Cultural Transmission Can Explain the Evolution of Cooperation

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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.

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, for an allele that determines cooperative behavior to increase in frequency, the reproductive cost to the actor that cooperates, c, must be less than the benefit to the recipient, b, times the 'relatedness' between the recipient and the actor, r. This 'relatedness' coefficient r measures the correlation between the gene in the actor and the gene in the recipient. This condition is also known as Hamilton's rule:

$$c < b \cdot r. \tag{1}$$

Eshel and Cavalli-Sforza (1982) have studied a relevant model for the evolution of cooperative behavior under vertical transmission. Their model included *assortative meeting*, or non-random encounters. That is, if a fraction m of the population interacts with an individual of the same phenotype, and $1 - m$ interacts randomly. Such assortative meeting may be due, for example, to population structure or active partner choice. In their model, cooperative behavior can evolve if [1]. (Eshel and Cavalli-Sforza, 1982, eq. 3.2)

$$c < b \cdot m, \tag{2}$$

where b and c are the benefit and cost of cooperation Here, m takes the role of the relatedness r.

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 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

[1]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).

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 then genetic trait, can lead to a better understanding of this important and enigmatic phenomenon.

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 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

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

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

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

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 $c < b$. **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.

	$\phi_2 = A$	$\phi_2 = B$
$\phi_1 = A$	$1 + b - c$	$1 - c$
$\phi_1 = B$	$1 + b$	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. $b > c > 0$.

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 $2\hat{p}(1 - \hat{p})$.

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.**

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**).

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

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

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

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

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

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

Equation 7 can be simplified to

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

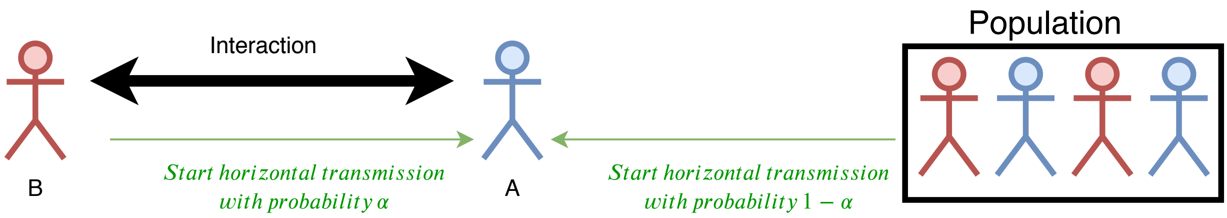


Figure 1: **Cultural horizontal transmission.** Transmission occurs between interacting partners with probability α (left) or between two random peers with probability $1 - \alpha$.

Results

Oblique and Horizontal Transmission

With only oblique and horizontal transmission, i.e. $v = 0$, Equation 4 becomes $\hat{p} = p$ and Equation 6 becomes

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

which gives the following result.

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*

$$T_A > T_B, \tag{11}$$

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

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 (see Figure 2c).

Vertical and Horizontal Transmission

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

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

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

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

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

and there are no additional equilibria.

Therefore, for cooperation to take over the population (for $\tilde{p} = 1$ to be globally stable) we require $\tilde{p}' > \tilde{p}$, that is,

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

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

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

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

$$(1 - c)(1 - T_B) + (1 + b)T_A > 1 \tag{16}$$

If $\alpha < 1$, we want to determine a condition for $\tilde{p}' > \tilde{p}$. We divide Equation 12 by $\tilde{p}$ and set $\bar{w} = 1 + \tilde{p}(b - c)$ to get

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

Rearranging, we get

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

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

$$\begin{aligned} &1 - (1 - \alpha)T_A - (1 + b)\alpha T_A - (1 - T_B)(1 - c) < \\ &\tilde{p}[-(1 + b - c)(1 - \alpha)T_B + (1 - c)(1 - \alpha)T_B + (1 + b)(1 - \alpha)T_A - (1 - \alpha)T_A]. \end{aligned} \tag{19}$$

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

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

Following the same steps to solve $\tilde{p}' = \tilde{p}$, we find that there can be a third, polymorphic equilibrium

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

Note that this is a legitimate equilibrium only if $0 < \tilde{p}^* < 1$.

Note that all parameters are positive. So, applying Equation 20, for $\tilde{p}' > \tilde{p}$ we require that either

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

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

We therefore have the following result and corollaries.

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

We define the initial frequency as $\tilde{p}_0$ and the cost boundaries

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

Applying eqs. 21, 22, and 23 we can summarize the possible outcomes:

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 $c < \gamma_2$.
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 $\gamma_1 < c$.
3. Coexistence of both phenotypes at $\tilde{p}^*$, if $T_A < T_B$ and $\gamma_2 < c < \gamma_1$.

Much of the literature on evolution of cooperation focuses on conditions for cooperation 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. $T_A = T_B$.

Corollary 1 (Condition for cooperation to increase from rarity)**.** *If the initial frequency of the cooperative phenotype if very close to zero, $\tilde{p}_0 \approx 0$, then its frequency will increase if*

$$T_A > T_B \;\; \textit{and} \;\; c < \gamma_1, \quad \textit{or} \quad T_A < T_B \;\; \textit{and} \;\; \gamma_2 < c < \gamma_1. \tag{25}$$

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, we get the following corollary that does have the form of Hamilton's rule.

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

$$c < b \cdot \frac{\alpha T}{1 - T}. \tag{26}$$

To verify, set $T_A = T_B$ in Equation 20.

This can be interpreted as a version of Hamilton's rule (Equation 1), where $\alpha T/(1-T)$ is the 'effective relatedness'. Figure 2a demonstrates this condition.

Corollary 3 (No assortment of transmission and cooperation)**.** *When $\alpha = 0$, then if 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 if high enough ($\tilde{p}_0 > \tilde{p}^*$).*

Here, the third equilibrium is

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

and the cost boundaries are

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

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 $\gamma_2(\alpha = 0) < \gamma_1(\alpha = 0) < 0 < c$. So 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 by setting $\tilde{p}' > \tilde{p}$, which gives*

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

This is proven in Equation 16. In this case there is complete assortment, and horizontal transmission always 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, Equation 29 is equivalent to $c < \gamma_1$. 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, Equation 29 is sufficient for increase in frequency of A up to $\tilde{p}^*(\alpha = 1) \approx \infty$.

Equation 29 can be written as

$$1 - (1 - c)(1 - T_B) < (1 + b)T_A, \tag{30}$$

which provides an interesting interpretation for the success of cooperation. Consider an interaction between two individuals: 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. $(1+b)T_A$ is the probability that the defector becomes cooperative and reproduces. This is the effective benefit for cooperation from this interaction. So, Equation 29 means 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. Therefore, we focus on local stability, rather than global stability. To proceed, we note that Equation 4 can give $\hat{p}'$ as a function of both p' and $\tilde{p}'$, Equation 6 gives p' as a function of $\tilde{p}$, and Equation 9 gives $\tilde{p}'$ as a function of $\hat{p}$. Combining these equations, we find an equation for $\hat{p}'$ as a function of $\hat{p}$, see Appendix A. We then determine the equilibria, which are solutions of $\hat{p}' = \hat{p}$, and analyse their local stability.

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

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

where

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

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,

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

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 B). Therefore, we find the derivative,

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

and investigate its sign at the equilibria,

$$f'(0) = \alpha bvT - cv(1-T),$$
$$f'(1) = -\alpha bvT + cv(1-T). \tag{35}$$

Therefore with symmetric horizontal transmission, fixation of the cooperative phenotype ($\hat{p} = 1$) occurs under the same condition as Corollary 1.1, Equation 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 $\hat{p} = 1$. By solving $f(\hat{p})/\left[\hat{p}(1-\hat{p})\right] = \beta_3 - \beta_1\hat{p} = 0$ we find the third equilibrium

$$\hat{p}^* = \frac{\beta_3}{\beta_1}. \tag{36}$$

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

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

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 cooperator phenotype A is the only locally stable legitimate equilibrium.

Similarly, if $T_B > T_A$, then

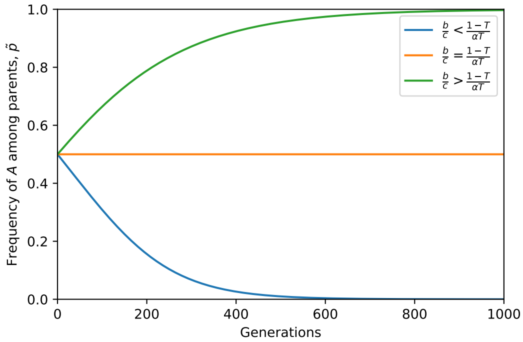
$$\beta_1 > [c(1-\alpha v) - b(1-\alpha v)](T_A - T_B) = (1-\alpha v)(c-b)(T_A - T_B) > 0, \tag{38}$$

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 cooperator phenotype A is the only locally stable legitimate equilibrium.

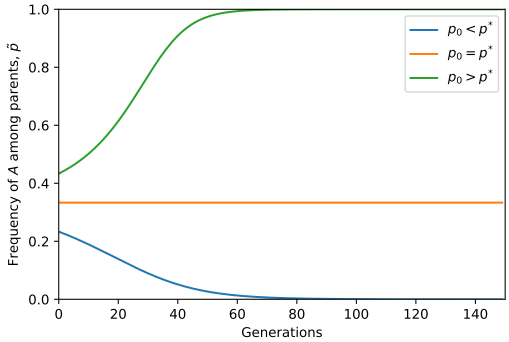
The following result summarizes these findings.

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 transmission bias $T_A - T_B$ and the coefficients β_1 and β_3:*

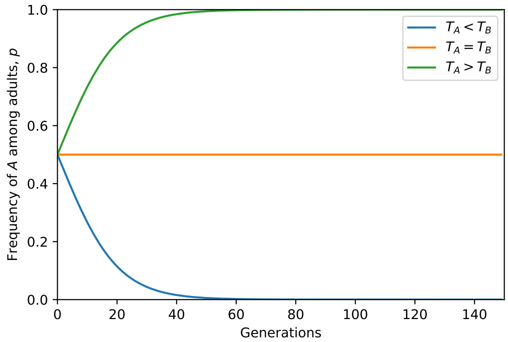
1. Fixation of cooperation, *if $T = T_A = T_B$ and $c < b \cdot \frac{\alpha T}{1-T}$; or if $T_A > T_B$ and* $0 < \beta_3$*; or if $T_A < T_B$ and $\beta_1 < \beta_3$.*
2. Fixation of the defection, *if $T = T_A = T_B$ and $c > b \cdot \frac{\alpha T}{1-T}$; or if $T_A > T_B$ and $\beta_1 < \beta_3 <$* 0*; or if $T_A < T_B$ and $\beta_3 < 0$.*
3. Coexistence of both phenotypes at $\hat{p}^*$, *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) $v = 1, T_A = T_B = T, \alpha \neq 0$



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



(c) $v = 0$

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)m and stable co-existence of cooperators and defectors (orange).

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 **??** 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 11). 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 or individual recognition. These results significantly further our understating of the cultural evolution of cooperation.

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 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 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 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 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 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 kin.

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). Therefore, other theories have been develop to explain the evolution of cooperation and altruism.

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,

$$c < b \cdot w. \tag{39}$$

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.

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,

$$c < b \cdot \frac{m}{m+n}. \tag{40}$$

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.

Eshel and Cavalli-Sforza (1982) have shown that with assortative meeting, i.e. probability m that individuals interact with within their phenotypic group, cooperation can evolve if $m > c/b$. In our Corollary 1.1 (Equation 26), cooperation evolves if $\alpha T/(1-T) > c/b$. So in our model $\alpha T/(1-T)$ is the effective relatedness, which is affected by α, the correlation between transmission and interaction, and T, the horizontal transmission rate.

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Appendices

Appendix A

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,

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

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

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

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

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) \tag{A3}$$

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

Appendix B

Denote $f(p) = \lambda(p'-p)$, where $\lambda > 0$, and assume $f(p^*) = 0$. We want a condition for $|p'-p^*| < |p-p^*|$.

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

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

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

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

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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