

# Non-Vertical Cultural Transmission and the Evolution of Cooperation

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## 10 Introduction

Cooperative behavior can reduce an individual's fitness and increase the fitness of its conspecifics or competitors (?). Nevertheless, cooperative behavior appears to occur in many non-human animals (?), including primates (?), rats (?), birds (??), and lizards (?). Evolution of cooperative behavior remains an important conundrum in evolutionary biology. Since the work of ? and ?, 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 ?, 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*:

$$24 \qquad c < b \cdot r. \qquad (1)$$

? 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<sup>1</sup> (?, eq. 3.2)

$$30 \qquad c < b \cdot m, \qquad (2)$$

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

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 (?). ? 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  $\varphi$ , then the condition for evolution of altruism in the case of sib-to-sib altruism is (?, Eq. 16)

$$c < b \cdot \varphi - \frac{1 - \varphi}{\varphi}. \qquad (3)$$

In this case  $\varphi$  takes the role of the relatedness  $r$  in ??, 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 more rapid than under pure vertical transmission (???). ? and ? 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

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<sup>1</sup>In an extended model, which allows an individual to encounter  $N$  individuals before choosing a partner, the righthand side is multiplied by  $E[N]$ , the expected number of encounters (?, eq. 4.6).

50 applied to cultural transmission, because models of cultural transmission are mathematically similar  
to those for transmission of infectious diseases (?). Importantly, their results depended on non-vertical  
52 transmission of the cooperation-determining microbes.

We therefore hypothesize that non-vertical cultural transmission can enhance the evolution of coop-  
54 eration. 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  
56 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  
58 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 investi-  
60 gate 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  
62 that treatment of cooperation as a cultural, rather than a genetic, trait can lead to a better understanding  
of its evolutionary dynamics.

## 64 Models

Consider a very large population whose members are characterized by their phenotype  $\phi$ , which can  
66 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  
68 population via oblique transmission with probability  $(1 - v)$ . Following ?, given that the parent  
phenotype is  $\phi$  and assuming uni-parental inheritance, the conditional probability that the phenotype  
70  $\phi'$  of the offspring is  $A$  is

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

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

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

Individuals are assumed to interact according to a *prisoner's dilemma*. Specifically, individuals  
78 interact in pairs; a cooperator suffers a fitness cost  $0 < c < 1$ , and its partner gains a fitness benefit  $b$ ,  
where we assume  $c < b$ . ?? shows the payoff matrix, i.e. the fitness of an individual with phenotype  
80  $\phi_1$  when interacting with a partner of phenotype  $\phi_2$ .

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

84 Horizontal cultural transmission occurs between pairs of individuals from the same generation. It  
occurs between social partners with probability  $\alpha$ , or between a random pair with probability  $1 - \alpha$   
86 (see ??). The assortment parameter  $\alpha$  is therefore the fraction of population that receives (horizontal

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

**Table 1: Payoff matrix for prisoner's dilemma.** The fitness of phenotype  $\phi_1$  when interacting with phenotype  $\phi_2$ .  $A$  is a cooperative phenotype,  $B$  is a defector phenotype,  $b$  is the benefit gained by an individual interacting with a cooperator, and  $c$  is the cost of cooperation.  $b > c > 0$ .

Phenotype $\phi_1$	Phenotype $\phi_2$	Frequency	Fitness of $\phi_1$	$P(\phi_1 = A)$ via horizontal transmission:	
				from partner, $\alpha$	from population, $(1 - \alpha)$
$A$	$A$	$\hat{p}^2$	$1 + b - c$	$1$	$\hat{p} + (1 - \hat{p})(1 - T_B)$
$A$	$B$	$\hat{p}(1 - \hat{p})$	$1 - c$	$1 - T_B$	$\hat{p} + (1 - \hat{p})(1 - T_B)$
$B$	$A$	$\hat{p}(1 - \hat{p})$	$1 + b$	$T_A$	$\hat{p}T_A$
$B$	$B$	$(1 - \hat{p})^2$	$1$	$0$	$\hat{p}T_A$

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

transmission) 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 (??).

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 ?? and ??, and the population mean fitness is

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

?? can be simplified to

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

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. ?? becomes  $\hat{p} = p$  and Eq. ?? becomes

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

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*

$$T_A > T_B, \quad (12)$$

*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 ??c).

### Vertical and Horizontal Transmission

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

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

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

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

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,

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

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

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

If  $\alpha < 1$ , divide both sides of Eq. ?? 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. ??, 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 ?? 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. ??, ??, and ??, 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  $\gamma_1$  and  $\gamma_2$  (??):*

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 ??b-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 ??.

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*

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

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*

$$c < b \cdot \frac{\alpha T}{1 - T}. \quad (24)$$

Inequality ?? is obtained by setting  $T_A = T_B$  in inequality ?? and can be interpreted as a version of Hamilton's rule (inequality ??), where  $\alpha T/(1 - T)$  can be regarded as the 'effective relatedness'. ??a 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 ( $\tilde{p}_0 > \tilde{p}^*$ ).*

??b illustrates these conditions, where the third equilibrium given by Eq. ?? becomes

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

and the cost boundaries are

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

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 ??, namely*

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

With perfect assortment, in inequality ?? horizontal transmission occurs together with the cooperative interaction. The same occurs in ?, and therefore this corollary is equivalent to their result (see their eq. 1).

In terms of the cost boundaries, inequality ?? 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 ?? is sufficient for increase in the frequency of A. Inequality ?? can be written as

$$1 - (1 - c)(1 - T_B) < (1 + b)T_A, \quad (28)$$

200 which provides an interesting interpretation for the success of cooperation. In the interaction between  
 202 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  
 204 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 ?? entails that cooperation can  
 206 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  
 208 interesting to examine the general effect of assortment on the evolution of cooperation. We denote the  
 assortment boundaries by

$$210 \quad a_1 = \frac{c(1 - T_B) - (1 + b)(T_A - T_B)}{b \cdot T_B}, \quad a_2 = \frac{c(1 - T_B) - (T_A - T_B)}{b \cdot T_A}. \quad (29)$$

Applying Eqs. ??, ??, and ??, we have the following corollary.

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

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

216 ??c 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  $\alpha$  (y-axis) is above  
 218 the orange line ( $a_1$ ), or if initially present at a high enough frequency (blue) if  $\alpha$  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  
 220 the blue line ( $a_2$ ), but can be maintained in coexistence with defection (yellow) if  $\alpha$  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 ??).

## 222 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  
 224 on global stability. To proceed, we note that Eq. ?? can give  $\hat{p}'$  as a function of both  $p'$  and  $\tilde{p}'$ . Eq.  
 ?? gives  $p'$  as a function of  $\tilde{p}$ , since  $\hat{p}$  is given in Eq. ?? as a function of  $\tilde{p}$  and Eq. ?? gives  $\tilde{p}'$  as a  
 226 function of  $\hat{p}$ . Combining these equations, we find an equation for  $\hat{p}'$  as a function of  $\hat{p}$  (shown in  
 Appendix ??). We then determine the equilibria, namely, solutions of  $\hat{p}' = \hat{p}$ , and analyse their local  
 228 stability.

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

$$230 \quad f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = \beta_1 \hat{p}^3 + \beta_2 \hat{p}^2 + \beta_3 \hat{p}, \quad (31)$$

where

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

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

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



236 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 ??), and

$$238 \quad f'(\hat{p}) = (1 - 2\hat{p})[\alpha bvT - cv(1 - T)], \quad (34)$$

with

$$240 \quad \begin{aligned} f'(0) &= \alpha bvT - cv(1 - T), \\ f'(1) &= -\alpha bvT + cv(1 - T). \end{aligned} \quad (35)$$

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

In the general case where  $T_A \neq T_B$ , the coefficient  $\beta_1$  is not necessarily zero, and  $f(\hat{p})$  is a cubic polynomial. Therefore, three equilibria may exist, two of which are  $\hat{p} = 0$  and  $\hat{p} = 1$ , and the third is

$$246 \quad \hat{p}^* = \frac{\beta_3}{\beta_1}. \quad (36)$$

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

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

250 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

$$258 \quad \beta_1 > [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) > 0, \quad (38)$$

260 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.

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

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

268 and define a vertical transmission threshold,

$$\hat{v} = \frac{T_B - T_A}{1 - T_A}. \quad (40)$$

270 The following result summarizes the possible outcomes.

272 **Result 3** (Vertical, oblique, and horizontal transmission of cooperation). *With vertical, horizontal,*  
 274 *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  $\hat{\gamma}_3$  (??) and the vertical threshold  $\hat{v}$  (??)*  
 :

- 276 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  $c > \hat{\gamma}_2$ .
- 278 2. Fixation of the defection: *if (iv)  $T = T_A = T_B$  and  $c > b \cdot \frac{\alpha T}{1-T}$ ; or if (va)  $T_A > T_B$  and*  
 $\hat{\gamma}_1 < c < \hat{\gamma}_2$  and  $v > \hat{v}$ ; or if (vb)  $T_A > T_B$  and  $c > \hat{\gamma}_1$  and  $c > \hat{\gamma}_2$  and  $v < \hat{v}$ ; or if (vi)  $T_A < T_B$   
 280 and  $c > \hat{\gamma}_1$ .
3. Coexistence of both phenotypes at  $\hat{p}^*$ : *if (viiia)  $T_A < T_B$  and  $v < \hat{v}$  and  $\hat{\gamma}_1 < c < \hat{\gamma}_2$ ; or if viib*  
 282  $T_A < T_B$  and  $v > \hat{v}$  and  $c > \hat{\gamma}_1$  and  $c > \hat{\gamma}_2$ .
4. Fixation of either phenotype depending on initial frequency: *if (viiiia)  $T_A > T_B$  and  $c > \hat{\gamma}_2$  and*  
 284  $v > \hat{v}$ ; or if (viiiib)  $T_A > T_B$  and  $c < \hat{\gamma}_2$  and  $v < \hat{v}$ .

## Discussion

286 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  
 288 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  
 290 of cooperation (Result ??). Under horizontal and vertical cultural transmission, cooperation, or  
 defection can fix, or coexist at a stable polymorphism, depending on the relationship between the  
 292 cost and benefit of cooperation, the horizontal bias, and the correlation between cooperation and  
 transmission (Result ??). Under a combination of vertical, oblique, and horizontal transmission the  
 294 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 ??). We saw that  
 296 it is likely to find configuration of parameters that results coexistence as can be seen in ??a. In figure  
 ??a the yellow area in which coexistence occur has horizontal bias that favor defection ( $T_B > T_A$ ) and  
 298 the cost is relatively small.

This study was partially inspired by the work of ?, who hypothesised that microbes that manipulate  
 300 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  
 302 changes in their hosts (??). 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  
 304 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  
 306 (genetically) unrelated (?). 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,  
 308 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  
 310 transmission of their microbial kin.

? showed that with assortative meeting, namely, a probability  $m$  that individuals interact within their  
 312 phenotypic group, cooperation can evolve if  $c < b \cdot m$ . Our results highlight another possibility  
 for assortment, namely, individuals interacting at rate  $\alpha$  with their cultural partners, resulting in  
 314 horizontal transmission. We show that high levels of assortment significantly increase the potential for  
 evolution of cooperation. With a high enough  $\alpha$ , cooperation can increase when initially rare (although

316 it will not fix) even when there is horizontal bias against cooperation ( $\alpha > (c(1 - T_B) + (T_B - T_A))/bT_A$ ,  
 see Result ??)

318 ? 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:  
 320 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.

322 An important implication of our results is that cooperation can evolve even in a fully mixed popu-  
 lation (i.e., in an unstructured population), without repeated interactions or individual recognition.  
 324 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.

## 326 Acknowledgements

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# Appendices

## 330 Appendix A

332 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 ??,

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

334 we substitute  $p'$  using ?? and  $\tilde{p}'$  using ??, we have

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

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

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

338 Using *SymPy* (?), a Python library for symbolic mathematics, we simplify ?? to eqs. ??-??.

## Appendix B

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

342 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

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

346 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  $-\frac{f(p)}{1-p} < 0$ .  
 348 Using a linear approximation for  $f(p)$  near 1, we have

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

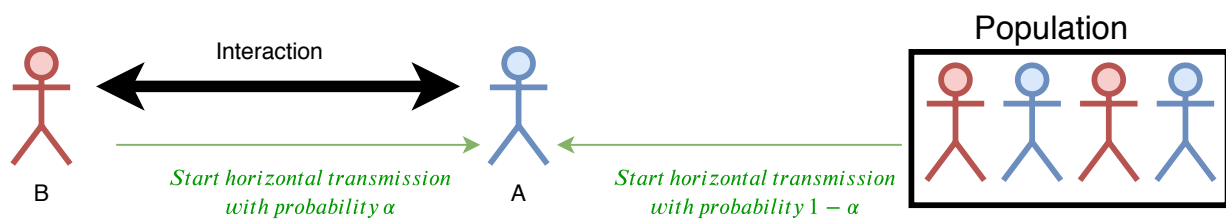
350 Therefore, if  $f'(1) < 0$  then there exists  $\epsilon > 0$  such that for any  $1 - \epsilon < 1 - p < 1$  it is guaranteed that  
 $1 - p' < 1 - p$ , that is,  $p'$  is closer than  $p$  to one.

## 352 References

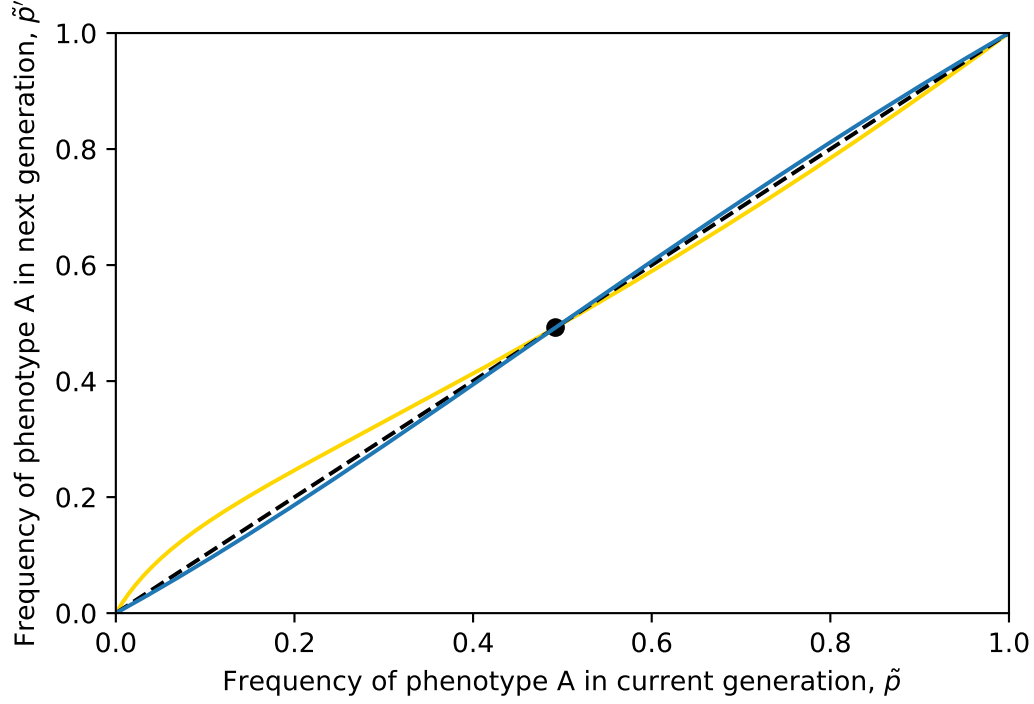
- Robert Axelrod and William D Hamilton. The evolution of cooperation. *Science*, 211(4489):1390–  
 354 1396, 1981.
- Luigi Luca Cavalli-Sforza and Marcus W Feldman. *Cultural transmission and evolution: A quantitative approach*. Number 16. Princeton University Press, 1981.
- Andrew P Dobson. The population biology of parasite-induced changes in host behavior. *The Quarterly Review of Biology*, 63(2):139–165, 1988.
- Lee Alan Dugatkin. *Cooperation among Animals: An Evolutionary Perspective*. Oxford University  
 360 Press on Demand, 1997.
- Ilan Eshel and Luigi Luca Cavalli-Sforza. Assortment of encounters and evolution of cooperativeness.  
 362 *Proceedings of the National Academy of Sciences*, 79(4):1331–1335, 1982.
- Marcus W Feldman, Luca L Cavalli-Sforza, and Joel R Peck. Gene-culture coevolution: models  
 364 for the evolution of altruism with cultural transmission. *Proceedings of the National Academy of Sciences*, 82(17):5814–5818, 1985.
- William D Hamilton. The genetical evolution of social behaviour. ii. *Journal of Theoretical Biology*,  
 366 7(1):17–52, 1964.
- Adrian V Jaeggi and Michael Gurven. Natural cooperators: food sharing in humans and other primates.  
*Evolutionary Anthropology: Issues, News, and Reviews*, 22(4):186–195, 2013.
- Indrikis Krams, Tatjana Krama, Kristine Igaune, and Raivo Mänd. Experimental evidence of reciprocal  
 370 altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, 62(4):599–605, 2008.
- Ohad Lewin-Epstein and Lilach Hadany. Host–microbiome coevolution can promote cooperation in  
 372 a rock–paper–scissors dynamics. *Proc. R. Soc. B Biol. Sci.*, 287(1920):20192754, feb 2020.  
 374 ISSN 0962-8452. doi: 10.1098/rspb.2019.2754. URL <https://royalsocietypublishing.org/doi/10.1098/rspb.2019.2754>.
- Ohad Lewin-Epstein, Ranit Aharonov, and Lilach Hadany. Microbes can help explain the evolution  
 376 of host altruism. *Nature Communications*, 8:14040, 2017.
- Stephen J Lycett and John AJ Gowlett. On questions surrounding the acheulean ‘tradition’. *World  
 378 Archaeology*, 40(3):295–315, 2008.
- Aaron Meurer, Christopher P Smith, Mateusz Paprocki, Ondřej Čertík, Sergey B Kirpichev, Matthew  
 380 Rocklin, AMiT Kumar, Sergiu Ivanov, Jason K Moore, Sartaj Singh, et al. Sympy: symbolic  
 382 computing in python. *PeerJ Computer Science*, 3:e103, 2017.

- Robert Poulin. Parasite manipulation of host behavior: an update and frequently asked questions. In  
 384 *Advances in the Study of Behavior*, volume 41, pages 151–186. Elsevier, 2010.
- Yoav Ram, Uri Liberman, and Marcus W Feldman. Evolution of vertical and oblique transmission  
 386 under fluctuating selection. *Proceedings of the National Academy of Sciences*, 115(6):E1174–  
 E1183, 2018.
- 388 George E Rice and Priscilla Gainer. “Altruism” in the albino rat. *Journal of Comparative and  
 Physiological Psychology*, 55(1):123, 1962.
- 390 Peter J Richerson and Robert Boyd. *Not by Genes Alone: How Culture Transformed Human Evolution*.  
 University of Chicago Press, 2008.
- 392 Barry Sinervo, Alexis Chainé, Jean Clobert, Ryan Calsbeek, Lisa Hazard, Lesley Lancaster, Andrew G  
 McAdam, Suzanne Alonzo, Gwynne Corrigan, and Michael E Hochberg. Self-recognition, color  
 394 signals, and cycles of greenbeard mutualism and altruism. *Proceedings of the National Academy of  
 Sciences*, 103(19):7372–7377, 2006.
- 396 Peter B Stacey and Walter D Koenig, editors. *Cooperative breeding in birds: long term studies of  
 ecology and behaviour*. Cambridge University Press, 1990.

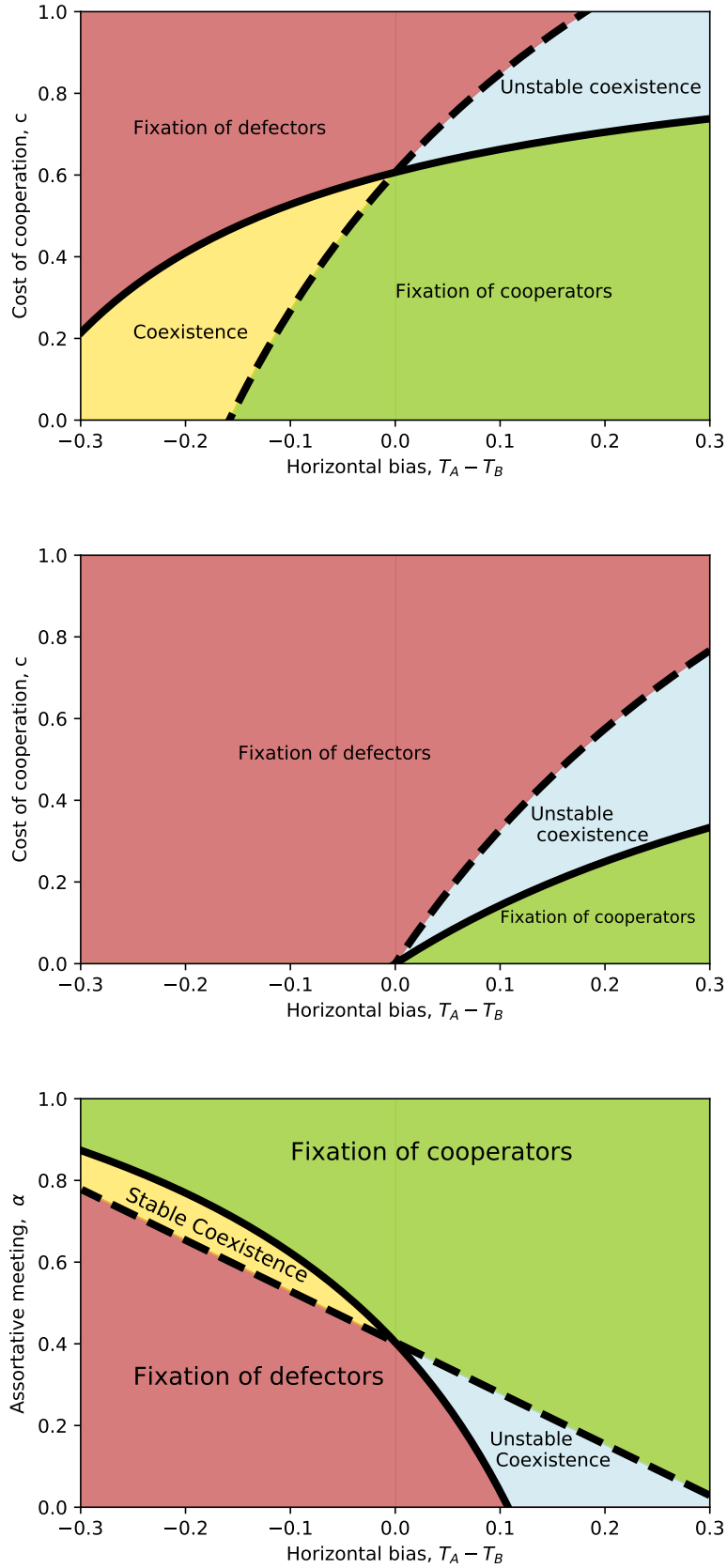
## 398 Figures



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

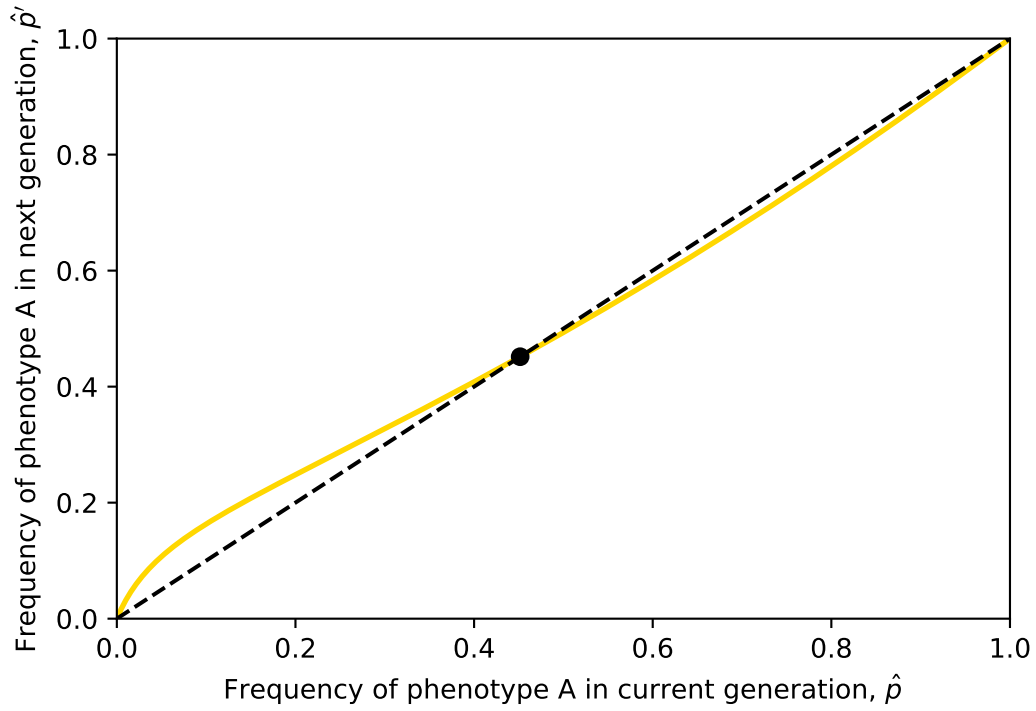


**Figure 2: Stable and unstable coexistence between cooperation and defection - without oblique transmission.** The frequency of the cooperative phenotype  $A$  among parents in the next generation  $\tilde{p}'$  is plotted as a function of the frequency in the current generation  $\tilde{p}$ . The line  $\tilde{p}' = \tilde{p}$  is shown as a dashed black line. The curves and dashed line intersect at the equilibrium  $\tilde{p}^*$  (black circle). When the curves are above the dashed line ( $\tilde{p} < \tilde{p}^*$ ) the frequency  $\tilde{p}$  increases towards  $\tilde{p}^*$ . When the curves are below the dashed line ( $\tilde{p} > \tilde{p}^*$ ) the frequency  $\tilde{p}$  decreases towards  $\tilde{p}^*$ . The yellow curve is **stable coexistence** and has the following parameters values:  $T_A = 0.4, T_B = 0.9, b = 12, c = 0.35, \alpha = 0.45$ . For those values we get that  $\gamma_2 < c < \gamma_1$  (??) The blue curve is **unstable coexistence** and has the following parameters values:  $T_A = 0.5, T_B = 0.1, b = 1.3, c = 0.904, \alpha = 0.4$ . For those values we can that  $\gamma_1 < c < \gamma_2$



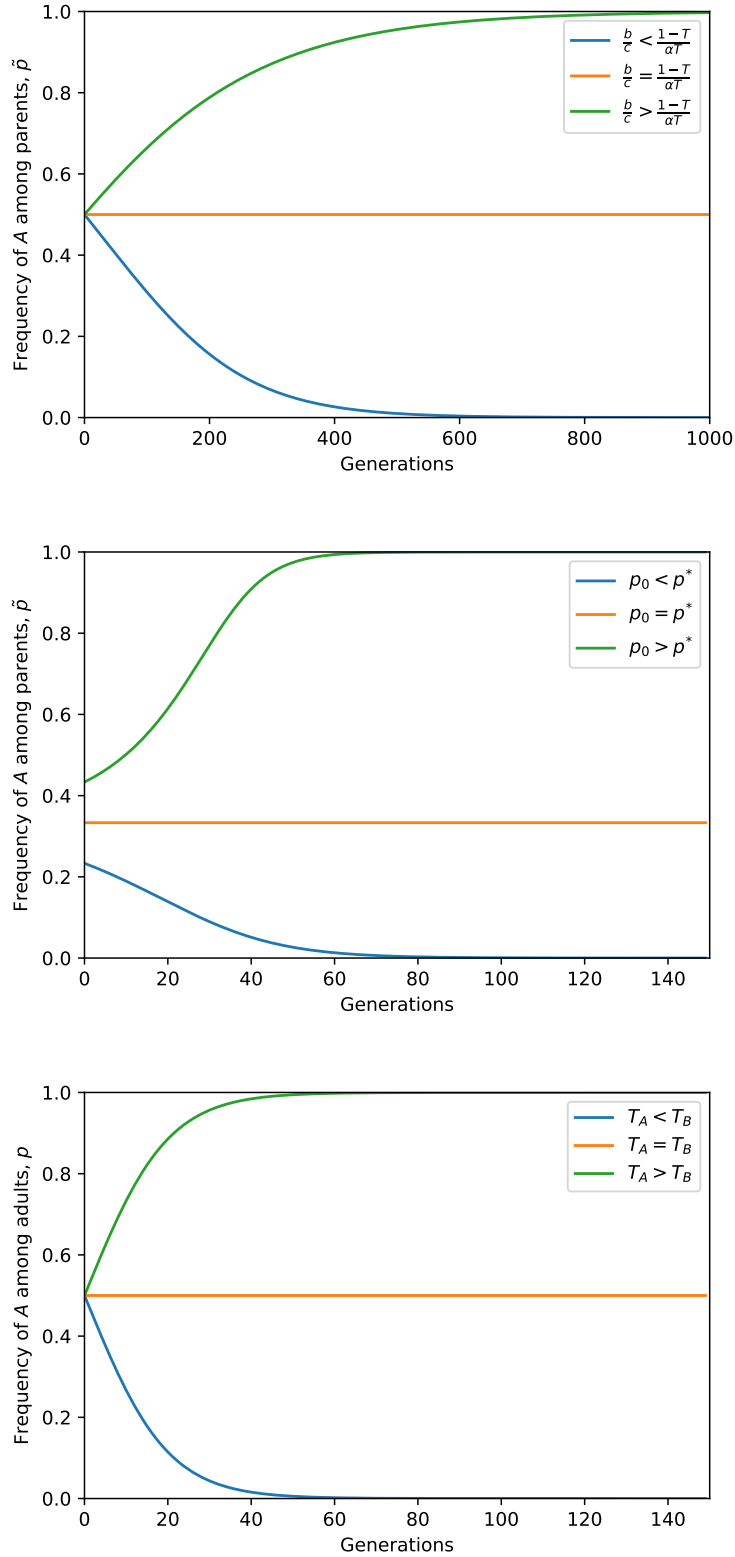
**Figure 3: Evolution of cooperation under vertical and horizontal cultural transmission.** The figure shows the global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial conditions - unstable coexistence (blue), and 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  $\gamma_1$  and  $\gamma_2$  (??) are the solid and dashed lines. **(c)** the assortment  $\alpha$  is on the y-axis; the assortment boundaries  $a_1$  and  $a_2$  (??) are the solid and dashed lines. Here,  $b = 0.3$ ,  $T_A = 0.4$ . In figure **(a)**  $\alpha = 0.7$  and in figure **(b)**  $\alpha = 0$ . In figure **(c)**  $c = 0.35$ .





**Figure 4: Stable coexistence between cooperation and defection - with oblique transmission.**

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  $\hat{p}$ . 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 curves are above the dashed line ( $\hat{p} < \hat{p}^*$ ) the frequency  $\hat{p}$  increases towards  $\hat{p}^*$ . When the curves are below the dashed line ( $\hat{p} > \hat{p}^*$ ) the frequency  $\hat{p}$  decreases towards  $\hat{p}^*$ . The curve is **stable coexistence** and has the following parameters values:  $T_A = 0.4$ ,  $T_B = 0.9$ ,  $b = 20$ ,  $c = 0.1$ ,  $\alpha = 1$ ,  $v = 0.4$ . For those values we get that  $0 < \beta_3 < \beta_1$  (??)



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