Gene-Culture Coinheritance of a Behavioral Trait

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Abstract: Many physical and behavioral traits in animals, including humans, are inherited both genetically and culturally. The presence of different inheritance systems affecting the same trait can result in complex evolutionary dynamics. Here, we present a general model that elucidates the distinct roles of cultural and genetic inheritance systems and their interaction in driving the evolution of complex phenotypes. In particular, we derive a Price equation that incorporates both cultural and genetic inheritance of a phenotype where the effects of genes and culture are additive. We then use this equation to investigate whether a genetically maladaptive phenotype can evolve under dual transmission. We examine the special case of altruism using an illustrative model and show that cultural selection can overcome genetic selection when the variance in culture is sufficiently high with respect to genes. We also show that the presence of cultural transmission can modify genetic selection when the interaction between genetic and cultural transmission of behaviors or traits can lead to an evolutionary process that operates in tandem with genetic transmission of (and selection on) a trait as mutually exclusive. However, their approach was limited to modeling genetic and nongenetic traits that jointly determine phenotype. However, their work considered cultural and genetic transmission from individuals that may not have contributed any genetic material. Given the importance of genetic and nongenetic inheritance in determining so many behavioral traits, it is imperative to develop a better theoretical understanding of how such coinheritance affects the evolution of behavioral traits.

In recent years, evolutionary theorists have begun to investigate the consequences of multiple inheritance systems (Otto et al. 1995; Bonduriansky and Day 2009; Day and Bonduriansky 2011). In a pair of articles, Day and Bondurianski used the Price equation to construct a general framework for modeling genetic and nongenetic traits that jointly determined phenotype. However, their approach was limited to vertical transmission of the nongenetic trait and thus kept track of only the reproductive fitness consequences of both systems of inheritance. While this approach gives a mathematically valid description of evolutionary change in a trait, it obscures the separate roles of genetic and nongenetic inheritance and selection in causing that change. In another recent article, El Mouden et al. (2014) developed a Price equation for cultural evolution and addressed the question of how potential conflicts between cultural and genetic selection might be resolved. However, their work considered cultural and genetic transmission of (and selection on) a trait as mutually exclusive alternatives and did not attempt to model the cotransmission of a single trait through both culture and genetics (for more on this point, see “Discussion”).

To account for the distinct causal roles of cultural and genetic selection, one needs to consider fitness measures in both systems of inheritance simultaneously. This is ultimately because ancestors in one system may not be identical to the ancestors in another. A fitness measure implies a mapping from ancestral to descendant individuals: ancestors who map...
(i.e., contribute hereditary material) to more descendants have higher fitness. Multiple inheritance systems mean the possibility of multiple mappings. For example, imagine a population of asexual organisms (as in fig. 1) with a phenotype $p$ determined by genetic and cultural inheritance. Let $p_a$ be the phenotype of an ancestor and $p_d$ the phenotype of her genetic descendant. If both genes and culture are inherited from the same ancestor and we assume no flaws in transmission and identical environmental effects, then $p_a = p_d$. However, if one’s genetic parent and cultural role model are not the same individual, then it is possible that $p_a \neq p_d$. If we consider the mapping solely from genetic parents to offspring, this discrepancy will appear simply to be an unexplained deviation between parents and offspring. However, also keeping track of the mapping between cultural role models and pupils, we might find that certain individuals map to more cultural descendants as a result of their phenotype because of selection in the cultural domain. Thus, what appears under one mapping to be an unexplained deviation between parent and offspring is revealed under another mapping to be a force of selection in its own right.

The argument above underscores the importance of considering fitness in each domain of inheritance when multiple forms of inheritance are present. This point was highlighted nearly 40 years ago by Richerson and Boyd (1978), who remarked that when both genes and culture determine a single phenotype, the value of the phenotype that maximizes genetic fitness may differ from the value that maximizes cultural fitness, leading to conflicts between the two inheritance systems. Modeling phenotype as the outcome of a nonzero sum game between cultural and genetic inheritance, they showed the conditions under which the Nash equilibrium phenotype would be the cultural fitness optimum and not the optimum value for genetic fitness. In the ensuing decades, cultural evolution theory has largely focused on the case when the genetic trait encodes a learning rule that determines how a cultural trait is acquired (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1988; Boyd et al. 2003; Guzmán et al. 2007; Lehmann et al. 2008). By contrast, the problem of conflict between inheritance systems that affect the same trait has received surprisingly little attention, with the notable exception of the model of Findlay (1992), which treated only vertical cultural transmission. This dearth of attention is particularly surprising, given the anthropological evidence for behavioral and social practices in humans that reduce reproductive fitness (Glanville 1987; Logan and Qirko

![Figure 1](https://example.com/figure1.png)

**Figure 1:** *a* Diagram shows the hereditary relationships between ancestors ($A_1$, $A_2$, $A_3$) and descendants ($D_1$, $D_2$, $D_3$). Solid lines indicate reproductive relationships, while dashed lines show cultural learning. While $A_3$ sired no offspring, he is the cultural learning model for all descendants. *b* Genotype, culture type, phenotypic, and fitness values for each ancestor and descendant (excepting fitness values). Each descendant has only one genetic and cultural ancestor; thus, each solid edge corresponds to $v_i = 1$, and each dashed edge corresponds to $v_i = 1$.
Examples include clubbing pregnant women to induce birth in Colombia (Reichel-Dolmatoff and Reichel-Dolmatoff 2013), unhygienic neonatal care practices in Bangladesh (McConville 1988), and folk medical practices such as ingesting rhino horn (Ayling 2013) or bloodletting (Wootton 2007). While these practices are undoubtedly inherited through cultural transmission, they are very likely also influenced by genetic inheritance, at the very least via broader behavioral traits with a significant genetic component, such as risk-taking, a trait that itself shows cross-cultural variation (Weber and Hsee 1998; Hsee and Weber 1999; Cesarini et al. 2009). Conflict between selection in the two inheritance domains provides a potential explanation for the spread of such maladaptive traits. Recent work (El Mouden et al. 2014; Morin 2014) has claimed that such conflicts will always be resolved in favor of reproductive fitness in the long term. Yet because this work has not explicitly modeled both types of selection acting on a trait simultaneously, the authors did not actually address the question of what happens to a trait that is under simultaneous, conflicting selection through genetic and cultural transmission. We take up this precise question, which reveals a more complex picture than previously recognized.

We derive a Price equation that explicitly incorporates both genetic and cultural inheritance. The Price equation is an exact description of an evolutionary process under a certain set of minimal assumptions (Price 1970; Frank 1998; Rice 2004). Soon after its introduction, Hamilton (1975) pointed out that the Price equation can apply equally well to cultural transmission, and recent authors have developed an exact description of an evolutionary process under a certain model to derive a Price equation that incorporates both domains of inheritance and their relevant fitness measures. Here, we use a simple additive model to derive a Price equation that incorporates both domains of inheritance and their relevant fitness measures directly. We then analyze the condition for the evolution of a phenotype when selection in the two domains is in conflict, taking altruistic behavior as a special case and extending our result to differing timescales of genetic and cultural transmission. Our model elucidates the conditions under which selection in one domain can overcome counterselection in the other domain. We end with a discussion of the implications of our results for understanding the evolution of potentially maladaptive behaviors.

**Gene-Culture Coinheritance of a Trait**

We model the change in a continuous phenotype, denoted by \( p \), that results from both genetic and cultural inheritance. We can take \( p \) to represent a behavioral trait, such as one of the big five personality traits (e.g., extraversion, agreeableness, conscientiousness; Goldberg 1993), or a morphological one such as body size. We assume that the effects of genetic and cultural inheritance are additive; that is, we express an individual’s phenotype as the following:

\[
p_i = c_i + g_j + \epsilon.
\]  

The final term, \( \epsilon \), is the effect of the environment that does not include cultural transmission (i.e., is not heritable). The two terms \( c_i \) and \( g_j \) will be referred to as the culture type and genotype, respectively. These terms only describe continuous variables and are not meant to imply any particular mode of inheritance (e.g., haploidy, diploidy). If we take extraversion as an example, \( g_j \) might represent a genetic predisposition toward extraversion (e.g., a polygenic score), while \( c_i \) might represent the overall exposure \( j \) has had to individuals of varying levels of extraversion, including the relative influence they have had on \( j \). Equation (1) is similar to the quantitative genetic formulation of Otto et al. (1995). The culture types and genotypes are determined by the corresponding values in \( j \)’s genetic and cultural ancestors. We assume that a descendant’s culture type and genotype are linear functions of her ancestors’ values given by

\[
g_j = \sum_{i=1}^{N} v_i g_i + \Delta g_j,
\]

\[
c_i = \sum_{j=1}^{N} \gamma_j c_j + \Delta c_i,
\]

where ancestral individuals are indexed by \( i \) and descendant individuals by \( j \). The coefficients \( v_i \) and \( \gamma_j \) are the weights that describe the degree of influence an ancestor \( i \) has on descendant \( j \) in the genetic and cultural domain, respectively. These weights are normalized so that \( \sum_{i=1}^{N} v_i = \sum_{j=1}^{N} \gamma_j = 1 \). For example, in a haploid organism, for an ancestor \( i \), all \( v_i \) are either 1 (if \( j \) is a descendant of \( i \)) or 0 (if \( j \) is not a descendant of \( i \)). In the diploid, sexually reproducing case, \( v_i = \{0, 1/2\} \), if we assume codominance. Similarly, the \( \gamma_j \) can accommodate any particular mode of information transfer from cultural parents to offspring. By normalizing these weights, we have assumed that all individuals have at least one genetic and cultural ancestor. While this assumption is perfectly natural for genetic reproduction, one can imagine traits for which some individuals might receive no cultural input or more cultural input than genetic. The delta terms \( \Delta g_j \) and \( \Delta c_i \) represent departures in \( j \) from the inherited genetic and cultural values. As an example, \( \Delta g_j \) may be nonzero in the event of mutation or recombination, while \( \Delta c_i \) may be nonzero because of individual learning or experience. This model generalizes that presented by El Mouden et al. (2014) to multiple inheritance, although our analysis and some conclusions differ.
Fitness captures the contribution of an ancestor to the next generation. In this model, that contribution, whether genetic or cultural, is determined by the weights given to an ancestor by her descendants, a formulation introduced by El Mouden et al. (2014). Thus, the fitness of an individual in either domain of inheritance is simply the sum of the weights given to an ancestor by all descendants. Specifically, we define the genetic fitness of an ancestor \( i \) as \( w_i = \sum_{j=1}^{N'} v_{ij} \) and the cultural fitness as \( s_i = \sum_{j=1}^{N'} \gamma_{ij} \), where the sums are taken over the descendant generation and \( N' \) is the number of descendants. If we recall the haploid case from above for \( v_{ij} \), then \( w_i \) is just the sum of \( i \)'s offspring. For \( s_i \), the values can range from 0 to a maximum of \( N' \), which occurs when \( i \) is the sole cultural ancestor of all descendants in the population. In the cultural domain, the definition of \( s_i \) shows that the total amount of influence an ancestor \( i \) has on descendant phenotypes is what matters most, not just the number of individuals over which \( i \) has had some nonzero influence.

Using these definitions and equation (1), we can derive the following Price equation to describe the evolutionary change in the mean value of the phenotype (see app. sec. A1; appendix is available online):

\[
\Delta \overline{p} = \frac{1}{\overline{w}} \text{cov}(w_i, g_i) + \frac{1}{\overline{w}} \text{cov}(s_i, c_i) + \langle \Delta g \rangle + \langle \Delta c \rangle. \tag{3}
\]

Note that angled brackets indicate averages over the descendant population, indexed by \( j \). Just as in the standard Price equation, the covariance terms represent the effects of selection and drift on evolutionary change (Rice 2004). Importantly, we can separate the effects of differential reproduction,

\[
\frac{1}{\overline{w}} \text{cov}(w_i, g_i),
\]

and differential influence in cultural transmission (e.g., due to content bias, model bias),

\[
\frac{1}{\overline{w}} \text{cov}(s_i, c_i).
\]

Note also the mean fitness,

\[
\overline{w} = \frac{N'}{N} = \bar{z},
\]

which is a direct result of the normalization conditions on \( \gamma_{ij} \) and \( v_{ij} \) and again implies that everyone receives the same amount of cultural input as genetic input and that cultural descendants must be equal to the total number of genetic offspring. The remaining terms are the effects due to spontaneous departure from one’s inherited information, such as mutation or recombination in genes or individual trial and error learning in culture. These terms differ somewhat from the transmission term in the standard Price equation, which is the fitness-weighted average departure of mean offspring phenotype from parental phenotype (\( E[w \Delta p] \)). This difference results from the fact that we are measuring the differences \( (\Delta g, \Delta c) \) between an individual offspring’s type and its ancestral contribution and then averaging over descendants.

The standard Price equation uses a single fitness measure and provides a mathematically valid description of evolutionary change. But in order to understand the effect of nongenetic inheritance, we need to keep track of two kinds of fitness. To see why, consider figure 1, which depicts an asexually reproducing population where descendants receive both genes and culture from ancestors, although not necessarily the same ancestors. Arrows with solid lines indicate parent-offspring relationships, and arrows with dashed lines indicate social learning relationships. Using only reproductive fitness (arrows with solid lines), we could capture the evolutionary change with the standard Price equation: \( \Delta \overline{p} = (1/\overline{w}) \text{cov}(w_i, \rho) + E[w \Delta p] = -1/3 + 1 = 2/3 \). This expression indicates that the effect of natural selection is to oppose increases in the phenotype, but it leads us to conclude that the transmission term, for reasons that are obscure, more than compensates for natural selection. Thus, it appears that natural selection has been overtaken by a faulty inheritance system. However, computing the terms in equation (3), we have \( \text{cov}(w_i, g_i) = 0, \text{cov}(s_i, c_i) = 2/3, \langle \Delta g \rangle = 0, \langle \Delta c \rangle = 0, \) and so \( \Delta \overline{p} = 0 + 2/3 + 0 + 0 = 2/3 \). Considering both genetic and cultural mappings, we see that there is in fact no natural selection on the phenotype in the genetic domain and no flaws in either inheritance system; however, there is positive selection in the cultural domain that produces evolutionary change. This is a distinctly different cause than was revealed by considering only the reproductive fitness mapping. In summary, if the two modes of inheritance were not explicitly described as in equation (1), then a departure in phenotype from one’s genetic ancestors would include the effect of cultural inheritance, while a departure in phenotype from one’s cultural ancestors would include genetic inheritance. By explicitly accounting for both inheritance mechanisms, our approach avoids confounding their evolutionary effects. In the remainder of the article, we explore the consequences of accounting for both cultural and genetic fitness explicitly.

It is worth noting that the distinction between ancestral and descendant individuals in this context is not meant to imply a nonoverlapping generations model. The Price equation examines evolutionary change over an arbitrary time step (Rice 2004); ancestors and descendants are simply the members of the same population separated by the given time step that can be mapped to one another. For example, if the time step is within a (reproductive) generation, an individual may serve as her own ancestor if she has simply persisted in the population. When the time step represents multiple generations, we can take ancestors and descendants to have their colloquial meanings. In a later section, we examine the consequences of assuming an explicitly nonoverlapping gen-
Conflict between Cultural and Genetic Selection

We can use equation (3) to examine evolutionary change when there are conflicts between cultural and genetic selection forces, that is, when $\Delta \bar{p} > 0$, even though $\text{cov}(s_c, p_c)$ and $\text{cov}(w_c, p_c)$ have opposite signs. For example, consider a socially acquired preference that leads to decreased reproduction, as in some cultural evolution models of the demographic transition (Ihara and Feldman 2004; Kolk et al. 2014). Let higher values of $p$ reduce fitness (i.e., $\text{cov}(w_c, p_c) < 0$). Then the mean phenotype in the population will increase when

$$\text{cov}(s_c, c) > -\left(\text{cov}(w_c, g_c) + \bar{\varphi}(\Delta g_c)\right),$$

where we have ignored the genetic transmission term $\langle \Delta g_c \rangle$ under the assumption that mutation and recombination effects are unbiased with respect to genotypic value. If the magnitude of cultural selection exceeds that of genetic selection (plus the effect of genetic transmission), then $\bar{p}$ can increase, despite being opposed by natural selection. In essence, a loss in reproductive fitness can be compensated for by increased importance as a learning model. However, the cultural transmission term means that this condition will be harder to meet if social learning biases individuals toward lower cultural values than their learning models, for example, as a result of biased learning error (Henrich 2004b).

Cultural Evolution of Altruism

Hamilton’s rule (Hamilton 1964a, 1964b) states that an altruistic allele will spread in the population when $rB > C$, where $B$ is the fitness benefit to a recipient of altruism, $C$ is the fitness cost to an altruist, and $r$ measures the assortment between altruists (often interpreted as a relatedness coefficient). Cultural evolution theorists have claimed that altruism is more likely to evolve under cultural evolution because this relatedness parameter for culture is likely to be higher than for genes (Fehr and Fischbacher 2003; Henrich 2004a; Boyd and Richerson 2010). This claim implies that cultural evolution makes the spread of altruism possible even when the classical form of Hamilton’s rule does not hold (El Mouden et al. 2014), that is, when genetic selection is opposed to altruism. To investigate this claim, the effect of evolutionary forces in the cultural and genetic domains must be compared directly, which has not been done before. Here we use our framework to derive the precise conditions under which cultural selection can favor altruism, despite being opposed by genetic selection.

By altruism we mean here a behavior that reduces the fitness (genetic and/or cultural) of a focal individual while increasing the fitness of others, when the fitness effects of others on the focal individual are ignored (Hamilton 1964a; Rousset 2013). We start by examining the most stringent case where fitness cost is both genetic and cultural, although there is no necessity for altruism to be costly with respect to both domains of inheritance. Let $p$ now represent the level of altruistic behavior and the cultural and genetic fitnesses be given by the following equations:

$$s_c = s_0 + \beta_{sp} p + \beta_{pc} \bar{p},$$
$$w_c = w_0 + \beta_{wp} p + \beta_{pc} \bar{p}.$$

The tilde over a variable indicates the mean value of that variable across $i$’s neighbors (i.e., the individuals with whom the focal can potentially interact). We have assumed that both kinds of fitness are linear functions of an individual’s own phenotype and the phenotypes of her neighbors, where $s_c$ and $w_c$ are the baseline fitnesses. As in the standard derivation of Hamilton’s rule using the Price equation, it is customary to identify $\beta_{sp}$ and $\beta_{pc}$ as the cost ($C$) to an altruist and benefit ($B$) to recipients of altruism, respectively (Frank 1998; Rice 2004; McElreath and Boyd 2008). We will use the same convention but add subscripts to indicate costs and benefits to genetic and cultural fitnesses: $\beta_{sp} = -C_g$, $\beta_{pc} = -C_c$, $\beta_{wp} = B_g$, $\beta_{pc} = B_c$. By labeling these terms, we will be able to more clearly interpret our key results. We can then derive the following condition (see app. sec. A2),

$$B_g (\beta_{ic} + \beta_{ig}) - C_g (1 + \beta_{ic}) >$$
$$-B_g (\beta_{ig} + \beta_{ig}) - C_g (1 + \beta_{ig}) \frac{\text{var}(g_c)}{\text{var}(c_c)},$$

where we have ignored the transmission terms. The left-hand side of equation (7) gives the cultural selection coefficient, while the term in brackets on the right-hand side is the genetic selection coefficient. It is immediately apparent that the genetic selection coefficient is different than it would be under purely genetic transmission of the phenotype (i.e., $B_g \beta_{ig} - C_g$, as follows from the canonical form of Hamilton’s rule) because of the presence of the additional regression coefficients $\beta_{ig}$ and $\beta_{ig}$. The same is true for the cultural selection coefficient, which would be $B_g \beta_{ic} - C_c$, under purely cultural transmission (El Mouden et al. 2014).

Of the three regression coefficients on the left-hand side, the first, $\beta_{ic}$, is the cultural relatedness term, and it describes how likely actors are to behave altruistically toward individuals with similar culture types. The second, $\beta_{ig}$, is one of the gene-culture relatedness terms and captures the correlation between an actor’s culture type and neighbor’s genotype. Thus, if individuals with higher culture type values are more likely to direct their altruism toward those with higher genotypic values, the cultural fitness benefit is greater. The final regression coefficient, $\beta_{ig}$, captures the correlation between an actor’s genotype and her culture type. The higher the cor-
relation between genes and culture, the more likely it is that a costly genotype will be paired with a costly culture type, making it more difficult for altruism to evolve.

Turning to the term in brackets on the right-hand side, the regression coefficient, \( \beta_{\text{ex}} \), is the regression of neighbor culture type on focal genotype. The term \( \beta_{\text{ex}} \) is the regression of focal culture type on focal genotype. Both of these terms mean that the presence of cultural transmission changes genetic selection on altruism (i.e., genetic selection is no longer given by \( B_t \beta_{\text{ex}} - C_t \)), since there are now gene–culture-relatedness terms to be taken into account. For example, if individuals with an altruistic genotype are more likely to direct their altruism toward those with an altruistic culture type, then genetic selection can favor altruism even with low genetic relatedness (\( \beta_{\text{ex}} \)); this suggests that a locus that causes individuals to preferentially interact with culturally similar individuals can be favored by natural selection even when it is costly.

When there is complete statistical independence of genetic and cultural transmission, all gene–culture correlations are 0 (\( \beta_{g} = \beta_{c} = \beta_{\text{ex}} = 0 \)), and equation (7) reduces to

\[
B_t \beta_{\text{ex}} - C_t > -B_t \bar{\beta}_{\text{ex}} - C_t \frac{\text{var}(g)}{\text{var}(c)}.
\]

The term in parentheses on the right-hand side is the genetic inclusive fitness from the canonical form of Hamilton’s rule, while the left-hand side is the corresponding expression for culture. Thus, when there are no gene–culture correlations, altruism will spread as long as cultural inclusive fitness only exceeds genetic inclusive fitness scaled by the ratio of the variances in the two domains. When the variance in culture types is sufficiently high with respect to variance in genotypes, cultural selection can overcome even considerable genetic selection. If we further consider the case when altruism is costly to genetic fitness but beneficial to cultural fitness, the left-hand side becomes \( B_t \beta_{\text{ex}} + C_t \), and the condition becomes even easier to meet.

From examination of equation (7), we see that cultural transmission affects the evolution of altruism in two important ways: (1) by introducing a cultural selection force that may overcome genetic selection and (2) by changing the nature of genetic selection itself. This latter effect means that for given values of \( B_t \) and \( C_t \), genetic selection may be positive in the presence of joint cultural and genetic transmission when it would have been negative under purely genetic transmission.

**Differing timescales of transmission.** Up to now we have considered evolutionary change over a single time step for both genetic and cultural transmission. However, measuring the effect of two selection processes operating under incongruent timescales over a single time period can cause problems of interpretation of the Price equation terms. Here we consider a model where cultural transmission occurs multiple times during a reproductive generation. We imagine a fixed population of size \( N \) with nonoverlapping reproductive generations. Within a reproductive generation, there are \( n \) nonoverlapping stages of cultural transmission. A cohort is born at the beginning of a reproductive generation and receives its initial cultural and genetic input from the outgoing generation. This cohort then moves through the \( n \) stages updating its culture types on the basis of the values of other cohort members in the previous stage. In effect, while the stages are nonoverlapping, all stages after the initial stage allow for horizontal transmission that alters the cohort’s culture types from its initial inheritance from the previous generation. Ignoring the effects of both genetic and cultural transmission, we can derive the following Hamilton’s rule–like condition (for model details and full results, see app. sec. A4):

\[
\sum_{t=1}^{n} S_t > -S_t \frac{\text{var}(g)}{\langle S_t \text{var}(c^{-1}) \rangle_t},
\]

where

\[
S_t = \frac{1}{\xi} [\beta_{g}(1 + \beta_{c}) + \beta_{c}(\beta_{\text{ex}} + \beta_{\text{ex}})]
\]

and

\[
S_2 = \frac{1}{\eta} [\beta_{g}(1 + \beta_{c}) + \beta_{c}(\beta_{\text{ex}} + \beta_{\text{ex}})]
\]

are the cultural and genetic selection coefficients, respectively (for details on the scaling factors \( 1/\xi \) and \( 1/\eta \), see app. sec. A4). The cultural selection coefficients are identified by superscript \( t \) to indicate the selection coefficient at each of the \( n \) stages of cultural transmission. The denominator on the right-hand side is the average cultural variance over the \( n \) stages, weighted by the selection coefficient relevant to that stage. It is easy to see that when \( n = 1 \), we have equation (7). For \( n > 1 \), we see that cumulative cultural selection must overcome the genetic selection coefficient scaled by a new ratio: that of genetic variance to the selection weighted average cultural variance over the \( n \) stages of cultural transmission. This selection weighted variance term is complex in that selection may vary over the \( n \) stages of cultural transmission, which will affect how the different variances are weighted, but these variances too will be affected by the magnitude of selection at the previous stage. A more explicit model will be required to explore how different selection trajectories (i.e., the sequence of \( S_t \) values) affect the overall effect on phenotypic evolution.

**Discussion**

**Coinherited Behaviors**

Our model is inspired by the fact that many complex traits (from psychological traits to disease risk) are likely affected by both genetic and cultural transmission. We use a gene-
culture Price equation to investigate the effect of conflicts between selection in the two domains of inheritance. Our Price equation framework provides a simple condition for when cultural selection can overcome genetic selection and steer the evolution of a phenotype.

This framework can be useful for making both quantitative and qualitative predictions. For instance, educational attainment is a complex trait that is clearly influenced by social learning. Epidemiological studies suggest a narrow-sense heritability of 0.4 (Branigan et al. 2013), while Kong et al. (2017) recently showed evidence for selection against genetic variants associated with higher educational attainment in an extensive data set from Iceland. If we assume that the remaining trait variance is due to culture, equation (4) can be used to calculate a threshold cultural selection value for the increase in educational attainment. In another example, Levy et al. (2016) found that culturally transmitted negative stereotypes about aging predicted later biomarkers of Alzheimer’s disease (reduced hippocampal volume and increased amyloid plaque development). Our model indicates that if these negative stereotypes are culturally selected for—perhaps because a rapidly changing environment makes older individuals seem less valuable as cultural role models—then cultural selection can increase the incidence and severity of Alzheimer’s biomarkers, especially because natural selection is likely to be very weak in this case.

Our results show the importance of the ratio of genetic to cultural variance in determining the relative strength of genetic and cultural selection. Although several studies have looked at genetic and cultural variation in humans, they currently do not report the necessary information to measure this ratio for a particular trait. Bell et al. (2009) compared $F_{ST}$ values for culture and genes in populations using the World Values Survey. Their results suggested greater between-population variation in culture than in genes, although these were across genomes and cultures and not with respect to a particular trait. Other studies have shown parallels in the patterns of linguistic and genetic diversity (Hunley et al. 2008; Perreault and Mathew 2012; Creanza et al. 2015; Longobardi et al. 2015) but again do not report the ratio of genetic to cultural variance for a particular trait. However, behavioral genetics is providing increasingly accurate heritability measures for behavioral traits. These studies, in combination with cultural measures (e.g., using cultural pedigrees), can offer empirical estimates of this ratio for evolving behaviors. Nonhuman animals provide even better prospects for measuring distinct genetic and cultural heritabilities, which we will show relate directly to our variance ratio. Songbirds in particular lend themselves to experimental designs where both genetic and cultural pedigrees can be manipulated (Danchin et al. 2011). Using an extended animal model, cultural and geneticheritabilities could be measured and the ratio of genetic to cultural variance estimated.

Related Work

Nearly 40 years ago, Richerson and Boyd (1978) used a game theoretic model to show that the Nash equilibrium value of a trait that is both genetically and culturally inherited could be that which optimizes cultural fitness. But surprisingly, given the intense attention gene-culture coevolution received, very little theoretical work has been done to follow up on the evolution of phenotypes that are directly coherited, as opposed to culturally inherited behavioral phenotypes and genetically inherited learning rules (e.g., Lehmann and Feldman 2008). Findlay (1992) modeled gene-culture transmission of a phenotype in a structured population but limited his analysis to vertical transmission. Another article close to our model is that of Lehmann et al. (2008), who model the evolution of a purely culturally inherited altruistic behavior in a subdivided population. In their model, Lehmann et al. (2008) consider the phenotype to be affecting either only cultural or only reproductive fitness and assume no genetic contribution to the phenotype. As such, their model can be recovered by modifying our Price equation (7) by setting $p_i = c$, which replaces the right-hand side of the condition with 0. Importantly, biological offspring in Lehmann et al.’s (2008) model serve as vectors of the cultural types of their parents, which means that even when their cultural trait affects only reproductive fitness, our corresponding $B_i$ and $C_i$ terms would be nonzero. That means that the transmission rate of different cultural types are not the same over the entire life cycle, and there is cultural (but no genetic) selection.

More recently, El Mouden et al. (2014, p. 235), using a Price equation to describe cultural evolution, claimed that cultural selection can increase genetic fitness (e.g., through altruism that benefits others) of a population only if genetic and cultural fitness is positively correlated. Our results contradict this claim: instead, we show that coinherited altruistic behaviors that increase mean genetic fitness of the population can evolve through cultural selection even when opposed by genetic selection. To give the simplest possible example, consider our equation (8) and an altruistic trait with $B_x > C_x$, but $\beta_{gx}B_x < C_x$. This trait would be opposed by genetic selection (more altruistic phenotypes would have lower genetic fitness). However, if it spreads through cultural selection (which happens when $\beta_{gx}B_x > C_x$ is sufficiently large, when more altruistic phenotypes have higher cultural fitness), it would increase the mean genetic fitness, despite the fact that cultural and genetic fitness is negatively correlated. At the heart of this discrepancy is the fact that the mathematical framework of El Mouden et al. (2014) considers competing hypotheticals where a trait is transmitted either purely culturally or purely genetically. Therefore, their model cannot directly address the question of which direction a trait will evolve under conflicting selection pressures and what the consequences of such evolution are for a population’s mean
fitness. In contrast, we allow both modes of inheritance to be present and make clear, direct comparisons between the effects of those inheritance systems. This framework allows us to further consider the consequences of assortment between individuals genetically and/or culturally as well as the assortment of the genotypes and culture types within individuals. We find that some assortment patterns can cause genetic selection to change direction to match cultural selection. Our results show that there is more complexity to the interaction of genetic and cultural selection, especially in structured populations.

El Mouden et al. (2014) also conclude that natural selection acting on the underlying learning rule that determines cultural selection will bring the two kinds of fitness into alignment. Specifically, El Mouden et al. (2014) consider a trait evolving under purely cultural transmission and consider how the learning rule, itself genetically transmitted, would evolve. In forthcoming work (E. Aguilar and E. Akçay, unpublished manuscript), we extend the approach in this article to derive the conditions for the simultaneous (genetic) evolution of a learning rule with a gene-culture coinherited trait. Our results in that work show that the conclusion of El Mouden et al. (2014) indeed holds in the special case when the phenotype is transmitted only culturally. However, when the trait is coinherited, the picture becomes more complex: learning rules that support maladaptive phenotypes can be maintained in some cases. More generally, the coevolution of transmission rules for genetic and cultural systems for coinherited traits needs to be explored further.

Our results on the importance of the ratio of genetic to cultural variance relates to a recent strand of work on extended inheritance. In a series of articles, Danchin et al. (2011, 2013) and Danchin and Wagner (2010) introduced the idea of inclusive heritability, which partitions the variance in the inheritable component of phenotype into the contributions from each system of inheritance. This allows for narrow-sense heritability to be expressed as the sum of the heritabilities in each domain (assuming no interactions between the inheritance systems). In our model, this means \( h^2 = h_c^2 + h_g^2 \) (where \( h_c^2 \) and \( h_g^2 \) are the genetic and cultural narrow-sense heritabilities). The relationship between these quantities and the term that appears in our results as the scaling factor of genetic selection is

\[
\frac{\text{var}(g)}{\text{var}(c)} = \frac{\text{var}(g) \cdot \text{var}(p)}{\text{var}(p) \cdot \text{var}(c)} = \frac{h_g^2}{h_c^2}.
\]

Thus, it is the ratio of the narrow-sense heritabilities that determines the relative importance of genetic selection in the evolution of a coinherited phenotype. This further demonstrates the relationship between inclusive heritability and the effects of selection acting in different domains of inheritance.

For most of the article, we do not model population structure explicitly, instead dealing with statistics of population structure, given by the gene-culture, culture-culture, and gene-culture correlation terms in equation (7) (which are calculated explicitly in the assortment model described in app. sec. A3). Findlay (1992) presented a model of explicit population structure and found that when within- and between-group selection had the same sign, gene-culture inheritance accelerated the rate of phenotypic evolution (vis-à-vis purely genetic inheritance) by increasing the correlation between parents and offspring as well as the heritable between-group variation. This result assumed vertical transmission of culture from genetic parent to offspring. A similarly explicit population structure model in our framework may yield different results because of the fact that phenotypic correlations between parents and offspring are likely to decrease when cultural and genetic parents differ. More generally, the effects of population structure needs to be further explored for their implications for the literature on cultural group selection.

**Limitations and Extensions**

The Price equation derives its power from its generality. Results derived from the Price equation will apply to all models in the class defined by the Price equation's basic assumptions. Therefore, results for explicit models in the same class can all be related to one another using the general results of the Price equation. In this sense, our above results are general for coinherence models that respect additivity. However, this generality comes at a cost. On its own, the Price equation cannot be used to iterate into the future and make statements about the long-term dynamics of a process, a property referred to as dynamical insufficiency (Frank 1998). Viewed from this perspective, the Price equation is analogous to a derivative for a discretized system over arbitrary time steps. The variance and regression terms in the conditions derived above can evolve across time steps depending on the explicit dynamical model employed. Long-term behavior of coinherence systems will require examination of specific dynamic models; for this reason, we include results for an explicit dynamical model in the appendix (see app. sec. A3). However, the Price equation does provide a recipe for model construction and interpretation, which is especially important for considering multiple inheritance systems where there are more degrees of freedom for choices of model assumptions.

The additive model we used in this article is both the simplest model and a natural extension of the standard assumption in quantitative genetics (Falconer and Mackay 1996). It is also easily generalizable to an extended animal model, which would be of particular use in experimental setups in nonhuman animals (Danchin et al. 2011). However, our framework can also be expanded by a simple method to a wide class of functions that determine phenotype and the effect
of the relative variances in the two domains still obtains (for details, see app. sec. A5).

In the course of deriving our results on the effects of selection, we often ignored the transmission terms \( \langle D_c \rangle \) and \( \langle D_g \rangle \). In relatively simple genetic systems, it may be safe to assume that the expected difference between parents and offspring is zero. However, culture very often makes this assumption untenable because the cultural transmission system allows for biased or directed mutation in the form of individual learning and other factors. For example, individuals may systematically differ from their parents because they learn more appropriate responses to their environment through their own trial-and-error learning. El Mouden et al. (2014) offered an interpretation of the transmission term as evolved biases in favor of reproductive fitness–maximizing behaviors. However, cultural transmission biases (or individual learning) may not always maximize reproductive fitness, especially under frequency dependence. Meanwhile, Henrich (2004a) took the transmission term to represent systematic error in cultural learning that biased individuals to trait values lower than their cultural parents. These examples hint at the diverse interpretations that can be ascribed to the transmission term, particularly in lieu of empirical evidence on how a specific trait is passed on. These effects also present important future directions for a more complete framework of gene-culture coevolution.

Conclusion

The Price equation offers a general statement of how evolutionary change can be partitioned among different evolutionary factors (Frank 2012). In using the Price equation, we have offered a framework for partitioning the evolution of a co-inherited trait across the distinct causes (selection, transmission effects, etc.) in each domain of inheritance. More broadly, none of the fundamental assumptions of our model are unique to cultural transmission, and thus our results hold well for nongenetic inheritance more generally and are a particular improvement when ancestors are not the same across all inheritance systems. As the importance of nongenetic inheritance systems becomes clearer, we propose that accounting for multiple inheritance systems explicitly, as we do in our framework, will contribute to a better theoretical understanding of the evolution of these traits.

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