits of increased ability to store and process adaptive cultural information. Cross-species evidence supports this assertion (92). A similar mechanism is thought to underlie increases in human longevity which may have evolved as a result of the expanding possibility for accumulating, benefitting from and especially transmitting beneficial cultural adaptations, knowledge and capital (93). Humans began to increase their lifespan, living longer in the upper paleolithic (~30kya), corresponding with the advent of behaviorally modern humans (94). Similarly, menopause, like longevity (95), may have emerged because it favored the transmission of accumulated adaptive cultural knowledge from older women to the young over the cost of ceased genetic reproduction (96). Other examples of mutualistic gene culture coevolution are shown in Table 4.

Preemptive cultural adaptation – Stage III

A subsequent pattern of gene-culture coevolution in which cultural adaptation preempts genetic adaptation is the third stage of the proposed human ETI. In cultural preemption, new cultural adaptations and cultural niche construction resolve adaptive challenges before genetic selection can respond, forestalling both genetic evolution and mutualistic gene-culture coevolution (114). The overall effect of cultural preemption is to reduce the fraction of adaptive information stored in and tied to genes and to increase that fraction in culture.

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 has changed (and relaxed) genetic selection in humans, increasing the likelihood that a daughter borne by cesarean will herself require one (115). 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 (116). Gestational surrogacy constitutes a preemptive cultural adaptation for reproduction where it

Genetic traits	Cultural traits	Sources
Brain size	Beneficial cultural traits	Muthukrishna et al., 2018; Navarrete et al., 2011; Rendell et al., 2011
Longevity and life history	Beneficial cultural traits	Caspari and Lee, 2004; Finch, 2010a; Gurven and Kaplan, 2007a; Kaplan and Robson, 2002a; Richerson and Boyd, 2020
Menopause	Beneficial cultural traits	Hawkes, 2003; Lahdenperä et al., 2004; Peccei, 1995
Docility	Collective and cooperative social structures	Gibbons, 2014; Leach, 2003; Theofanopoulou et al., 2017; Wilson, 1991; Wrangham, 2019
Shortened foregut, vestigial appendix	Cooking, food processing	Carmody and Wrangham, 2009; Wrangham and Conklin-Brittain, 2003; Wrangham et al., 1999
Lactase persistence	Dairying	Gerbault et al., 2011a; Ingram et al., 2009; Itan et al., 2009; Liebert et al., 2017; Tishkoff et al., 2007
Linguistic ability	Expressive human languages	Blasi et al., 2019; DeMille et al., 2018; Hunley, 2015

Table 4. Examples of mutualistic gene-culture coevolution, which predominate in stage II.

Adaptive challenge or gene-culture conflict	Preemptive cultural adaptation	Sources
Complex societies (C) conflict with social instincts (G), hampering social efficacy (x).	The "work-arounds" hypothesis	Richerson and Boyd, 1999
Modern agriculture creates surplus calories (C), leading to unbalanced diets, nutrient deficiencies, obesity (x).	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 (x).	Further medical technology, assisted living	Finch, 2010; Gurven and Kaplan, 2007; Kaplan and Robson, 2002a; Robson and Kaplan, 2003
Individual inability to reproduce (A).	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
Dental hygiene (C) lengthens tooth life, causing impaction of third molar (x).	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 (x).	Non-diary 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 (x).	Gluten-free foods	Hall et al., 2009; Pasquali et al., 2017; Zeder, 2016
Artificial light and longer workdays (C) conflict with sleep requirements (G), disrupting sleep schedules (x).	Sleeping drugs, shades, sleeping masks	Nunn et al., 2016; Samson and Nunn, 2015; Wright et al., 2012
Time-saving devices and communication technology (C) reduced need for collective work (G) leading to isolation, depression (x).	Therapy, antidepressants	Ambrose, 2010; Berland, 2009; Carter, 2014; Hidaka, 2012; Richerson and Christiansen, 2013; Stout et al., 2011
Work saving devices reduce labor (C) conflicting with need for exercise (G), decreasing general health (x).	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 5. Examples of cultural preemption in gene-culture coevolution which characterize stage 3. Cultural preemption occurs when cultural adaptations preempt genetic adaptation and relax genetic selection for solutions to adaptive challenges (A). This occurs commonly in domains in which prior genetic (G) and cultural (C) traits are in conflict (x). Note that most or all preemptive cultural adaptations are group-level cultural traits.

would otherwise be impossible. Both of these solutions require group-level support. Indeed, many preemptive cultural adaptations are group-level cultural traits (Table 5). As Mitteroecker (117) points out, gene-culture coevolution operates differently now that human bodies are evolving exclusively within modern societies.

V. Current status

Currently our species appears to be entering a stage of preemptive cultural adaptation. While prior human evolution is replete with evidence for the mutualistic 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). This is suggested by a consideration of the empirical metrics.

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 vastly more healthy and capable than humans without those cultural adaptations (37). Furthermore, cultural adaptations such as reproductive technology, and medical practice are increasingly disrupting the genotype-phenotype link. However, the transition is far from complete. For example, humans currently employ only a limited set of mechanisms to directly select the genotype of their offspring, including amniocentesis or sex-selective abortion (157). More invasive genetic germline intervention techniques such as pre-implantation genetic diagnosis (158) and human gene editing (159) are rare. Despite significant ethical concerns with these techniques, their increasing technical sophistication and decreasing costs make them likely to become more common. However, the genetic component of phenotypic variation is still strong, as genotype still plays an overwhelmingly large role in shaping human traits (160).

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 mentioned above showed that the onset of statehood increased genetic mixture among pre-existing groups (74). The same pattern can be observed in other "melting pot" societies which generally play an interesting role in gene-culture coevolution, breaking down genetically distinct groups through genetic admixture, dissolving old cultures through acculturation, conformity and coersion, and facilitating the growth of new group cultures. Importantly, this type of cultural group selection can occur without conquest or the loss of human lives.

Today, it is clear that the majority of human cultural adaptation comes from those group-level cultural traits such as food production, defense, education and health care all of which have become highly centralized and specialized. Thus, while there is still major variation in human fitness within societies, societal factors play an important role in determining individual health and fitness (161). Overall, we estimate the human species to have recently passed out of stage II and into stage III, but still be a long way from completing a coupled evolutionary transition.

VI. Predictions

The coupled transition hypothesis allows us to make simple predictions, some of which are readily measurable.

Inheritance-based predictions

If culture continues to replace genes as the primary inheritance system as we presume, then we can make a series of predictions based on the increasing importance of cultural inheritance.

1. By relaxing selection on genetic variation, cultural adaptations in medicine will allow genetic traits that would previously have been maladaptive to accumulate. This has the ratcheting effect of driving increased dependency on cultural systems, such as can be seen in human fertilization and birth (116, 126–130).
2. Reduced selection for individual genetic reproduction. Despite clear evidence of positive selection for fertility in some populations (85), we expect a long-term average relaxation of selection against non-biologically reproducing individuals, as the advantage to groups of culturally inherited skills overtakes that of more individuals. We also predict increased group control of reproduction, child-rearing and education. Mechanisms including norms and laws that support and prescribe reproduction, childcare and education, reproductive technology, and increased investment of non-relatives in raising children serve to increase the role of cultural groups in determining individual reproduction (162–165)
3. Increased importance of cultural group identity. Individual 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 (e.g. 166).

Individuality-based predictions

If group resources, capacities and traits become more influential than those of individuals, a set of simple predictions can be made.

1. Individuals outsource increasing degrees of their extended phenotypes (and therefore fitness) to their cultural groups. This occurs when people invest resources in and accept support from communities or organizations, coupling their future success to group-level outcomes. Examples include connecting a home to municipal utilities for water, gas or electricity or investing money in a business venture.
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 integrated and robust communication within groups (167–169) .
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 (170). Group differentiation can also exacerbate group polarization (171–173), competition, and conflict (e.g. wars, identity politics, economic competition, social strife) (174) when resources are in limited.

It should be noted that in an individuality transition the levels of social organization change over time, and the type of cultural group which comes to matter most cannot be easily predicted.

VII. Discussion: Causation in human socio-biological 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 result of the factors of unique human traits, such as our cooperative ability and capacity for cumulative culture. But explaining human uniqueness itself has remained out of reach. Evolutionary theories have often shied away from long-term directional change (175) despite the appreciation of slow, cumulative change and self-reinforcing systems in evolutionary transitions (25). A broader view suggests that our position as a species along a coupled evolutionary transition is the most parsimonious explanation of human uniqueness, and a source of ultimate causation in human sociobiological evolution.

Many of the proximate explanations of social science can be ordered and explained, at least in part, by the unique position 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? Institutionalized education is a group-structured cultural inheritance system which serves to disseminate cultural adaptations. Education therefore improves 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. Similarly, we can consider research-supported medicine as a group-level health system which increases T_P and T_ω.

The value of the coupled transition hypothesis as an ultimate cause of human behavior can be seen in how it might 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 (176). Why would human fertility decline when individuals are on average more comfortable and healthier than ever? The correlates and proximate causes are broadly understood: total fertility rate (TFR) declines across societies with increasing education and economic development (177).

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 (124, 178). 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 cost to biological reproduction (179–183). Another evolutionary theory explains the demographic transition as a result of cultural changes which occur when social networks expand to include more non-kin (184), causing a decline in the amount of reproduction-focused communication people experience, resulting in decreased reproduction in favor of other behavioral strategies (185). But both evolutionary explanations rest on unexplained aspects of human uniqueness; they explain how a change is unfolding but not why.

The demographic transition reveals a negative relationship between social and reproductive success which has been recognized for a decades (186, 187). However, if human adaptation is shifting from genetic to cultural systems of selection and inheritance, then the coupled transition is expected to favor cultural reproduction over genetic reproduction. Therefore, the historical decline in the fertility across societies is perhaps the strongest evidence of the cultural preemption of genetic inheritance. The same logic also presents the coupled transition as the ultimate cause of the human demographic transition.

VIII. Conclusion

Building on dual inheritance theory (24), 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 environmental interaction 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. We note that both cultural and environmental change are far from equilibrium, perhaps partly as a result of the human ETI. We speculate that, in the long term, culture will continue to grow in influence over human evolution, until genes become secondary structures that hold human biological design blueprints but are ultimately governed by culture.

Contrary to suggestions that the human ETI has stalled because the correlations between genes and culture is decreasing (15, 16), 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 coupled transition framework highlights the incompleteness of popular conceptions of a ‘technological singularity’ (188), but may contribute to more dispassionate research on ‘post-biological’ evolution (189).

The framework outlined above makes clear the need for a more organized research program on long term 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. 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. Third, better historical and current estimates of the strength of culture-driven group selection on human genes are needed. 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 a coupled transition in inheritance and individuality. Nevertheless, the coupled evolutionary transition provides a uniquely parsimonious explanation for both social and biological aspects of ongoing human evolution. And, given the available evidence, we estimate that a coupled transition in human evolution is underway and accelerating.

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