

# Cultural Transmission Can Explain the Evolution of Cooperative Behavior

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# Introduction

Cooperative behavior can harm 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), for example rats (Rice and Gainer, 1962) and birds (Krams et al., 2008). Evolution of cooperative behavior remains an important conundrum in evolutionary biology. Three major theories have been proposed to explain the evolution of cooperative behavior:

1. *Kin selection* theory posits that natural selection can favor cooperation between related individuals. The importance of relatedness to the evolution of cooperation and altruism was shown by Hamilton (1964). According to Hamilton, an allele that determines altruistic behavior should increase in frequency when the reproductive cost to the actor that cooperates,  $c$ , is less than the benefit to the recipient,  $b$ , times the genetic relatedness between the recipient and the actor,  $r$ . This is also known as Hamilton's Rule:

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

There is an ongoing debate about the extent to which kin selection explains the evolution of cooperation and altruism. For example, it has been suggested that it can explain the cooperative behavior of worker castes of eusocial insects like the honey bee. The most significant argument against kin selection is that in some cases cooperation among unrelated individuals appears to have evolved (Wilson, 2005). According to Wilson (2005), this makes Hamilton's rule incomplete, although Foster et al. (2006) reject this claim and argue that altruism cannot evolve without relatedness. They refer to Hamilton, who claimed that relatedness can arise without recent common ancestry. Wilson (2005) also criticizes kin selection on the grounds that environmental or ecological factors are probably more important than relatedness in determining social actions. However, Foster et al. (2006) argue that kin selection does not ignore ecology, and Hamilton's rule suggests that environmental factors causing a high benefit-to-cost ratio will favor cooperation.

2. *Reciprocity* entails that repeated interactions or individual recognition are key components of the evolution of cooperation. In *direct reciprocity* there are repeated encounters between the same two individuals, and at every encounter each individual has a choice between cooperation and defection. Hence, it may eventually pay off to cooperate if it may cause your partner to cooperate in the future. This game-theoretic framework, known as the *repeated prisoner's dilemma*, can only lead to the evolution of cooperation if the cost is less than the benefit  $b$  times the probability of another encounter between the same two individuals,  $w$ ,

$$c < b \cdot w. \quad (2)$$

Direct reciprocity assumes that both players are in a position to cooperate, but it can not explain cooperation in asymmetric interactions such as human philanthropy.

*Indirect reciprocity* has also been suggested to explain the evolution of cooperation. Nowak (2006) claims that direct reciprocity is like a barter economy based on the immediate exchange of goods, while indirect reciprocity resembles the invention of currency. The currency that "fuels the engines" of indirect reciprocity is *reputation*. However, reciprocity assumes repeated interactions and therefore has difficulty in explaining the evolution of cooperation if interactions are not repeated.

3. *Group selection* theory posits that cooperation is favored because it imparts an advantage to the whole group, if selection acts at the group level in addition to the individual level. A common model for group selection divides the population into groups in which there are cooperators that help other group members and defectors that do not. Individuals reproduce proportionally to their fitness, and offspring are added to the same group as their parents. If a group reaches a certain size it can split to two groups, so groups that grow faster will split more often. Groups with cooperators grow faster

than groups without cooperators, and cooperation can evolve in this model when the cost  $c$  is less than the benefit  $b$  times the ratio between the the number of groups  $m$  and the sum of  $m$  and the maximum group size  $n$ ,

$$c < b \cdot \frac{m}{m + n}. \quad (3)$$

Group selection has been criticized by biologists who advocate a gene-centered view of evolution. It has also been criticized because for cooperation to take over the population it must have higher fitness than defection, while under group selection theory the fitness of cooperators at the individual level is lower than the fitness of defectors. Thus a trait with a lower fitness taking over the population is a contradiction Eldakar and Wilson (2011) reject this argument, claiming that it is a tautology and does not qualify as an argument against group selection. The distinction between individual and group selection requires a comparison of fitness differentials within and between groups in a multi-group population, and when a trait evolves by group selection, despite having lower fitness within a group, that group might have higher average fitness in competition with other groups, all things considered.

These theories assume that cooperation is genetically determined, which raises the question: *Is it possible that cooperation is determined by non-genetic factors?* Culture has significant impact on the behavior of humans (Ihara and Feldman, 2004; Jeong et al., 2018) as well as non-human animals (Bonner, 2018). Here we attempt to determine to what extent the evolution of cooperative behavior can be explained by *cultural transmission*, which allows an individual to acquire attitudes and 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. They showed that under vertical (parent-to-offspring) cultural transmission, Hamilton's rule does not govern the evolution of parent-to-offspring or sib-to-sib altruism.

*Non-vertical transmission* may be either horizontal or oblique: horizontal transmission occurs between individuals from the same generation, while oblique transmission occurs from adults to unrelated offspring. Evolution under either of these transmission models can be more rapid than under pure vertical transmission (Cavalli-Sforza and Feldman, 1981; Ram et al., 2018). Lewin-Epstein et al. (2017) have demonstrated that non-vertical transmission, mediated by microbes that manipulate their host behavior, can help to explain the evolution of cooperative behavior. Interestingly, 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).

Here we hypothesize that non-vertical cultural transmission can explain the evolution of cooperation. To test this hypothesis, we suggest a model in which behavioral changes are mediated by cultural transmission that can occur during social interactions. For example, if an individual interacts with a cooperative individual, it might learn that cooperation is a positive behavior and will be cooperative in the future. We develop cultural evolution models that include both vertical and non-vertical transmission of cooperation and investigate these models using mathematical analysis and simulations. Our results demonstrate cultural transmission can facilitate the evolution of cooperation even when genetic transmission cannot. These results suggest that further research on the evolution of cooperation should account for non-vertical transmission and that treatment of cooperation as a cultural, rather than genetic trait, can lead to a better understanding of this important and enigmatic phenomenon.

## 98 Models

We focus on the evolution of cooperation in a fully mixed population where cooperation is modeled using the *prisoner's dilemma*.

Consider a very large population whose members are characterized by their phenotype  $\phi$ , 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  $\phi$  and assuming uni-parental inheritance, the conditional probability that the phenotype  $\phi'$  of the offspring is  $A$  is

$$P(\phi' = A \mid \phi) = \begin{cases} v + (1 - v)p, & \text{if } \phi = A \\ (1 - v)p, & \text{if } \phi = B \end{cases}, \quad (4)$$

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 with  $\tilde{p}$ . Therefore, the frequency  $\hat{p}$  of phenotype  $A$  among juveniles (after selection and vertical and oblique transmission) is

$$\begin{aligned} \hat{p} &= \tilde{p}[v + (1 - v)p] + (1 - \tilde{p})[(1 - v)p] \\ &= v\tilde{p} + (1 - v)p. \end{aligned} \quad (5)$$

Individuals 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  $b > c > 0$ . **Table 1** shows the payoff matrix, i.e. the fitness of an individual with phenotype  $\phi_1$  when interacting with a partner of phenotype  $\phi_2$ .

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

Table 1: **Payoff matrix for prisoner's dilemma.** The fitness of phenotype  $\phi_1$  when interacting with phenotype  $\phi_2$ .  $A$  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.  $b > c > 0$ .

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 peers. It may occur between social partners with probability  $\alpha$ , or between a random pair with probability  $1 - \alpha$  (see **Figure 1**). Horizontal transmission is not always successful, as one peer 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**).

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

Phenotype $\phi_1$	Phenotype $\phi_2$	Frequency	Fitness of $\phi_1$	$P(\phi_1 = A)$ via horizontal transmission:	
				from partner, $\alpha$	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.**

transmission, is

$$\begin{aligned}
 p' = & \hat{p}^2[\alpha + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
 & + \hat{p}(1 - \hat{p})[\alpha(1 - T_B) + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
 & + (1 - \hat{p})\hat{p}[\alpha T_A + (1 - \alpha)\hat{p}T_A] \\
 & + (1 - \hat{p})^2[(1 - \alpha)\hat{p}T_A],
 \end{aligned} \tag{6}$$

which simplifies to

$$p' = \hat{p}^2(T_B - T_A) + \hat{p}(1 + T_A - T_B). \tag{7}$$

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

$$\begin{aligned}
 \bar{w}p' = & \hat{p}^2(1 + b - c)[\alpha + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
 & + \hat{p}(1 - \hat{p})(1 - c)[\alpha(1 - T_B) + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
 & + (1 - \hat{p})\hat{p}(1 + b)[\alpha T_A + (1 - \alpha)\hat{p}T_A] \\
 & + (1 - \hat{p})^2[(1 - \alpha)\hat{p}T_A],
 \end{aligned} \tag{8}$$

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

$$\bar{w} = 1 + \hat{p}(b - c). \tag{9}$$

Equation 8 can be simplified to

$$\begin{aligned}
 \bar{w}p' = & \hat{p}^2(1 + b - c)(1 - (1 - \hat{p})(1 - \alpha)T_B) \\
 & + \hat{p}(1 - \hat{p})(1 - c)(\hat{p}(1 - \alpha)T_B + 1 - T_B) \\
 & + (1 - \hat{p})\hat{p}(1 + b)(\hat{p}(1 - \alpha) + \alpha)T_A \\
 & + (1 - \hat{p})^2\hat{p}(1 - \alpha)T_A.
 \end{aligned} \tag{10}$$

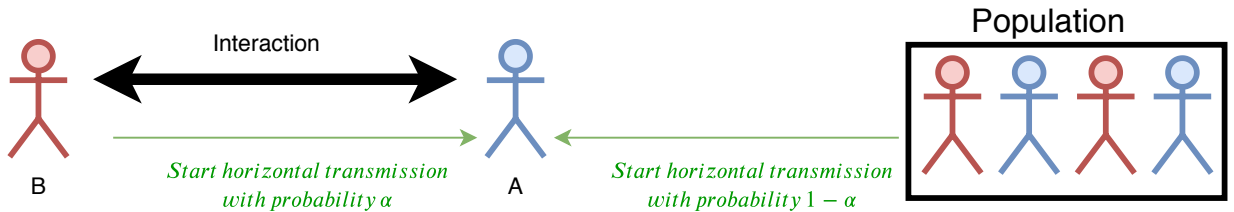


Figure 1: **Cultural horizontal transmission.** Transmission occurs between interacting partners with probability  $\alpha$  (left) or between two random peers with probability  $1 - \alpha$ .

## 136 Results

### Without Oblique Transmission

138 With only vertical and horizontal transmission, i.e.  $v = 1$ , Equation 5 becomes  $\hat{p} = \tilde{p}$ , and Equation 10 for the change in frequency  $p'$  of phenotype  $A$  among parents can be written as

$$\begin{aligned}
 \bar{w}\tilde{p}' &= \tilde{p}^2(1 + b - c)[1 - (1 - \tilde{p})(1 - \alpha)T_B] \\
 &+ \tilde{p}(1 - \tilde{p})(1 - c)[\tilde{p}(1 - \alpha)T_B + 1 - T_B] \\
 &+ \tilde{p}(1 - \tilde{p})(1 + b)[\tilde{p}(1 - \alpha) + \alpha]T_A \\
 &+ (1 - \tilde{p})^2\tilde{p}(1 - \alpha)T_A.
 \end{aligned}
 \tag{11}$$

We find the following result and corollaries.

142 **Result 1: Vertical and horizontal transmission of cooperation.** From Equation 11, if

$$c \cdot (1 - T_B) < b \cdot \alpha T_A + (T_A - T_B)[1 + b\tilde{p}(1 - \alpha)], \tag{12}$$

144 then  $\tilde{p}' > \tilde{p}$ , and the frequency of the cooperator phenotype  $A$  among parents increases every generation.

146 **Corollary 1.1: Symmetric horizontal transmission.** If  $T = T_A = T_B$ , then

$$c < b \cdot \frac{\alpha T}{1 - T}, \tag{13}$$

148 which can be seen as a cultural version of *Hamilton's rule* (Equation 1), where  $r_H = \alpha T / (1 - T)$  can be thought of as *horizontal relatedness*. Therefore, if the cost  $c$  is less than the benefit  $b$  times the horizontal relatedness  $r_H$ , then cooperation will take over of the population (see **Figure 2a**).

**Corollary 1.2: Complete correlation between transmission and cooperation.**

152 In this case  $\alpha = 1$ , and horizontal transmission can only occur as a result of cooperative interactions. Therefore, Equation 12, which determines the conditions for evolution of cooperation, becomes

$$c \cdot (1 - T_B) < b \cdot T_A + (T_A - T_B). \tag{14}$$

This is equivalent to a result by Lewin-Epstein et al. (2017, eq. 1).

156 Equation 14 can be written as

$$1 - (1 - T_B)(1 - c) < T_A \cdot (1 + b), \tag{15}$$

158 which provides an interesting interpretation for the success of cooperation. Consider an interaction between two individuals: a cooperator and a defector.  $(1 - T_B)(1 - c)$  is the probability that the cooperator remains cooperative and also reproduces. Therefore,  $1 - (1 - T_B)(1 - c)$  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.  $T_A \cdot (1 + b)$  is the probability that the defector becomes cooperative and reproduces. This is the effective benefit for cooperation from this interaction. So, Equation 15 means that cooperation can evolve if the effective cost is less than the effective benefit.

**Corollary 1.3: No correlation between transmission and cooperation.**

166 In this case  $\alpha = 0$ , and horizontal transmission is entirely independent from cooperative interactions. Then, Equation 12 becomes

$$c \cdot (1 - T_B) < b \cdot \tilde{p} (T_A - T_B) + (T_A - T_B). \tag{16}$$

Therefore, since all the parameters are positive, cooperation cannot take over the population (and furthermore will become extinct) if cooperators do not have a horizontal transmission bias, i.e. if  $T_A \leq T_B$ . When such a bias does exist,  $T_A > T_B$ , then cooperation will evolve if  $\tilde{p} > \tilde{p}^*$ , where (see also **Figure 2b**)

$$\tilde{p}^* = \frac{c}{b} \cdot \frac{1 - T_B}{T_A - T_B} - \frac{1}{b}. \quad (17)$$

A sufficient condition for evolution of cooperation is that  $\tilde{p}^* < 0$ , namely

$$c < \frac{T_A - T_B}{1 - T_B}. \quad (18)$$

## Without Vertical Transmission

With only oblique and horizontal transmission, i.e.  $v = 0$ , Equation 5 becomes  $\hat{p} = p$  and Equation 7 becomes

$$p' = p^2(T_B - T_A) + p(1 + T_A - T_B), \quad (19)$$

which gives the following result.

**Result 2: Oblique and horizontal transmission of cooperation.** If there is a horizontal transmission bias in favor of cooperation, namely

$$T_A > T_B, \quad (20)$$

then  $p' > p$ , and the frequency of the cooperator phenotype among adults increases every generation. Therefore, cooperation will evolve if the cooperator phenotype has a horizontal transmission bias (see **Figure 2c**).

## With Vertical and Oblique Transmission

In this case  $0 < v < 1$ , and the recursion system is more complex. Therefore, we focus on local stability, rather than global stability. To proceed, we note that Equation 5 can give  $\hat{p}'$  as a function of both  $p'$  and  $\tilde{p}'$ , Equation 7 gives  $p'$  as a function of  $\tilde{p}$ , and Equation 10 gives  $\tilde{p}'$  as a function of  $\hat{p}$ . Combining these equations, we find an equation for  $\hat{p}'$  as a function of  $\hat{p}$ , see Appendix B. We then determine the equilibria, which are solutions of  $\hat{p}' = \hat{p}$ , and analyse their local stability.

We apply Equation 5, Equation 7, and Equation 10 to obtain the function  $f(\hat{p})$ , see Appendix B:

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = \beta_1 \hat{p}^3 + \beta_2 \hat{p}^2 + \beta_3 \hat{p}, \quad (21)$$

where

$$\begin{aligned} \beta_1 &= [c(1 - v) - b(1 - \alpha v)](T_A - T_B), \\ \beta_2 &= -\beta_1 - \beta_3, \\ \beta_3 &= \alpha b v T_A - c v (1 - T_B) + (T_A - T_B). \end{aligned} \quad (22)$$

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

$$f(\hat{p}) = \hat{p}(1 - \hat{p})[\alpha b v T - c v (1 - T)]. \quad (23)$$

Clearly the only two equilibria are the fixations of either phenotype,  $\hat{p} = 0$  and  $\hat{p} = 1$ . These equilibria are locally stable if  $f'(\hat{p}) < 0$  (Appendix C). Therefore, we find the derivative,

$$f'(\hat{p}) = (1 - 2\hat{p})[\alpha bvT - cv(1 - T)], \quad (24)$$

and investigate its sign at the equilibria,

$$\begin{aligned} f'(0) &= \alpha bvT - cv(1 - T), \\ f'(1) &= -\alpha bvT + cv(1 - T). \end{aligned} \quad (25)$$

Therefore with symmetric horizontal transmission, fixation of the cooperative phenotype ( $\hat{p} = 1$ ) occurs under the same condition as Corollary 1.1, Equation 13.

In the general case where  $T_A \neq T_B$ , the coefficient  $\beta_1$  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  $\hat{p} = 1$ . By solving  $f(\hat{p})/[\hat{p}(1 - \hat{p})] = \beta_3 - \beta_1\hat{p} = 0$  we find the third equilibrium

$$\hat{p}^* = \frac{\beta_3}{\beta_1}. \quad (26)$$

Note that the sign of this cubic at positive (negative) infinity is equal (opposite) to the sign of  $\beta_1$ . If  $T_A > T_B$ , then

$$\beta_1 < [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) < 0, \quad (27)$$

since  $c < b$  and  $1 > \alpha v$ , the sign of the cubic at positive and negative infinity is 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  $\hat{p}^* < 0$  and therefore  $f'(0) > 0$  and  $f'(1) < 0$ , that is, fixation of the cooperators phenotype  $A$  is the only locally stable legitimate equilibrium.

Similarly, if  $T_B > T_A$ , then

$$\beta_1 > [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) > 0, \quad (28)$$

since  $c < b$ , and  $1 > \alpha v$ . So the sign of the cubic at positive and negative infinity is positive and negative, respectively. First, if  $\beta_3 < 0$  then  $\hat{p}^* < 0$  and therefore  $f'(0) < 0$  and  $f'(1) > 0$ , that is, 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 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  $f'(1) < 0$ , that is, fixation of the cooperators phenotype  $A$  is the only locally stable legitimate equilibrium.

The following result summarizes these findings.

**Result 3: Oblique and vertical transmission of cooperation.** The cultural evolution of a cooperators phenotype will follow one of the following scenarios, depending on the horizontal transmission bias  $T_A - T_B$  and the coefficients  $\beta_1$  and  $\beta_3$ :

1. *Fixation of the cooperative phenotype A,*

(a) if  $T = T_A = T_B$  and  $c < b \cdot \frac{\alpha T}{1 - T}$ , or

(b) if  $T_A > T_B$  and  $0 < \beta_3$ , or



(c) if  $T_A < T_B$  and  $\beta_1 < \beta_3$ .

238 2. *Fixation of the defector phenotype B,*

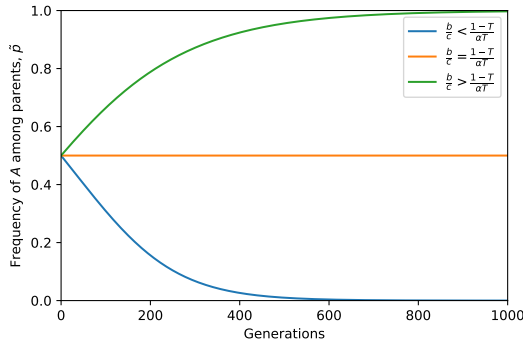
(a) if  $T = T_A = T_B$  and  $c > b \cdot \frac{\alpha T}{1-T}$ , or

240 (b) if  $T_A > T_B$  and  $\beta_1 < \beta_3 < 0$ , or

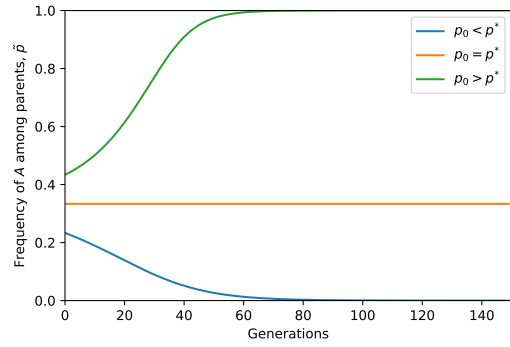
(c) if  $T_A < T_B$  and  $\beta_3 < 0$ .

242 3. *Protected polymorphism, or co-existence of both phenotypes,* if  $T_A < T_B$  and  $0 < \beta_3 < \beta_1$ .

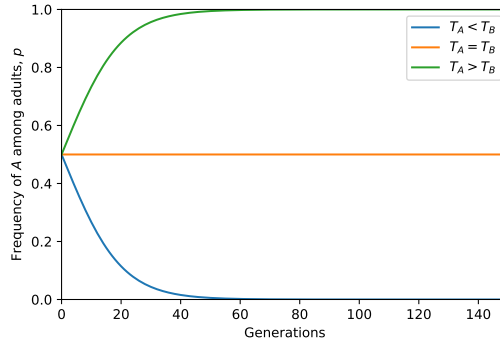
4. *Fixation of either phenotype depending on initial frequency,* if  $T_A > T_B$  and  $\beta_3 < \beta_1$ .



(a)  $\nu = 1, T_A = T_B = T, \alpha \neq 0$



(b)  $\nu = 1, \alpha = 0$



(c)  $\nu = 0$

Figure 2: **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 co-existence of cooperators and defectors (orange).

## 244 Discussion

We hypothesized that non-vertical transmission can explain the evolution of cooperation. We studied fully mixed and very large populations with a prisoner's dilemma payoff. We found that under horizontal and vertical cultural transmissions, if Equation 12 is satisfied, cooperation will take over fully mixed populations (Result 1). Under oblique and horizontal transmission, horizontal transmission bias for the cooperative phenotype is sufficient and necessary for evolution of cooperation (Result 2, Equation 20). Under a combination of vertical, oblique, and horizontal transmission the dynamics are further complicated. Yet, we find that cooperation can evolve and in some cases be maintained together with defection (Result 4). Importantly, our results demonstrate that cooperation can evolve

even in a fully mixed population (i.e. in an unstructured population), without repeating interactions  
254 or individual recognition. These results significantly further our understating of the cultural evolution  
of cooperation.

256 This study was partially inspired by Lewin-Epstein et al. (2017). They hypothesised that microbes  
that manipulate their hosts to act altruistically can be favored by selection, and may play a role in  
258 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  
260 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  
262 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  
264 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 the vertical transmission of the  
266 microbes of the receiving individual. Kin selection among microbes could therefore favor microbes  
that induce cooperative behavior in their hosts, thereby increasing the transmission of their microbial  
268 kin.

Eshel and Cavalli-Sforza (1982) have studied a relevant model for the evolution of cooperative behavior  
270 under vertical transmission. Their model included *assortative meeting*, or non-random encounters.  
This assortment may be due, for example, to population structure or active partner choice. In this  
272 model, cooperative behavior can evolve if (Eshel and Cavalli-Sforza, 1982, eq. 3.2)

$$c < b \cdot m, \quad (29)$$

274 where  $b$  and  $c$  are the benefit and cost of cooperation, and  $m$  is the fraction of the population that meets  
an individual of the same phenotype rather than a random individual<sup>1</sup>. As a version of Hamilton's  
276 rule,  $m$  can be interpreted as the effective relatedness. In our Corollary 1.1 (Equation 13), cooperation  
evolves if  $c < b \cdot \alpha T / (1 - T)$ . So in our model  $\alpha T / (1 - T)$  is the effective relatedness, which is  
278 affected by  $\alpha$ , the correlation between transmission and interaction, and  $T$ , the horizontal transmission  
rate.

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<sup>1</sup>In 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).

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## 334 Appendices

### Appendix A

- 336 We start with Equation 11 and we want to investigate when  $\tilde{p} < \tilde{p}'$ , that is, when

$$\begin{aligned} \bar{w}\tilde{p} &< \tilde{p}^2(1+b-c)(1-(1-\tilde{p})(1-\alpha)T_B) \\ &+ \tilde{p}(1-\tilde{p})(1-c)(\tilde{p}(1-\alpha)T_B + 1 - T_B) \\ &+ \tilde{p}(1-\tilde{p})(1+b)(\tilde{p}(1-\alpha) + \alpha)T_A \\ &+ (1-\tilde{p})^2\tilde{p}(1-\alpha)T_A. \end{aligned} \quad (A1)$$

- 338 First divide by  $\tilde{p}$  to obtain

$$\begin{aligned} \bar{w} &< \tilde{p}(1+b-c)(1-(1-\tilde{p})(1-\alpha)T_B) \\ &+ (1-\tilde{p})(1-c)(\tilde{p}(1-\alpha)T_B + 1 - T_B) \\ &+ (1-\tilde{p})(1+b)(\tilde{p}(1-\alpha) + \alpha)T_A \\ &+ (1-\tilde{p})^2(1-\alpha)T_A. \end{aligned} \quad (A2)$$

- 340 We know that the mean fitness  $\bar{w} = 1 + \tilde{p}(b-c)$ , thus Equation A2 becomes

$$\begin{aligned} 1 + \tilde{p}(b-c) &< \tilde{p}(1+b-c)(1-(1-\tilde{p})(1-\alpha)T_B) \\ &+ (1-\tilde{p})(1-c)(\tilde{p}(1-\alpha)T_B + 1 - T_B) \\ &+ (1-\tilde{p})(1+b)(\tilde{p}(1-\alpha) + \alpha)T_A \\ &+ (1-\tilde{p})^2(1-\alpha)T_A. \end{aligned} \quad (A3)$$

- 342 which we simplify to inequality Equation 12.

## Appendix B

344 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  $\hat{p}$ . We start from eq. 5,

$$346 \quad \hat{p}' = v\tilde{p}' + (1-v)p' \quad (\text{B1})$$

Substituting  $p'$  using eq. 7 and  $\tilde{p}'$  using eq. 10, we have

$$\begin{aligned} \hat{p}' = & \frac{v}{\bar{w}} \left\{ \hat{p}^2(1+b-c) \left[ 1 - (1-\hat{p})(1-\alpha)T_B \right] \right\} \\ & + \frac{v}{\bar{w}} \left\{ \hat{p}(1-\hat{p})(1-c) \left[ \hat{p}(1-\alpha)T_B + 1 - T_B \right] \right\} \\ 348 \quad & + \frac{v}{\bar{w}} \left\{ \hat{p}(1-\hat{p})(1+b) \left[ \hat{p}(1-\alpha) + \alpha \right] T_A \right\} \\ & + \frac{v}{\bar{w}} (1-\hat{p})^2 \hat{p} (1-\alpha) T_A \\ & + (1-v)\hat{p}^2(T_B - T_A) + (1-v)\hat{p}(1+T_A - T_B), \end{aligned} \quad (\text{B2})$$

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

350 We define  $f(\hat{p})$  to be

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) \quad (\text{B3})$$

352 Using *SymPy* (Meurer et al., 2017), a Python library for symbolic mathematics, we simplify Equation  
B3 to Equation 21 and Equation 22.

## 354 Appendix C

We show that  $f'(\hat{p}^*) < 0$  is a sufficient condition for local stability an equilibrium  $\hat{p}^*$ . We will write  
356  $f(\hat{p})$  as a Taylor approximation around the equilibrium  $\hat{p}^*$ .

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = f(\hat{p}^*) + f'(\hat{p}^*)(\hat{p} - \hat{p}^*) + R_2(\hat{p}) \quad (\text{C1})$$

358 Where  $R_2(\hat{p})$  is the remainder. Since  $\hat{p}^*$  is an equilibrium  $f(\hat{p}^*) = 0$ .

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = f'(\hat{p}^*)(\hat{p} - \hat{p}^*) + R_2(\hat{p}) \quad (\text{C2})$$

360 Neglecting the remainder(?) and we get:

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = f'(\hat{p}^*)(\hat{p} - \hat{p}^*) \quad (\text{C3})$$

362 And we get:

$$\begin{aligned} f'(\hat{p}^*) &= \bar{w} \left( \frac{\hat{p}' - \hat{p}}{\hat{p} - \hat{p}^*} \right) \\ &= \bar{w} \left( \frac{\hat{p}' - \hat{p}^* + \hat{p}^* - \hat{p}}{\hat{p} - \hat{p}^*} \right) = \bar{w} \left( \frac{\hat{p}' - \hat{p}^*}{\hat{p} - \hat{p}^*} - 1 \right). \end{aligned} \quad (\text{C4})$$

364 In order for the equilibrium  $\hat{p}^*$  to be stable we demand that if  $\hat{p} > \hat{p}^*$  then  $\hat{p}' - \hat{p}^* < \hat{p} - \hat{p}^*$  and if  
 $\hat{p} < \hat{p}^*$  we demand that  $-(\hat{p}' - \hat{p}^*) < -(\hat{p} - \hat{p}^*)$ . In other words,  $\frac{\hat{p}' - \hat{p}^*}{\hat{p} - \hat{p}^*} < 1$  for every  $\hat{p}$ . Therefore,

$$366 \quad f'(\hat{p}^*) = \bar{w} \left( \frac{\hat{p}' - \hat{p}^*}{\hat{p} - \hat{p}^*} - 1 \right) < 0. \quad (\text{C5})$$

Therefore,  $f'(\hat{p}^*)$  is a sufficient condition for stability of  $\hat{p}^*$ .