# Gene-culture co-inheritance of a behavioral trait

Elliot G. Aguilar[1] and Erol Akçay[2]

Department of Biology, University of Pennsylvania

433 S University Ave. Philadelphia, PA 19104

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[1] elliot.g.aguilar@gmail.com

[2] eakcay@sas.upenn.edu

**Abstract**

Human behavioral traits are complex phenotypes that result from both genetic and cultural transmission. But different inheritance systems need not favor the same phenotypic outcome. What happens when there are conflicting selection forces in the two domains? To address this question, 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. Finally, we show how our basic result can be extended to nonadditive effects models. We discuss the implications of our results for understanding the evolution of maladaptive behaviors.

# 1   Introduction

Behavioral traits are complex phenotypes that result from the interaction between genes and environment (Turkheimer, 2000). In species with social learning, a significant component of what has traditionally been called the environment may be cultural transmission. While behavioral genetics seeks to find the genetic basis of increasingly complex behavioral phenotypes, such as educational attainment or political participation (Ward et al., 2014; Fowler et al., 2008), a true understanding of the evolution of behavioral traits means reckoning with how genetic and cultural transmission interact to affect evolutionary outcomes.

When there are multiple domains of inheritance, the concept of fitness must be tailored to each domain. Nearly forty years ago, Richerson & Boyd (1978) pointed

out that optimum value of a phenotype that maximizes genetic fitness may differ from the value that maximizes cultural fitness, leading to conflicts between the two inheritance systems. In the ensuing decades, evolutionary theorists have studied numerous cases of the co-evolution of genetic and cultural traits (Boyd and Richerson, 1988; Cavalli-Sforza and Feldman, 1981), such as genetically encoded learning rules and culturally acquired helping behaviors (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 far less attention. This is curious, given the likelihood that many human behaviors are both genetically and culturally determined. For instance, fertility itself may result from genetic predispositions towards fitness maximization and culturally acquired preferences for family size (Kolk et al., 2014). In this paper, we take up the question of how conflict between selection in different domains of inheritance affects the evolution of a trait.

In order to address the question of conflicting selection in the cultural and genetic domains, we derive a Price equation that explicitly incorporates both forms of inheritance. The Price equation is an exact description of an evolutionary process under a certain set of minimal assumptions (Price et al., 1970; Frank, 1998; Rice, 2004). As early as (Hamilton, 1975) it was pointed out that the Price equation can apply equally well to cultural transmission, and recent authors have developed it for that purpose (Henrich, 2004a; El Mouden et al., 2014). Others have also extended the Price equation to include multiple forms of inheritance (Day and Bondurriansky, 2011; Helanterä and Uller, 2010), though they considered separate traits being transmitted in each domain. Here, we use a simple additive model to

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35  derive a Price equation that incorporates both domains of inheritance and their rel-

36  evant fitness measures directly. We then analyze the condition for the evolution

37  of a phenotype when selection in the two domains is in conflict. We take altruism

38  as a special case and present an illustrative model to explore the implications of

39  our results. The model shows that selection in one domain can overcome counter-

40  selection in the other domain under the right conditions. We then extend our Price

41  equation framework to more complicated models. We end with a discussion of the

42  implications of our results for understanding the evolution of maladaptive behav-

43  iors.

## 2  Gene-Culture Price equation

45  We model the evolution of a trait that results from both genetic and cultural inheri-

46  tance. Evolution here means the change in the phenotypes in a population, not only

47  the change in the genetic or culturally inherited information that underlies them.

48  An individual's phenotype is represented by a continuous variable, $p$. We can take

49  this to represent a behavioral trait, such as one of the big five personality traits (e.g.

50  extraversion, agreeableness, conscientousness, etc.) (Goldberg, 1993). We assume

51  that the effects of genetic and cultural inheritance are additive, i.e., we express an

52  individual's phenotype as

$$p_j = c_j + g_j + e \,. \tag{1}$$

53  The final term, $e$, is the effect of the environment that does not include cultural

54  transmission (i.e. is not heritable). The two terms, $c_j$ and $g_j$ will be referred to as

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the culture-type and genotype, respectively. These terms only describe the state of the continuous variables, and are not meant to imply any particular mode of inhertiance (e.g. haploidy, diploidy, etc.). Equation (1) is similar to the quantitative genetic formulation in Otto et al. (Otto et al., 1995). The culture- and geno-types 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

$$g_j = \sum_{i=1}^{N} \nu_{ij} g_i + \Delta g_j \qquad (2a)$$

$$c_j = \sum_{i=1}^{N} \gamma_{ij} c_i + \Delta c_j \,, \qquad (2b)$$

where $\nu_{ij}, \gamma_{ij} \in [0,1]$ and $\sum_{i=1}^{N} \nu_{ij} = \sum_{i=1}^{N} \gamma_{ij} = 1$; these values are the weights that describe the degree of influence an ancestor $i$ has on descendant $j$ in the genetic or cultural domain. For generality, we have taken the sums over all $N$ individuals in the ancestral population. When $i$ is not a genetic ancestor to $j$, then $\nu_{ij} = 0$; when $i$ is not a cultural ancestor, $\gamma_{ij} = 0$. The delta terms, $\Delta g_j$ and $\Delta c_j$ , 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 $\Delta c_j$ may be nonzero due to individual learning or experience. This model generalizes that presented by El Mouden et al. (El Mouden et al., 2014), though our analysis and conclusions differ.

Equation (1) explicitly identifies the two modes of inheritance that affect the phenotype in question. This formulation keeps cultural and genetic lineages separate, ensuring that a descendant will not inherit via genes information that its

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74 ancestor inherited via social learning and vice versa. Equations (2) ensure that the

75 effects of selection and transmission in the two domains of inheritance are kept sep-

76 arate. This is an important point: if the two modes of inheritance were not explicitly

77 described, then a departure in phenotype from one's genetic ancestors would in-

78 clude the effect of cultural inheritance, while a departure in phenotype from one's

79 cultural ancestors would include genetic inheritance. Equations (2) allows us to

80 avoid confounding the effects of the two modes of inheritance.

81 Fitness captures the contribution of an ancestor to the next generation. In this

82 model, that contribution, whether genetic or cultural, is determined by the weights

83 given to an ancestor by her descendants. Thus, the fitness of an individual in either

84 domain of inheritance is simply the sum of the weights given to an ancestor by

85 all descendants. Specifically we define the genetic fitness of an ancestor $i$ as $w_i = $

86 $\sum_{j=1}^{N'} \nu_{ij}$ and the cultural fitness, $s_i = \sum_{j=1}^{N'} \gamma_{ij}$, where the sums are taken over the

87 descendant generation. For example, for a haploid organism, all $\nu_{ij}$ are either $1$

88 or $0$, and $w_i$ is simply equal to the number of offspring (in the diploid, sexually

89 reproducing case, $\nu_{ij} = \{0, 1/2\}$). In the cultural domain, the definition of $s_i$ shows

90 that the total amount of influence an ancestor $i$ has on descendant phenotypes is

91 what matters most, not just the number of individuals over which $i$ has had some

92 non-zero influence.

93 Using these definitions and equation 1, we can derive the following Price equa-

94 tion to describe the evolutionary change in the mean value of the phenotype (see

95 A–1),

$$\Delta \bar{p} = \frac{1}{\bar{w}} \text{cov}(w, g) + \frac{1}{\bar{w}} \text{cov}(s, c) + \langle \Delta g \rangle + \langle \Delta c \rangle . \tag{3}$$

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96    Just as in the standard Price equation, the covariance terms represent the effects of

97    selection and drift (Rice, 2004) on evolutionary change. Importantly, we can sep-

98    arate the effects of differential reproduction ($\frac{1}{\bar{w}}\mathrm{cov}(w, g)$) and differential influence

99    in cultural transmission ($\frac{1}{\bar{w}}\mathrm{cov}(s, c)$). Importantly, $\bar{s} = \bar{w}$, which is equivalent to

100   everyone receiving some cultural input. The remaining terms are the effects due

101   to spontaneous departure from one's inherited information, such as mutation or

102   recombination in genes, or individual trial-and-error learning in culture. This ap-

103   proach means that each of the four terms in equation 3 can be given a clear biolog-

104   ical interpretation and, crucially, that each term represents an exclusive evolution-

105   ary effect.

106        We can use equation (3) to examine evolutionary change when there are con-

107   flicts between cultural and genetic selective forces. Is it possible for a trait that is

108   favored by social learning but detrimental to reproductive fitness to evolve? For

109   example, let us imagine a socially acquired preference that leads to decreased re-

110   production, as in some cultural evolution models of the demographic transition

111   (Ihara and Feldman, 2004; Kolk et al., 2014). Let higher values of $p$ reduce fitness,

112   that is to say, $cov(w, p) < 0$. Then we have the following condition,

$$cov(s, c) > -cov(w, g) - \bar{w}\langle \Delta c \rangle, \tag{4}$$

113   where we have ignored the genetic transmission term $\langle \Delta g \rangle$ under the assumption

114   that mutation and recombination effects are unbiased with respect to genotypic

115   value. Putting aside for the moment the cultural transmission term, this condi-

116   tion states that the mean value of $p$ can increase—despite reducing reproductive

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fitness—so long as the covariance between cultural value and influence on descen-

dants exceeds the absolute value of the covariance between genotype and repro-

ductive fitness. In essence, a loss in reproductive fitness can be compensated for by

increased importance as a learning model. However, 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).

Intuitively, whether individuals give higher or lower weights to ancestors with

higher cultural values determines the direction of evolution of $p$. This can be seen

by observing that the cultural covariance term can be rewritten as

$$cov(s_i, c_i) = N' \left\langle cov(\gamma_{ij}, c_i) \right\rangle = N' \left\langle \beta_{\gamma c}^j \right\rangle var(c), \tag{5}$$

where the brackets indicate the mean over the descendant population and $N'$ is the

descendant population size. The term inside the brackets applies to an *individual

descendant*; it is the correlation between the weight that particular descendant as-

cribes to ancestors and those ancestors' cultural values (computed for all potential

ancestors). When this term is positive, it means that, on average, greater weight is

given to ancestors with higher values of $c$. We can now rewrite eq. (4) as a new

inequality that shows explicitly how strong the bias in favor of higher $c$ must be in

order for there to be positive evolutionary change,

$$\left\langle \beta_{\gamma c}^j \right\rangle > -\frac{1}{N} \left[ \frac{\beta_{wg}}{\bar{w}} \frac{var(g)}{var(c)} + \frac{\langle \Delta c \rangle}{var(c)} \right] \tag{6}$$

Condition (4) gives us the criterion for maladaptive phenotypes with respect to how

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135   ancestors' $c$ values translate into cultural fitness. The condition in (6) allows us to

136   see the same condition from the 'descendant's point of view'. The correlation term

137   $\beta^j_{\gamma c}$ characterizes the learning rule a descendant $j$ employs. It is the population av-

138   erage of the learning rule employed by descendants that determines the direction

139   of evolutionary change. Importantly, we also see that the strength of the genetic

140   selection term (first term inside the brackets) is modified by the relative variance in

141   genotypes and culture-types. This is a result of having multiple selection terms in

142   our Price equation. In fact, Hamilton (1975) pointed out a similar effect in his multi-

143   level selection version of the Price equation, where the variances corresponded to

144   individual and group level characters (Hamilton, 1975). It is important to point out

145   here that while group and individual level variances are just different ways of par-

146   titioning the population variance (and hence have to add up to the total variance),

147   here we have variances of two different variables whose values are unconstrained

148   by one other. We will see this ratio play an important role in the next section.

## 2.1   Cultural Evolution of Altruism

150   We now examine a question that has received considerable attention in the cul-

151   tural evolution literature: whether cultural transmission can lead to the evolution

152   of altruism even when natural selection would not (Henrich, 2004a; Boyd and Rich-

153   erson, 2009; Boyd et al., 2011; Lehmann et al., 2008; Lehmann and Feldman, 2008;

154   André and Morin, 2011). To be precise, by altruism we mean a behavior that re-

155   duces the fitness (genetic and/or cultural) of a focal individual while increasing

156   the fitness of others, when the fitness effects of others on the focal individual are

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157 ignored (Hamilton, 1964; Rousset, 2013). For the moment we will assume that the

158 fitness cost is both genetic and cultural; later we explore the effect of relaxing this

159 assumption. Let $p$ now represent the level of altruistic behavior and the cultural

160 and genetic fitnesses be given by the following equations:

$$s_i = s_0 + \beta_{sp}p_i + \beta_{s\tilde{p}}\tilde{p}_i \tag{7}$$

$$w_i = w_0 + \beta_{wp}p_i + \beta_{w\tilde{p}}\tilde{p}_i \tag{8}$$

161 The tilde over a variable indicates the mean value of that variable across $i$'s neigh-

162 bors. We have assumed both kinds of fitness are linear functions of an individu-

163 als own phenotype and the phenotypes of her neighbors, where $s_o$ and $w_0$ are the

164 baseline fitnesses. As in the standard derivation of Hamilton's rule using the Price

165 equation, it is customary to identify $\beta_{wp}$ and $\beta_{w\tilde{p}}$ as the cost ($C$) to an altruist and

166 benefit ($B$) to recipients of altruism, respectively (Frank, 1998; Rice, 2004; McElreath

167 and Boyd, 2008). We will use the same convention, but add subscripts to indicate

168 costs and benefits to genetic *and* cultural fitnesses.

169
$$\begin{aligned}
\beta_{wp} &\Rightarrow -C_g \\
\beta_{cp} &\Rightarrow -C_c \\
\beta_{w\tilde{p}} &\Rightarrow B_g \\
\beta_{c\tilde{p}} &\Rightarrow B_c
\end{aligned}$$

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By labeling these terms, we'll be able to more clearly interpret our key results. We can derive the following condition (*see* A–2),

$$B_c(\beta_{tildecc} + \beta_{\tilde{g}c}) - C_c(1 + \beta_{gc}) > -\left[B_g(\beta_{tildegg} + \beta_{\tilde{c}g}) - C_g(1 + \beta_{cg})\right]\frac{var(g)}{var(c)}, \quad (9)$$

where we've ignored the transmission terms. Written this way, we can see that the left-hand side is the cultural selection coefficient, where selection must also account for correlations between an actor's culture-type and neighbor genotypes, as well as any correlation between her own culture-type and genotype. Similarly, the right-hand side features the genetic selection coefficient in brackets, where we have again correlations between culture-types and genotypes. Importantly, the inequality says that the cultural selection coefficient must exceed the genetic selection coefficient, again, as in (6), scaled by the ratio of the variance in genotypes to cultural types. Thus, even relatively weak cultural selection can overcome genetic selection if the variance in culture-types is sufficiently high compared to the variance in genotypes.

Below we will explore the consequences of (9) using a simple illustrative model.


# 3  An illustrative model

We imagine a population of haploid individuals interacting assortatively in each generation. These interactions determine the reproductive output of each individual and, potentially, their cultural influence on the next generation. Each individual possesses two loci with a single 'allele' at each locus. At the first locus, alleles are transmitted genetically, from a single parent to her offspring; at the other locus, a

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189 'cultural allele' is acquired from a single cultural parent. An individual's pheno-

190 type is determined by the combined additive effect of the alleles at the two loci in

191 the following way: when two individuals interact they play a prisoner's dilemma;

192 each individual employs a mixed strategy where the phenotype, $p$, is the proba-

193 bility of playing 'cooperate'. Those with both the genetic and cultural alleles for

194 altruism play a pure strategy of cooperate; those with only the genetic or cultural

195 allele, play cooperate half of the time; finally, an individual that lacks both the ge-

196 netic and cultural alleles will play a pure strategy of defect. Thus we have four

197 types of individuals in the population $\{0,0\}, \{0,1\}, \{1,0\}, \{1,1\}$, with phenotypes

198 $p_{00} = 1$, $p_{01} = p_{10} = 1/2$, $p_{11} = 1$.

199    An individual of type $\psi$ has an expected reproductive fitness of

$$w_\psi = w_0 + B_g \tilde{p}_\psi - C_g p_\psi \tag{10}$$

200 where $w_0$ is the baseline fitness, $\tilde{p}_\psi$ is the expected phenotype of a type $\psi$ individ-

201 ual's opponent in the game, and $p_\psi$ is the phenotype of a type $\psi$ individual.

202    Players in the model interact assortatively with respect to both genes and cul-

203 ture. The correlation between the genotypes of a player and her opponent is $f_g$,

204 while the correlation in culture-types is $f_c$. If individuals were interacting with

205 kin, $f_g$ would be the probability of being identical-by-descent, and $f_c$ would be the

206 analogous value computed for a cultural genealogy Aguilar and Ghirlanda (2015).

207 For our purposes, we can ignore the specific nature of the assortment mechanism

208 and just say that with some probability, $f_g$, an individual chooses a partner of iden-

209 tical genotype, and otherwise selects her partner at random (with an analogous

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210 situation for culture-type). Then the probability of having an opponent of a certain

211 type will be conditional on one's own type. For example, the probability that a type

212 $\{1, 1\}$ interacts with another $\{1, 1\}$ is,

$$P(1,1|1,1) = f_g f_c + f_c(1 - f_g)q_g + f_g(1 - f_c)q + (1 - f_c)(1 - f_g)q_g q_c \qquad (11)$$

213 where $q_g$ and $q_c$ are the population frequencies of the genetic and cultural altruistic

214 alleles. The first term is the probability that two $\{1, 1\}$ individuals are identical due

215 to assortment; the second is the probability of being identical due to assortment for

216 culture but not genes; the third is the probability of being identical due to assort-

217 ment for genes and not culture; and the final term is the probability of not being

218 identical due to assortment either genetically or culturally. These conditional prob-

219 abilities then determine the expected phenotype of an individual's opponent in the

220 game, $\tilde{p}_\psi$. Further details on the model are provided in SI–1.

221     Offspring inherit their parent's genetic allele. They must then choose a cultural

222 model whose allele they will inherit at the cultural locus. Below, we consider two

223 models for how cultural models are chosen.

## 3.1   Model 1: Neutral cultural trait

225 First, we assume that the cultural propensity of altruism is neutral for cultural fit-

226 ness. In other words, ancestors are chosen as cultural parents without regard to

227 their cultural traits, so the probability of acquiring the cultural propensity for al-

228 truism will just be $q_c$, the population frequency of the cultural allele in the parental

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229 generation. We can use (9) to determine the condition for the increase in the al-

230 truistic phenotype by multiplying both sides of the inequality by $var(c)$ and com-

231 puting the covariances directly from the model. We have no cultural selection, so

232 $B_c = C_c = 0$. Since culture is chosen at random, genetic and cultural type are

233 uncorrelated, so that $cov(c, g) = cov(\tilde{c}, g) = cov(\tilde{g}, g) = 0$. Thus, (9) reduces to

$$B_g f_g > C_g,$$

234 the canonical form of Hamilton's rule. This result follows directly from the cul-

235 tural allele being chosen at random. Under random copying the expected change

236 in the frequency of the cultural allele is zero and the only change in mean pheno-

237 type will be due to changes in the frequency of the genetic allele. Further, with

238 no correlations between the genetic and cultural allele, the only forces affecting the

239 evolution of the genetic allele will be the reproductive fitness effects. However, it

240 should be noted that due to the dual inheritance of altruism, the value of the phe-

241 notype may be maintained at significant levels in the population if the frequency of

242 the cultural allele is high. Take the extreme case where $q_c = 1$. Even if the inequal-

243 ity above is not met and the genetic allele is driven to extinction, the cultural allele

244 will be unaffected and the mean value of the phenotype in the population will be

245 $\bar{p} = q_c/2 = 1/2$. In other words, there will be no perfect altruists, but everyone will

246 be a 'half' altruist. As the mean reproductive fitness, $\bar{w}$ depends on the mean phe-

247 notype, this could have important implications for population growth, including
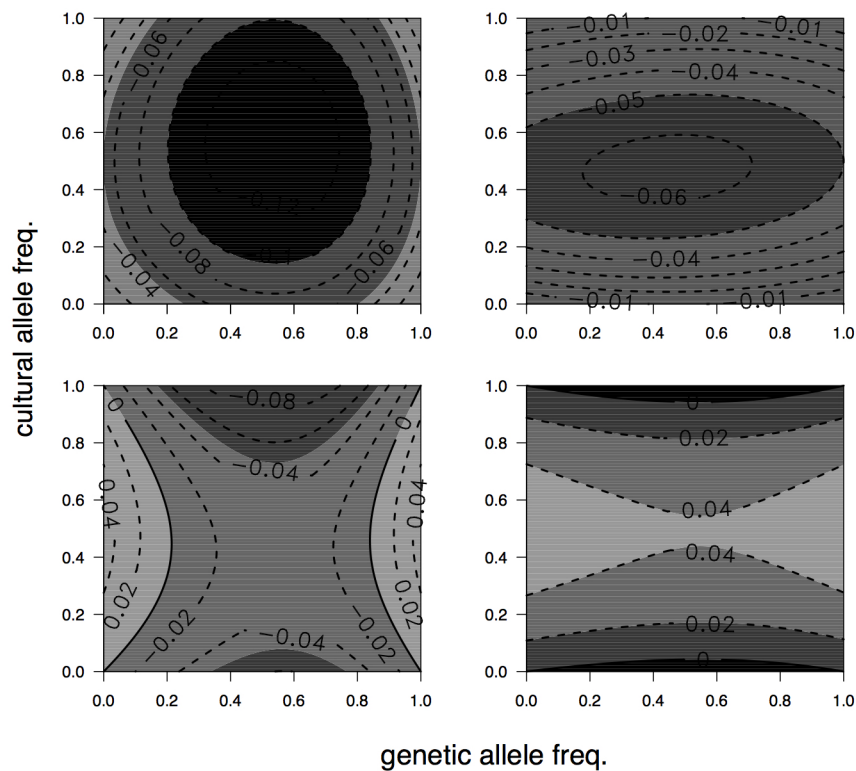
248 eventual extinction.

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Figure 1: Surfaces showing the selection differential on the altruistic phenotype for fixed values $B_c^z = 2$, $C_c^z = 1$, $B_g = 1$, $C_g = 1$, and varied values of assortment probabilities, $f_g, f_c$. Lighter shades indicate higher values. The zero contour is the solid line. (Top left) $f_c = 0.1$ and $f_g = 0.1$; (Top right) $f_c = 0.1$, $f_g = 0.9$; (Bottom left) $f_c = .9$, $f_g = 0.1$; (Bottom right) $f_c = 0.9$, $f_g = 0.9$. Higher cultural assortment values lead to positive selection differentials, especially for mid-range values of $q_c$.

## 3.2  Model 2: Cultural prisoner's dilemma

Next, we consider a case where offspring no longer choose their cultural parent at random. In particular, we assume that individuals meet to play the prisoner's dilemma, this time with respect to both reproduction and cultural propagation. For simplicity, we'll imagine individuals producing cultural 'gametes' or behavioral tokens that can then be acquired or observed by offspring. The number of cultural gametes, $z$, that an individual of type $\psi$ produces is,

$$z_\psi = z_0 + B_c^z \tilde{p}_\psi - C_c^z p_\psi \tag{12}$$

The terms $B_c^z$ and $C_c^z$ are the gametic fitness benefit and cost, with $B_c = B_c^z/\bar{z}$, $C_c = C_c^z/\bar{z}$ (see SI–2). Recall that in the previous section cultural fitness was defined in terms of the total influence ($s_i = \sum_{j=1}^{N'} \gamma_{ij}$) an ancestor has on the descendant population. In this model, offspring have a single cultural ancestor (i.e. $\gamma_{ij} = 1$), and $s_i$ is just the total number of descendant individuals who count $i$ as an ancestor. The number of offspring available as cultural descendants is determined by the reproductive output of the population, thus,

$$s_i = \frac{z_i}{\bar{z}} \bar{w} \, . \tag{13}$$

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263 Substituting (12) and (13) into the gene-culture Price equation and making simpli-

264 fications, we obtain:

$$B_c^z f_c - C_c^z > - \left[ B_g f_g - C_g \right] \frac{q_g(1 - q_g)}{q_c(1 - q_c)} \frac{\bar{z}}{\bar{w}} \,. \tag{14}$$

265 In this condition we see an explicit dependence on the frequency of the cultural

266 and genetic alleles. Using the definition of cultural fitness given in (13), we see that

267 $\bar{w}/\bar{z} = s_i/z_i$, the number of cultural descendants per gamete produced. We can

268 rename this term the cultural viability, $v_z$. When $v_z$ is high, the RHS is reduced and

269 a weaker cultural selection coefficient can still lead to an increase in the altruistic

270 phenotype. But what does this viability term actually mean? We can view it as the

271 average effort spent by one ancestor per cultural descendant. As that effort grows,

272 $v_z$ decreases, and the effect of genetic selection increases. Thus, as individuals must

273 expend more effort to gain influence over a cultural descendant, condition (14) will

274 be harder to meet.

275 The ratio of the variances in (14), means that if the genetic allele is at very high

276 or very low frequency ($q_g$ close to 0 or 1) and $q_c$ is in the mid-range, the direction

277 of evolution of the phenotype will be determined mostly by cultural selection. In

278 Figure 1, we plot the the values of the overall effect of selection on the altruistic phe-

279 notype (i.e. LHS-RHS in (14)) under different values of model parameters. We see

280 that when assortment is low in both domains (Figure 1, top-left), the altruistic phe-

281 notype is largely selected against. Conversely, when assortment in both domains is

282 high (Figure 1, bottom-right), altruism is selected for. The more interesting case is

283 when $f_c$ is high and $f_g$ is low (Figure 1, bottom-left); even though genetic selection

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here is against altruism, the increased variance in culture when $q_c$ is near $0.5$ can lead to a positive overall selection effect.

We defined altruism with respect to both cultural and genetic fitnesses. In model I cultural transmission was neutral with respect to the altruistic phenotype, while in model II there was also a cultural fitness cost to the phenotype. Another possibility is that a phenotype may be beneficial in the cultural domain while detrimental to reproduction. We can simply change the sign of the cost term on the LHS of (14) and see this has the effect of making the condition easier to meet. It is therefore important in addressing the evolution of a co-inherited trait that its relationship to fitness be specified with respect to both domains of inheritance.

# 4   Non-additive phenotypes

The results described above all assumed an additive phenotype function, which is a standard starting point in social evolution and population genetics theory (Van Cleve, 2015). However, biological reality may be much more complicated, particularly when trying to incorporate the effects of multiple inheritance systems. One way to deal with this problem in evolutionary theory has been to observe that most genetic variants have small effects on phenotypes and genetic variation in the population is small, in which case, an additive approximation gives satisfactory results (Taylor and Frank, 1996; Akçay and Van Cleve, 2012). In this section, we translate this approach to phenotypes that are jointly determined by genes and culture.

We begin by assuming that an individual descendant $j$'s phenotype is given

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305  by a function $p_j(c_j, g_j)$, where the arguments are the heritable cultural and ge-

306  netic information descendant possessed by the descendant. This information in

307  turn is a function of the heritable cultural and genetic information of the ances-

308  tors, which implies that we can instead write the phenotype mapping function as

309  $p_j(c_1, \ldots, c_N, g_1, \ldots, g_N)$, a direct function of the ancestral culture-types and geno-

310  types. Assuming that all $p_j$ are differentiable with respect to ancestral values, we

311  can make a first-order Taylor approximation of $p_j$ around the point $(\bar{\mathbf{c}}, \bar{\mathbf{g}}) = (\bar{c}, \cdots, \bar{c}, \bar{g}, \cdots, \bar{g})$.

312  We then substitute this expansion into $\Delta\bar{p} = \frac{1}{N}\sum_{i=1}^{N} p_j - \bar{p}$ to arrive at a Price equa-

313  tion for the non-additive case (*see* SI–2),

$$\Delta\bar{p} = \frac{N}{N'}cov(\mathcal{S}_i, c_i) + \frac{N}{N'}cov(W_i, g_i) + \langle p_j(\bar{\mathbf{c}}, \bar{\mathbf{g}})\rangle - \bar{p}\,, \tag{15}$$

314  where $\mathcal{S}_i = \sum_{j=1}^{N'} \left.\frac{\partial p_j}{\partial c_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})}$ and $W_i = \sum_{j=1}^{N'} \left.\frac{\partial p_j}{\partial g_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})}$, refer to *generalized fitnesses* in

315  the sense that we are measuring not only the number of descendant individuals

316  an ancestor has, but also the combined effect of that ancestor on her descendants'

317  phenotypes. For example, in a haploid genetic model in the absence of mutation,

318  where the 'phenotype' of interest is just the genotype, then $\frac{\partial p_j}{\partial g_i} = 1$ when $i$ is a

319  genetic ancestor of $j$, while $\frac{\partial p_j}{\partial g_k} = 0$ for all individuals $k$ that are not genetic ancestors

320  to $j$. In this case, the generalized fitness just reduces to the number of descendant

321  individuals who count $i$ as an ancestor. Similarly, in the model presented in the first

322  section, the partial derivative of the phenotype function $p_j$ with respect to $c_i$ will

323  yield $\gamma_{ij}$, and $\mathcal{S}_i = s_i$. The advantage of this formulation is that more complicated

324  phenotype mapping functions can be incorporated into the idea of a generalized

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325 fitness.

326     Equation (15) looks similar to equation (3); first, we have two covariance terms

327 that account for the effect of selection (now with respect to generalized fitness).

328 We've replaced the inverse of the mean fitness with a more direct measure of pop-

329 ulation growth, $(N/N')^{-1}$; this is because generalized fitness refers to the effect of

330 an ancestor on the phenotypes in the next generation, and is no longer synonymous

331 merely with her contribution to the growth of the population. The remaining term,

332 $\langle p_j(\overline{\mathbf{c}}, \overline{\mathbf{g}}) \rangle - \bar{p}$, denotes the effect of transmission. Specifically, we see that this is the

333 difference between (1) the average phenotype that would occur if every individual

334 inherited the mean values of $c$ and $g$, and (2) the mean phenotype among ancestors

335 $(\bar{p})$. This isolates the effect of the phenotype functions among descendants, $p_j$, on

336 evolutionary change.

337     From eq. 15 we can simply derive a condition for the evolution of a maladaptive

338 trait. When $\Delta \bar{p} > 0$, we have,

$$\beta_{\mathcal{S}_i, c_i} > -\left[ \beta_{W_i, g_i} \frac{var(g)}{var(c)} - \frac{(\langle p_j(\overline{\mathbf{c}}, \overline{\mathbf{g}}) \rangle - \bar{p})}{var(c)} \right] \tag{16}$$

339 This result is exactly analogous to (4) in the first section and can be summarized

340 similarly: a loss in generalized reproductive fitness can be compensated for by a

341 gain in generalized cultural fitness. Again, we have assumed that the rules of trans-

342 mission remain constant over the timescale being considered in the Price equation.

343     This approach could of course be extended to higher order expansions of the

344 phenotype function: in SI–2 we show that the infinite expansion of the pheno-

345 type function leads to a more precise definition of generalized fitness than appears

19

346 in this example. Most importantly, without making assumptions about either the

347 phenotype mapping function or the fitness function, we have shown an important

348 relationship between these two fundamental concepts in evolutionary theory.

# 5   Discussion

350 In animals capable of social learning, phenotypes may result from both genetic and

351 cultural inheritance. We derived a Price equation for the evolution of a trait that is

352 transmitted via both modes of inheritance. Under our model of additive effects

353 of genes and culture, the forces of selection and transmission in each domain are

354 explicitly represented. We showed that even weak selection in the cultural domain

355 can overcome selection in the genetic domain so long as the variance in culture is

356 sufficiently high relative to variance in genes (ignoring the effects of transmission).

357     The additive model we used in this paper is both the simplest model and a nat-

358 ural extension of the standard assumption in quantitative genetics (Falconer and

359 Mackay, 1996). However, even under this simple model we observed some non-

360 trivial results. In our formulation we made an important assumption that the mean

361 cultural fitness was equal to the mean reproductive fitness (i.e. $\bar{s} = \bar{w}$). We jus-

362 tify this assumption for many behavioral traits, such as personality traits, simply

363 because every individual must possess them. However, for other traits, some indi-

364 viduals may never receive cultural input. For example, though underlying genetic

365 variation may determine one's reading ability, one may never be taught to read. In

366 these cases, the equality of $\bar{s}$ and $\bar{w}$ will not necessarily hold. As we saw in our

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367 second illustrative model, when the mean number of replications for culture and

368 reproduction are not the same—in this case $\bar{z}$ and $\bar{w}$—the conversion factor $\bar{z}/\bar{w}$

369 scaled the effect of genetic selection. In the event that cultural replication might

370 affect fewer individuals than are actually born, $\bar{z}/\bar{w} < 1$, and the effect genetic se-

371 lection is further reduced.

372    We also assumed here that the rules of cultural transmission are stable on the

373 timescale of evolutionary change. This is also the case for genetic transmission, and

374 is standard in all Price equation formulations. However, it is not unreasonable to

375 assume that cultural transmission itself may be subject to evolution, and there is

376 an extensive literature on the evolution of cultural transmission (Rogers et al., 2009;

377 Boyd and Richerson, 1988; Henrich, 2004a; Lehmann and Feldman, 2008). We have

378 taken the existence of cultural transmission as a given, which allowed us to focus on

379 the effect of combined inheritance on a single trait. Given the evidence for the evo-

380 lutionary history of cultural transmission in the human lineage (Lind et al., 2013), it

381 is reasonable to assume that a number of traits evolved under the combined influ-

382 ence of genetic and cultural transmission. Therefore, it will be important to address

383 in future work the simultaneous evolution of the cultural transmission rule, which

384 in this paper is characterized by $\langle \beta^j_{\gamma c} \rangle$, the descendant mean of the correlation be-

385 tween $\gamma_{ij}$ and $c_i$.

386    In the course of deriving our results on the effects of selection, we often ignored

387 the transmission terms, $\langle \Delta c \rangle$ and $\langle \Delta g \rangle$. In relatively simple genetic systems, it may

388 be safe to assume that the expected difference between parents and offspring is

389 zero. However, culture very often can make this assumption untenable, as the cul-

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tural 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. (2015) offered an interpretation of the transmission term as evolved biases in favor of reproductive fitness maximizing behaviors. Meanwhile, Henrich (2004) 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 co-evolution.

Our results show the importance of the ratio of genetic to cultural variance in scaling the effect of genetic selection. It is interesting to consider empirical estimates of cultural and genetic diversity to gauge the expected relative strength of genetic selection. Bell et al. compared $F_{st}$ values for culture and genes in populations using the World Values Survey (Bell et al., 2009). Their results suggested greater-between population variation in culture than in genes. Unfortunately, these results say little about the within-group variance in culture relative to genes. Other studies have shown parallels in the patterns of linguistic and genetic diversity (Perreault and Mathew, 2012; Longobardi et al., 2015), but again provided no information about the ratio of genetic to cultural variance. However, this question is well-suited to empirical study; given our results, empirical estimates of the ratio can shed light

22

413 on qualitative expectations about the evolution of behavioral traits.

414     The ratio of genetic to cultural variance also has an important relationship to the

415 narrow-sense heritability ($h^2$), which measures the proportion of phenotypic vari-

416 ance attributable to the 'heritable' component of phenotype (Falconer and Mackay,

417 1996). In a series of papers, Danchin and co-authors (Danchin and Wagner, 2010;

418 Danchin et al., 2011, 2013) introduced the idea of 'inclusive heritability', which par-

419 titions the variance in the heritable component of phenotype into the contributions

420 from each system of inheritance. This allows for narrow-sense heritability to be ex-

421 pressed as the sum of the heritabilities in each domain (assuming no interactions

422 between the inheritance systems). In our model, this means $h^2 = h_g^2 + h_c^2$ (where

423 $h_g^2$ and $h_c^2$ are the genetic and cultural heritabilities). The ratio of these heritabili-

424 ties is exactly the term that appears in our results as the scaling factor of genetic

425 selection, demonstrating the importance of inclusive heritability when considering

426 evolutionary outcomes.

427     Other authors have presented extensions of the Price equation to multiple sys-

428 tems of inheritance (Day and Bonduriansky, 2011; Helanterä and Uller, 2010). In

429 particular, Day & Bondurianski wrote coupled Price equations to describe the co-

430 evolution of two traits where one was transmitted genetically and the other by a

431 nongenetic mode of inheritance (e.g. culture). However, in their model, selection

432 in both domains acted on biological reproduction. Cultural transmission allows

433 for the propagation of hereditary information to individuals who are not biologi-

434 cal offspring, and the extent of success in cultural transmission need not coincide

435 with reproductive success. Our model allows for cultural and genetic fitness to di-

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436 verge. El Mouden et al. also compared evolution under cultural transmission to

437 that under genetic transmission using a Price equation (El Mouden et al., 2014).

438 However, this approach confounds the effects of culture and genes, since genes

439 cause transmission effects with respect to culture and vice versa. By contrast, our

440 model allows all the evolutionary effects of the two systems of inheritance to be

441 expressed simultaneously.

442 In our section on non-additivity, we took an unusual approach to deriving the

443 Price equation. Most models of social evolution make an explicit assumption about

444 the fitness function (e.g. linearity, as in our derivation of the gene-culture Hamil-

445 ton's rule) and an implicit assumption about the phenotype function (e.g. $p = g$, as

446 in the phenotypic gambit). By contrast, we made no assumptions about the form

447 of the phenotype function, with the exception of differentiability, and were able

448 to derive a definition of fitness that similarly relied on no previous assumptions

449 about the fitness function. This approach demonstrates the relationship between

450 how phenotypes are actually constructed from inherited information and fitness it-

451 self. Also, our notion of generalized fitness incorporates both the idea of the fitness

452 of a specific lineage and the fitness of a particular type. The relationship between

453 generalized fitness and other important fitness concepts, such as inclusive fitness,

454 are worth exploring, but beyond the scope of the present paper.

455 Richerson & Boyd (1978) also assumed that phenotype was a generic function

456 of genotype and culture-type, though they included a 'penetrance' parameter that

457 determined the relative importance of the two kinds of inheritance (Richerson and

458 Boyd, 1978). They analyzed equilibrium phenotype when cultural and genetic fit-

24

ness were maximized at different phenotypic values. They found that under certain conditions, the equilibrium phenotype could be the cultural-fitness maximizing phenotype, even when the 'penetrance' parameter was under genetic control. These intriguing results are in qualitative agreement with ours, though they deserve further investigation.

Our model was inspired by the idea that behavioral traits can be influenced by both genetic and cultural evolution. Research into the evolutionary basis of human behavior has long puzzled over the existence of maladaptive behaviors (Glanville, 1987; Logan and Qirko, 1996). These are behaviors that persist via cultural transmission despite detrimental reproductive fitness effects, such as clubbing pregnant women to induce birth in Colombia (Reichel-Dolmatoff and Reichel-Dolmatoff, 2013), unhygenic neonatal care practices in Bangladesh (McConville, 1988), and folk medical practices like ingesting rhino horn (Ayling, 2013) or bloodletting (Wootton, 2007). While these practices are likely spread almost exclusively by cultural transmission, other maladaptive behaviors, such as the cross-cultural variation in risk-taking (Weber and Hsee, 1998; Hsee and Weber, 1999), may have a significant genetic component. The demographic transition provides another potential example of a dually inherited trait. In fact, Kolk et al. (Kolk et al., 2014) presented a model in which reproductive behavior resulted from a genetic predisposition and exposure to cultural models. Our model demonstrates more broadly the possibility that maladaptive behvioral traits may evolve under dual transmission, despite their reproductive fitness costs.

25

## 5.1 Conclusions

The Price equation offers a general statement of how evolutionary change can be partitioned among different evolutionary factors (Frank, 2012). Its generality arises from its relative lack of assumptions. However, in applying the Price equation to any system, it is important to be clear about the assumptions being made based on knowledge of that system. We have applied the Price equation to the evolution of a behavioral trait that is jointly determined by culture and genes. We've made our assumptions clear: an additive phenotype function and the stability of transmission rules over the evolutionary timescale. Using only these assumptions we show the conditions under which a maladaptive trait may evolve, and when altruism will be favored. While the validity of our assumptions may rightfully be challenged, the results follow clearly. Any departure from these results must be based on a difference in the underlying assumptions, an important point that can be obscured when directly comparing specific mechanistic models. We also move beyond the additive phenotype function assumption, and point toward a general framework for dealing with phenotypes that receive different heritable inputs. As the importance of nongenetic inheritance systems becomes clearer, we believe this framework will contribute to a better theoretical understanding of evolution.

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# Appendices

## A–1 Derivation of Gene Culture Price equation.

The phenotype of individual $j$ is given by,

$$p_j = \sum_{i=1}^{N} \nu_{ij} g_i + \Delta g_j + \sum_{i=1}^{N} \gamma_{ij} c_i + \Delta c_j + e \tag{A–1}$$

where the coefficients $\nu_{ij}$ and $\gamma_{ij}$ represent the influence an ancestor $i$ has on descendant $j$ in the genetic and cultural domains, respectively (Note: $\sum_{i=1}^{N} \nu_{ij} = \sum_{i=1}^{N} \gamma_{ij} = 1$). The mean value of $p$ in the descendant generation is,

$$\bar{p'} = \frac{1}{N'} \sum_{j=1}^{N'} \sum_{i=1}^{N} \nu_{ij} g_i + \frac{1}{N'} \sum_{j=1}^{N'} \Delta g_j + \frac{1}{N'} \sum_{j=1}^{N'} \sum_{i=1}^{N} \gamma_{ij} c_i + \frac{1}{N'} \sum_{j=1}^{N'} \Delta c_j \tag{A–2}$$

where $e$ is assumed to have mean zero. Reversing the orders of the double sum terms and noting that $w_i = \sum_{j=1}^{N'} \nu_{ij}$, and $s_i = \sum_{j=1}^{N'} \gamma_{ij}$, we can rewrite eq. A–2 as,

$$\bar{p'} = \frac{1}{N'} \sum_{i=1}^{N} g_i w_i + \frac{1}{N'} \sum_{i=1}^{N} c_i s_i + \frac{1}{N'} \sum_{j=1}^{N'} \Delta g_j + \frac{1}{N'} \sum_{j=1}^{N'} \Delta c_j \tag{A–3}$$

Using the definition of covariance ($cov(x, y) = E[xy] - E[x]E[y]$) we can replace the first two terms on the RHS,

$$\bar{p'} = \frac{N}{N'} \mathrm{cov}(w, g) + \frac{N}{N'} \mathrm{cov}(s, c) + \langle \Delta g \rangle + \langle \Delta c \rangle + \frac{N}{N'} (\bar{w}\bar{g} + \bar{s}\bar{c}) \tag{A–4}$$

33

623 The angle brackets here mean averages over the descendant population. Noting

624 $N\bar{w} = N\bar{s} = N'$ we can rewrite the final term on the RHS as $\bar{g} + \bar{c}$.[1] Subtracting the

625 mean phenotype in the ancestral population, $\bar{p} = \bar{g} + \bar{c}$, we have (3).

626     The cultural covariance term in (3) takes the 'ancestral' point of view, in that it in-

627 cludes ancestral cultural values and their fitnesses. However, we can be re-express

628 this term from the descendant point of view with the following quick restatement,

$$\text{cov}(s, c) = \overline{cs} - \bar{c}\bar{s}$$

$$= \tfrac{1}{N} \sum_{i=1}^{N} \sum_{j=1}^{N'} c_i \gamma_{ij} - \bar{c}\bar{s} = \sum_{j=1}^{N'} \langle c_i \gamma_{ij} \rangle - \bar{c}\bar{s}$$

$$= \sum_{j=1}^{N'} \text{cov}(c_i, \gamma_{ij}) + \sum_{j=1}^{N'} \bar{c}\bar{\gamma}_j - \bar{c}\bar{s}$$

$$= \sum_{j=1}^{N'} \text{cov}(\gamma_{ij}, c_i) + \bar{c}\tfrac{N'}{N} - \bar{c}\bar{s}$$

$$= N' \langle \text{cov}(\gamma_{ij}, c_i) \rangle \tag{A–5}$$

629 Where the final mean is taken over the descendant population.

## A–2    Derivation of Gene-culture Hamilton's rule

631 We begin with the following cultural and genetic fitness functions:

$$s_i = s_0 + \beta_{sp}p_i + \beta_{s\tilde{p}}\tilde{p} = s_0 + \beta_{sp}c_i + \beta_{sp}g_i + \beta_{s\tilde{p}}\tilde{c}_i + \beta_{s\tilde{p}}\tilde{g}_i \tag{A–6}$$

$$w_i = w_0 + \beta_{wp}p_i + \beta_{w\tilde{p}}\tilde{p} = w_0 + \beta_{wp}c_i + \beta_{wp}g_i + \beta_{w\tilde{p}}\tilde{c}_i + \beta_{w\tilde{p}}\tilde{g}_i \tag{A–7}$$

---

[1]In this derivation we assume that for every descendant $j$ there exists some ancestor $i$ for whom $\gamma_{ij} > 0$.

632  The tilde over a variable indicates the mean value of that variable across $i$'s neigh-

633  bors. We have assumed both kinds of fitness are linear functions of an individuals

634  own phenotype and the phenotypes of her neighbors. As in the standard derivation

635  of Hamilton's rule using the Price equation, it is customary to identify $\beta_{wp}$ and $\beta_{w\tilde{p}}$

636  as the cost ($C$) to an altruist and benefit ($B$) to recipients of altruism, respectively.

637  We will use the same convention, but add subscripts to indicate costs and benefits

638  to genetic *and* cultural fitnesses"

639
$$\begin{aligned}
\beta_{wp} &\Rightarrow C_g \\
\beta_{sp} &\Rightarrow C_c \\
\beta_{w\tilde{p}} &\Rightarrow B_g \\
\beta_{s\tilde{p}} &\Rightarrow B_c
\end{aligned}$$

Substituting A–7 into our Price equation in 3, though ignoring the transmission terms, we have,

$$\bar{w}\Delta\bar{p} = B_c \left[cov(\tilde{c}, c) + cov(\tilde{g}, c)\right] + C_c \left[var(c) + cov(g, c)\right]$$
$$+ B_g \left[cov(\tilde{c}, g) + cov(\tilde{g}, g)\right] + C_g \left[cov(c, g) + var(g)\right] \quad \text{(A–8)}$$

640  The equation above allows us to derive a condition for the evolution of the altru-

641  istic trait $p$ in the population. Using $cov(x, y) = \beta_{xy}var(y)$, where $\beta_{xy}$ is the linear

642  regression coefficient of $x$ on $y$, and dividing through by $var(c)$, we can rearrange

643  the above expression to find,

$$B_c(\beta_{\tilde{c}c} + \beta_{\tilde{g}c}) > -C_c(1 + \beta_{gc}) - \{C_g(1 + \beta_{cg}) + B_g(\beta_{\tilde{c}g} + \beta_{\tilde{g}g})\} \frac{var(g)}{var(c)}. \quad \text{(A–9)}$$

35

# Supplementary Information

## SI–1   Model I

We imagine a population of haploid individuals who, once born, select a cultural parent to copy. Each individual has two loci with a single allele present at each. The allele at the first locus is genetically transmitted while the allele at the second is received from a cultural parent. Individuals interact assortatively, with some probability of being genetically identical due to assortment, ($f_g$), and culturally identical due to assortment, ($f_c$). At discrete time steps individuals meet a random kin member and play a prisoner's dilemma according to a mixed strategy. The phenotype, $p$, is the probability of playing cooperate. The two loci mean four types of individuals $\{0,0\}, \{0,1\}, \{1,0\}, \{1,1\}$, with phenotypes, $p_{00} = 0, p_{01} = 1/2, p_{10} = 1/2, p_{11} = 1$.

The expected reproductive fitnesses for each type are

$$w_{00} = w_0 + B_g(P(11|00) + P(01|00)/2 + P(10|00)/2)$$

$$w_{01} = w_0 + B_g(P(11|01) + P(01|01)/2 + P(10|01)/2) - C_g/2$$

$$w_{10} = w_0 + B_g(P(11|10) + P(01|10)/2 + P(10|10)/2) - C_g/2$$

$$w_{11} = w_0 + B_g(P(11|11) + P(01|11)/2 + P(10|11)/2) - C_g \,.$$

The conditional probabilities are probability of encountering a certain type given one's own type. For example, $P(10|00)$ should be read as the "probability of encountering a $\{1,0\}$ given that the player is a $\{0,0\}$." Rather than enumerate all of these

1

658 conditional probabilities we take advantage of the following identity:

$$P(g_o, c_o | g_p, c_p) = P(g_o | g_p) P(c_o | c_p) , \tag{SI–1}$$

where the $o$ subscript indicates the opponent and $p$ the player. We need only specify the following conditional probabilities,

$$P(g_o = 1 | g_p = 1) = (1 - f_g)q_g + f_g \tag{SI–2}$$

$$P(g_o = 1 | g_p = 0) = (1 - f_g)q_g \tag{SI–3}$$

$$P(c_o = 1 | c_p = 1) = (1 - f_c)q_c + f_c \tag{SI–4}$$

$$P(c_o = 1 | c_p = 0) = (1 - f_c)q_c . \tag{SI–5}$$

659 Note that the remaining marginal conditional probabilities are given by

$$P(g_o = 0 | g_p = 0) = 1 - P(g_o = 1 | g_p = 0) \tag{SI–6}$$

$$P(g_o = 0 | g_p = 1) = 1 - P(g_o = 1 | g_p = 1) \tag{SI–7}$$

$$P(c_o = 0 | c_p = 0) = 1 - P(c_o = 1 | c_p = 0) \tag{SI–8}$$

$$P(c_o = 0 | c_p = 1) = 1 - P(c_o = 1 | c_p = 1) . \tag{SI–9}$$

660 Using (SI–1) we can calculate all the conditional probabilities of encounters be-
661 tween types.

662     To find the condition for the evolution of the altruistic phenotype, we need only
663 substitute all the relevant terms in (9). As $B_c = C_c = 0$, we can remove those terms.

2

664 We then only have to calculate the following,

$$\beta_{cg} var(g) = 0 \tag{SI–10}$$

$$var(g) = \tfrac{1}{4} q_c (1 - q_c) \tag{SI–11}$$

$$\beta_{\tilde{g}g} var(g) = \tfrac{1}{4} f_g q_g (1 - q_g) \tag{SI–12}$$

$$\beta_{\tilde{c}g} var(g) = 0 \tag{SI–13}$$

665 Substituting these terms into (9) we arrive at 12.

## SI–2   Model II

666

In this model, individuals encounter one another and play a prisoner's dilemma. This time, the game determines both the reproductive fitness and cultural fitness of the players. We imagine individuals producing 'cultural gametes', or behavioral tokens. The probability of acquiring a given cultural allele will be determined by the proportion that allele constitutes of all the available cultural gametes. The expected number of cultural gametes produced by individuals of each type are:

$$z_{00} = z_0 + B_c^z(P(11|00) + P(01|00)/2 + P(10|00)/2)$$

$$z_{01} = z_0 + B_c^z(P(11|01) + P(01|01)/2 + P(10|01)/2) - C_c^z/2$$

$$z_{10} = z_0 + B_c^z(P(11|10) + P(01|10)/2 + P(10|10)/2) - C_c^z/2$$

$$z_{11} = z_0 + B_c^z(P(11|11) + P(01|11)/2 + P(10|11)/2) - C_c^z \,.$$

3

667     It is important to note that the terms $B_c^z$ and $C_c^z$ are the gametic fitness benefit

668   and cost, as opposed to $B_c$ and $C_c$ that appear in (9). The cultural fitness of an

669   individual $i$ is $s_i = z_i \frac{\bar{w}}{\bar{z}}$, which we can substitute into the cultural covariance term

670   from (2),

$$\frac{1}{\bar{w}} cov(s_i, c_i) = \frac{B_c^z}{\bar{z}} cov(z_i, c_i) \tag{SI–14}$$

671   We can then rewrite (9) as,

$$B_c^z(\beta_{\tilde{c}c} + \beta_{\tilde{g}c}) - C_c^z(1 + \beta_{cg}) > -\left[B_g(\beta_{\tilde{c}g} + \beta_{\tilde{g}g}) - C_g(1 + \beta_{cg})\right]\frac{var(g)}{var(c)}\frac{\bar{z}}{\bar{w}} \tag{SI–15}$$

672   Again, we compute the relevant terms:

$$\beta_{\tilde{c}c} = f_c \tag{SI–16}$$

$$\beta_{\tilde{g}c} = 0 \tag{SI–17}$$

$$\beta_{\tilde{c}g} = 0 \tag{SI–18}$$

$$\beta_{\tilde{g}g} = f_g \tag{SI–19}$$

$$\beta_{cg} = 0 \tag{SI–20}$$

$$var(c) = \tfrac{1}{4} q_c(1 - q_c) \tag{SI–21}$$

$$var(g) = \tfrac{1}{4} q_g(1 - q_g) \,. \tag{SI–22}$$

673   Substituting these terms into (9) gives us (14).

# Non-additive phenotypes

We assume that all descendant individuals have a (potentially) unique function for mapping from heritable inputs to phenotype, $p_j(f_j(c_1, \cdots, c_N), h_j(g_1, \cdot, g_N))$. Assuming that the change in phenotype is small over small fluctuations in heritable inputs (e.g. because we are considering small evolutionary time scales), we can take a first order Taylor approximation of a phenotype function around the point $(\bar{c}, \cdots, \bar{c}, \bar{g}, \cdots, \bar{g}) = (\bar{\mathbf{c}}, \bar{\mathbf{g}})$,

$$
p_j \approx p_j(\bar{\mathbf{c}}, \bar{\mathbf{g}}) + \sum_{i=1}^{N} \left.\frac{\partial p_j}{\partial c_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})} (c_i - \bar{c}) + \sum_{i=1}^{N} \left.\frac{\partial p_j}{\partial g_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})} (g_i - \bar{c}).
$$

To obtain the Price equation, we can substitute the above expression into $\Delta \bar{p} = \bar{p}' - \bar{p}$,

$$
\begin{aligned}
\Delta \bar{p} \approx \quad & \frac{1}{N'} \sum_{j=1}^{N'} p_j(\bar{\mathbf{c}}, \bar{\mathbf{g}}) + \frac{1}{N'} \sum_{j=1}^{N'} \sum_{i=1}^{N} c_i \left.\frac{\partial p_j}{\partial c_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})} + \frac{1}{N'} \sum_{j=1}^{N'} \sum_{i=1}^{N} g_i \left.\frac{\partial p_j}{\partial g_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})} \quad \text{(SI–23)} \\
& -\frac{\bar{c}}{N'} \sum_{j=1}^{N'} \sum_{i=1}^{N} \left.\frac{\partial p_j}{\partial c_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})} - \frac{\bar{g}}{N'} \sum_{j=1}^{N'} \sum_{i=1}^{N} \left.\frac{\partial p_j}{\partial g_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})} - \bar{p} \quad \text{(SI–24)}
\end{aligned}
$$

Switching the order of all the summations, and defining the quantities, $\mathcal{S}_i = \sum_{j=1}^{N'} \left.\frac{\partial p_j}{\partial c_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})}$, and $W_i = \sum_{j=1}^{N'} \left.\frac{\partial p_j}{\partial g_i}\right|_{(\bar{\mathbf{c}},\bar{\mathbf{g}})}$, we can write,

$$
\begin{aligned}
\Delta \bar{p} \quad &= \frac{N}{N'} \left[ cov(\mathcal{S}_i, c_i) + cov(W_i, g_i) + \bar{c}\bar{\mathcal{S}} + \bar{g}\bar{W} \right] - \frac{N}{N'} \bar{c}\bar{\mathcal{S}}_i - \frac{N}{N'} \bar{g}\bar{W} \quad \text{(SI–25)} \\
& \quad + \frac{1}{N'} \sum_{j=1}^{N'} p_j(\bar{\mathbf{c}}, \bar{\mathbf{g}}) - \bar{p} \quad \text{(SI–26)}
\end{aligned}
$$

Cancelling terms we arrive at Eq. (SI–23).

5

If we continue our expansion of the phenotype function, we arrive at the following result,

$$\Delta \bar{p} = \frac{N}{N'} cov(\mathcal{S}_i, c_i) + \frac{N}{N'} cov(\mathcal{W}_i, g_i) + \frac{N}{N'} cov(\mathcal{I}_i, g_i) + \overline{p_j(\bar{\mathbf{c}}, \bar{\mathbf{g}})} - \bar{p} \qquad \text{(SI–27)}$$

where,

$$\mathcal{S}_i = \sum_{j=1}^{N'} \left( \frac{\partial p_j}{\partial c_i} + \frac{1}{2} \sum_{k=1}^{N} \frac{\partial^2 p_j}{\partial c_i \partial c_k} (c_k - \bar{c}) + \frac{1}{3!} \sum_{k=1}^{N} \sum_{l=1}^{N} \frac{\partial^3 p_j}{\partial c_i \partial c_k \partial c_l} (c_k - \bar{c})(c_l - \bar{c}) + \cdots \right)$$

$$\mathcal{W}_i = \sum_{j=1}^{N'} \left( \frac{\partial p_j}{\partial g_i} + \frac{1}{2} \sum_{k=1}^{N} \frac{\partial^2 p_j}{\partial g_i \partial g_k} (g_k - \bar{g}) + \frac{1}{3!} \sum_{k=1}^{N} \sum_{l=1}^{N} \frac{\partial^3 p_j}{\partial g_i \partial g_k \partial g_l} (g_k - \bar{g})(g_l - \bar{g}) + \cdots \right)$$

$$\mathcal{I}_i = \sum_{j=1}^{N'} \Big( \frac{1}{2} \sum_{k=1}^{N} \frac{\partial^2 p_j}{\partial g_i \partial c_k} (c_k - \bar{c}) + \frac{1}{3!} \sum_{k=1}^{N} \sum_{l=1}^{N} \frac{\partial^3 p_j}{\partial g_i \partial c_k \partial c_l} (c_k - \bar{c})(c_l - \bar{c})$$

$$+ \frac{1}{3!} \sum_{k=1}^{N} \sum_{l=1}^{N} \frac{\partial^3 p_j}{\partial g_i \partial c_k \partial g_l} (c_k - \bar{c})(g_l - \bar{g}) + \dots \Big).$$

The dots represent higher order terms in the expansion. The $\mathcal{S}_i$ and $\mathcal{W}_i$ terms are exclusive to the cultural and genetic domains, while the $\mathcal{I}_i$ term captures interactions between the two forms of inheritance. The additional covariance term captures the effect of interactions between genes and culture. In expanding these phenotype functions in a Taylor series, we've been able to directly relate the concepts of fitness to phenotype while making only minimal assumptions about either.

6