

Cultural Transmission Can Explain the Evolution of Cooperation

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August 10, 2020

Introduction

Cooperative behavior can reduce an individual's fitness and increase the fitness of its conspecifics or competitors (Axelrod and Hamilton, 1981). Nevertheless, cooperative behavior appears to occur in many non-human animals (Dugatkin, 1997), including primates (Jaeggi and Gurven, 2013), rats (Rice and Gainer, 1962), birds (Stacey and Koenig, 1990; Krams et al., 2008), and lizards (Sinervo et al., 2006). Evolution of cooperative behavior remains an important conundrum in evolutionary biology. Since the work of Hamilton (1964) and Axelrod and Hamilton (1981), theories for the evolution of cooperative and altruistic behaviors have been intertwined often under the rubric of kin selection.

Kin selection theory posits that natural selection is more likely to favor cooperation between more closely related individuals. The importance of relatedness to the evolution of cooperation and altruism was shown by Hamilton (1964), who showed that an allele that determines cooperative behavior will increase in frequency if the reproductive cost to the actor that cooperates, c , is less than the benefit to the recipient, b , times the relatedness, r , between the recipient and the actor. This relatedness coefficient r measures a probability that an allele sampled from the cooperator is identical by descent to one at the same locus in the recipient. This condition is known as "Hamilton's rule":

$$c < b \cdot r. \quad (1)$$

Eshel and Cavalli-Sforza (1982) studied a related model for the evolution of cooperative behavior under vertical transmission. Their model included *assortative meeting*, or non-random encounters, where a fraction m of individuals in the population each interact with an individual of the same phenotype, and a fraction $1 - m$ interacts with a randomly chosen individual. Such assortative meeting may be due, for example, to population structure or active partner choice. In their model, cooperative behavior can evolve if¹ (Eshel and Cavalli-Sforza, 1982, eq. 3.2)

$$c < b \cdot m, \quad (2)$$

where b and c are the benefit and cost of cooperation. Here m in (2) takes the role of the relatedness r in (1).

Here we study the evolution of a cooperative behavior that is subject to *cultural transmission*, which allows an individual to acquire attitudes or behavioral traits from other individuals in its social group through imitation, learning, or other modes of communication (Cavalli-Sforza and Feldman, 1981; Richerson and Boyd, 2008). Feldman et al. (1985) introduced the first model for the evolution of altruism by cultural transmission and showed that under vertical (parent-to-offspring) cultural transmission, the conditions for the initial increase of altruism entails a modification of Hamilton's rule in the cases of parent-to-offspring or sib-to-sib altruism.

Non-vertical cultural transmission may be either viewed as horizontal or oblique: horizontal transmission occurs between individuals from the same generation, while oblique transmission occurs to offspring from the generation to which their parents belong. Evolution under either of these transmission models can be more rapid than under pure vertical transmission (Cavalli-Sforza and Feldman, 1981; Lycett and Gowlett, 2008; Ram et al., 2018). Lewin-Epstein et al. (2017) have demonstrated that non-vertical transmission, mediated by microbes that manipulate their host's behavior, can help to explain the evolution of cooperative behavior. Some of their analysis can be applied to cultural transmission, because models of cultural transmission are mathematically similar to those for transmission of infectious diseases (Cavalli-Sforza and Feldman, 1981).

We hypothesize that non-vertical cultural transmission can enhance the evolution of cooperation, and to test this hypothesis we suggest a model in which behavioral changes are mediated by cultural

¹In an extended model, which allows an individual to encounter N individuals before choosing a partner, the righthand side is multiplied by $E[N]$, the expected number of encounters (Eshel and Cavalli-Sforza, 1982, eq. 4.6).

transmission that can occur during social interactions. For example, if an individual interacts with a cooperative individual, it might learn that cooperation is an advantageous behavior and will be cooperative in the future. Our cultural evolution models include both vertical and non-vertical transmission of cooperation, and we investigate these models using mathematical analysis and simulations. Our results demonstrate that cultural transmission can facilitate the evolution of cooperation even when genetic transmission can not, and that treatment of cooperation as a cultural, rather than a genetic, trait can lead to a better understanding of its evolutionary dynamics.

Models

Consider a very large population whose members are characterized by their phenotype ϕ , which can be of two types, $\phi = A$ for cooperators or $\phi = B$ for defectors. An offspring inherits its phenotype from its parent via vertical transmission with probability v or from a random individual in the parental population via oblique transmission with probability $(1 - v)$. Following Ram et al. (2018), given that the parent phenotype is ϕ and assuming uni-parental inheritance, the conditional probability that the phenotype ϕ' of the offspring is A is

$$P(\phi' = A \mid \phi) = \begin{cases} v + (1 - v)p, & \text{if } \phi = A \\ (1 - v)p, & \text{if } \phi = B \end{cases}, \quad (3)$$

where $p = P(\phi = A)$ is the frequency of A among all adults in the parental generation.

Not all adults become parents due to natural selection, and we denote the frequency of phenotype A among parents by \tilde{p} . Therefore, the frequency \hat{p} of phenotype A among juveniles (after selection and vertical and oblique transmission) is

$$\begin{aligned} \hat{p} &= \tilde{p}[v + (1 - v)p] + (1 - \tilde{p})[(1 - v)p] \\ &= v\tilde{p} + (1 - v)p. \end{aligned} \quad (4)$$

Individuals are assumed to interact according to a *prisoner's dilemma*. Specifically, individuals interact in pairs; a cooperator suffers a fitness cost $0 < c < 1$, and its partner gains a fitness benefit b , where we assume $c < b$. **Table 1** shows the payoff matrix, i.e. the fitness of an individual with phenotype ϕ_1 when interacting with a partner of phenotype ϕ_2 .

[TABLE 1 HERE]

Social interactions occur randomly: two individuals with phenotype A interact with probability \hat{p}^2 , two individuals with phenotype B interact with probability $(1 - \hat{p})^2$, and two individuals with different phenotypes interact with probability $2\hat{p}(1 - \hat{p})$.

Horizontal cultural transmission occurs between pairs of individuals from the same generation. It occurs between social partners with probability α , or between a random pair with probability $1 - \alpha$ (see **Figure 1**). The assortment parameter α is therefore the fraction of population that receives (horizontal transmission) from the social interaction partner, and $1 - \alpha$ receives randomly. Horizontal transmission is not always successful, as one partner may reject the other's phenotype. The probability for successful horizontal transmission of phenotypes A and B are T_A and T_B , respectively (**Table 2**).

[TABLE 2 HERE]

88 Therefore, the frequency p' of phenotype A among adults in the next generation, after horizontal transmission, is

$$\begin{aligned}
 p' = & \hat{p}^2[\alpha + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
 & + \hat{p}(1 - \hat{p})[\alpha(1 - T_B) + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
 & + (1 - \hat{p})\hat{p}[\alpha T_A + (1 - \alpha)\hat{p}T_A] \\
 & + (1 - \hat{p})^2[(1 - \alpha)\hat{p}T_A] ,
 \end{aligned}
 \tag{5}$$

which simplifies to

$$p' = \hat{p}^2(T_B - T_A) + \hat{p}(1 + T_A - T_B).
 \tag{6}$$

94 The frequency of A among parents (i.e. after selection) follows a similar dynamic, but also includes the effect of natural selection, and is therefore

$$\begin{aligned}
 \bar{w}\tilde{p}' = & \hat{p}^2(1 + b - c)[\alpha + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
 & + \hat{p}(1 - \hat{p})(1 - c)[\alpha(1 - T_B) + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
 & + (1 - \hat{p})\hat{p}(1 + b)[\alpha T_A + (1 - \alpha)\hat{p}T_A] \\
 & + (1 - \hat{p})^2[(1 - \alpha)\hat{p}T_A] ,
 \end{aligned}
 \tag{7}$$

96 where fitness values are taken from **Table 1** and **Table 2**, and the population mean fitness is

$$\bar{w} = 1 + \hat{p}(b - c).
 \tag{8}$$

98 Equation 7 can be simplified to

$$\begin{aligned}
 \bar{w}\tilde{p}' = & \hat{p}^2(1 + b - c)(1 - (1 - \hat{p})(1 - \alpha)T_B) \\
 & + \hat{p}(1 - \hat{p})(1 - c)(\hat{p}(1 - \alpha)T_B + 1 - T_B) \\
 & + (1 - \hat{p})\hat{p}(1 + b)(\hat{p}(1 - \alpha) + \alpha)T_A \\
 & + (1 - \hat{p})^2\hat{p}(1 - \alpha)T_A .
 \end{aligned}
 \tag{9}$$

100 where $\hat{p} = v\tilde{p} + (1 - v)p$.

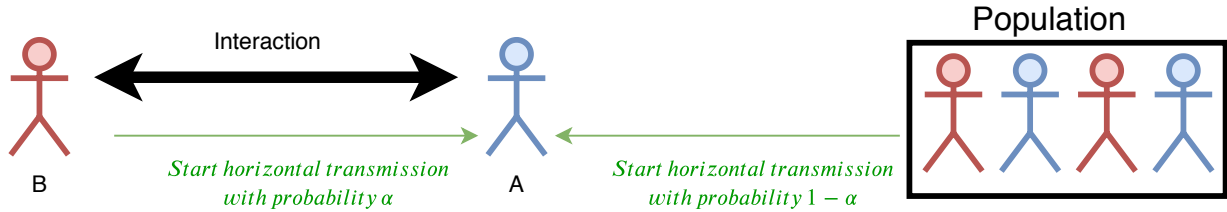


Figure 1: **Cultural horizontal transmission.** Transmission occurs between interacting partners with probability α (left) or between two random peers with probability $1 - \alpha$.

Results

102 Oblique and Horizontal Transmission

With only oblique and horizontal transmission, i.e. $v = 0$, Eq. 4 becomes $\hat{p} = p$ and Eq. 6 be-
 104 comes

$$p' = p^2(T_B - T_A) + p(1 + T_A - T_B),
 \tag{10}$$

106 which gives the following result.

108 **Result 1** (Oblique and horizontal transmission of cooperation). *Without vertical transmission ($v = 0$), if there is a horizontal transmission bias in favor of cooperation, namely*

$$110 \quad T_A > T_B, \quad (11)$$

then $p' > p$, and the frequency of the cooperator phenotype among adults increases every generation.

112 Therefore, in the absence of vertical transmission, selection plays no role in the evolution of cooperation. Hence, cooperation will evolve if the cooperator phenotype has a horizontal transmission bias
114 (see Figure 4c).

Vertical and Horizontal Transmission

116 With only vertical and horizontal transmission, i.e. $v = 1$, Eq. 4 becomes $\hat{p} = \tilde{p}$, and Eq. 9 for the frequency of the cooperative phenotype among parents in the next generation \tilde{p}' can be written
118 as

$$\begin{aligned} \bar{w}\tilde{p}' &= \tilde{p}^2(1+b-c)[1-(1-\tilde{p})(1-\alpha)T_B] \\ &\quad + \tilde{p}(1-\tilde{p})(1-c)[\tilde{p}(1-\alpha)T_B + 1 - T_B] \\ &\quad + \tilde{p}(1-\tilde{p})(1+b)[\tilde{p}(1-\alpha) + \alpha]T_A \\ &\quad + (1-\tilde{p})^2\tilde{p}(1-\alpha)T_A. \end{aligned} \quad (12)$$

120 Fixation of either cooperation, $\tilde{p} = 1$, or defection, $\tilde{p} = 0$, are equilibria of Eq. 12, that is, they solve $\tilde{p}' = \tilde{p}$. We therefore assume for the remainder of the analysis that $0 < \tilde{p} < 1$.

122 If $\alpha = 1$, then $\tilde{p}' = \tilde{p}$ is reduced to

$$\tilde{p}(1-\tilde{p})[(1+b)T_A + (1-c)(1-T_B) - 1] = 0, \quad (13)$$

124 and there are no additional equilibria. For cooperation to take over the population (for $\tilde{p} = 1$ to be globally stable) we require $\tilde{p}' > \tilde{p}$; that is,

$$126 \quad \tilde{p}^2(1+b-c) + \tilde{p}(1-\tilde{p})[(1-c)(1-T_B) + (1+b)T_A] > \bar{w}\tilde{p}. \quad (14)$$

We divide by \tilde{p} , set $\bar{w} = 1 + \tilde{p}(b-c)$, and rearrange to get

$$128 \quad (1-\tilde{p})[(1-c)(1-T_B) + (1+b)T_A] > 1 - \tilde{p}. \quad (15)$$

Dividing by $(1-\tilde{p})$ we find that $\tilde{p}' > \tilde{p}$ if

$$130 \quad (1-c)(1-T_B) + (1+b)T_A > 1 \quad (16)$$

132

If $\alpha < 1$, divide both sides of Eq. 12 by \tilde{p} and set $\bar{w} = 1 + \tilde{p}(b-c)$. Then $\tilde{p}' > \tilde{p}$ if

$$\begin{aligned} 1 + \tilde{p}(b-c) &< \tilde{p}(1+b-c)(1-(1-\tilde{p})(1-\alpha)T_B) \\ &\quad + (1-\tilde{p})(1-c)(\tilde{p}(1-\alpha)T_B + 1 - T_B) \\ &\quad + (1-\tilde{p})(1+b)(\tilde{p}(1-\alpha) + \alpha)T_A \\ &\quad + (1-\tilde{p})^2(1-\alpha)T_A. \end{aligned} \quad (17)$$

Rearranging, we get

$$\begin{aligned} 1 - \tilde{p} &< -\tilde{p}(1+b-c)(1-\tilde{p})(1-\alpha)T_B \\ &\quad + (1-\tilde{p})(1-c)(\tilde{p}(1-\alpha)T_B + 1 - T_B) \\ &\quad + (1-\tilde{p})(1+b)(\tilde{p}(1-\alpha) + \alpha)T_A \\ &\quad + (1-\tilde{p})^2(1-\alpha)T_A. \end{aligned} \quad (18)$$

136

138 Diving by $(1 - \tilde{p})$ and rearranging so that free terms are on the left and terms with \tilde{p} are on the right, we have

$$1 - (1 - \alpha)T_A - (1 + b)\alpha T_A - (1 - T_B)(1 - c) < \tilde{p}[-(1 + b - c)(1 - \alpha)T_B + (1 - c)(1 - \alpha)T_B + (1 + b)(1 - \alpha)T_A - (1 - \alpha)T_A]. \quad (19)$$

140 Simplifying, we find that $\tilde{p}' > \tilde{p}$ if and only if

$$c(1 - T_B) - b\alpha T_A - (T_A - T_B) < \tilde{p} \cdot b(1 - \alpha)(T_A - T_B). \quad (20)$$

142 Besides the fixation states $\tilde{p} = 0$ and $\tilde{p} = 1$, there may be an actual polymorphic equilibrium of $\tilde{p}' = \tilde{p}$ in Eq. 12, namely

$$144 \quad \tilde{p}^* = \frac{c(1 - T_B) - b\alpha T_A - (T_A - T_B)}{b(1 - \alpha)(T_A - T_B)}, \quad (21)$$

which is legitimate if $0 < \tilde{p}^* < 1$.

Since all parameters are positive, we can apply inequality 20 and see that for $\tilde{p}' > \tilde{p}$ we require that either

$$T_A > T_B \quad \text{and} \quad \tilde{p} > \tilde{p}^*, \quad \text{or} \quad (22)$$

$$T_A < T_B \quad \text{and} \quad \tilde{p} < \tilde{p}^*. \quad (23)$$

146 We summarize these findings in the following result and corollaries.

148 **Result 2** (Vertical and horizontal transmission of cooperation). *Without oblique transmission ($v = 1$), fixation, extinction, and coexistence of both phenotypes are possible.*

150 Let the initial frequency of the alternative phenotype be \tilde{p}_0 and denote the cost boundaries by

$$\gamma_1 = \frac{b\alpha T_A + (T_A - T_B)}{1 - T_B}, \quad \gamma_2 = \frac{b\alpha T_B + (1 + b)(T_A - T_B)}{1 - T_B}. \quad (24)$$

152 Then, applying 21, 22, and 23, we summarize the possible outcomes which are illustrated in Figure 2:

- 154 1. Fixation of cooperation, if $T_A > T_B$ and $c < \gamma_1$; or if $T_A > T_B$ and $\gamma_1 < c < \gamma_2$ and $\tilde{p}_0 > \tilde{p}^*$; or if $T_A < T_B$ and $c < \gamma_2$.
- 156 2. Fixation of defection, if $T_A > T_B$ and $\gamma_2 < c$; or if $T_A > T_B$ and $\gamma_1 < c < \gamma_2$ and $\tilde{p}_0 < \tilde{p}^*$; or if $T_A < T_B$ and $\gamma_1 < c$.
- 158 3. Coexistence of both phenotypes at \tilde{p}^* , if $T_A < T_B$ and $\gamma_2 < c < \gamma_1$.

160 Note that cooperation and defection can coexist stably if there is horizontal bias for defection and the cost of cooperation is large but not too large. The recursion dynamic for this case is illustrated in Figure 3.

162 Much of the literature on evolution of cooperation focuses on conditions for an initially rare cooperative phenotype to invade a population of defectors. The next corollary deals with such a condition, followed by a corollary that deals with symmetric horizontal transmission, i.e. $T_A = T_B$.

166 **Corollary 1** (Condition for cooperation to increase when initially rare). *If the initial frequency of the cooperative phenotype is very close to zero, $\tilde{p}_0 \approx 0$, then this frequency will increase if*

$$168 \quad T_A > T_B \quad \text{and} \quad c < \gamma_1, \quad \text{or} \quad T_A < T_B \quad \text{and} \quad \gamma_2 < c < \gamma_1. \quad (25)$$

In general, these conditions cannot be formulated in the form of Hamilton's rule ($c < b \cdot r$) due to the horizontal transmission bias $T_A - T_B$. Without horizontal transmission bias, i.e., with $T_A = T_B$, these conditions reduce to the following form of Hamilton's rule.

Corollary 2 (Symmetric horizontal transmission). *If $T = T_A = T_B$, then cooperation will take over the population if*

$$c < b \cdot \frac{\alpha T}{1 - T}. \quad (26)$$

Inequality 26 is obtained by setting $T_A = T_B$ in inequality 20 and can be interpreted as a version of Hamilton's rule (inequality 1), where $\alpha T/(1 - T)$ can be regarded as the 'effective relatedness'. Figure 4a demonstrates this condition.

Corollary 3 (No assortment of transmission and cooperation). *If $\alpha = 0$ and there is horizontal bias for cooperation ($T_A > T_B$) and (1) the cost is low compared to the bias ($c < (T_A - T_B)/(1 - T_B)$), then cooperation will fix from any positive frequency; or (2) the cost is low compared to the benefit ($c < (1 + b)(T_A - T_B)(1 - T_B)$), then cooperation will fix if the initial frequency is high enough ($\tilde{p}_0 > \tilde{p}^*$).*

Figure 2b illustrates these conditions, where the third equilibrium given by Eq. 21 becomes

$$\tilde{p}^*(\alpha = 0) = \frac{c(1 - T_B) - (T_A - T_B)}{b(T_A - T_B)}, \quad (27)$$

and the cost boundaries are

$$\gamma_1(\alpha = 0) = \frac{T_A - T_B}{1 - T_B}, \quad \gamma_2(\alpha = 0) = (1 + b) \frac{T_A - T_B}{1 - T_B}. \quad (28)$$

If $T_A > T_B$ then $0 < \gamma_1(\alpha = 0) < \gamma_2(\alpha = 0)$. So either $c < \gamma_1(\alpha = 0)$ or $\gamma_1(\alpha = 0) < c < \gamma_2(\alpha = 0)$ will allow fixation of cooperation, the latter only if the initial frequency is high enough. If $T_A < T_B$ then $\gamma_2(\alpha = 0) < \gamma_1(\alpha = 0) < 0 < c$, and defection will fix.

Corollary 4 (Complete assortment of transmission and cooperation). *When $\alpha = 1$, there are only two equilibria, $\tilde{p} = 0$ and $\tilde{p} = 1$. The condition for evolution of cooperation (i.e. global stability of $\tilde{p} = 1$) is found from inequality 16, namely*

$$c < \frac{b \cdot T_A + (T_A - T_B)}{1 - T_B}. \quad (29)$$

With complete assortment, in inequality 16 horizontal transmission occurs together with the cooperative interaction. The same occurs in Lewin-Epstein et al. (2017), and therefore this corollary is equivalent to their result (see their eq. 1).

In terms of the cost boundaries, inequality 29 is equivalent to $c < \gamma_1$, and if $T_A > T_B$ then that suffices for fixation of cooperation. If $T_B > T_A$ then $\gamma_2(\alpha = 1) < 0$ and again, (29) is sufficient for increase in the frequency of A. Inequality 29 can be written as

$$1 - (1 - c)(1 - T_B) < (1 + b)T_A, \quad (30)$$

which provides an interesting interpretation for the success of cooperation. In the interaction between a cooperator and a defector, $(1 - c)(1 - T_B)$ is the probability that the cooperator remains cooperative and also reproduces. Therefore, $1 - (1 - c)(1 - T_B)$ is the probability that either the cooperator becomes

a defector, or that it fails to reproduce. This is the effective cost for cooperation from this interaction, while $(1 + b)T_A$ is the probability that the defector becomes cooperative and reproduces, which is the effective benefit for cooperation from this interaction. Thus inequality (29) entails that cooperation can evolve if the effective cost for cooperation is less than the effective benefit.

With Vertical and Oblique Transmission

In this case $0 < v < 1$, and the recursion system is more complex, and we focus on local rather than on global stability. To proceed, we note that Eq. 4 can give \hat{p}' as a function of both p' and \tilde{p}' . Eq. 6 gives p' as a function of \tilde{p} , since \hat{p} is given in Eq. 4 as a function of \tilde{p} and Eq. 9 gives \tilde{p}' as a function of \hat{p} . Combining these equations, we find an equation for \hat{p}' as a function of \hat{p} (shown in Appendix Appendix A). We then determine the equilibria, namely, solutions of $\hat{p}' = \hat{p}$, and analyse their local stability.

We apply Eqs. 4, 6, and 9 to obtain the function $f(\hat{p})$ (see Appendix Appendix A):

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = \beta_1 \hat{p}^3 + \beta_2 \hat{p}^2 + \beta_3 \hat{p}, \quad (31)$$

where

$$\begin{aligned} \beta_1 &= [c(1 - v) - b(1 - \alpha v)](T_A - T_B), \\ \beta_2 &= -\beta_1 - \beta_3, \\ \beta_3 &= \alpha b v T_A - c v(1 - T_B) + (T_A - T_B). \end{aligned} \quad (32)$$

If $T = T_A = T_B$ then $\beta_1 = 0$ and $\beta_3 = -\beta_2 = \alpha b v T - c v(1 - T)$, and $f(\hat{p})$ becomes a quadratic polynomial:

$$f(\hat{p}) = \hat{p}(1 - \hat{p})[\alpha b v T - c v(1 - T)]. \quad (33)$$

Clearly the only two equilibria are the fixations $\hat{p} = 0$ and $\hat{p} = 1$. These equilibria are locally stable if $f'(\hat{p}) < 0$ near the equilibrium (Appendix Appendix B), and

$$f'(\hat{p}) = (1 - 2\hat{p})[\alpha b v T - c v(1 - T)], \quad (34)$$

with

$$\begin{aligned} f'(0) &= \alpha b v T - c v(1 - T), \\ f'(1) &= -\alpha b v T + c v(1 - T). \end{aligned} \quad (35)$$

Therefore with symmetric horizontal transmission, fixation of the cooperative phenotype ($\hat{p} = 1$) occurs under the same condition as Corollary 1.1, namely Eq. 26.

In the general case where $T_A \neq T_B$, the coefficient β_1 is not necessarily zero, and $f(\hat{p})$ is a cubic polynomial. Therefore, three equilibria may exist, two of which are $\hat{p} = 0$ and $\hat{p} = 1$, and the third is

$$\hat{p}^* = \frac{\beta_3}{\beta_1}. \quad (36)$$

Note that the sign of the cubic (Eq. 31) at positive (negative) infinity is equal (opposite) to the sign of β_1 . If $T_A > T_B$, then

$$\beta_1 < [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) < 0, \quad (37)$$

since $c < b$ and $1 > \alpha v$. Hence the signs of the cubic at positive and negative infinity are negative and positive, respectively. First, if $\beta_3 < \beta_1$ then $1 < \hat{p}^*$ and therefore $f'(0) < 0$ and $f'(1) > 0$; that is, fixation of the defector phenotype B is the only locally stable legitimate (i.e. between 0 and 1) equilibrium. Second, if $\beta_1 < \beta_3 < 0$ then $0 < \hat{p}^* < 1$ and therefore $f'(0) < 0$ and $f'(1) < 0$, that

is, both fixations are locally stable and \hat{p}^* separates the domains of attraction. Third, if $0 < \beta_3$ then
 244 $\hat{p}^* < 0$ and therefore $f'(0) > 0$ and $f'(1) < 0$; that is, fixation of the cooperator phenotype A is the
 only locally stable legitimate equilibrium.

246 Similarly, if $T_B > T_A$, then

$$\beta_1 > [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) > 0, \quad (38)$$

248 since $c < b$ and $1 > \alpha v$, and the signs of the cubic at positive and negative infinity are positive and
 negative, respectively. First, if $\beta_3 < 0$ then $\hat{p}^* < 0$ and therefore $f'(0) < 0$ and $f'(1) > 0$; that is,
 250 fixation of the defector phenotype $A = B$ is the only locally stable legitimate equilibrium. Second,
 if $0 < \beta_3 < \beta_1$ then $0 < \hat{p}^* < 1$ and therefore $f'(0) > 0$ and $f'(1) > 0$; that is, both fixations
 252 are locally unstable and \hat{p}^* is a stable polymorphic equilibrium. Third, if $\beta_1 < \beta_3$ then $\hat{p}^* > 1$ and
 therefore $f'(0) > 0$ and $f'(1) < 0$, and fixation of the cooperator phenotype A is the only locally
 254 stable legitimate equilibrium.

The following result summarizes these findings.

256 **Result 3** (Vertical, oblique, and horizontal transmission of cooperation). *The cultural evolution of*
a cooperator phenotype will follow one of the following scenarios, depending on the horizontal
 258 *transmission bias $T_A - T_B$ and the coefficients β_1 and β_3 :*

1. Fixation of cooperation: if (i) $T = T_A = T_B$ and $c < b \cdot \frac{\alpha T}{1-T}$; or (ii) if $T_A > T_B$ and $0 < \beta_3$; or
 260 (iii) if $T_A < T_B$ and $\beta_1 < \beta_3$.
2. Fixation of the defection: if (iv) $T = T_A = T_B$ and $c > b \cdot \frac{\alpha T}{1-T}$; or (v) if $T_A > T_B$ and $\beta_1 < \beta_3 < 0$;
 262 or (vi) if $T_A < T_B$ and $\beta_3 < 0$.
3. Coexistence of both phenotypes at \hat{p}^* : if (vi) $T_A < T_B$ and $0 < \beta_3 < \beta_1$.
- 264 4. Fixation of either phenotype depending on initial frequency: if (vii) $T_A > T_B$ and $\beta_3 < \beta_1$.

Discussion

266 We hypothesized that non-vertical transmission can explain the evolution of cooperation and evaluated
 this hypothesis using a deterministic discrete-time evolutionary model with fitnesses in the form of
 268 payoffs from a prisoner's dilemma game.. Under oblique and horizontal transmission, horizontal
 transmission bias for the cooperative phenotype was found to be sufficient and necessary for evolution of
 270 cooperation (Result 1). Under horizontal and vertical cultural transmission, cooperation, or defection
 can fix, or coexist at a stable polymorphism, depending on the relationship between the cost and
 272 benefit of cooperation, the horizontal bias, and the correlation between cooperation and transmission
 (Result 2). Under a combination of vertical, oblique, and horizontal transmission the dynamics are
 274 much more complicated. However, we show that under some conditions cooperation can evolve, and
 can even be maintained in stable coexistence with defection (Result 3).

276 This study was partially inspired by the work of Lewin-Epstein et al. (2017), who hypothesised that
 microbes that manipulate their hosts to act altruistically can be favored by selection, and may play a role
 278 in the widespread occurrence of cooperative behavior. Indeed, it has been shown that microbes can
 mediate behavioral changes in their hosts (Dobson, 1988; Poulin, 2010). Therefore, natural selection
 280 on microbes may favor manipulation of the host so that it cooperates with others. Microbes can be
 transmitted *horizontally* from one host to another during host interactions, and following horizontal
 282 transfer, the recipient host may carry microbes that are closely related to the microbes of the donor
 host, even when the two hosts are (genetically) unrelated (Lewin-Epstein et al., 2017). Microbes can
 284 also be transferred vertically, from parent to offspring, and a microbe that induces its host to cooperate
 with another host, and thereby increases the latter's fitness, will increase its vertical transmission

286 from the receiving individual. Kin selection among microbes could therefore favor those that induce cooperative behavior in their hosts, thereby increasing the transmission of their microbial kin.

288 Eshel and Cavalli-Sforza (1982) showed that with assortative meeting, namely, a probability m that individuals interact within their phenotypic group, cooperation can evolve if $c < b \cdot m$. Our results
 290 highlight another possibility for assortative meeting, namely, individuals interacting at rate α with their cultural partners, resulting in horizontal transmission. We show that high levels of assortative meeting
 292 significantly increase the potential for evolution of cooperation. With a high enough α , cooperation can increase when initially rare (although it will not fix) even when there is horizontal bias against
 294 cooperation ($\alpha > (c(1 - T_B) + (T_B - T_A))/bT_A$, see Result 2)

An important implication of our results is that cooperation can evolve even in a fully mixed population (i.e., in an unstructured population), without repeated interactions or individual recognition. This highlights the potential importance of non-vertical cultural transmission for explaining complex evolutionary phenomena, and furthers our understating of the cultural evolution of cooperation.

Acknowledgements

300 We thank Lilach Hadany and Ayelet Shavit for discussions and comments. This work was supported in part by the Israel Science Foundation 552/19 (YR), and Minerva Stiftung Center for Lab Evolution (YR).

302 Appendices

Appendix A

304 We want to find the frequency of juveniles with phenotype A in next generation \hat{p}' as a function of frequency of juveniles with phenotype A in the current generation \hat{p} . Starting from Equation 4,

$$306 \quad \hat{p}' = v\tilde{p}' + (1 - v)p', \quad (\text{A1})$$

we substitute p' using Equation 6 and \tilde{p}' using Equation 9, we have

$$\begin{aligned} \hat{p}' = & \frac{v}{\bar{w}} \left\{ \hat{p}^2(1 + b - c) [1 - (1 - \hat{p})(1 - \alpha)T_B] \right\} \\ & + \frac{v}{\bar{w}} \left\{ \hat{p}(1 - \hat{p})(1 - c) [\hat{p}(1 - \alpha)T_B + 1 - T_B] \right\} \\ 308 \quad & + \frac{v}{\bar{w}} \left\{ \hat{p}(1 - \hat{p})(1 + b) [\hat{p}(1 - \alpha) + \alpha] T_A \right\} \\ & + \frac{v}{\bar{w}} (1 - \hat{p})^2 \hat{p}(1 - \alpha)T_A \\ & + (1 - v)\hat{p}^2(T_B - T_A) + (1 - v)\hat{p}(1 + T_A - T_B), \end{aligned} \quad (\text{A2})$$

where $\bar{w} = 1 + \hat{p}(b - c)$. We define $f(\hat{p})$ as

$$310 \quad f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) \quad (\text{A3})$$

Using *SymPy* (Meurer et al., 2017), a Python library for symbolic mathematics, we simplify Equation A3 to eqs. 31-32.

Appendix B

314 Denote $f(p) = \lambda(p' - p)$, where $\lambda > 0$, and assume $f(p^*) = 0$; i.e., p^* is an equilibrium. We want a condition for $|p' - p^*| < |p - p^*|$.

316 If $p > p^* = 0$, we want a condition for $p' < p$, or $\frac{p'}{p} < 1$, or $\lambda \frac{p' - p}{p} < 0$, or $\frac{f(p)}{p} < 0$. Using a linear approximation for $f(p)$ near 0, we have

$$\begin{aligned} p' < p &\Leftrightarrow \\ \frac{f'(0) \cdot p + O(p^2)}{p} < 0 &\Leftrightarrow \\ f'(0) + O(p) &< 0. \end{aligned} \tag{B1}$$

Therefore, by definition of big-O notation, if $f'(0) < 0$ then there exists $\epsilon > 0$ such that for any $0 < p < \epsilon$, it is guaranteed that $0 < p' < p$, that is, p' is closer than p to zero.

If $p < p^* = 1$, we want a condition for $1 - p' < 1 - p$, or $\frac{1 - p'}{1 - p} < 1$, or $\lambda \frac{-(p' - p)}{1 - p} < 0$, or $-\frac{f(p)}{1 - p} < 0$. Using a linear approximation for $f(p)$ near 1, we have

$$\begin{aligned} 1 - p' < 1 - p &\Leftrightarrow \\ \frac{f'(1)(p - 1) + O((p - 1)^2)}{p - 1} < 0 &\Leftrightarrow \\ f'(1) - O(1 - p) &< 0. \end{aligned} \tag{B2}$$

324 Therefore, if $f'(1) < 0$ then there exists $\epsilon > 0$ such that for any $1 - \epsilon < 1 - p < 1$ it is guaranteed that $1 - p' < 1 - p$, that is, p' is closer than p to one.

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	$\phi_2 = A$	$\phi_2 = B$
$\phi_1 = A$	$1 + b - c$	$1 - c$
$\phi_1 = B$	$1 + b$	1

Table 1: **Payoff matrix for prisoner's dilemma.** The fitness of phenotype ϕ_1 when interacting with phenotype ϕ_2 . A is a cooperative phenotype, B is a defector phenotype, b is the benefit gained by an individual interacting with a cooperator, and c is the cost of cooperation. $b > c > 0$.

Phenotype ϕ_1	Phenotype ϕ_2	Frequency	Fitness of ϕ_1	$P(\phi_1 = A)$ via horizontal transmission:	
				from partner, α	from population, $(1 - \alpha)$
A	A	\hat{p}^2	$1 + b - c$	1	$\hat{p} + (1 - \hat{p})(1 - T_B)$
A	B	$\hat{p}(1 - \hat{p})$	$1 - c$	$1 - T_B$	$\hat{p} + (1 - \hat{p})(1 - T_B)$
B	A	$\hat{p}(1 - \hat{p})$	$1 + b$	T_A	$\hat{p}T_A$
B	B	$(1 - \hat{p})^2$	1	0	$\hat{p}T_A$

Table 2: **Interaction frequency, fitness, and transmission probabilities.**

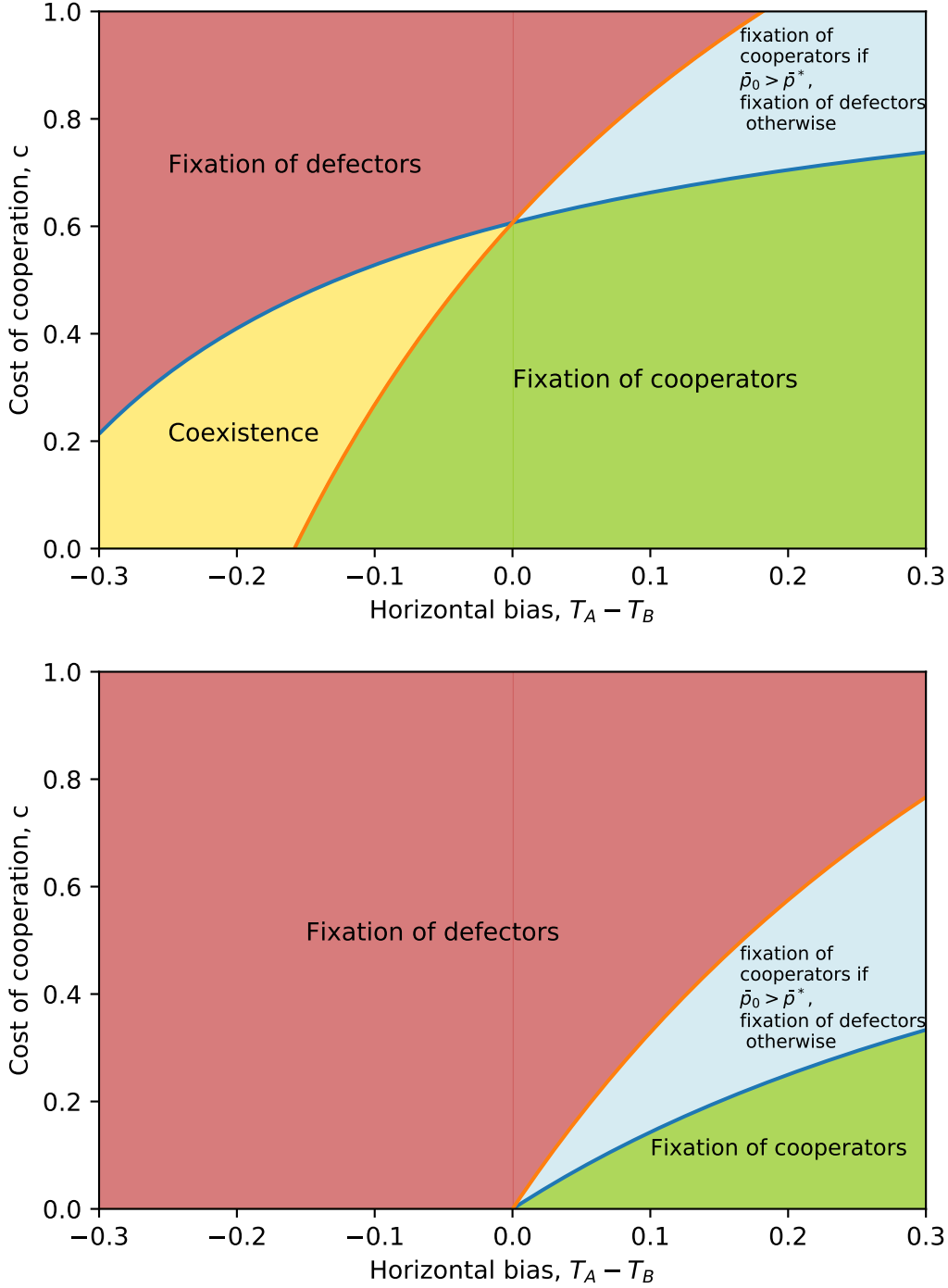


Figure 2: **Vertical and horizontal transmission.** The figure illustrates combinations of horizontal bias, $T_A - T_B$, and cost of cooperation, c , that lead to either global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial frequencies (blue), or coexistence of cooperation and defection (yellow). The blue and orange curves show the cost boundaries γ_1 and γ_2 (Equation 24). Here, benefit of cooperation is $b = 1.3$, horizontal transmission of cooperation $T_A = 0.4$, c and T_B vary on the y- and x-axes. **Up:** With $\alpha = 0.7 > 0$, coexistence is possible (yellow). **Down:** With $\alpha = 0$, coexistence is not possible.

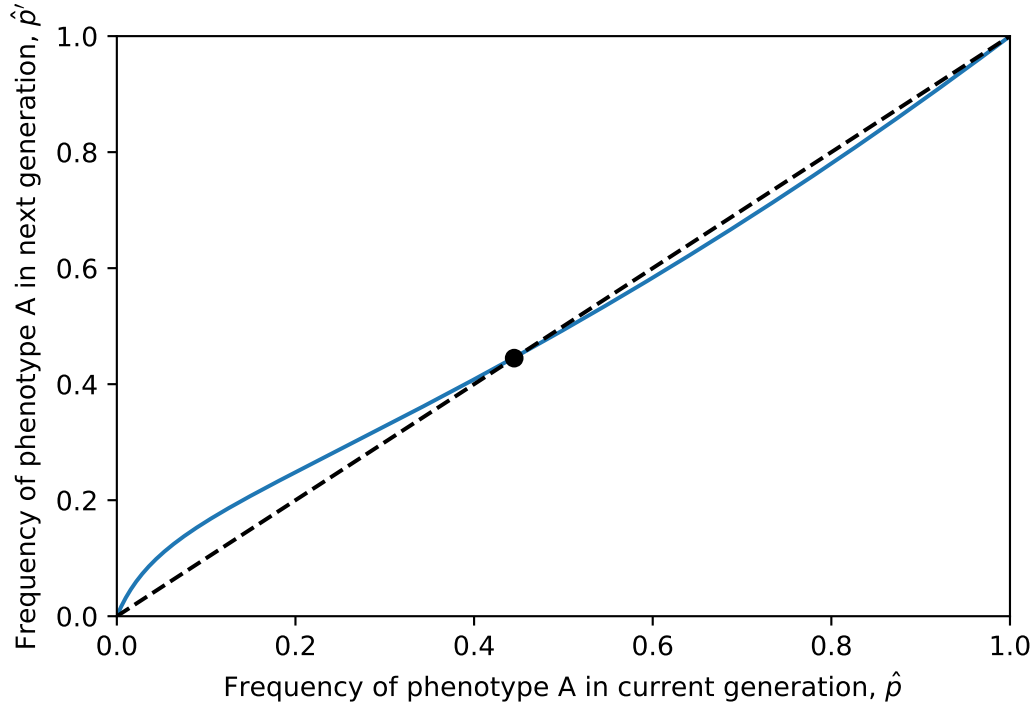


Figure 3: **Stable coexistence between cooperation and defection.** The frequency of the cooperative phenotype A among juveniles in the next generation \hat{p}' is plotted in blue as a function of the frequency in the current generation \hat{p} for $T_A < T_B$ and $\gamma_2 < c < \gamma_1$. The line of $\hat{p}' = \hat{p}$ is in dashed black. The curve and dashed line intersect at the equilibrium \hat{p}^* . The blue curve is above the black dashed line $\hat{p} < \hat{p}^*$, so that the frequency increases towards \hat{p}^* . The blue curve is below the black dashed line when $\hat{p} > \hat{p}^*$, so that the frequency decreases towards \hat{p}^* .

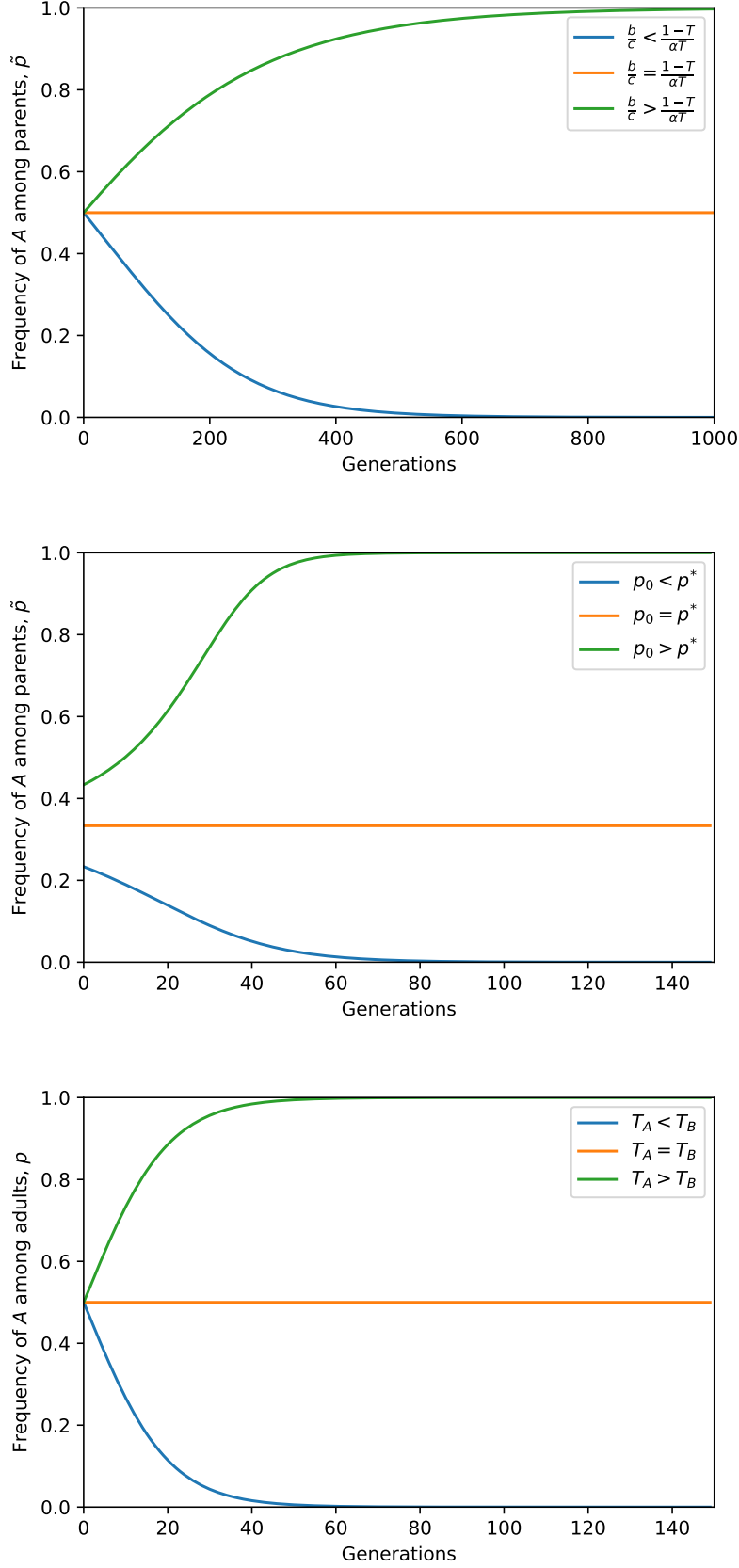


Figure 4: **Numerical results for cultural evolution of cooperation.** Shown are dynamics of (a-b) \tilde{p} , the frequency of parents with cooperative phenotype A; (c) p , the frequency of adults with cooperative phenotype A. The figure demonstrates fixation of cooperation (green), extinction of cooperation (blue), and stable coexistence of cooperators and defectors (orange). Parameters: (a) $v = 1$, $T_A = T_B = T$, $\alpha \neq 0$; (b) $v = 1$, $\alpha = 0$; (c) $v = 0$.