Non-Vertical Cultural Transmission and the Evolution of Cooperation

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Abstract

We construct models for the cultural evolution of cooperation in a well-mixed population with vertical, horizontal, and oblique transmission. Conditions are found for fixation of cooperation, fixation of defection, and stable coexistence between cooperation and defection, and comparisons are drawn with Hamilton's rule. A spatial model is constructed and its results are compared to the well-mixed model. We show that assortment between cooperation and horizontal transmission facilitates the evolution of cooperation and increases the population mean fitness.

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 demonstrated 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*:

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

Eshel and Cavalli-Sforza (1982) studied a related model for the evolution of cooperative behavior. 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 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 in Eq. 2 takes the role of the relatedness r in Eq. 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. They showed that under a combination of genetic and 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. For example, if the fidelity of cultural transmission of altruism is φ, then the condition for evolution of altruism in the case of sib-to-sib altruism is (Feldman et al., 1985, Eq. 16)

$$c < b \cdot \varphi - \frac{1 - \varphi}{\varphi}\,. \tag{3}$$

In this case φ takes the role of the relatedness r in Eq. 1, but the effective benefit $b \cdot \varphi$ is further reduced by $(1 - \varphi)/\varphi$.

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 be more rapid than under pure vertical transmission (Cavalli-Sforza and Feldman,

[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).

1981; Lycett and Gowlett, 2008; Ram et al., 2018). Lewin-Epstein et al. (2017) and Lewin-Epstein and Hadany (2020) 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). Importantly, their results depended on non-vertical transmission of the cooperation-determining microbes.

We therefore hypothesize that non-vertical cultural transmission can enhance 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. That is, if there exists assortative meeting in the choice of the social interaction partner, or assortative learning in choice of the cultural transmission partner. 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

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

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

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

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.

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

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

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

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

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

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

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

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

Eq. 8 can be simplified to

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

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

Results

Oblique and Horizontal Transmission

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

$$p' = p^2(T_B - T_A) + p(1 + T_A - T_B), \tag{11}$$

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*

$$T_A > T_B, \tag{12}$$

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

If $T_A = T_B$, then $p' = p$ and the population is static. 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 5c).

Vertical and Horizontal Transmission

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

$$
\begin{aligned}
\bar{w}\tilde{p}' = {} & \tilde{p}^2(1+b-c)[1-(1-\tilde{p})(1-\alpha)T_B] \\
& + \tilde{p}(1-\tilde{p})(1-c)[\tilde{p}(1-\alpha)T_B + 1 - T_B] \\
& + \tilde{p}(1-\tilde{p})(1+b)[\tilde{p}(1-\alpha)+\alpha]T_A \\
& + (1-\tilde{p})^2\tilde{p}(1-\alpha)T_A.
\end{aligned}
\tag{13}
$$

Fixation of either cooperation, $\tilde{p} = 1$, or defection, $\tilde{p} = 0$, are equilibria of Eq. 13, 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

$$\tilde{p}(1-\tilde{p})\big[(1+b)T_A + (1-c)(1-T_B) - 1\big] = 0, \tag{14}$$

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,

$$\tilde{p}^2(1+b-c) + \tilde{p}(1-\tilde{p})\big[(1-c)(1-T_B) + (1+b)T_A\big] > \bar{w}\tilde{p}. \tag{15}$$

Factoring out $\tilde{p}(1-\tilde{p})$ and setting $\bar{w} = 1 + \tilde{p}(b-c)$, we find that $\hat{p}' > \hat{p}$ if

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

If $\alpha < 1$, divide both sides of Eq. 13 by $\tilde{p}$ and set $\bar{w} = 1 + \tilde{p}(b-c)$. Then $\tilde{p}' > \tilde{p}$ if

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

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

$$c(1-T_B) - b\alpha T_A - (T_A - T_B) < \tilde{p} \cdot b(1-\alpha)(T_A - T_B). \tag{18}$$

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. 13, namely

$$\tilde{p}^* = \frac{c(1-T_B) - b\alpha T_A - (T_A - T_B)}{b(1-\alpha)(T_A - T_B)}, \tag{19}$$

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

Since all parameters are positive, we can apply inequality 18 and see that for $\tilde{p}' > \tilde{p}$ we require that either

$$T_A > T_B \quad \text{and} \quad \tilde{p} > \tilde{p}^*, \quad \text{or} \tag{20}$$

$$T_A < T_B \quad \text{and} \quad \tilde{p} < \tilde{p}^*. \tag{21}$$

We define the initial frequency of the cooperator phenotype among parents, $\tilde{p}_0$, and the *cost boundaries*,

$$\gamma_1 = \frac{b\alpha T_A + (T_A - T_B)}{1 - T_B}, \quad \gamma_2 = \frac{b\alpha T_B + (1+b)(T_A - T_B)}{1 - T_B}. \tag{22}$$

Then, applying Eqs. 19, 20, and 21, we summarize the possible outcomes in following result and corollaries.

Result 2 (Vertical and horizontal transmission of cooperation)**.** *With vertical and horizontal but without oblique transmission ($v = 1$), the cultural evolution of a cooperator phenotype will follow one of the following scenarios, depending on the cost boundaries γ_1 and γ_2 (Eq. 22):*

1. Fixation of cooperation*: if* (i) $T = T_A = T_B$ *and* $c < b \cdot \frac{\alpha T}{1-T}$*; or if* (ii) $T_A > T_B$ *and* $c < \gamma_1$*; or if* (iii) $T_A < T_B$ *and* $c < \gamma_2$.
2. Fixation of defection*: if* (iv) $T = T_A = T_B$ *and* $c > b \cdot \frac{\alpha T}{1-T}$*; or if* (vi) $T_A > T_B$ *and* $\gamma_2 < c$*; or if* (vi) $T_A < T_B$ *and* $\gamma_1 < c$.
3. Fixation of either phenotype depending on initial frequency*: if* (vii) $T_A > T_B$ *and* $\gamma_1 < c < \gamma_2$.
4. Coexistence of both phenotypes at $\tilde{p}^*$*: if* (viii) $T_A < T_B$ *and* $\gamma_2 < c < \gamma_1$.

These conditions are illustrated in Figure 3b-c. 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 2.

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. $T_A = T_B$.

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*

$$T_A > T_B \;\; \textit{and} \;\; c < \gamma_1, \quad \textit{or} \quad T_A < T_B \;\; \textit{and} \;\; \gamma_2 < c < \gamma_1. \tag{23}$$

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*

$$c < b \cdot \frac{\alpha T}{1 - T}. \tag{24}$$

Inequality 24 is obtained by setting $T_A = T_B$ in inequality 18 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 5a 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 3b illustrates these conditions, where the third equilibrium given by Eq. 19 becomes

$$\tilde{p}^*(\alpha = 0) = \frac{c(1 - T_B) - (T_A - T_B)}{b(T_A - T_B)}, \tag{25}$$

and the cost boundaries are

$$\gamma_1(\alpha = 0) = \frac{T_A - T_B}{1 - T_B}, \quad \gamma_2(\alpha = 0) = (1 + b)\frac{T_A - T_B}{1 - T_B}. \tag{26}$$

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 (Perfect 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*

$$c < \frac{b \cdot T_A + (T_A - T_B)}{1 - T_B}. \tag{27}$$

With perfect 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 27 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, inequality 27 is sufficient for increase in the frequency of A. Inequality 27 can be written as

$$1 - (1-c)(1-T_B) < (1+b)T_A, \tag{28}$$

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 27 entails that cooperation can evolve if the effective cost for cooperation is less than the effective benefit.

Given the previous two corollaries for no assortment and perfect assortment ($\alpha = 0$ and $\alpha = 1$), it is interesting to examine the general effect of assortment on the evolution of cooperation. We denote the assortment boundaries by

$$a_1 = \frac{c(1-T_B) - (1+b)(T_A - T_B)}{b \cdot T_B}, \quad a_2 = \frac{c(1-T_B) - (T_A - T_B)}{b \cdot T_A}. \tag{29}$$

Applying Eqs. 19, 20, and 21, we have the following corollary.

Corollary 5 (Intermediate assortment of transmission and cooperation)**.** *The cooperative phenotype will increase from rarity if the assortment is high enough, or specifically if*

$$\begin{aligned} &T_A > T_B \ \ \textit{and} \ \ a_2 < \alpha, \quad \textit{or} \\ &T_A < T_B \ \ \textit{and} \ \ a_1 < \alpha\,. \end{aligned} \tag{30}$$

Figure 3c demonstrates these conditions. With horizontal bias for cooperation ($T_A > T_B$; positive x-axis) cooperation fixes in the population from any initial positive frequency (green) if α (y-axis) is above the orange line (a_1), or if initially present at a high enough frequency (blue) if α is above the blue line (a_2). With horizontal bias for defection ($T_B > T_A$; negative x-axis) cooperation fixes if $alpha$ is above the blue line (a_2), but can be maintained in coexistence with defection (yellow) if α is above the orange line (a_1). Without horizontal bias ($T_A = T_B$) fixation occurs if $\frac{c}{b} \cdot \frac{1-T}{T} < \alpha$ (inequality 24).

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. 5 can give $\hat{p}'$ as a function of both p' and $\tilde{p}'$. Eq. 7 gives p' as a function of $\tilde{p}$, since $\hat{p}$ is given in Eq. 5 as a function of $\tilde{p}$ and Eq. 10 gives $\tilde{p}'$ as a function of $\hat{p}$. Combining these equations, we find an equation for $\hat{p}'$ as a function of $\hat{p}$ (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. 5, 7, and 10 to obtain the function $f(\hat{p})$ (see Appendix Appendix A):

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

where

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

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

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

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

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

with

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

Therefore with symmetric horizontal transmission, fixation of the cooperative phenotype ($\hat{p} = 1$) occurs under the same condition as Corollary 1.1, namely Eq. 24.

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

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

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

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

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 $\hat{p}^* < 0$ 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 $1 > \alpha v$, 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, 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 $f'(1) < 0$, and fixation of the cooperator phenotype A is the only locally stable legitimate equilibrium.

We redefine the cost boundaries, the *cost boundaries*,

$$\hat{\gamma}_1 = \frac{bv\alpha T_A + (T_A - T_B)}{v(1-T_B)}, \quad \hat{\gamma}_2 = \frac{bv\alpha T_B + (1+b)(T_A - T_B)}{v(1-T_B) + (1-v)(T_A - T_B)}, \tag{39}$$

and define a vertical transmission threshold,

$$\hat{v} = \frac{T_B - T_A}{1 - T_A} \,. \tag{40}$$

The following result summarizes the possible outcomes.

Result 3 (Vertical, oblique, and horizontal transmission of cooperation)**.** *With vertical, horizontal, and oblique transmission, the cultural evolution of a cooperator phenotype will follow one of the following scenarios depending on the cost boundaries $\hat{\gamma}_1$ and $\hat{\gamma}_3$ (Eq. 39) and the vertical threshold $\hat{v}$ (Eq. 40) :*

1. Fixation of cooperation*: if* (i) $T = T_A = T_B$ *and* $c < b \cdot \frac{\alpha T}{1-T}$*; or if* (ii) $T_A > T_B$ *and* $c < \hat{\gamma}_1$*; or if* (iiia) $T_A < T_B$ *and* $v > \hat{v}$ *and* $c < \hat{\gamma}_2$*; or if* (iiib) $T_A < T_B$ *and* $v < \hat{v}$ *and* $c > \hat{\gamma}_2$.
2. Fixation of the defection*: if* (iv) $T = T_A = T_B$ *and* $c > b \cdot \frac{\alpha T}{1-T}$*; or if* (v) $T_A > T_B$ *and* $\hat{\gamma}_1 < c < \hat{\gamma}_2$*; or if* (vi) $T_A < T_B$ *and* $c > \hat{\gamma}_1$.
3. Coexistence of both phenotypes at $\hat{p}^*$*: if* (viia) $T_A < T_B$ *and* $v < \hat{v}$ *and* $c < \hat{\gamma}_1$ *and* $c < \hat{\gamma}_2$*; or if* (viib) $T_A < T_B$ *and* $v > \hat{v}$ *and* $c < \hat{\gamma}_1$ *and* $c > \hat{\gamma}_2$.
4. Fixation of either phenotype depending on initial frequency*: if* (viii) $T_A > T_B$ *and* $c > \hat{\gamma}_2$ *and* $c > \hat{\gamma}_1$ *and* $v > \hat{v}$.

Discussion

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 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 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 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 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). We saw that it is likely to find configuration of parameters that results coexistence as can be seen in Figure 3a. In figure Figure 3a the yellow area in which coexistence occur has horizontal bias that favor defection ($T_B > T_A$) and the cost is relatively small.

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 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 its vertical transmission 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.

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 highlight another possibility for assortment, namely, individuals interacting at rate α with their cultural partners, resulting in horizontal transmission. We show that high levels of assortment 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 cooperation ($\alpha > \big(c(1 - T_B) + (T_B - T_A)\big)/bT_A$, see Result 2)

Feldman et al. (1985) studied the dynamics of an altruistic phenotype with vertical cultural transmission and a gene that modifies the transmission of the phenotype. Their results are very sensitive to this genetic modification: without it, the conditions for invasion of the altruistic phenotype reduce to Hamilton's rule. Further work is needed to include such genetic modification of cultural transmission to our model.

Woodcock (2006) showed the importance of non-vertical transmission for the evolution of cooperation. In their model the individuals interact according to standard prisoner dilemma game. However, they do not link between interaction and transmission. In terms of our model they have chosen the assortative meeting coefficient α to be zero. Our results are more general since it shows the importance of assortative meeting for the evolution of cooperation.

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.

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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 Eq. 5,

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

we substitute p' using Eq. 7 and $\tilde{p}'$ using Eq. 10, we have

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

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 Eq. A3 to eqs. 31-32.

Appendix B

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 $|p' - p^*| < |p - p^*|$.

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

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

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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Figures

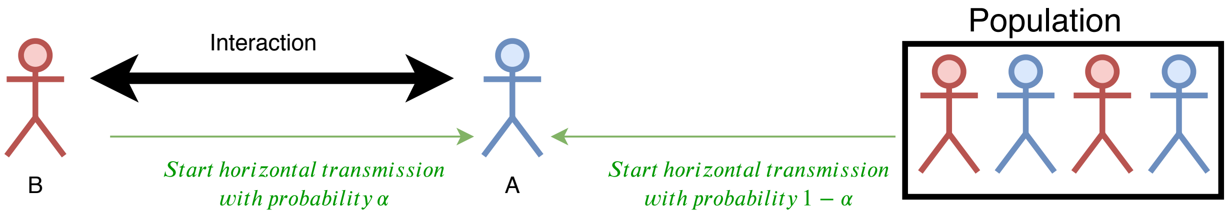

Figure 1: Cultural horizontal transmission with assortment. Transmission occurs between interacting partners with probability α (left) or between two random peers with probability $1 - \alpha$.

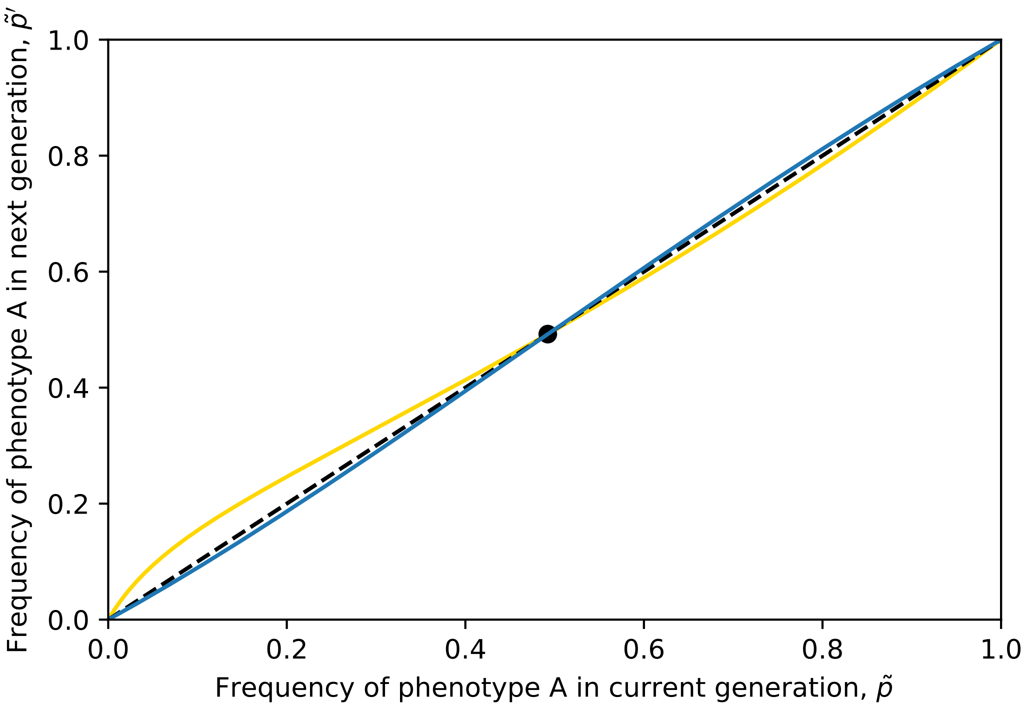

Figure 2: Stable and unstable coexistence between cooperation and defection without oblique transmission. The curves show the frequency of the cooperative phenotype A among parents in the next generation $\tilde{p}'$ vs. the current generation $\tilde{p}$ (Eq. 13). The dashed black line is $\tilde{p}' = \tilde{p}$. The curves and the dashed line intersect at the polymorphic equilibrium $\tilde{p}^*$ (black circle). When the curves are above the dashed line, $\tilde{}'p > \tilde{p}$, then $\tilde{p}$ increase. When the curves are below the dashed line, $\tilde{}'p < \tilde{p}$, then $\tilde{p}$ decreases. The yellow curve, for which the polymorphic equilibrium is stable, is given by $T_A = 0.4$, $T_B = 0.9$, $b = 12$, $c = 0.35$, and $\alpha = 0.45$, which give $\gamma_2 < c < \gamma_1$ (Eq. 22) The blue curve, for which the equilibrium is unstable, is given by $T_A = 0.5$, $T_B = 0.1$, $b = 1.3$, $c = 0.904$, and $\alpha = 0.4$, which give $\gamma_1 < c < \gamma_2$. In both cases there is no oblique transmission, $v = 1$; see Figure 4 for $v < 1$.

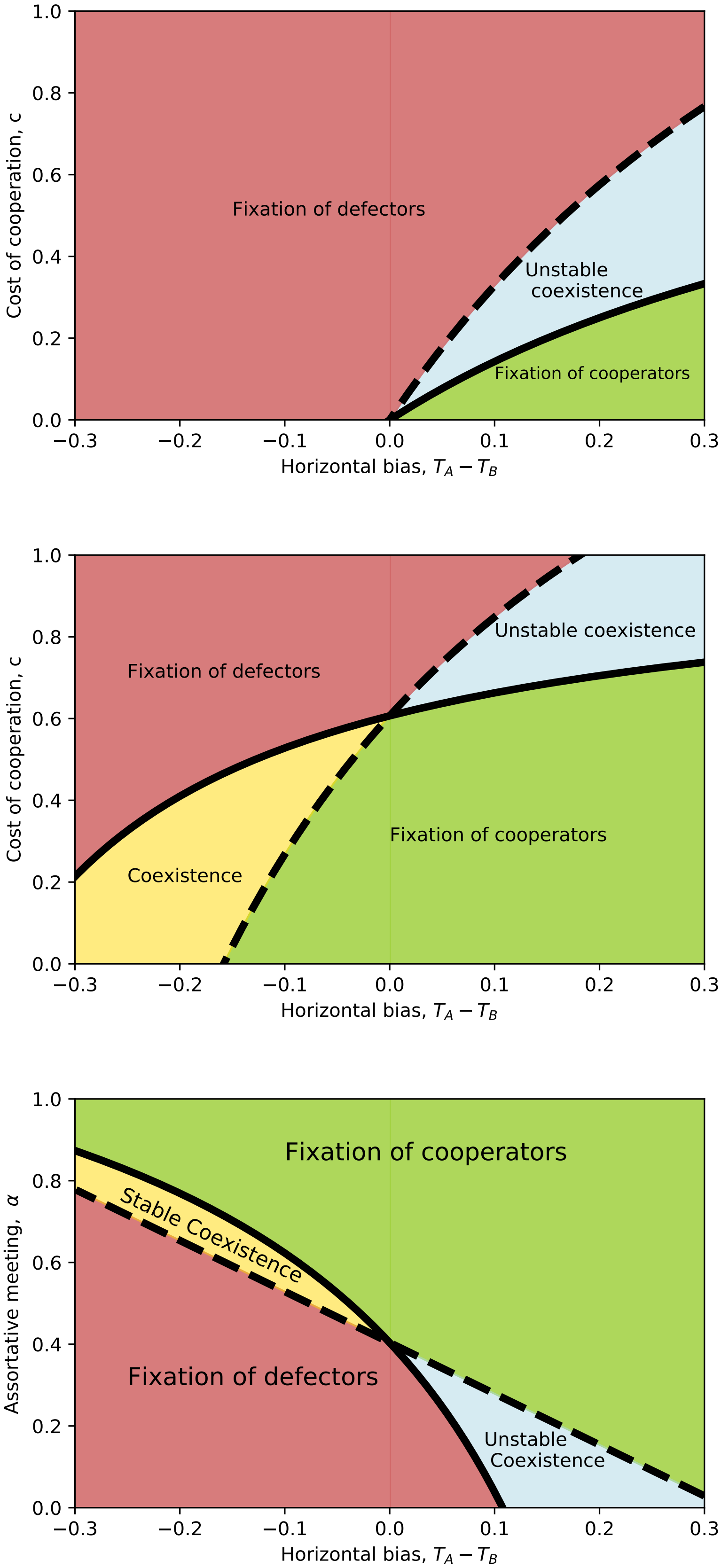

Figure 3: Evolution of cooperation under vertical and horizontal cultural transmission. The figure shows the global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial conditions, i.e. unstable coexistence (blue), and stable coexistence of cooperation and defection (yellow). In all cases the horizontal bias ($T_A - T_B$) is on the x-axis. (**a-b**) the cost of cooperation c is on the y-axis; the cost boundaries γ_1 and γ_2 (Eq. 22) are the solid and dashed lines. (**c**) the assortment α is on the y-axis; the assortment boundaries a_1 and a_2 (Eq. 29) are the solid and dashed lines. Here, $b = 1.3$, $T_A = 0.4$. (**a**) $\alpha = 0$.(**b**) $\alpha = 0.7$. (**c**) $c = 0.35$.

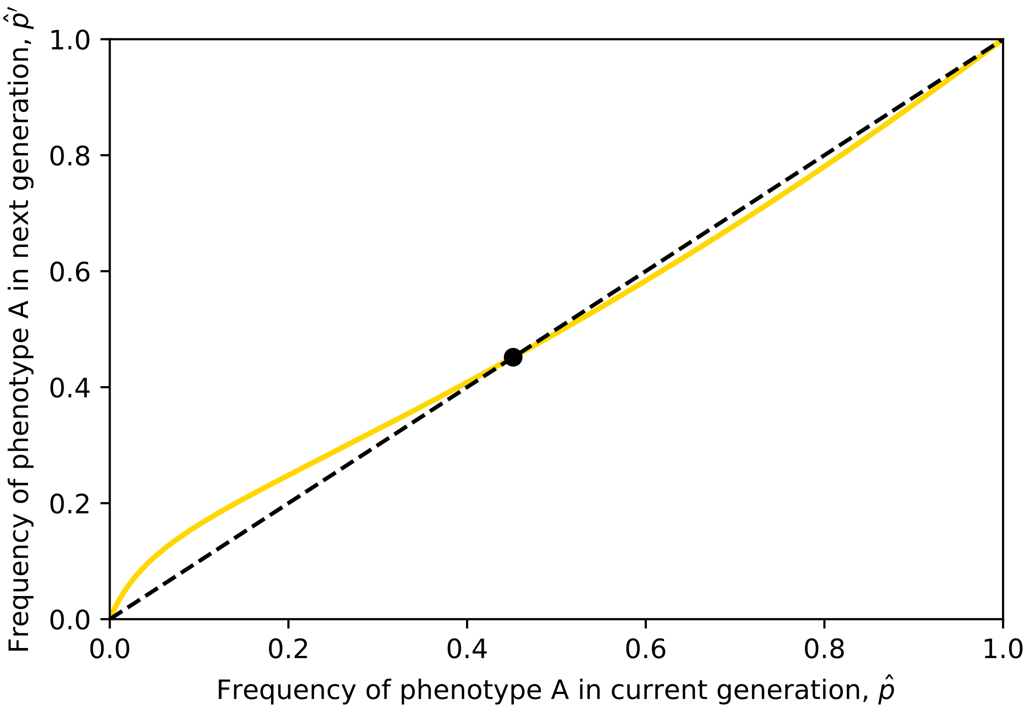

Figure 4: Stable coexistence between cooperation and defection with oblique transmission. The curve shows the frequency of the cooperative phenotype A among juveniles in the next generation $\hat{p}'$ vs. the current generation $\hat{p}$ (Eq. 5). The dashed black line is $\hat{p}' = \hat{p}$. The curve and the dashed line intersect at the stable equilibrium $\hat{p}^*$ (black circle). When $\hat{p} < \hat{p}^*$ then the curve is above the dashed line, $\hat{p}' > \hat{p}$, and $\hat{p}$ increases towards $\hat{p}^*$. When $\hat{p} > \hat{p}^*$ then the curve is below the dashed line, $\hat{p}' < \hat{p}$, and $\hat{p}$ decreases towards $\hat{p}^*$. Here, $T_A = 0.4$, $T_B = 0.9$, $b = 20$, $c = 0.1$, $\alpha = 1$, and $v = 0.4$, which give $0 < \beta_3 < \beta_1$ (Eq. 32).

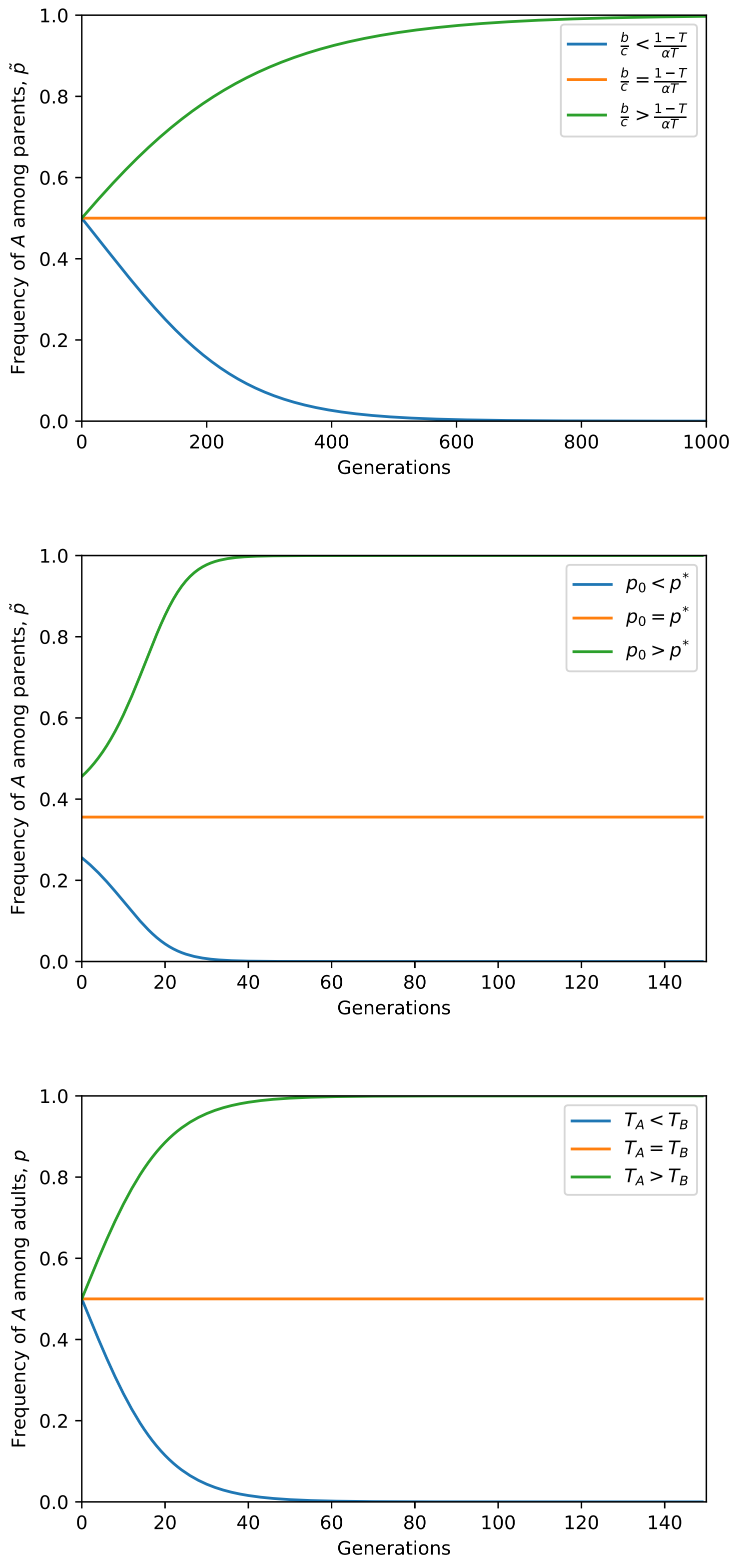

Figure 5: Dynamics of the frequency of cooperation. The frequency $\tilde{p}$ of parents with cooperative phenotype A in **(a-b)** and the frequency p of adults with cooperative phenotype A in **(c)**. The different lines correspond to parameter values that lead to fixation of cooperation (green), extinction of cooperation (red), or stable coexistence of cooperators and defectors (yellow). **(a)** $v = 1$, $T_A = T_B = T = 0.2$, $\alpha = 0.5 \neq 0$, $\tilde{p}_0 = 0.5$ and $c = 0.1$; **(b)** $v = 1$, $\alpha = 0$, $\tilde{p}^* \approx 0.35$, $T_A = 0.65$, $T_B = 0.1$, $b = 1.3$ and $c = 0.65$; **(c)** $v = 0$, $\alpha = 0.5$, $p_0 = 0.5$, $T_A = 0.5$, $b = 1.3$ and $c = 0.5$.