Non-Vertical Cultural Transmission and the Evolution of Cooperation

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August 19, 2020

Introduction

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

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

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

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

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

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, 1981; Lycett and Gowlett, 2008; Ram et al., 2018). Lewin-Epstein et al. (2017) have demonstrated

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[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).

50 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 trans-
52 mission, because models of cultural transmission are mathematically similar to those for transmission of infectious diseases (Cavalli-Sforza and Feldman, 1981).

54 We hypothesize that non-vertical cultural transmission can enhance the evolution of cooperation, and to test this hypothesis we suggest a model in which behavioral changes are mediated by cultural
56 transmission that can occur during social interactions. For example, if an individual interacts with a cooperative individual, it might learn that cooperation is an advantageous behavior and will be cooper-
58 ative 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
60 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
62 can lead to a better understanding of its evolutionary dynamics.

Models

64 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
66 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
68 the parent phenotype is ϕ and assuming uni-parental inheritance, the conditional probability that the phenotype ϕ' of the offspring is A is

70
$$P(\phi' = A \mid \phi) = \begin{cases} v + (1 - v)p, & \text{if } \phi = A \\ (1 - v)p, & \text{if } \phi = B \end{cases}, \tag{4}$$

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

72 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
74 vertical and oblique transmission) is

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

76 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
78 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. $b > c > 0$.

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.

80 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
82 phenotypes interact with probability $2\hat{p}(1 - \hat{p})$.

Horizontal cultural transmission occurs between pairs of individuals from the same generation. It
84 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
86 (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
88 probability for successful horizontal transmission of phenotypes A and B are T_A and T_B, respectively (Table 2).

90 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
96 the effect of natural selection, and is therefore

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

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

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

100 Eq. 8 can be simplified to

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

102 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.

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 4c).

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 summarize these findings in 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.*

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

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

Then, applying Eqs. 19, 20, and 21, we summarize the possible outcomes which are illustrated in Figure 3:

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 $\gamma_2 < c < \gamma_1$.

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*

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

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 4a demonstrates this condition.

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

Figure 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*

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

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 **??**).

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 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 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 $\beta_3 = -\beta_2 = \alpha b v T - c v (1 - T)$, and $f(\hat{p})$ becomes 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 $\hat{p} = 0$ and $\hat{p} = 1$. These equilibria are locally stable if $f'(\hat{p}) < 0$ near the equilibrium (Appendix B), and

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

with

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

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

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* (i) $T = T_A = T_B$ *and* $c < b \cdot \frac{\alpha T}{1 - T}$; *or if* (ii) $T_A > T_B$ *and* $0 < \beta_3$; *or if* (iii) $T_A < T_B$ *and* $\beta_1 < \beta_3$.

2. Fixation of the defection: *if* (iv) $T = T_A = T_B$ *and* $c > b \cdot \frac{\alpha T}{1 - T}$; *or if* (v) $T_A > T_B$ *and* $\beta_1 < \beta_3 < 0$; *or if* (vi) $T_A < T_B$ *and* $\beta_3 < 0$.

3. Coexistence of both phenotypes at $\hat{p}^*$: *if* (vi) $T_A < T_B$ *and* $0 < \beta_3 < \beta_1$.

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

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 assortatment, 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.

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

Acknowledgements

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.

338 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

$$1 - p' < 1 - p \Leftrightarrow$$

340
$$\frac{f'(1)(p-1) + O\big((p-1)^2\big)}{p-1} < 0 \Leftrightarrow \qquad\qquad\text{(B2)}$$

$$f'(1) - O(1-p) < 0.$$

Therefore, if $f'(1) < 0$ then there exists $\epsilon > 0$ such that for any $1 - \epsilon < 1 - p < 1$ it is guaranteed that
342 $1 - p' < 1 - p$, that is, p' is closer than p to one.

References

344 Robert Axelrod and William D Hamilton. The evolution of cooperation. *Science*, 211(4489):1390–1396, 1981.

346 Luigi Luca Cavalli-Sforza and Marcus W Feldman. *Cultural transmission and evolution: A quantitative approach*. Number 16. Princeton University Press, 1981.

348 Andrew P Dobson. The population biology of parasite-induced changes in host behavior. *The Quarterly Review of Biology*, 63(2):139–165, 1988.

350 Lee Alan Dugatkin. *Cooperation among Animals: An Evolutionary Perspective*. Oxford University Press on Demand, 1997.

352 Ilan Eshel and Luigi Luca Cavalli-Sforza. Assortment of encounters and evolution of cooperativeness. *Proceedings of the National Academy of Sciences*, 79(4):1331–1335, 1982.

354 Marcus W Feldman, Luca L Cavalli-Sforza, and Joel R Peck. Gene-culture coevolution: models for the evolution of altruism with cultural transmission. *Proceedings of the National Academy of*
356 *Sciences*, 82(17):5814–5818, 1985.

William D Hamilton. The genetical evolution of social behaviour. ii. *Journal of Theoretical Biology*,
358 7(1):17–52, 1964.

Adrian V Jaeggi and Michael Gurven. Natural cooperators: food sharing in humans and other primates.
360 *Evolutionary Anthropology: Issues, News, and Reviews*, 22(4):186–195, 2013.

Indrikis Krams, Tatjana Krama, Kristine Igaune, and Raivo Mänd. Experimental evidence of reciprocal
362 altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, 62(4):599–605, 2008.

Ohad Lewin-Epstein, Ranit Aharonov, and Lilach Hadany. Microbes can help explain the evolution
364 of host altruism. *Nature Communications*, 8:14040, 2017.

Stephen J Lycett and John AJ Gowlett. On questions surrounding the acheulean 'tradition'. *World*
366 *Archaeology*, 40(3):295–315, 2008.

Aaron Meurer, Christopher P Smith, Mateusz Paprocki, Ondřej Čertík, Sergey B Kirpichev, Matthew
368 Rocklin, AMiT Kumar, Sergiu Ivanov, Jason K Moore, Sartaj Singh, et al. Sympy: symbolic computing in python. *PeerJ Computer Science*, 3:e103, 2017.

370 Robert Poulin. Parasite manipulation of host behavior: an update and frequently asked questions. In *Advances in the Study of Behavior*, volume 41, pages 151–186. Elsevier, 2010.

372 Yoav Ram, Uri Liberman, and Marcus W Feldman. Evolution of vertical and oblique transmission under fluctuating selection. *Proceedings of the National Academy of Sciences*, 115(6):E1174–
374 E1183, 2018.

George E Rice and Priscilla Gainer. "Altruism" in the albino rat. *Journal of Comparative and Physiological Psychology*, 55(1):123, 1962.

Peter J Richerson and Robert Boyd. *Not by Genes Alone: How Culture Transformed Human Evolution*. University of Chicago Press, 2008.

Barry Sinervo, Alexis Chaine, Jean Clobert, Ryan Calsbeek, Lisa Hazard, Lesley Lancaster, Andrew G McAdam, Suzanne Alonzo, Gwynne Corrigan, and Michael E Hochberg. Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. *Proceedings of the National Academy of Sciences*, 103(19):7372–7377, 2006.

Peter B Stacey and Walter D Koenig, editors. *Cooperative breeding in birds: long term studies of ecology and behaviour*. Cambridge University Press, 1990.
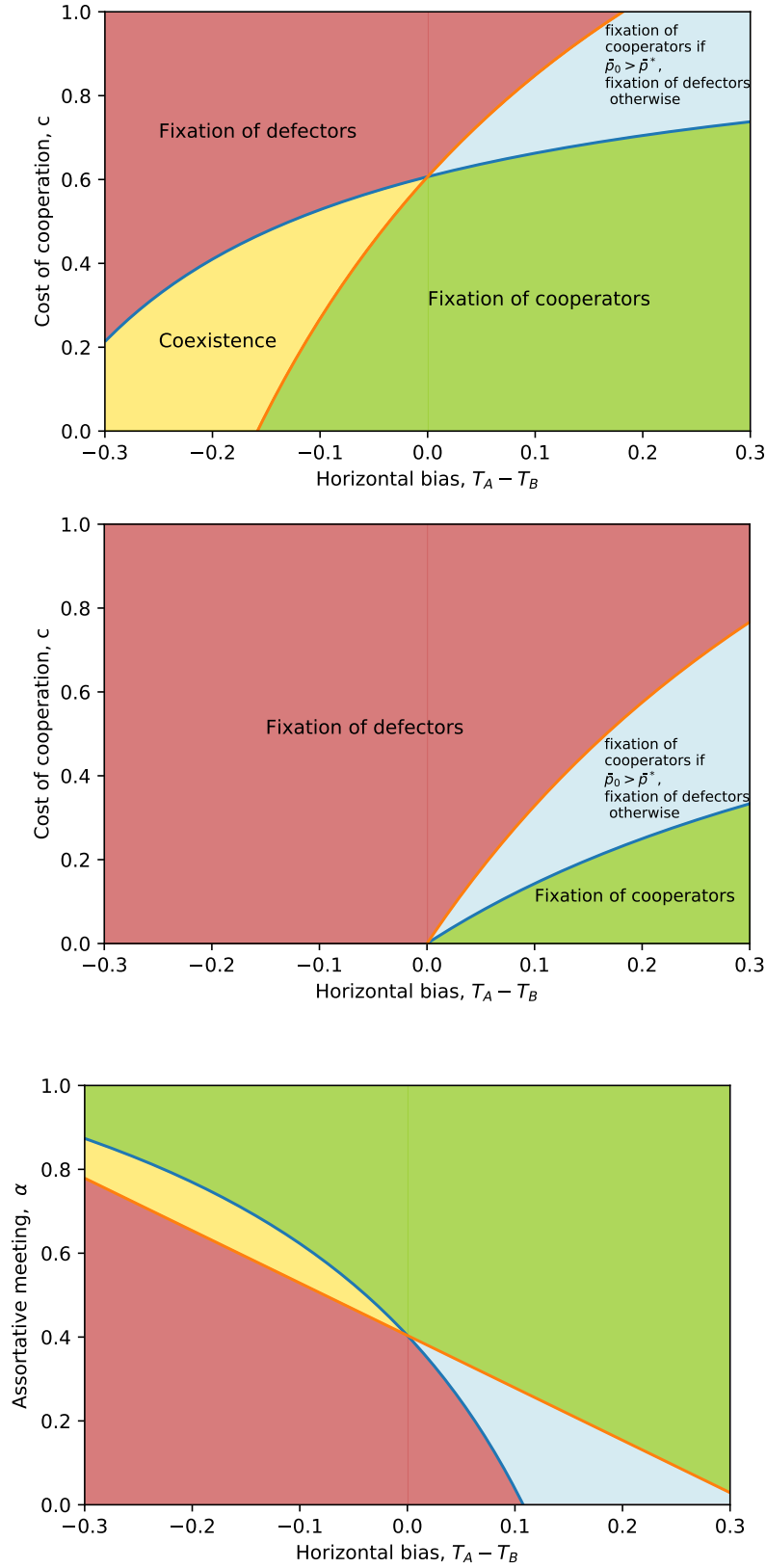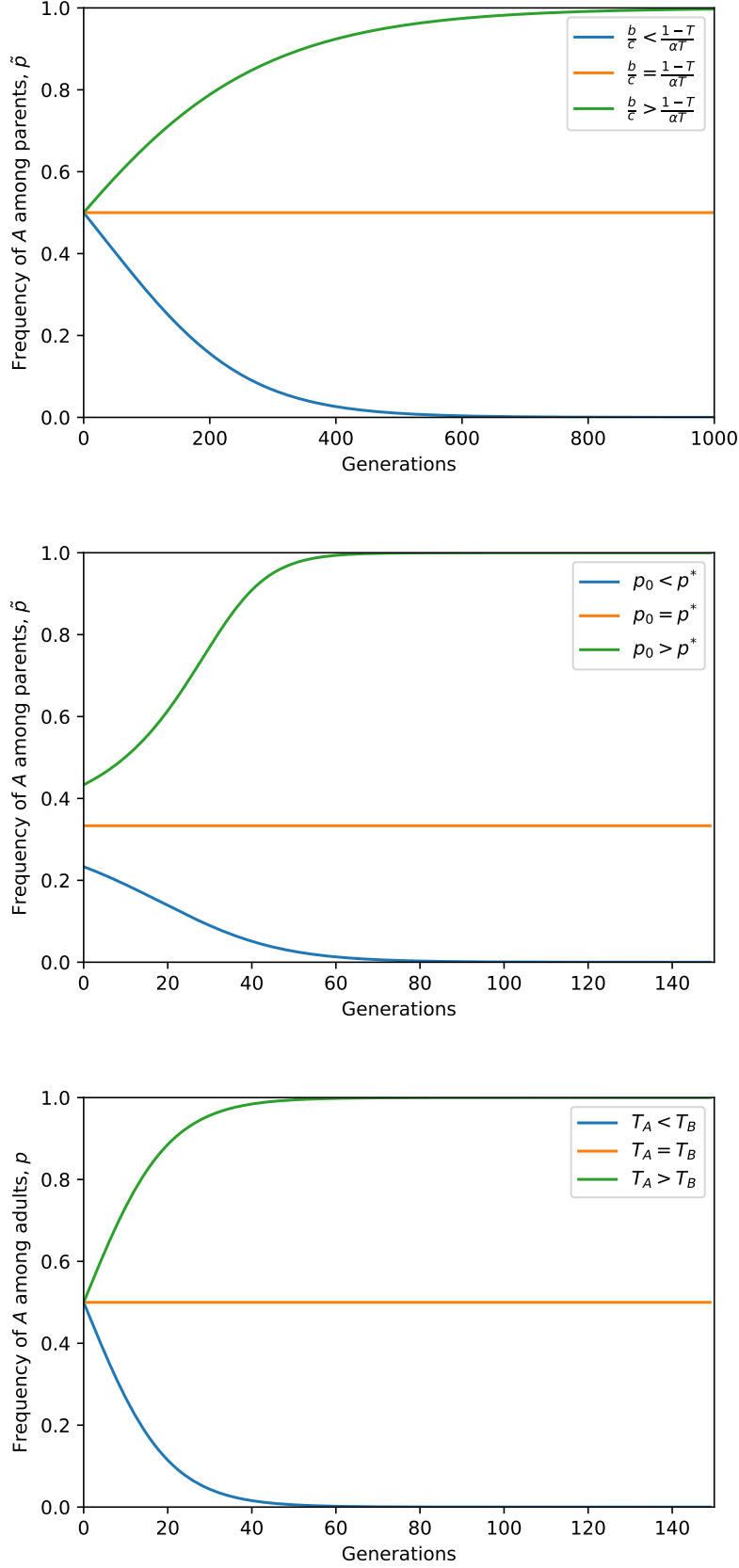
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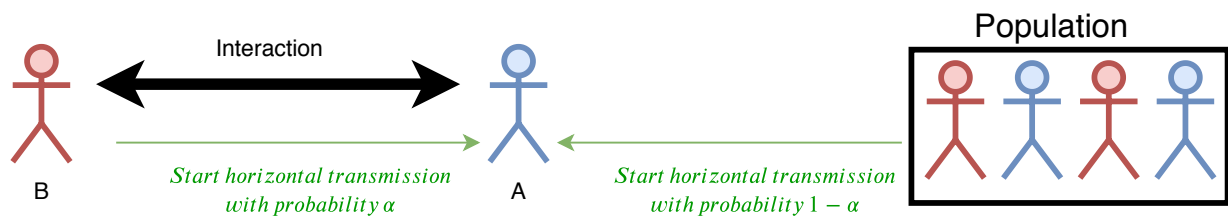
Figure 1: Cultural horizontal transmission. Transmission occurs between interacting partners with probability α (left) or between two random peers with probability $1 - \alpha$.
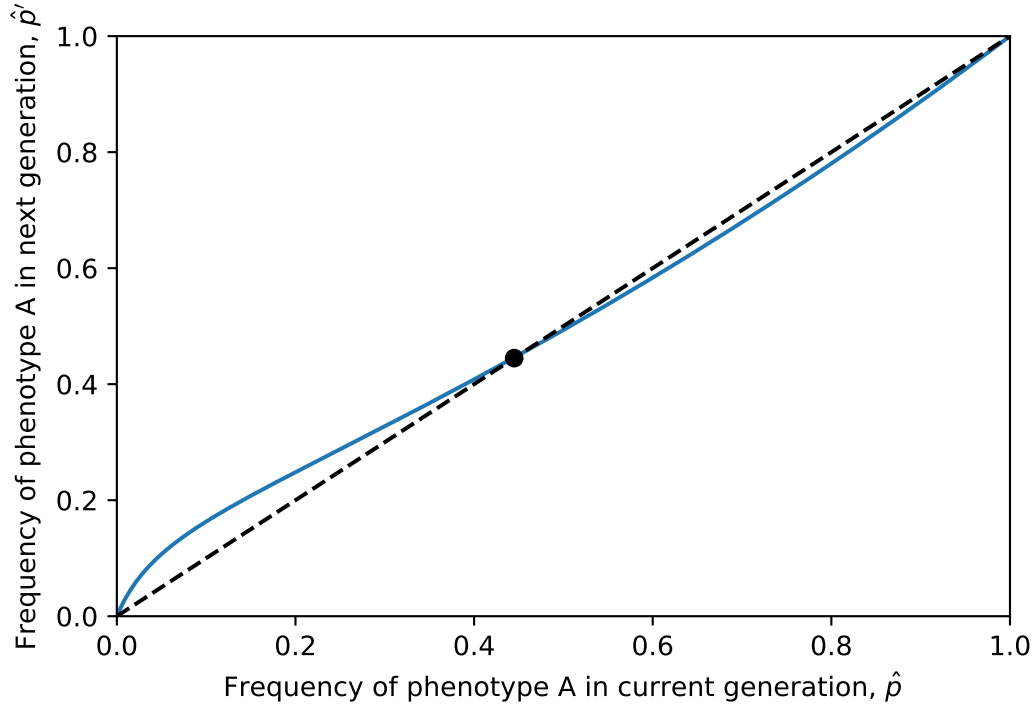
Figure 2: Stable coexistence between cooperation and defection. The frequency of the cooperative phenotype A among juveniles in the next generation $\hat{p}'$ is plotted as a function of the frequency in the current generation $\hat{p}$ for $T_A < T_B$ and $\gamma_2 < c < \gamma_1$. The line $\hat{p}' = \hat{p}$ is shown as a dashed black line. The curve and dashed line intersect at the equilibrium $\hat{p}^*$ (black circle). When the curve is above the dashed line ($\hat{p} < \hat{p}^*$) the frequency $\hat{p}$ increases towards $\hat{p}^*$. When the curve is below the dashed line ($\hat{p} > \hat{p}^*$) the frequency $\hat{p}$ decreases towards $\hat{p}^*$.

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 (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, $b = 1.3$, $T_A = 0.4$.

Figure 4: 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) $v = 1, T_A = T_B = T$, $\alpha \neq 0$; (b) $v = 1, \alpha = 0$; (c) $v = 0$.

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