

Gene-culture co-inheritance of a behavioral trait

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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

12 out that optimum value of a phenotype that maximizes genetic fitness may differ
13 from the value that maximizes cultural fitness, leading to conflicts between the two
14 inheritance systems. In the ensuing decades, evolutionary theorists have studied
15 numerous cases of the co-evolution of genetic and cultural traits (Boyd and Richer-
16 son, 1988; Cavalli-Sforza and Feldman, 1981), such as genetically encoded learn-
17 ing rules and culturally acquired helping behaviors (Boyd et al., 2003; Guzmán
18 et al., 2007; Lehmann et al., 2008). By contrast, the problem of conflict between
19 inheritance systems that affect the same trait has received far less attention. This
20 is curious, given the likelihood that many human behaviors are both genetically
21 and culturally determined. For instance, fertility itself may result from genetic pre-
22 dispositions towards fitness maximization and culturally acquired preferences for
23 family size (Kolk et al., 2014). In this paper, we take up the question of how conflict
24 between selection in different domains of inheritance affects the evolution of a trait.

25 In order to address the question of conflicting selection in the cultural and ge-
26 netic domains, we derive a Price equation that explicitly incorporates both forms
27 of inheritance. The Price equation is an exact description of an evolutionary pro-
28 cess under a certain set of minimal assumptions (Price et al., 1970; Frank, 1998;
29 Rice, 2004). As early as (Hamilton, 1975) it was pointed out that the Price equa-
30 tion can apply equally well to cultural transmission, and recent authors have de-
31 veloped it for that purpose (Henrich, 2004a; El Mouden et al., 2014). Others have
32 also extended the Price equation to include multiple forms of inheritance (Day and
33 Bonduriansky, 2011; Helanterä and Uller, 2010), though they considered separate
34 traits being transmitted in each domain. Here, we use a simple additive model to

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.

44 **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, conscientiousness, 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

$$p_j = c_j + g_j + e . \quad (1)$$

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

55 the culture-type and genotype, respectively. These terms only describe the state
56 of the continuous variables, and are not meant to imply any particular mode of
57 inheritance (e.g. haploidy, diploidy, etc.). Equation (1) is similar to the quantitative
58 genetic formulation in Otto et al. (Otto et al., 1995). The culture- and geno-types
59 are determined by the corresponding values in j 's genetic and cultural ancestors.
60 We assume that a descendant's culture-type and genotype are linear functions of
61 her ancestors' values given by

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

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

62 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
63 describe the degree of influence an ancestor i has on descendant j in the genetic or
64 cultural domain. For generality, we have taken the sums over all N individuals in
65 the ancestral population. When i is not a genetic ancestor to j , then $\nu_{ij} = 0$; when i is
66 not a cultural ancestor, $\gamma_{ij} = 0$. The delta terms, Δg_j and Δc_j , represent departures
67 in j from the inherited genetic and cultural values. As an example, Δg_j may be
68 nonzero in the event of mutation or recombination, while Δc_j may be nonzero due
69 to individual learning or experience. This model generalizes that presented by El
70 Mouden et al. (El Mouden et al., 2014), though our analysis and conclusions differ.

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

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 ν_{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),

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

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 ($\frac{1}{\bar{w}}\text{cov}(w, g)$) and differential influence
99 in cultural transmission ($\frac{1}{\bar{w}}\text{cov}(s, c)$). 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, $\text{cov}(w, p) < 0$. Then we have the following condition,

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

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

117 fitness—so long as the covariance between cultural value and influence on descen-
118 dants exceeds the absolute value of the covariance between genotype and repro-
119 ductive fitness. In essence, a loss in reproductive fitness can be compensated for by
120 increased importance as a learning model. However, this condition will be harder
121 to meet if social learning biases individuals toward lower cultural values than their
122 learning models, for example, as a result of biased learning error (Henrich, 2004b).

123 Intuitively, whether individuals give higher or lower weights to ancestors with
124 higher cultural values determines the direction of evolution of p . This can be seen
125 by observing that the cultural covariance term can be rewritten as

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

126 where the brackets indicate the mean over the descendant population and N' is the
127 descendant population size. The term inside the brackets applies to an *individual*
128 *descendant*; it is the correlation between the weight that particular descendant as-
129 cribes to ancestors and those ancestors' cultural values (computed for all potential
130 ancestors). When this term is positive, it means that, on average, greater weight is
131 given to ancestors with higher values of c . We can now rewrite eq. (4) as a new
132 inequality that shows explicitly how strong the bias in favor of higher c must be in
133 order for there to be positive evolutionary change,

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

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

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 $\beta_{\gamma c}^j$ 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.

149 **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

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:

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

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

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_0 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 β_{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.

$$\beta_{wp} \Rightarrow -C_g$$

$$\beta_{cp} \Rightarrow -C_c$$

$$\beta_{w\tilde{p}} \Rightarrow B_g$$

$$\beta_{c\tilde{p}} \Rightarrow B_c$$

169

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

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

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

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

183 **3 An illustrative model**

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

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 ψ has an expected reproductive fitness of

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

200 where w_0 is the baseline fitness, \tilde{p}_ψ is the expected phenotype of a type ψ individ-
201 ual’s opponent in the game, and p_ψ is the phenotype of a type ψ 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

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,

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

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}_ψ . 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.

224 **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

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

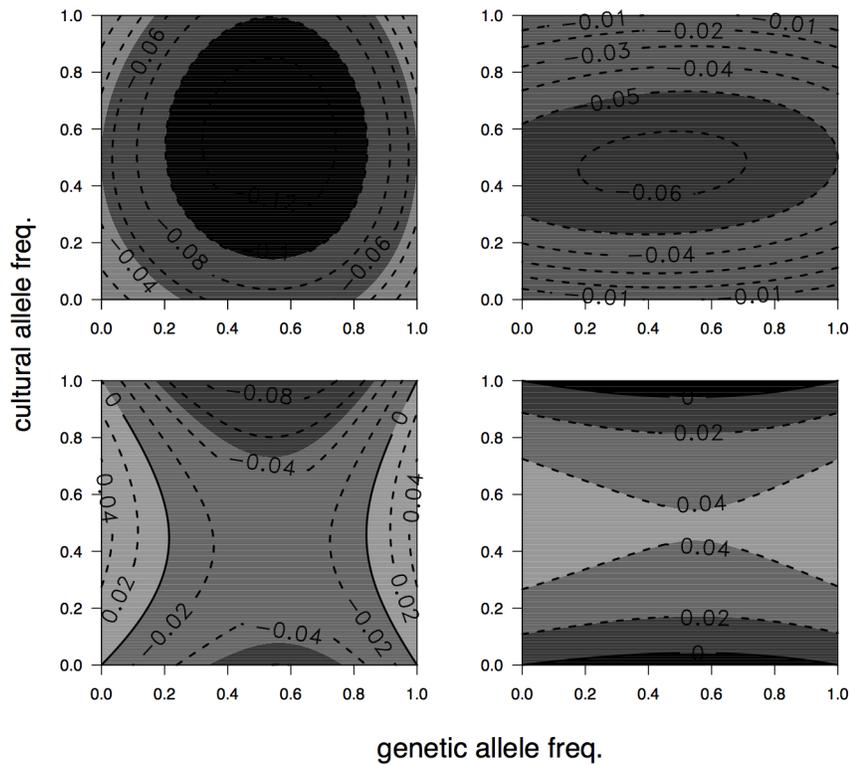


Figure 1: Surfaces showing the selection differential on the altruistic phenotype for fixed values $B_c^z = 2$, $C_c^z = 1$, $B_g = 1$, $C_g = 1$, and varied values of assortment probabilities, f_g, f_c . Lighter shades indicate higher values. The zero contour is the solid line. (Top left) $f_c = 0.1$ 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 .

249 3.2 Model 2: Cultural prisoner's dilemma

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

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

256 The terms B_c^z and C_c^z are the gametic fitness benefit and cost, with $B_c = B_c^z/\bar{z}$,
257 $C_c = C_c^z/\bar{z}$ (see SI-2). Recall that in the previous section cultural fitness was defined
258 in terms of the total influence ($s_i = \sum_{j=1}^{N'} \gamma_{ij}$) an ancestor has on the descendant
259 population. In this model, offspring have a single cultural ancestor (i.e. $\gamma_{ij} = 1$),
260 and s_i is just the total number of descendant individuals who count i as an ancestor.
261 The number of offspring available as cultural descendants is determined by the
262 reproductive output of the population, thus,

$$s_i = \frac{z_i}{\bar{z}} \bar{w}. \quad (13)$$

263 Substituting (12) and (13) into the gene-culture Price equation and making simpli-
264 fications, we obtain:

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

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

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

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

294 **4 Non-additive phenotypes**

295 The results described above all assumed an additive phenotype function, which is a
296 standard starting point in social evolution and population genetics theory (Van Cleve,
297 2015). However, biological reality may be much more complicated, particularly
298 when trying to incorporate the effects of multiple inheritance systems. One way to
299 deal with this problem in evolutionary theory has been to observe that most genetic
300 variants have small effects on phenotypes and genetic variation in the population
301 is small, in which case, an additive approximation gives satisfactory results (Tay-
302 lor and Frank, 1996; Akçay and Van Cleve, 2012). In this section, we translate this
303 approach to phenotypes that are jointly determined by genes and culture.

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

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 $p_j(c_1, \dots, c_N, g_1, \dots, g_N)$, 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 $(\bar{\mathbf{c}}, \bar{\mathbf{g}}) = (\bar{c}_1, \dots, \bar{c}_N, \bar{g}_1, \dots, \bar{g}_N)$.
 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),

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

314 where $\mathcal{S}_i = \sum_{j=1}^{N'} \frac{\partial p_j}{\partial c_i} \Big|_{(\bar{\mathbf{c}}, \bar{\mathbf{g}})}$ and $W_i = \sum_{j=1}^{N'} \frac{\partial p_j}{\partial g_i} \Big|_{(\bar{\mathbf{c}}, \bar{\mathbf{g}})}$, 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 γ_{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

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 $\langle p_j(\bar{c}, \bar{g}) \rangle - \bar{p}$, 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,

$$\beta_{S_i, c_i} > - \left[\beta_{W_i, g_i} \frac{\text{var}(g)}{\text{var}(c)} - \frac{\langle p_j(\bar{c}, \bar{g}) \rangle - \bar{p}}{\text{var}(c)} \right] \quad (16)$$

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

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.

349 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

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 $\langle \beta_{\gamma c}^j \rangle$, the descendant mean of the correlation be-
385 tween γ_{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-

390 tural transmission system allows for biased or directed ‘mutation’ in the form of
391 individual learning and other factors. For example, individuals may systemati-
392 cally differ from their parents because they learn more appropriate responses to
393 their environment through their own trial-and-error learning. El Mouden et al.
394 (2015) offered an interpretation of the transmission term as evolved biases in favor
395 of reproductive fitness maximizing behaviors. Meanwhile, Henrich (2004) took the
396 transmission term to represent systematic error in cultural learning that biased in-
397 dividuals to trait values lower than their cultural parents. These examples hint at
398 the diverse interpretations that can be ascribed to the transmission term, particu-
399 larly in lieu of empirical evidence on how a specific trait is passed on. These effects
400 also present important future directions for a more complete framework of gene-
401 culture co-evolution.

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

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-

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-

459 ness were maximized at different phenotypic values. They found that under cer-
460 tain conditions, the equilibrium phenotype could be the cultural-fitness maximiz-
461 ing phenotype, even when the ‘penetrance’ parameter was under genetic control.
462 These intriguing results are in qualitative agreement with ours, though they de-
463 serve further investigation.

464 Our model was inspired by the idea that behavioral traits can be influenced
465 by both genetic and cultural evolution. Research into the evolutionary basis of
466 human behavior has long puzzled over the existence of maladaptive behaviors
467 (Glanville, 1987; Logan and Qirko, 1996). These are behaviors that persist via cul-
468 tural transmission despite detrimental reproductive fitness effects, such as club-
469 bing pregnant women to induce birth in Colombia (Reichel-Dolmatoff and Reichel-
470 Dolmatoff, 2013), unhygienic neonatal care practices in Bangladesh (McConville,
471 1988), and folk medical practices like ingesting rhino horn (Ayling, 2013) or blood-
472 letting (Wootton, 2007). While these practices are likely spread almost exclusively
473 by cultural transmission, other maladaptive behaviors, such as the cross-cultural
474 variation in risk-taking (Weber and Hsee, 1998; Hsee and Weber, 1999), may have
475 a significant genetic component. The demographic transition provides another po-
476 tential example of a dually inherited trait. In fact, Kolk et al. (Kolk et al., 2014)
477 presented a model in which reproductive behavior resulted from a genetic predis-
478 position and exposure to cultural models. Our model demonstrates more broadly
479 the possibility that maladaptive behavioral traits may evolve under dual transmis-
480 sion, despite their reproductive fitness costs.

481 **5.1 Conclusions**

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

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613 Appendices

614 A-1 Derivation of Gene Culture Price equation.

615 The phenotype of individual j is given by,

$$p_j = \sum_{i=1}^N \nu_{ij} g_i + \Delta g_j + \sum_{i=1}^N \gamma_{ij} c_i + \Delta c_j + e \quad (\text{A-1})$$

616 where the coefficients ν_{ij} and γ_{ij} represent the influence an ancestor i has on de-
 617 scendant j in the genetic and cultural domains, respectively (Note: $\sum_{i=1}^N \nu_{ij} =$
 618 $\sum_{i=1}^N \gamma_{ij} = 1$). The mean value of p in the descendant generation is,

$$\bar{p}' = \frac{1}{N'} \sum_{j=1}^{N'} \sum_{i=1}^N \nu_{ij} g_i + \frac{1}{N'} \sum_{j=1}^{N'} \Delta g_j + \frac{1}{N'} \sum_{j=1}^{N'} \sum_{i=1}^N \gamma_{ij} c_i + \frac{1}{N'} \sum_{j=1}^{N'} \Delta c_j \quad (\text{A-2})$$

619 where e is assumed to have mean zero. Reversing the orders of the double sum
 620 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,

$$\bar{p}' = \frac{1}{N'} \sum_{i=1}^N g_i w_i + \frac{1}{N'} \sum_{i=1}^N c_i s_i + \frac{1}{N'} \sum_{j=1}^{N'} \Delta g_j + \frac{1}{N'} \sum_{j=1}^{N'} \Delta c_j \quad (\text{A-3})$$

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

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

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

$$\begin{aligned}
 \text{cov}(s, c) &= \overline{cs} - \bar{c}\bar{s} \\
 &= \frac{1}{N} \sum_{i=1}^N \sum_{j=1}^{N'} c_i \gamma_{ij} - \bar{c}\bar{s} = \sum_{j=1}^{N'} \langle c_i \gamma_{ij} \rangle - \bar{c}\bar{s} \\
 &= \sum_{j=1}^{N'} \text{cov}(c_i, \gamma_{ij}) + \sum_{j=1}^{N'} \bar{c} \bar{\gamma}_j - \bar{c}\bar{s} \\
 &= \sum_{j=1}^{N'} \text{cov}(\gamma_{ij}, c_i) + \bar{c} \frac{N'}{N} - \bar{c}\bar{s} \\
 &= N' \langle \text{cov}(\gamma_{ij}, c_i) \rangle
 \end{aligned} \tag{A-5}$$

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

630 **A-2 Derivation of Gene-culture Hamilton’s rule**

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

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

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

¹In 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 β_{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"

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

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

$$\begin{aligned} \bar{w}\Delta\bar{p} = & B_c [\text{cov}(\tilde{c}, c) + \text{cov}(\tilde{g}, c)] + C_c [\text{var}(c) + \text{cov}(g, c)] \\ & + B_g [\text{cov}(\tilde{c}, g) + \text{cov}(\tilde{g}, g)] + C_g [\text{cov}(c, g) + \text{var}(g)] \quad (\text{A-8}) \end{aligned}$$

640 The equation above allows us to derive a condition for the evolution of the altru-
 641 istic trait p in the population. Using $\text{cov}(x, y) = \beta_{xy}\text{var}(y)$, where β_{xy} is the linear
 642 regression coefficient of x on y , and dividing through by $\text{var}(c)$, we can rearrange
 643 the above expression to find,

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

644 **Supplementary Information**

645 **SI-1 Model I**

646 We imagine a population of haploid individuals who, once born, select a cultural
647 parent to copy. Each individual has two loci with a single allele present at each.
648 The allele at the first locus is genetically transmitted while the allele at the second is
649 received from a cultural parent. Individuals interact assortatively, with some prob-
650 ability of being genetically identical due to assortment, (f_g) , and culturally identical
651 due to assortment, (f_c) . At discrete time steps individuals meet a random kin mem-
652 ber and play a prisoner's dilemma according to a mixed strategy. The phenotype, p ,
653 is the probability of playing cooperate. The two loci mean four types of individuals
654 $\{0, 0\}$, $\{0, 1\}$, $\{1, 0\}$, $\{1, 1\}$, with phenotypes, $p_{00} = 0$, $p_{01} = 1/2$, $p_{10} = 1/2$, $p_{11} = 1$.

The expected reproductive fitnesses for each type are

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

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

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

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

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

658 conditional probabilities we take advantage of the following identity:

$$P(g_o, c_o | g_p, c_p) = P(g_o | g_p) P(c_o | c_p), \quad (\text{SI-1})$$

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

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

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

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

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

659 Note that the remaining marginal conditional probabilities are given by

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

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

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

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

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.

664 We then only have to calculate the following,

$$\beta_{cg} \text{var}(g) = 0 \quad (\text{SI-10})$$

$$\text{var}(g) = \frac{1}{4} q_c (1 - q_c) \quad (\text{SI-11})$$

$$\beta_{\bar{g}g} \text{var}(g) = \frac{1}{4} f_g q_g (1 - q_g) \quad (\text{SI-12})$$

$$\beta_{\bar{c}g} \text{var}(g) = 0 \quad (\text{SI-13})$$

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

666 **SI-2 Model II**

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:

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

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

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

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

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),

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

671 We can then rewrite (9) as,

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

672 Again, we compute the relevant terms:

$$\beta_{\bar{c}c} = f_c \quad (\text{SI-16})$$

$$\beta_{\bar{g}c} = 0 \quad (\text{SI-17})$$

$$\beta_{\bar{c}g} = 0 \quad (\text{SI-18})$$

$$\beta_{\bar{g}g} = f_g \quad (\text{SI-19})$$

$$\beta_{cg} = 0 \quad (\text{SI-20})$$

$$\text{var}(c) = \frac{1}{4}q_c(1 - q_c) \quad (\text{SI-21})$$

$$\text{var}(g) = \frac{1}{4}q_g(1 - q_g) . \quad (\text{SI-22})$$

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

674 Non-additive phenotypes

We assume that all descendant individuals have a (potentially) unique function for mapping from heritable inputs to phenotype, $p_j(f_j(c_1, \dots, c_N), h_j(g_1, \cdot, g_N))$. 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 $(\bar{c}, \dots, \bar{c}, \bar{g}, \dots, \bar{g}) = (\bar{\mathbf{c}}, \bar{\mathbf{g}})$,

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

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

$$\Delta \bar{p} \approx \frac{1}{N'} \sum_{j=1}^{N'} p_j(\bar{\mathbf{c}}, \bar{\mathbf{g}}) + \frac{1}{N'} \sum_{j=1}^{N'} \sum_{i=1}^N c_i \frac{\partial p_j}{\partial c_i} \Big|_{(\bar{\mathbf{c}}, \bar{\mathbf{g}})} + \frac{1}{N'} \sum_{j=1}^{N'} \sum_{i=1}^N g_i \frac{\partial p_j}{\partial g_i} \Big|_{(\bar{\mathbf{c}}, \bar{\mathbf{g}})} \quad (\text{SI-23})$$

$$- \frac{\bar{c}}{N'} \sum_{j=1}^{N'} \sum_{i=1}^N \frac{\partial p_j}{\partial c_i} \Big|_{(\bar{\mathbf{c}}, \bar{\mathbf{g}})} - \frac{\bar{g}}{N'} \sum_{j=1}^{N'} \sum_{i=1}^N \frac{\partial p_j}{\partial g_i} \Big|_{(\bar{\mathbf{c}}, \bar{\mathbf{g}})} - \bar{p} \quad (\text{SI-24})$$

676 Switching the order of all the summations, and defining the quantities, $\mathcal{S}_i = \sum_{j=1}^{N'} \frac{\partial p_j}{\partial c_i} \Big|_{(\bar{\mathbf{c}}, \bar{\mathbf{g}})}$,

677 and $W_i = \sum_{j=1}^{N'} \frac{\partial p_j}{\partial g_i} \Big|_{(\bar{\mathbf{c}}, \bar{\mathbf{g}})}$, we can write,

$$\Delta \bar{p} = \frac{N}{N'} [\text{cov}(\mathcal{S}_i, c_i) + \text{cov}(W_i, g_i) + \bar{c}\bar{\mathcal{S}} + \bar{g}\bar{W}] - \frac{N}{N'} \bar{c}\bar{\mathcal{S}} - \frac{N}{N'} \bar{g}\bar{W} \quad (\text{SI-25})$$

$$+ \frac{1}{N'} \sum_{j=1}^{N'} p_j(\bar{\mathbf{c}}, \bar{\mathbf{g}}) - \bar{p} \quad (\text{SI-26})$$

678 Cancelling terms we arrive at Eq. (SI-23).

679 If we continue our expansion of the phenotype function, we arrive at the follow-
 680 ing result,

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

681 where,

$$\begin{aligned} \mathcal{S}_i &= \sum_{j=1}^{N'} \left(\frac{\partial p_j}{\partial c_i} + \frac{1}{2} \sum_{k=1}^N \frac{\partial^2 p_j}{\partial c_i \partial c_k} (c_k - \bar{c}) + \frac{1}{3!} \sum_{k=1}^N \sum_{l=1}^N \frac{\partial^3 p_j}{\partial c_i \partial c_k \partial c_l} (c_k - \bar{c})(c_l - \bar{c}) + \dots \right) \\ \mathcal{W}_i &= \sum_{j=1}^{N'} \left(\frac{\partial p_j}{\partial g_i} + \frac{1}{2} \sum_{k=1}^N \frac{\partial^2 p_j}{\partial g_i \partial g_k} (g_k - \bar{g}) + \frac{1}{3!} \sum_{k=1}^N \sum_{l=1}^N \frac{\partial^3 p_j}{\partial g_i \partial g_k \partial g_l} (g_k - \bar{g})(g_l - \bar{g}) + \dots \right) \\ \mathcal{I}_i &= \sum_{j=1}^{N'} \left(\frac{1}{2} \sum_{k=1}^N \frac{\partial^2 p_j}{\partial g_i \partial c_k} (c_k - \bar{c}) + \frac{1}{3!} \sum_{k=1}^N \sum_{l=1}^N \frac{\partial^3 p_j}{\partial g_i \partial c_k \partial c_l} (c_k - \bar{c})(c_l - \bar{c}) \right. \\ &\quad \left. + \frac{1}{3!} \sum_{k=1}^N \sum_{l=1}^N \frac{\partial^3 p_j}{\partial g_i \partial c_k \partial g_l} (c_k - \bar{c})(g_l - \bar{g}) + \dots \right). \end{aligned}$$

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