

# Non-Vertical Cultural Transmission, Assortment, and the Evolution of Cooperation

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## Abstract

We study the cultural evolution of cooperation under vertical, horizontal, and oblique transmission. Conditions are found for fixation and coexistence of cooperation and defection. We find that the evolution of cooperation is facilitated by horizontal transmission, especially when there is an association between cooperation and transmission, and that the effect of oblique transmission depends on the bias in horizontal transmission. Stable coexistence of cooperation and defection can occur. A spatial model is constructed and compared to results from an unstructured model. Comparisons are drawn with Hamilton's rule and the concepts of relatedness and assortment.

## 18 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 condition is known as *Hamilton's rule*:

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

where the relatedness coefficient  $r$  measures the probability that an allele sampled from the cooperator is identical by descent to one at the same locus in the recipient.

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<sup>1</sup> (Eshel and Cavalli-Sforza, 1982, eq. 3.2)

$$c < b \cdot m, \quad (2)$$

where  $b$  and  $c$  are the benefit and cost of cooperation. Here  $m$  in inequality 2 takes the role of the relatedness coefficient  $r$  in inequality 1.

The role of assortment in the evolution of altruism was emphasized by Fletcher and Doebeli (2009). They found that in a *public-goods* game, altruism will evolve if cooperative individuals experience more cooperation, on average, than defecting individuals, and “thus, the evolution of altruism requires (positive) assortment between focal *cooperative* players and cooperative acts in their interaction environment.” With some change in parameters, this condition is summarized by (Fletcher and Doebeli, 2009, eq. 2.3)

$$c < b \cdot (p_C - p_D), \quad (3)$$

where  $p_C$  is the probability that a cooperator receives help, and  $p_D$  is the probability that a defector receives help.<sup>2</sup> See Bijma and Aanen (2010) for treatment of non-public-goods games.

In this paper 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 demonstrated that if the fidelity of cultural transmission of

<sup>1</sup>In an extended model, which allows an individual to encounter  $N$  individuals before choosing a partner, the righthand side is multiplied by  $E[N]$ , the expected number of encounters (Eshel and Cavalli-Sforza, 1982, eq. 4.6).

<sup>2</sup>Inequality 3 generalizes inequality 1 and inequality 2 by substituting  $p_C = r + p$ ,  $p_D = p$  and  $p_C = m + (1 - m)p$ ,  $p_D = (1 - m)p$ , respectively, where  $p$  is the frequency of cooperators.

altruism is  $\varphi$ , then the condition for evolution of altruism in the case of sib-to-sib altruism is (Feldman et al., 1985, Eq. 16)

$$c < b \cdot \varphi - \frac{1 - \varphi}{\varphi}. \quad (4)$$

In inequality 4,  $\varphi$  takes the role of relatedness ( $r$  in inequality 1) or assortment ( $m$  in inequality 2), but the effective benefit  $b \cdot \varphi$  is reduced by  $(1 - \varphi)/\varphi$ . This shows that under a combination of genetic and cultural transmission, the condition for the evolutionary success of altruism entails a modification of Hamilton's rule (1).

Cultural transmission may be viewed as vertical, horizontal or oblique: vertical transmission occurs between parents and offspring, horizontal transmission occurs between individuals from the same generation, and oblique transmission occurs to offspring from the generation to which their parents belong (i.e. from non-parental adults). Evolution under either of these transmission models can be more rapid than under pure vertical transmission (Cavalli-Sforza and Feldman, 1981; Lycett and Gowlett, 2008; Ram et al., 2018). Both Woodcock (2006) and Lewin-Epstein et al. (2017) demonstrated that non-vertical transmission can help explain the evolution of cooperative behavior (the former using simulations with cultural transmission, the latter using a model where cooperation is mediated by microbes that manipulate their host's behavior.) Some of the analyses by Lewin-Epstein et al. (2017) can be applied to cultural transmission, because models of cultural transmission are mathematically similar to those for transmission of infectious diseases (Cavalli-Sforza and Feldman, 1981).

Here, we study cultural-evolution models of cooperation that include both vertical and non-vertical transmission. We investigate these models using mathematical analysis and simulations. In our models behavioral changes are mediated by cultural transmission that can occur specifically during social interactions. For instance, there may be an association between the choice of partner for social interaction and the choice of partner for cultural transmission. As another example, when an individual interacts with an individual of a different phenotype, exposure to the latter may lead the former to convert its phenotype. Our results demonstrate that cultural transmission can enhance the evolution of cooperation even when genetic transmission cannot, partly because it facilitates the generation of assortment (Fletcher and Doebeli, 2009), and partly because non-vertical transmission can protect traits from the effect of natural selection (Ram et al., 2018). This further emphasizes that treatment of cooperation as a cultural trait, rather than a genetic one, can lead to a broader understanding of its evolutionary dynamics.

## Models

Consider a large population whose members can be one of two phenotypes:  $\phi = A$  for cooperators or  $\phi = B$  for defectors. An offspring inherits its phenotype from its parent via vertical transmission with probability  $v$  or from a random individual in the parental population via oblique transmission with probability  $(1 - v)$ . Following Ram et al. (2018), given that the parent phenotype is  $\phi$  and assuming uni-parental inheritance, the conditional probability that the phenotype  $\phi'$  of the offspring is  $A$  is

$$P(\phi' = A \mid \phi) = \begin{cases} v + (1 - v)p, & \text{if } \phi = A \\ (1 - v)p, & \text{if } \phi = B \end{cases}, \quad (5)$$

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

$$\begin{aligned}\hat{p} &= \tilde{p}[v + (1 - v)p] + (1 - \tilde{p})[(1 - v)p] \\ &= v\tilde{p} + (1 - v)p.\end{aligned}\tag{6}$$

102 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  
104  $b$ , where we assume  $c < b$ . Table 1 shows the payoff matrix, i.e. the fitness of an individual with  
phenotype  $\phi_1$  when interacting with a partner of phenotype  $\phi_2$ .

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

Horizontal cultural transmission occurs between pairs of individuals from the same generation. It  
110 occurs between socially interacting partners with probability  $\alpha$ , or between a random pair with  
probability  $1 - \alpha$  (see Figure 1). However, horizontal transmission is not always successful, as one  
112 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).

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

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

which simplifies to

$$118 \quad p' = \hat{p}^2(T_B - T_A) + \hat{p}(1 + T_A - T_B).\tag{8}$$

The frequency of  $A$  among parents (i.e. after selection) follows a similar dynamic, but also includes  
120 the effect of natural selection, and is therefore

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

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

$$\bar{w} = 1 + \hat{p}(b - c).\tag{10}$$

124 Eq. 9 can be simplified to

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

126 Table 3 summarizes the model variables and parameters.

## Results

### Oblique and Horizontal Transmission

With only oblique and horizontal transmission, i.e.  $v = 0$ , Eq. 6 becomes  $\hat{p} = p$  and Eq. 8 becomes

$$p' = p^2(T_B - T_A) + p(1 + T_A - T_B) , \quad (12)$$

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*

$$T_A > T_B , \quad (13)$$

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

That is, in the absence of vertical transmission, selection plays no role in the evolution of cooperation (i.e.  $b$  and  $c$  are missing from Eq. 12). The dynamics are determined solely by differential horizontal transmission of the two phenotypes, namely, the relative tendency of each phenotype to be horizontally transmitted to peers (see Figure 5c). Note that without bias in horizontal transmission,  $T_A = T_B$ , phenotype frequencies are static,  $p' = p$ .

### Vertical and Horizontal Transmission

With only vertical and horizontal transmission, i.e.  $v = 1$ , Eq. 6 becomes  $\hat{p} = \tilde{p}$ , and Eq. 11 for the frequency of the cooperative phenotype among parents in the next generation  $\tilde{p}'$  can be written as

$$\begin{aligned} \bar{w}\tilde{p}' &= \tilde{p}^2(1 + b - c)[1 - (1 - \tilde{p})(1 - \alpha)T_B] \\ &\quad + \tilde{p}(1 - \tilde{p})(1 - c)[\tilde{p}(1 - \alpha)T_B + 1 - T_B] \\ &\quad + \tilde{p}(1 - \tilde{p})(1 + b)[\tilde{p}(1 - \alpha) + \alpha]T_A \\ &\quad + (1 - \tilde{p})^2\tilde{p}(1 - \alpha)T_A . \end{aligned} \quad (14)$$

Fixation of either cooperation,  $\tilde{p} = 1$ , or defection,  $\tilde{p} = 0$ , are equilibria of Eq. 14, solving  $\tilde{p}' = \tilde{p}$ . We assume for the remainder of the analysis that  $0 < \tilde{p} < 1$ .

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

$$\tilde{p}(1 - \tilde{p})[(1 + b)T_A + (1 - c)(1 - T_B) - 1] = 0 , \quad (15)$$

and there are no additional equilibria. For cooperation to take over the population (i.e., for  $\tilde{p} = 1$  to be globally stable) we require  $\tilde{p}' > \tilde{p}$ ; that is,

$$\tilde{p}^2(1 + b - c) + \tilde{p}(1 - \tilde{p})[(1 - c)(1 - T_B) + (1 + b)T_A] > \bar{w}\tilde{p} . \quad (16)$$

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

$$(1 - c)(1 - T_B) + (1 + b)T_A > 1 . \quad (17)$$

If  $\alpha < 1$ , divide both sides of Eq. 14 by  $\tilde{p}$  and set  $\bar{w} = 1 + \tilde{p}(b - c)$ . Then  $\tilde{p}' > \tilde{p}$  if

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

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

$$c(1 - T_B) - b\alpha T_A - (T_A - T_B) < \tilde{p} \cdot b(1 - \alpha)(T_A - T_B). \tag{19}$$

In addition to the fixation states  $\tilde{p} = 0$  and  $\tilde{p} = 1$ , there may be an actual polymorphic equilibrium of  $\tilde{p}' = \tilde{p}$  in Eq. 14, namely

$$\tilde{p}^* = \frac{c(1 - T_B) - b\alpha T_A - (T_A - T_B)}{b(1 - \alpha)(T_A - T_B)}, \tag{20}$$

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

Since all parameters are positive, we can apply inequality 19 and see that a requirement for  $\tilde{p}' > \tilde{p}$  is that either

$$T_A > T_B \quad \text{and} \quad \tilde{p} > \tilde{p}^*, \quad \text{or} \tag{21}$$

$$T_A < T_B \quad \text{and} \quad \tilde{p} < \tilde{p}^*. \tag{22}$$

We define the *cost boundaries*,

$$\gamma_1 = \frac{b\alpha T_A + (T_A - T_B)}{1 - T_B}, \quad \gamma_2 = \frac{b\alpha T_B + (1 + b)(T_A - T_B)}{1 - T_B}. \tag{23}$$

Then, applying Eqs. 20, 21, and 22, we summarize the possible outcomes in the 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 cooperation exhibits one of the following scenarios, depending on the cost boundaries  $\gamma_1$  and  $\gamma_2$  (Eq. 23):*

1. Fixation of cooperation: if (i)  $T_A \geq T_B$  and  $c < \gamma_1$ ; or if (ii)  $T_A < T_B$  and  $c < \gamma_2$ .
2. Fixation of defection: if (iii)  $T_A \geq T_B$  and  $\gamma_2 < c$ ; or if (iv)  $T_A < T_B$  and  $\gamma_1 < c$ .
3. Stable coexistence: if (v)  $T_A < T_B$  and  $\gamma_2 < c < \gamma_1$ .
4. Unstable coexistence: if (vi)  $T_A > T_B$  and  $\gamma_1 < c < \gamma_2$ .

These conditions are illustrated in Figure 2.

Cooperation and defection can coexist stably at frequencies  $\tilde{p}^*$  and  $1 - \tilde{p}^*$  (Eq. 20) if there is horizontal transmission bias for defection,  $T_A < T_B$ , and the cost of cooperation is intermediate,  $\gamma_2 < c < \gamma_1$ ; see yellow area in Figure 2b. When unstable coexistence occurs, phenotype A will fix if its initial frequency is  $p > \tilde{p}^*$ , and phenotype B will fix if its initial frequency is  $1 - p > 1 - \tilde{p}^*$ ; this occurs when there is horizontal transmission bias for cooperation,  $T_A > T_B$ , and the cost is intermediate,  $\gamma_1 < c < \gamma_2$ . Figure 4a shows the mapping  $\tilde{p} \rightarrow \tilde{p}'$ ; see blue areas in Figure 2a and Figure 2b.

**Corollary 1** (Symmetric horizontal transmission). *If  $T = T_A = T_B$ , then cooperation will take over the population if*

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

Note that the right-hand side equals  $\gamma_1$  when  $T = T_A = T_B$ . This condition is obtained by setting  $T = T_A = T_B$  in inequality 19 and can be interpreted as a version of Hamilton's rule ( $c < b \cdot r$ , inequality 1) or as a version of inequality 3, where  $\alpha T/(1 - T)$  can be regarded as the *effective relatedness* or *effective assortment*, respectively. Figure 5a illustrates this condition.

The condition in inequality 24 demonstrates the importance of the social association  $\alpha$ . The following corollaries provide additional demonstrations.

**Corollary 2** (No social association of transmission and cooperation). *Without social association ( $\alpha = 0$ ), cooperation can take over the population if there is horizontal transmission bias for cooperation,  $T_A > T_B$ , and if either*

$$c < \frac{T_A - T_B}{1 - T_B} \quad \text{or} \quad \tilde{p}_0 > \tilde{p}^* = \frac{c(1 - T_B) - (T_A - T_B)}{b(T_A - T_B)} . \quad (25)$$

Figure 2a illustrates these conditions, which are obtained by setting  $\alpha = 0$  in Eqs. 20 and 23. If there is horizontal transmission bias for cooperation ( $T_A > T_B$ ) then cooperation can evolve from any initial frequency if the cost is low enough,  $c < \gamma_1$  (green area below solid line). If the cost is not low enough, cooperation can also evolve if its initial frequency is high enough and the cost is not too high,  $c < \gamma_2$  (blue area between solid and dashed lines).

We can interpret these condition as follows. First, when cooperators are rare, they will mostly interact with defectors. Therefore, for cooperation to increase in frequency and fix, the *effective cost of cooperation* must be lower than the horizontal transmission of cooperation,  $1 - (1 - c)(1 - T_B) < T_A$ , which is equivalent to the first of the two inequalities in Eq. 25. Second, if  $T_A$  is not large enough, cooperation will fix if the initial frequency is higher than the threshold  $\tilde{p}^*$ ; thus, this threshold must be below one, which entails  $1 - (1 - c)(1 - T_B) < T_A + b(T_A - T_B)$ . That is, the effective cost of cooperation must be lower than the combined effect of horizontal transmission of cooperation,  $T_A$ , and the benefit of cooperation multiplied by the transmission bias,  $b(T_A - T_B)$ .

**Corollary 3** (Perfect social association of transmission and cooperation). *With perfect social association ( $\alpha = 1$ ), the only equilibria are the fixation states,  $\tilde{p} = 0$  and  $\tilde{p} = 1$ , and cooperation will evolve from any initial frequency (i.e.,  $\tilde{p}' > \tilde{p}$ ) if*

$$c < \frac{b \cdot T_A + (T_A - T_B)}{1 - T_B} . \quad (26)$$

This condition is obtained from inequality 17, and the right-hand side equals  $\gamma_1$  when  $\alpha = 1$  (Eq. 23). Perfect social association (horizontal transmission always occurs during the cooperative interaction) is also assumed in the model studied by Lewin-Epstein et al. (2017), and therefore this corollary is equivalent to the result in their eq. 1.

Inequality 26 can also be written as  $1 - (1 - c)(1 - T_B) < (1 + b)T_A$ , 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 of cooperation* from this interaction. Similarly,  $(1 + b)T_A$  is

the probability that during an interaction between a cooperator and a defector, the defector becomes cooperative and reproduces, which is the *effective benefit of cooperation* from this interaction. Thus, inequality 26 entails that cooperation can evolve if the effective cost of cooperation is less than the effective benefit during an interaction between a cooperator and a defector.

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

$$a_1 = \frac{c(1 - T_B) - (1 + b)(T_A - T_B)}{b \cdot T_B}, \quad a_2 = \frac{c(1 - T_B) - (T_A - T_B)}{b \cdot T_A}. \quad (27)$$

Applying Eqs. 20, 21, and 22, we have the following corollary.

**Corollary 4** (Intermediate association of transmission and cooperation). *Cooperation will increase from rarity if social association is high enough, specifically if  $a_2 < \alpha$ .*

Figure 2c demonstrates these conditions. With horizontal transmission bias for cooperation ( $T_A > T_B$ ), cooperation can fix from any initial frequency if  $a_2 < \alpha$  (green area in positive x-axis). With horizontal bias favoring defection ( $T_A < T_B$ ), cooperation can fix from any frequency if social association is high,  $a_1 < \alpha$  (green area with  $T_A < T_B$ ), and can also increase when rare and reach stable coexistence with defection if social association is intermediate,  $a_2 < \alpha$  (yellow area). Without horizontal bias ( $T_A = T_B$ ) fixation of cooperation occurs if social association is high enough;  $\frac{c}{b} \cdot \frac{1-T}{T} < \alpha$  (inequality 24; in this case  $a_1 = a_2$ ).

## With Vertical and Oblique Transmission

With both vertical and oblique transmission,  $0 < v < 1$ , the recursion system is more complex and we focus on local rather than on global stability. To proceed, note that Eq. 6 gives  $\hat{p}'$  as a function of both  $p'$  and  $\tilde{p}'$ . Eq. 8 gives  $p'$  as a function of  $\tilde{p}$ , since  $\hat{p}$  is given in Eq. 6 as a function of  $\tilde{p}$  and Eq. 11 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), determine the equilibria, namely, solutions of  $\hat{p}' = \hat{p}$ , and analyse their local stability.

Applying Eqs. 6, 8, and 11 gives the function  $f(\hat{p})$  (see Appendix Appendix A):

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = \beta_1 \hat{p}^3 + \beta_2 \hat{p}^2 + \beta_3 \hat{p}, \quad (28)$$

where

$$\begin{aligned} \beta_1 &= [c(1 - v) - b(1 - \alpha v)](T_A - T_B), \\ \beta_2 &= -\beta_1 - \beta_3, \\ \beta_3 &= \alpha b v T_A - c v (1 - T_B) + (T_A - T_B). \end{aligned} \quad (29)$$

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:

$$f(\hat{p}) = \hat{p}(1 - \hat{p})[\alpha b v T - c v (1 - T)]. \quad (30)$$

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 (see Appendix Appendix B), where

$$f'(\hat{p}) = (1 - 2\hat{p})[\alpha b v T - c v (1 - T)], \quad (31)$$



with

$$\begin{aligned} f'(0) &= \alpha b v T - c v (1 - T), \\ f'(1) &= -\alpha b v T + c v (1 - T). \end{aligned} \quad (32)$$

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

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

$$\hat{p}^* = \frac{\beta_3}{\beta_1}. \quad (33)$$

Note that the sign of the cubic (Eq. 28) at positive (negative) infinity is equal (opposite) to the sign of  $\beta_1$ . If  $T_A > T_B$ , then

$$\beta_1 < [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) < 0, \quad (34)$$

since  $c < b$  and  $\alpha v < 1$ . 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  $f'(1) < 0$  so that 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  $T_A < T_B$ , then

$$\beta_1 > [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) > 0, \quad (35)$$

since  $c < b$  and  $\alpha v < 1$ , 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  $A$  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.

Define new cost boundaries,  $\hat{\gamma}_1$  and  $\hat{\gamma}_2$ ,

$$\hat{\gamma}_1 = \frac{b v \alpha T_A + (T_A - T_B)}{v(1 - T_B)}, \quad \hat{\gamma}_2 = \frac{b v \alpha T_B + (1 + b)(T_A - T_B)}{v(1 - T_B) + (1 - v)(T_A - T_B)}, \quad (36)$$

and a vertical transmission threshold,

$$\hat{v} = \frac{T_B - T_A}{1 - T_A}. \quad (37)$$

First, assume  $T_A < T_B$ .  $\beta_3 < 0$  requires  $\hat{\gamma}_1 < c$ , and for  $\beta_3 < \beta_1$  we need  $c[v(1 - T_B) + (1 - v)(T_A - T_B)] > b v \alpha T_B + (1 + b)(T_A - T_B)$ . Note that the expression in the square brackets is positive if and only if  $v > \hat{v}$ . Thus, for  $\beta_3 < \beta_1$  we need  $v > \hat{v}$  and  $\hat{\gamma}_2 < c$  or  $v < \hat{v}$  and  $c < \hat{\gamma}_2$ , and for  $0 < \beta_3 < \beta_1$  we need  $v > \hat{v}$  and  $\hat{\gamma}_2 < c < \hat{\gamma}_1$ , or  $v < \hat{v}$  and  $c < \min(\hat{\gamma}_1, \hat{\gamma}_2)$ . For  $\beta_1 < \beta_3$  we need  $v > \hat{v}$  and  $c < \hat{\gamma}_2$  or  $v < \hat{v}$  and  $\hat{\gamma}_2 < c$ . However, some of these conditions cannot be met, since  $v < \hat{v}$  implies  $c < 1 < \hat{\gamma}_2$ .

Second, when  $T_A > T_B$   $\beta_3 > 0$  requires  $\hat{\gamma}_1 > c$ . For  $\beta_1 < \beta_3$  we need  $c[v(1 - T_B) + (1 - v)(T_A - T_B)] < b v \alpha T_B + (1 + b)(T_A - T_B)$ . Thus for  $\beta_1 < \beta_3$  we need  $v > \hat{v}$  and  $c < \hat{\gamma}_2$  or  $v < \hat{v}$  and  $c > \hat{\gamma}_2$ . But  $\hat{v} < 0$  when  $T_A > T_B$ , and therefore we have  $\beta_1 < \beta_3$  if  $c < \hat{\gamma}_2$ . Similarly, we have  $\beta_3 < \beta_1$  if  $c > \hat{\gamma}_2$ .

304 The following result summarizes the possible outcomes.

306 **Result 3** (Vertical, oblique, and horizontal transmission of cooperation). *With vertical, horizontal,*  
 308 *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  $\hat{\gamma}_2$  (Eq. 36) and the vertical transmission*  
*threshold  $\hat{v}$  (Eq. 37) :*

- 310 1. Fixation of cooperation: if (i)  $T_A \geq T_B$  and  $c < \hat{\gamma}_1$ ; or if (ii)  $T_A < T_B$  and  $v > \hat{v}$  and  $c < \hat{\gamma}_2$ .
- 312 2. Fixation of defection: if (iii)  $T_A \geq T_B$  and  $\hat{\gamma}_2 < c$ ; or if (iv)  $T_A < T_B$  and  $\hat{\gamma}_1 < c$ .
- 314 3. Stable Coexistence: if (v)  $T_A < T_B$  and  $v < \hat{v}$  and  $c < \hat{\gamma}_1$ ; or if (vi)  $T_A < T_B$  and  $v > \hat{v}$  and  $\hat{\gamma}_2 < c < \hat{\gamma}_1$ .
- 314 4. Unstable coexistence: if (vii)  $T_A > T_B$  and  $\hat{\gamma}_1 < c < \hat{\gamma}_2$ .

These conditions are illustrated in Figure 3ab.

316 Much of the literature on evolution of cooperation focuses on conditions for initially rare cooperative  
 318 phenotype to invade a population of defectors. The next corollary deals with such a condition.

**Corollary 5** (Condition for cooperation to increase from rarity). *If the initial frequency of cooperation*  
 320 *is very close to zero,  $\hat{p}_0 \approx 0$ , then its frequency will increase if*

$$c < \hat{\gamma}_1 = \frac{bv\alpha T_A + (T_A - T_B)}{v(1 - T_B)}. \quad (38)$$

322 This condition merges the conditions for fixation of cooperation and for stable coexistence, which both  
 324 lead to the instability of  $\hat{p} = 0$ , the fixation of defection. Importantly, increasing social association  $\alpha$   
 326 increases the boundary cost ( $\partial\hat{\gamma}_1/\partial\alpha > 0$ ), making it easier for cooperation to increase from rarity.  
 328 Similarly, increasing the horizontal transmission of cooperation increases the boundary ( $\partial\hat{\gamma}_1/\partial T_A >$   
 330  $0$ ), making it easier for cooperation to evolve. However, increasing the horizontal transmission of  
 defection can either increase or decrease the boundary depending on  $\text{sign}(\partial\hat{\gamma}_1/\partial T_B) = \text{sign}(bv\alpha T_A +$   
 $T_A - 1)$ . Therefore, increasing  $T_B$  increases the boundary when  $T_A > \frac{1}{1+bv}$  but when this applies we  
 get that  $\hat{\gamma}_1 > 1$  which guarantees cooperation will evolve from rarity since  $c < 1$ . When  $T_A < \frac{1}{1+bv}$   
 increasing  $T_B$  decreases the boundary.

Increasing the vertical transmission  $v$  can either increase or decrease the boundary, depending on the  
 332 horizontal transmission bias,  $T_A - T_B$  (because  $\text{sign}(\partial\hat{\gamma}_1/\partial v) = -\text{sign}(T_A - T_B)$ .) When  $T_A < T_B$  we  
 334 get  $\partial\hat{\gamma}_1/\partial v > 0$  and therefore, as the vertical transmission increases the boundary on the cost increases  
 336 making it easier for cooperation to evolve from rarity. Similarly, when  $T_A > T_B$  we get  $\partial\hat{\gamma}_1/\partial v < 0$  and  
 338 therefore, as the vertical transmission increases the boundary on the cost decreases making it harder  
 for cooperation to evolve from rarity. We got that when  $T_A > T_B$  vertical transmission is interfering  
 cooperation to evolve by decreasing the maximum cost that the cooperates can pay and stil evolve  
 from rarity.

In general, this condition cannot be formulated in the form of Hamilton's rule due to the horizontal  
 340 transmission bias  $T_A - T_B$ . Without horizontal transmission bias, i.e., with  $T = T_A = T_B$ , these condi-  
 tions reduce to a form of Hamilton's rule.

342

In Corollary 4, we examined the effect of social association on evolution of cooperation in the case of  
 344 perfect vertical transmission ( $v = 1$ ). A more general case can be stated for  $0 < v \leq 1$ . Consider the

social association boundaries

$$\hat{a}_1 = \frac{c \cdot v(1 - T_A) - (T_A - T_B)(1 + b - c)}{b \cdot v \cdot T_B}, \quad \hat{a}_2 = \frac{c \cdot v(1 - T_B) - (T_A - T_B)}{b \cdot v \cdot T_A}. \quad (39)$$

Then the following applies.

348

**Corollary 6** (Intermediate association of transmission and cooperation). *Cooperation will increase from rarity if social association is high enough, specifically if  $\hat{a}_2 < \alpha$ .*

Figure 3cd illustrates this conditions.

352 Note that  $\partial \hat{a}_2 / \partial v = bT_A(T_A - T_B)$ .  $\partial \hat{a}_2 / \partial v > 0$  when  $T_A > T_B$  and therefore, as the vertical transmission  $v$  increases a greater value of social association is required for fixation of cooperation from  
354 rarity. Similarly, when  $T_B > T_A$   $T_A > T_B$  we get  $\partial \hat{a}_2 / \partial v < 0$  and therefore, as  $v$  decreases a greater value of social association is required for fixation of cooperation from rarity.

356

**Corollary 7** (Necessary condition for fixation of cooperation). *Fixation of cooperation is possible only if the vertical transmission rate is high enough,*

358

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

360 This condition does not guarantee fixation of cooperation. Rather, if this condition does not apply then cooperation cannot fix. When horizontal transmission is biased for cooperation,  $T_A > T_B$ , cooperation  
362 can fix with any vertical transmission rate, i.e.  $\hat{v} < 0$ . In contrast, if the horizontal transmission is biased for defection,  $T_A < T_B$ , cooperation can fix only if the vertical transmission rate is high enough:  
364 in this case oblique transmission can prevent fixation of cooperation, see Figure 3bd.

## 366 Modifiers of social association

We now analyze the evolution of social association under perfect vertical transmission,  $v = 1$ . We  
368 assume a population at a stable coexistence of the two phenotypes, cooperation  $A$  and defection  $B$ , such that the frequency of  $A$  among parents is  $\tilde{p}^*$  (Eq. 20). Note that for stable coexistence to occur, we  
370 assume horizontal bias for defection,  $T_A < T_B$ , and an intermediate cost of cooperation,  $\gamma_2 < c < \gamma_1$  (Eq. 23)

372 The stable population mean fitness is  $\bar{w}^* = 1 + \tilde{p}^*(b - c)$  (Eq. 10), which is increasing in  $\tilde{p}^*$ . Therefore, to determine the effect of increasing  $\alpha$  on the stable population mean fitness, we must analyze its effect  
374 on  $\tilde{p}^*$ ,

$$\frac{\partial \tilde{p}^*}{\partial \alpha} = \frac{bT_A - c(1 - T_B) + (T_A - T_B)}{b(1 - \alpha)^2(T_B - T_A)}. \quad (41)$$

376 Note that stable coexistence implies  $c < \gamma_1$ , and because  $\alpha < 1$ , we have

$$c < \gamma_1 = \frac{b\alpha T_A + (T_A - T_B)}{1 - T_B} < \frac{bT_A + (T_A - T_B)}{1 - T_B}. \quad (42)$$

378 Therefore,  $bT_A - c(1 - T_B) - (T_B - T_A) > 0$ , and since  $T_A < T_B$ , the derivative  $\partial \tilde{p}^* / \partial \alpha$  is positive, and the population mean fitness increases as social association  $\alpha$  increases.

380 We found that if the social association increases, the population mean fitness will increase. But can an allele that increases the social association evolve? To answer this question, we extend our model

382 to include a “modifier locus” (Lieberman and Feldman, 1986; Lieberman, 1988). The function of this  
 384 modifier locus is to determine the social association. It has no direct effect on fitness. We assume  
 386 that the modifier locus has two alleles,  $M$  and  $m$ , which induce association probabilities  $\alpha_1$  and  $\alpha_2$ ,  
 388 respectively, and that initially only  $M$  is present. Suppose that the population evolves to a stable  
 equilibrium when only  $M$  is present; we check the local stability of this equilibrium to the introduction  
 of the allele  $m$  at the modifier locus. This is called “external stability”; For more details on external  
 stability, see Altenberg et al. (2017).

We define the frequencies of the pheno-genotypes  $AM$ ,  $BM$ ,  $Am$ , and  $Bm$  as  $\tilde{\mathbf{p}} = (\tilde{p}_1, \tilde{p}_2, \tilde{p}_3, \tilde{p}_4)$ . The  
 390 frequencies of the pheno-genotypes in the next generation are defined by the recursion system

$$\begin{aligned}
 \bar{w}\tilde{p}'_1 &= \tilde{p}_1(\tilde{p}_1 + \tilde{p}_3)(1 + b - c)(1 - (1 - \alpha_1)(\tilde{p}_2 + \tilde{p}_4)T_B) \\
 &\quad + \tilde{p}_1(\tilde{p}_2 + \tilde{p}_4)(1 - c)(1 - \alpha_1 T_B(\tilde{p}_1 + \tilde{p}_3) - T_B(\tilde{p}_2 + \tilde{p}_4)) \\
 &\quad + \tilde{p}_2(\tilde{p}_1 + \tilde{p}_3)(1 + b)T_A(\tilde{p}_1 + \tilde{p}_3 + \alpha_1(\tilde{p}_2 + \tilde{p}_4)) \\
 &\quad + \tilde{p}_2(\tilde{p}_2 + \tilde{p}_4)(\tilde{p}_1 + \tilde{p}_3)(1 - \alpha_1)T_A \\
 \bar{w}\tilde{p}'_2 &= \tilde{p}_2(\tilde{p}_2 + \tilde{p}_4)(1 - (1 - \alpha_1)(\tilde{p}_1 + \tilde{p}_3)T_A) \\
 &\quad + \tilde{p}_2(\tilde{p}_1 + \tilde{p}_3)(1 + b)(1 - \alpha_1 T_A(\tilde{p}_2 + \tilde{p}_4) - T_A(\tilde{p}_1 + \tilde{p}_3)) \\
 &\quad + \tilde{p}_1(\tilde{p}_2 + \tilde{p}_4)(1 - c)(\alpha_1 T_B + (1 - \alpha_1)(\tilde{p}_2 + \tilde{p}_4)T_B) \\
 &\quad + \tilde{p}_1(\tilde{p}_1 + \tilde{p}_3)(1 + b - c)(1 - \alpha_1)(\tilde{p}_2 + \tilde{p}_4)T_B \\
 \bar{w}\tilde{p}'_3 &= \tilde{p}_3(\tilde{p}_1 + \tilde{p}_3)(1 + b - c)(1 - (1 - \alpha_2)(\tilde{p}_2 + \tilde{p}_4)T_B) \\
 &\quad + \tilde{p}_3(\tilde{p}_2 + \tilde{p}_4)(1 - c)(1 - \alpha_2 T_B(\tilde{p}_1 + \tilde{p}_3) - T_B(\tilde{p}_2 + \tilde{p}_4)) \\
 &\quad + \tilde{p}_4(\tilde{p}_1 + \tilde{p}_3)(1 + b)T_A(\tilde{p}_1 + \tilde{p}_3 + \alpha_2(\tilde{p}_2 + \tilde{p}_4)) \\
 &\quad + \tilde{p}_4(\tilde{p}_2 + \tilde{p}_4)(\tilde{p}_1 + \tilde{p}_3)(1 - \alpha_2)T_A \\
 \bar{w}\tilde{p}'_4 &= \tilde{p}_4(\tilde{p}_2 + \tilde{p}_4)(1 - (1 - \alpha_2)(\tilde{p}_1 + \tilde{p}_3)T_A) \\
 &\quad + \tilde{p}_4(\tilde{p}_1 + \tilde{p}_3)(1 + b)(1 - \alpha_2 T_A(\tilde{p}_2 + \tilde{p}_4) - T_A(\tilde{p}_1 + \tilde{p}_3)) \\
 &\quad + \tilde{p}_3(\tilde{p}_2 + \tilde{p}_4)(1 - c)(\alpha_2 T_B + (1 - \alpha_2)(\tilde{p}_2 + \tilde{p}_4)T_B) \\
 &\quad + \tilde{p}_3(\tilde{p}_1 + \tilde{p}_3)(1 + b - c)(1 - \alpha_2)(\tilde{p}_2 + \tilde{p}_4)T_B ,
 \end{aligned} \tag{43}$$

392 where  $\bar{w} = 1 + (b - c) \cdot (\tilde{p}_1 + \tilde{p}_3)$  is the population mean fitness.

The local stability of  $\tilde{\mathbf{p}}^* = (\tilde{p}^*, 1 - \tilde{p}^*, 0, 0)$ , the equilibrium when only allele  $M$  is present (see Eq. 20),  
 394 to the introduction of allele  $m$  is determined by the linear approximation  $\mathbf{L}^*$  of the transformation  
 in Eq. 43 near  $\tilde{\mathbf{p}}^*$  (i.e., the Jacobian of the transformation at the equilibrium).  $\mathbf{L}^*$  is known to have  
 396 a block structure, with the diagonal blocks occupied by the matrices  $\mathbf{L}_{in}^*$  and  $\mathbf{L}_{ex}^*$ . The latter is the  
 external stability matrix: the linear approximation to the transformation near  $\tilde{\mathbf{p}}^*$  involving only the  
 398 pheno-genotypes  $Am$  and  $Bm$ . Because we assume that  $\tilde{\mathbf{p}}^*$  is internally stable (i.e. locally stable  
 to small perturbations in the frequencies of  $AM$  and  $BM$ ), the stability of  $\tilde{\mathbf{p}}^*$  is determined by the  
 400 eigenvalues of the external stability matrix  $\mathbf{L}_{ex}^*$ , which is derived from Eq. 43 as

$$\mathbf{L}_{ex}^* = \frac{1}{\bar{w}^*} \begin{bmatrix} \frac{\partial \tilde{p}'_3}{\partial \tilde{p}_3}(\tilde{\mathbf{p}}^*) & \frac{\partial \tilde{p}'_3}{\partial \tilde{p}_4}(\tilde{\mathbf{p}}^*) \\ \frac{\partial \tilde{p}'_4}{\partial \tilde{p}_3}(\tilde{\mathbf{p}}^*) & \frac{\partial \tilde{p}'_4}{\partial \tilde{p}_4}(\tilde{\mathbf{p}}^*) \end{bmatrix} . \tag{44}$$

402 If the eigenvalues of  $\mathbf{L}_{ex}^*$  are less than 1, then the equilibrium  $\tilde{\mathbf{p}}$  is externally stable and allele  $m$  cannot  
 invade the population of allele  $M$ .

$$\begin{aligned}
\frac{\partial \tilde{p}'_3}{\partial \tilde{p}_3}(\tilde{\mathbf{p}}^*) &= b(\tilde{p}^* - (1 - \alpha_2)T_B(\tilde{p}^* - \tilde{p}^{*2})) + (1 - c)(1 + \tilde{p}^*T_B - T_B) \\
\frac{\partial \tilde{p}'_3}{\partial \tilde{p}_4}(\tilde{\mathbf{p}}^*) &= bT_A\tilde{p}^*(\tilde{p}^* + \alpha_2(1 - \tilde{p}^*)) + \tilde{p}^*T_A \\
\frac{\partial \tilde{p}'_4}{\partial \tilde{p}_3}(\tilde{\mathbf{p}}^*) &= (1 - \tilde{p}^*)(1 - c)T_B + b\tilde{p}^*(1 - \alpha_2)(1 - \tilde{p}^*)T_B \\
\frac{\partial \tilde{p}'_4}{\partial \tilde{p}_4}(\tilde{\mathbf{p}}^*) &= 1 - \tilde{p}^*T_A + b\tilde{p}^*(1 - \alpha_2T_A(1 - \tilde{p}^*) - T_A\tilde{p}^*)
\end{aligned} \tag{45}$$

## With Population Structure

Social association may also emerge from a population's structure. Consider a population colonizing a 2D grid of size 100-by-100, where each site is inhabited by one individual, similarly to Lewin-Epstein and Hadany (2020). Each individual is characterized by its phenotype: either cooperator,  $A$ , or defector,  $B$ . At the beginning, each cell in the grid is randomly colonized with either a cooperator or a defector, with equal probability. In each generation individuals interact with their neighbors, i.e. individuals that inhabit adjacent sites, in a prisoner's dilemma game (Table 1) and with horizontal cultural transmission. As before,  $T_A$  and  $T_B$  are the probabilities of transmitting phenotypes  $A$  and  $B$  during horizontal transmission. At each generation, half of the individuals are randomly chosen to "initiate" interactions. Initiators then interact with a random neighbor in a prisoners' dilemma game and a random neighbor (with replacement) for horizontal cultural transmission (as both the game and the transmission are symmetrical, the expected number of each of these interactions per individual per generation is 1). Therefore, the effective social association  $\alpha$  in this model is the probability that the same neighbor is picked for both interactions, or  $\alpha = 1/m$ , where  $m$  is the number of neighbors. On an infinite grid,  $m = 8$ , but on a finite grid  $m$  can be lower in edge neighborhoods close to the grid border.

The order of the interactions across the lattice at each generation is random. After all interactions take place, and individual's fitness is determined by  $w = 1 + b \cdot n_b - c \cdot n_c$ , where  $n_b$  is the number interactions of that individual with cooperative neighbors, and  $n_c$  is the total number of interactions that that individual had ( $n_b \leq n_c$ ). Then a new generation is generated, and sites can be settled by offspring of any parent, not just neighbor parents. Thus, selection is global, rather than local, in accordance with our deterministic model. The parent is randomly drawn with probability proportional to its fitness, divided by the average fitness of all potential parents. Offspring then have the same phenotype as their parents.

Figure 6 shows that the highest cost of cooperation ( $c$ ) that permits the evolution of cooperation in simulations of the spatial model roughly agrees with the conditions derived in Result 2. An example for stable coexistence is shown in Figure 8. Simulating a spatial model with local selection (i.e. sites can only be settled by offspring of neighbor parents) had only a minor affect, eliminating the stable coexistence.

This comparison between the deterministic well-mixed model and the stochastic spatial model demonstrates that the derived conditions can be useful for predicting the dynamics of complex scenarios. Moreover, our spatial model shows how social association ( $\alpha$ ) can emerge from local interactions between individuals in a structured population.

## 438 Discussion

We studied the evolution of cooperation under non-vertical transmission using deterministic discrete-time evolutionary models with fitnesses in the form of payoffs from a prisoner's dilemma game. Under oblique and horizontal cultural transmission, horizontal transmission bias in favor of the cooperative phenotype was found to be necessary and sufficient for evolution of cooperation (Result 1). Under a combination of vertical, oblique, and horizontal transmission, cooperation or defection can either fix or coexist at a stable polymorphism, depending on the relationship between the cost and benefit of cooperation, the horizontal bias, and the association between cooperation and transmission (Results 2 and 3). Importantly, cooperation can increase from rarity (i.e. invade a population of defectors) if and only if (inequality 38),

$$448 \quad c \cdot v(1 - T_B) < b \cdot v\alpha T_A + (T_A - T_B) , \quad (46)$$

that is, if the effective cost of cooperation (left-hand side) is smaller than the effective benefit plus the horizontal transmission bias (right-hand side). Remarkably, stable coexistence between cooperation and defection can be maintained if horizontal transmission is biased for defection ( $T_A < T_B$ ) and both the cost of cooperation and social association are intermediate (yellow areas in Figures 2-3).

We find that increasing social association ( $\alpha$ ) increases the opportunity for evolution of cooperation (Corollaries 4 and 6, Figures 2c and 3cd). Without social association, the benefit of cooperation cannot facilitate its evolution; cooperation can only succeed under horizontal transmission bias ( $T_A > T_B$ , Corollary 2). Indeed, horizontal transmission plays a major role in the evolution of cooperation. Mostly, increasing the transmission of cooperation ( $T_A$ ) or decreasing the transmission of defection ( $T_B$ ) facilitates the evolution of cooperation (Corollaries 5 and 6, Figure 2). However, in specific cases increasing the transmission of defection can be advantageous for cooperation (Corollaries 5 and 6). The effect of oblique transmission is more complex (Corollary 6). When there is horizontal transmission bias for cooperation ( $T_A > T_B$ ), increasing the rate of oblique transmission ( $1 - v$ ) will facilitate the evolution of cooperation (Figure 3ac). In contrast, when the bias is for defection ( $T_A < T_B$ ), high rates of vertical transmission ( $v$ ) are advantageous for cooperation, and there must be sufficient rate of vertical transmission ( $v > \hat{v}$ , Corollary 7, Figure 3bd) for cooperation to fix in the population.

The conditions derived from our deterministic well-mixed model provide a good approximation to results of simulations of a complex stochastic spatial model (Figure 6). In this spatial model, individuals can only interact with and transmit to their neighbors. This model demonstrates that social association between cooperation and transmission can arise in a structured population in which both types of interactions are local.

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 incorporate such genetic modification of cultural transmission into our model.

Woodcock (2006) stressed the significance of non-vertical transmission for the evolution of cooperation. He executed simulations with prisoner's dilemma payoffs but without horizontal transmission or social association ( $\alpha = 0$ ). Nevertheless, his results demonstrated that it is possible to sustain altruistic behavior via cultural transmission for a substantial length of time. Our results provide strong evidence for his hypothesis that horizontal transmission can have an important role in the evolution of cooperation.

To understand the role of horizontal transmission, we first discuss the role of *assortment*. Eshel and Cavalli-Sforza (1982) showed that altruism can evolve when there is enough *assortative meeting*, namely, a tendency for individuals to interact within their phenotypic group. Fletcher and Doebeli

(2009) further argued that a general explanation for the evolution of altruism is given by *assortment*:  
 486 the correlation between individuals that carry an altruistic trait and the amount of altruistic behavior  
 488 in their interaction group (see also Bijma and Aanen (2010)). They therefore suggested that to explain  
 the evolution of altruism, we should seek mechanisms that generate assortment, such as population  
 structure, repeated interactions, and individual recognition. Our results highlight another mechanism  
 490 for generating assortment: an association between social interactions and horizontal transmission  
 that creates a correlation between one's partner for interaction and partner for transmission. This  
 492 mechanism does not require population structure, repeated interactions, or individual recognition.  
 We show that high levels of such social association greatly increase the potential for evolution of  
 494 cooperation (Figure 2). With enough social association ( $\alpha > (c(1-T_B) + (T_B - T_A))/bT_A$ ), cooperation  
 can increase in frequency when initially rare even when there is horizontal transmission bias against  
 496 it ( $T_A < T_B$ , see Result 2).

How does non-vertical transmission generate assortment? Lewin-Epstein et al. (2017) and Lewin-  
 498 Epstein and Hadany (2020) suggested that microbes that manipulate their hosts to act altruistically  
 can be favored by selection, which may help to explain the evolution of cooperation. From the kin  
 500 selection point-of-view, if microbes can be transmitted *horizontally* from one host to another during  
 host interactions, then following horizontal transmission the recipient host will carry microbes that are  
 502 closely related to those of the donor host, even when the two hosts are (genetically) unrelated. From the  
 assortment point-of-view, infection by behavior-determining microbes during interactions effectively  
 504 generates assortment because a recipient of help may be infected by a behavior-determining microbe  
 and consequently become a helper. Cultural horizontal transmission can similarly generate assortment  
 506 between the cooperative phenotype and the benefit of cooperation if cultural transmission and helping  
 interactions occur between the same individuals, which in our model occurs with probability  $\alpha$ .

508 Thus, with horizontal transmission, “assortment between focal cooperative players and cooperative  
 acts in their interaction environment” (Fletcher and Doebeli, 2009) is generated not because *the helper*  
 510 *is likely to be helped*, but rather because *the helped is likely to become a helper*. These conclusions  
 highlight the importance of non-vertical cultural transmission in explaining complex evolutionary  
 512 phenomena, and furthers our understating of the cultural evolution of cooperation.

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## Appendices

### 518 Appendix A

We want to find the frequency of juveniles with phenotype  $A$  in next generation  $\hat{p}'$  as a function of  
 520 frequency of juveniles with phenotype  $A$  in the current generation  $\hat{p}$ . Starting from Eq. 6,

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

522 substitute for  $p'$  using Eq. 8 and for  $\tilde{p}'$  using Eq. 11, we have

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

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

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

526 Using *SymPy* (Meurer et al., 2017), a Python library for symbolic mathematics, Eq. A3 simplifies to eqs. 28-29.

## 528 Appendix B

Let  $f(p) = \lambda(p' - p)$ , where  $\lambda > 0$ , and we know that  $f(0) = 0$  and  $f(1) = 0$  since 0,1 are equilibrium.

532 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

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

534 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 to zero than  $p$ .

536 If  $p < p^* = 1$ , we want a condition for  $1 - p' < 1 - p$ , or  $\frac{1-p'}{1-p} < 1$ , or  $\lambda \frac{-(p'-p)}{1-p} < 0$ , or  $-\frac{f(p)}{1-p} < 0$ . Using a linear approximation for  $f(p)$  near 1, we have

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

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

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## Tables

**Table 1: Payoff matrix for prisoner's dilemma.**

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

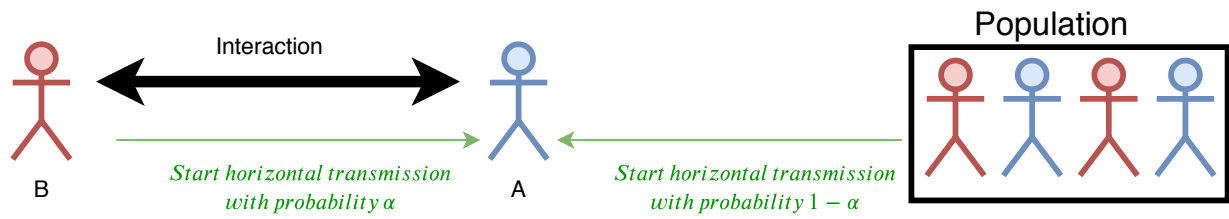
The fitness of phenotype  $\phi_1$  when interacting with phenotype  $\phi_2$ .  $A$  is a cooperative phenotype,  $B$  is a defector phenotype,  $b$  is the benefit gained by an individual interacting with a cooperator, and  $c$  is the cost of cooperation.  $0 < b < c$ .

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

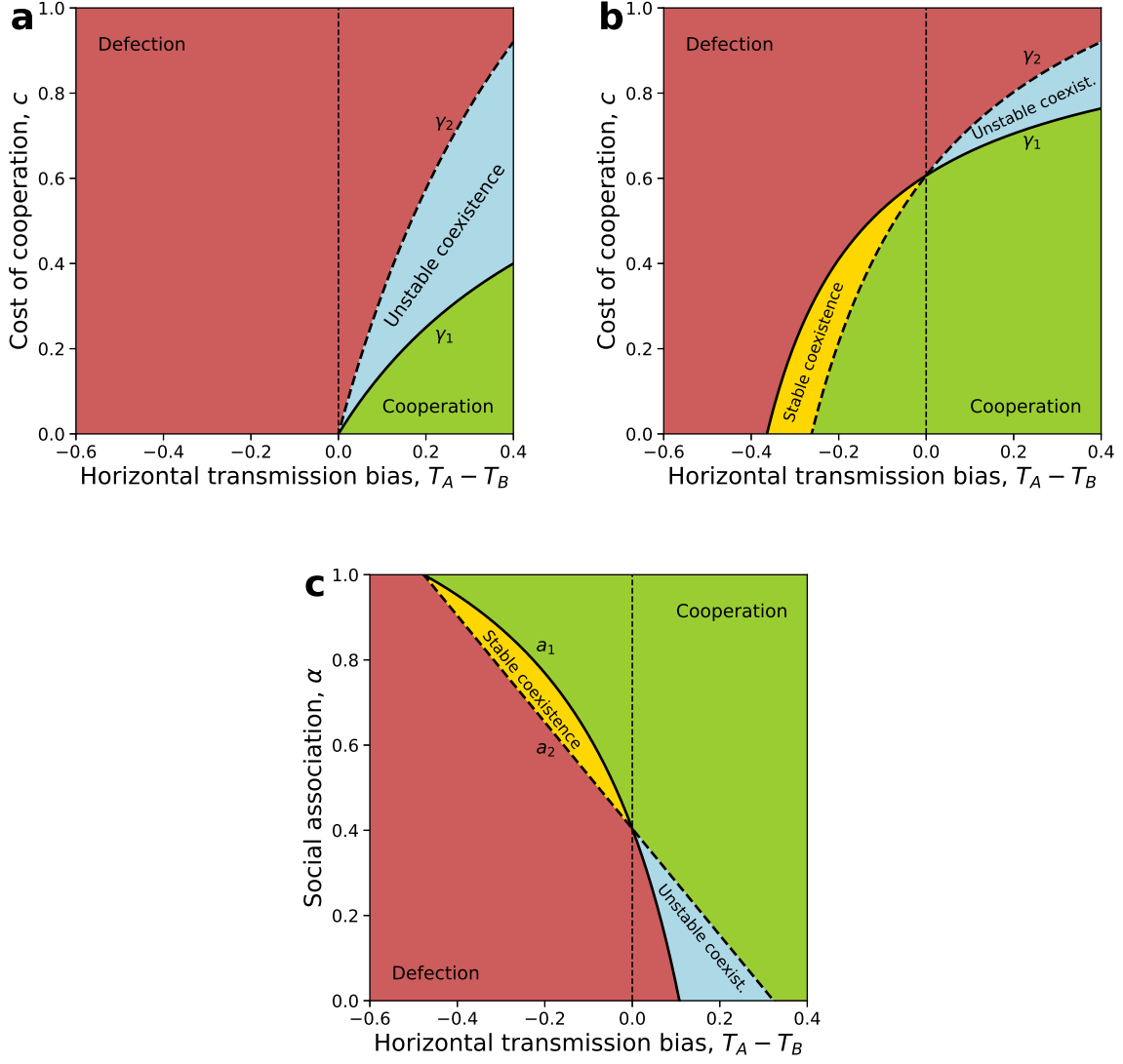
Phenotype $\phi_1$	Phenotype $\phi_2$	Frequency	Fitness of $\phi_1$	$P(\phi_1 = A)$ via horizontal transmission:	
				from partner, $\alpha$	from population, $(1 - \alpha)$
$A$	$A$	$\hat{p}^2$	$1 + b - c$	$1$	$\hat{p} + (1 - \hat{p})(1 - T_B)$
$A$	$B$	$\hat{p}(1 - \hat{p})$	$1 - c$	$1 - T_B$	$\hat{p}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

**Table 3: Model variables and parameters.**

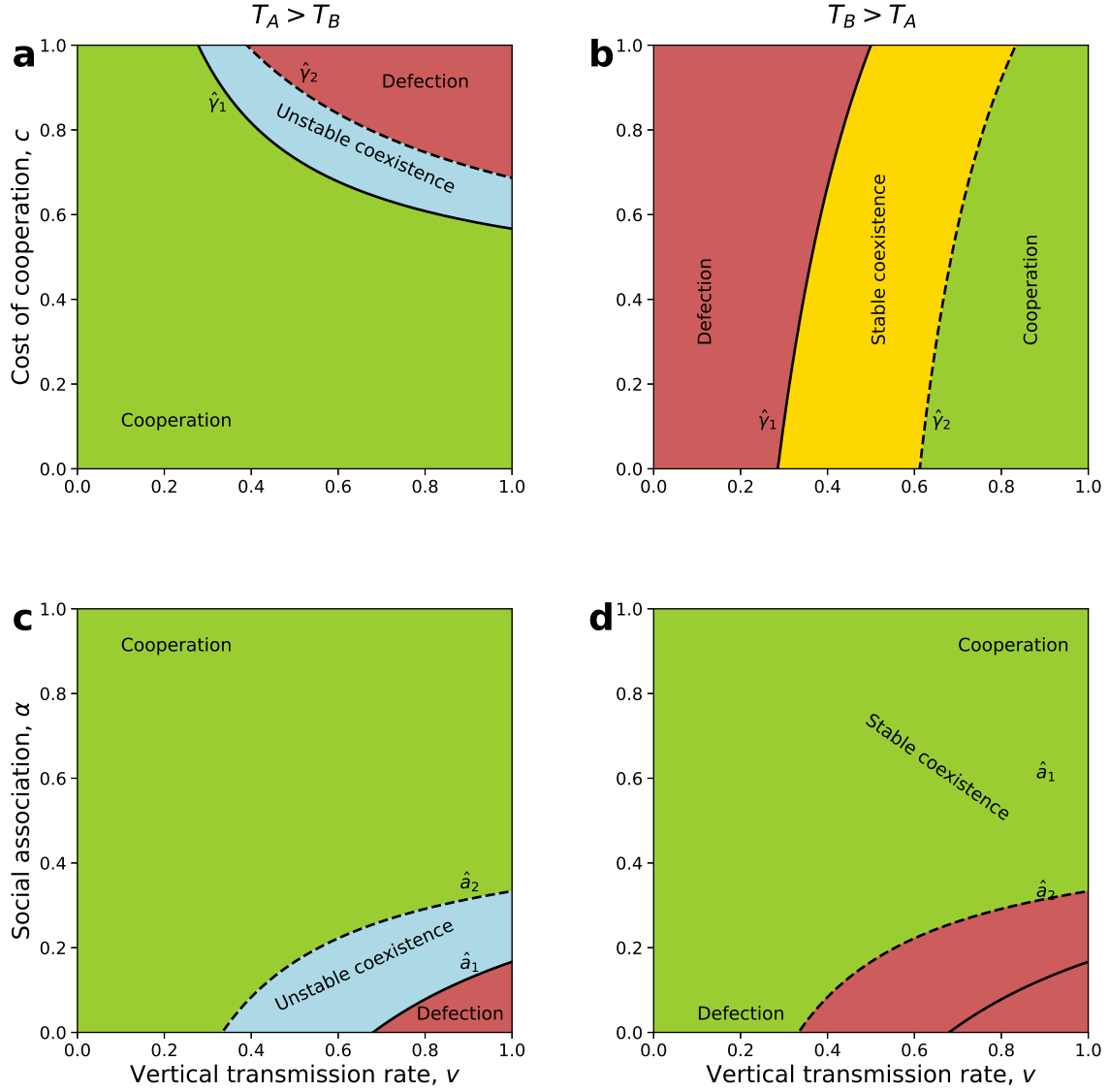
Symbol	Description	Values
$A$	Cooperator phenotype	
$B$	Defector phenotype	
$p$	Frequency of phenotype $A$ among adults	$[0, 1]$
$\tilde{p}$	Frequency of phenotype $A$ among parents	$[0, 1]$
$\hat{p}$	Frequency of phenotype $A$ among juveniles	$[0, 1]$
$v$	Vertical transmission rate	$[0, 1]$
$c$	Cost of cooperation	$(0, 1)$
$b$	Benefit of cooperation	$c < b$
$\alpha$	Probability of social association	$[0, 1]$
$T_A, T_B$	Horizontal transmission rates of phenotype $A$ and $B$	$[0, 1]$



**Figure 1: Cultural horizontal transmission with assortment.** Transmission occurs between interacting partners with probability  $\alpha$  (left) or between two random peers with probability  $1 - \alpha$ , where  $\alpha$  is the *social association* parameter.

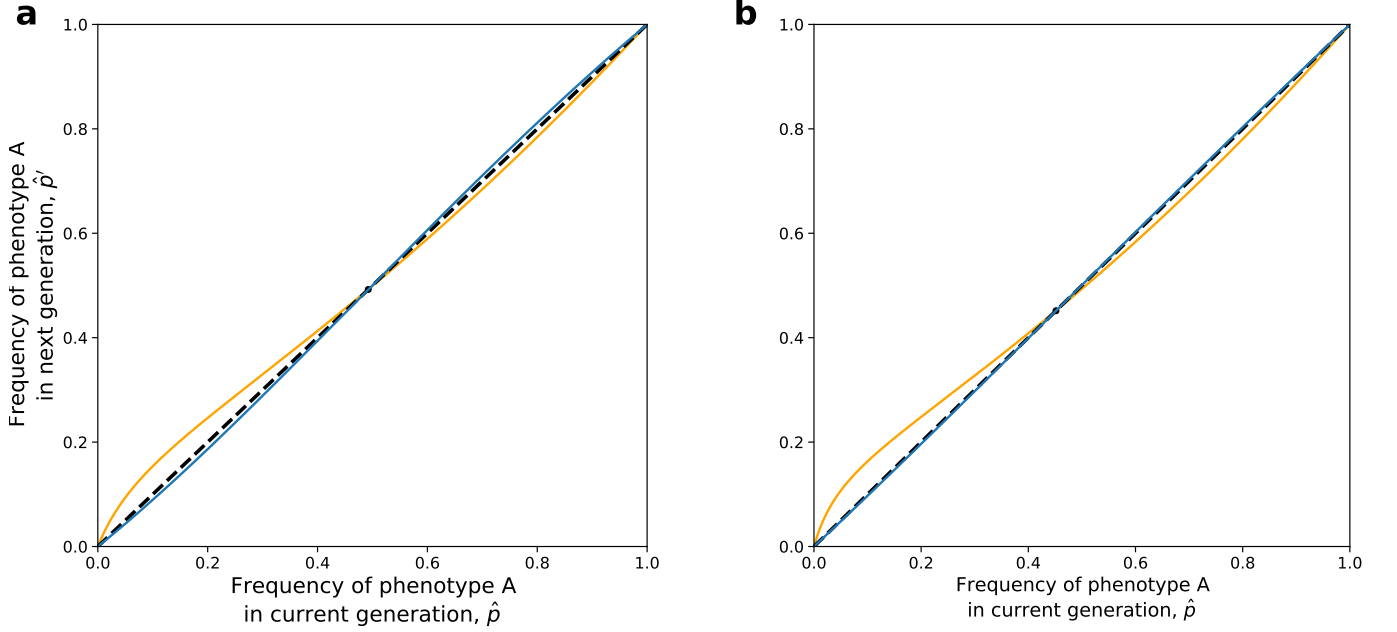


**Figure 2: Evolution of cooperation under vertical and horizontal cultural transmission.** The figure shows the global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial conditions, i.e. unstable coexistence (blue), 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  $\gamma_1$  and  $\gamma_2$  (Eq. 23) are the solid and dashed lines, respectively. **(c)** social association  $\alpha$  is on the y-axis; the social association boundaries  $a_1$  and  $a_2$  (Eq. 27) are the solid and dashed lines, respectively. Here,  $b = 1.3$ ,  $T_A = 0.4$ . **(a)**  $\alpha = 0$ . **(b)**  $\alpha = 0.7$ . **(c)**  $c = 0.35$ .



**Figure 3: Evolution of cooperation under vertical, oblique, and horizontal cultural transmission.**

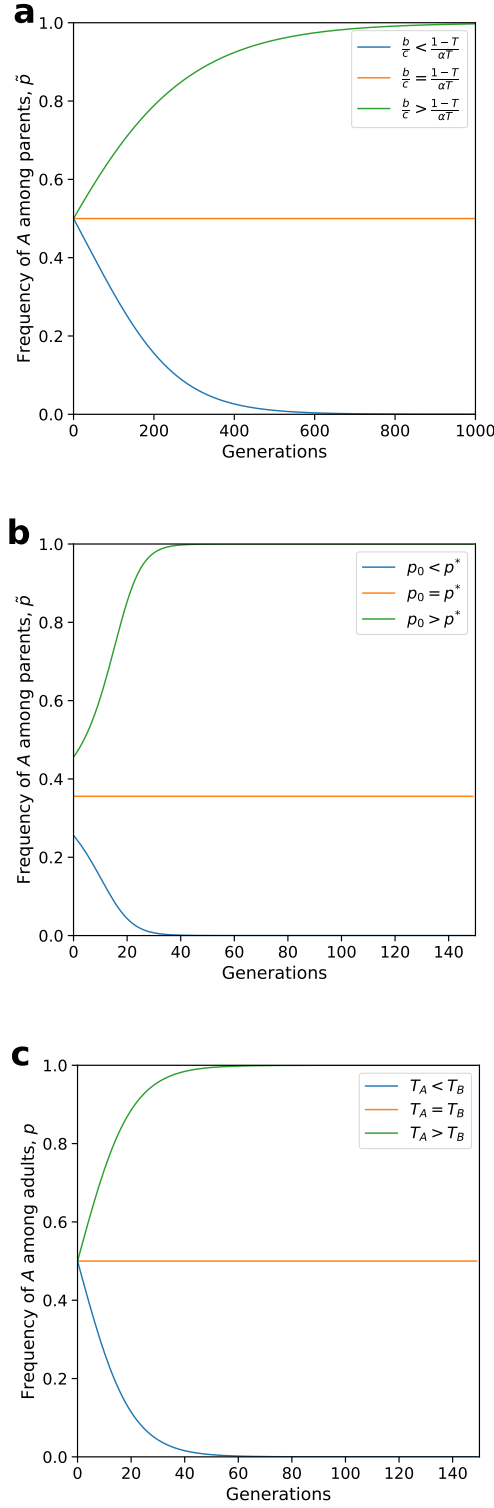
The figure shows the global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial conditions, i.e. unstable coexistence (blue), and stable coexistence of cooperation and defection (yellow). In all cases the vertical transmission rate  $\nu$  is on the x-axis. **(a-b)** The cost of cooperation  $c$  is on the y-axis and the cost boundaries  $\hat{\gamma}_1$  and  $\hat{\gamma}_2$  (Eq. 36) are represented by the solid and dashed lines, respectively. **(c-d)** The social association  $\alpha$  is on the y-axis and the social association boundaries  $\hat{a}_1$  and  $\hat{a}_2$  (Eq. 39) are represented by the solid and dashed lines, respectively. Horizontal transmission is biased in **(a,c)** for cooperation,  $T_A > T_B$ , and in **(b,d)** for defection,  $T_A < T_B$ . Here,  $T_A = 0.5$ , and **(a)**  $b = 1.2$ ,  $T_B = 0.4$ ,  $\alpha = 0.4$ ; **(b)**  $b = 2$ ,  $T_B = 0.7$ ,  $\alpha = 0.7$ ; **(c)**  $b = 1.2$ ,  $T_B = 0.4$ ,  $c = 0.5$ ; **(d)**  $b = 2$ ,  $T_B = 0.7$ ,  $c = 0.5$ .



**Figure 4: Stable and unstable coexistence between cooperation and defection.** The curves show the frequency  $\hat{p}'$  of the cooperative phenotype  $A$  among juveniles in the next generation vs. that in current generation  $\hat{p}$  (Eq. 6). The dashed black line is  $\hat{p}' = \hat{p}$ . The curves and the dashed line intersect at the stable equilibrium  $\hat{p}^*$  (black circle). When  $\hat{p} < \hat{p}^*$  the curve is above the dashed line,  $\hat{p}' > \hat{p}$ , and  $\hat{p}$  increases towards  $\hat{p}^*$ . When  $\hat{p} > \hat{p}^*$  the curve is below the dashed line,  $\hat{p}' < \hat{p}$ , and  $\hat{p}$  decreases towards  $\hat{p}^*$ .

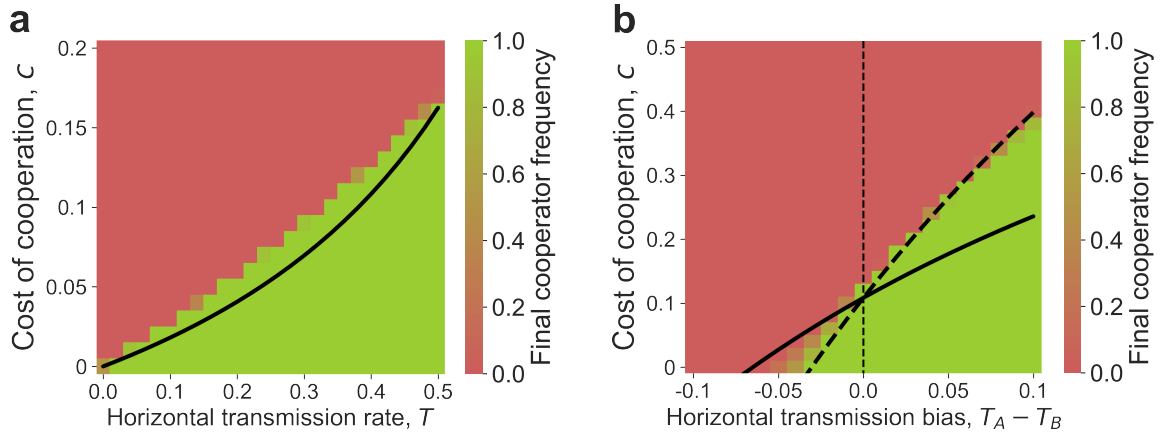
(a) There is no oblique transmission,  $\nu = 1$ . The orange curve, for which the polymorphic equilibrium is stable, is given by  $T_A = 0.4$ ,  $T_B = 0.9$ ,  $b = 12$ ,  $c = 0.35$ , and  $\alpha = 0.45$ , which give  $\gamma_2 < c < \gamma_1$  (Eq. 23). The blue curve, for which the equilibrium is unstable, is given by  $T_A = 0.5$ ,  $T_B = 0.1$ ,  $b = 1.3$ ,  $c = 0.904$ , and  $\alpha = 0.4$ , which give  $\gamma_1 < c < \gamma_2$ .

(b) Oblique transmission exists. The orange curve is parameterized by  $T_A = 0.4$ ,  $T_B = 0.9$ ,  $b = 20$ ,  $c = 0.1$ ,  $\alpha = 1$ , and  $\nu = 0.4$ , which give  $0 < \beta_3 < \beta_1$  (Eq. 29). The blue curve is parameterized by  $T_A = 0.5$ ,  $T_B = 0.4$ ,  $b = 1.2$ ,  $c = 0.487$ ,  $\alpha = 0.09$  and  $\nu = 0.6$ , which give  $\beta_1 < \beta_3 < 0$ .

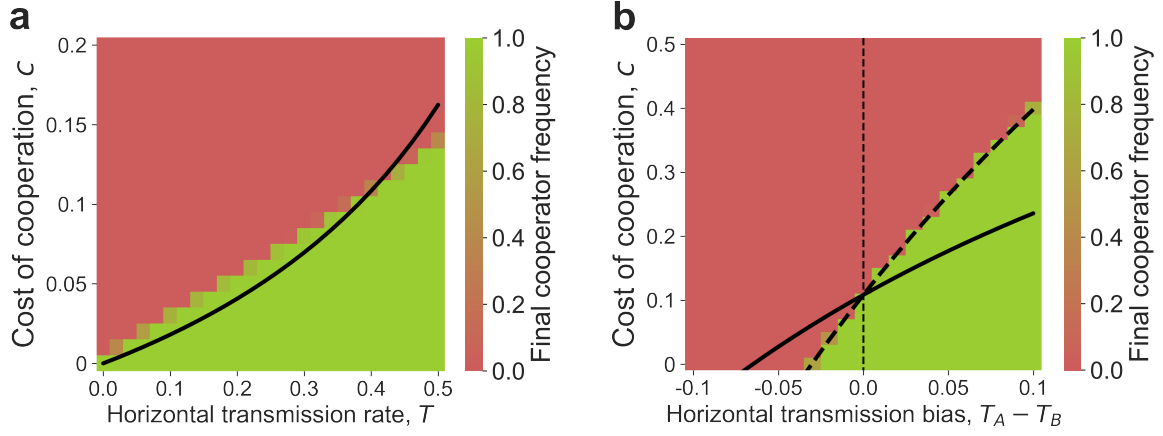


**Figure 5: Dynamics of the frequency of cooperation.** The frequency  $\tilde{p}$  of parents with cooperative phenotype A in (a-b) and the frequency  $p$  of adults with cooperative phenotype A in (c). The different lines correspond to parameter values that lead to fixation of cooperation (green), 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  $c = 0.5$ .

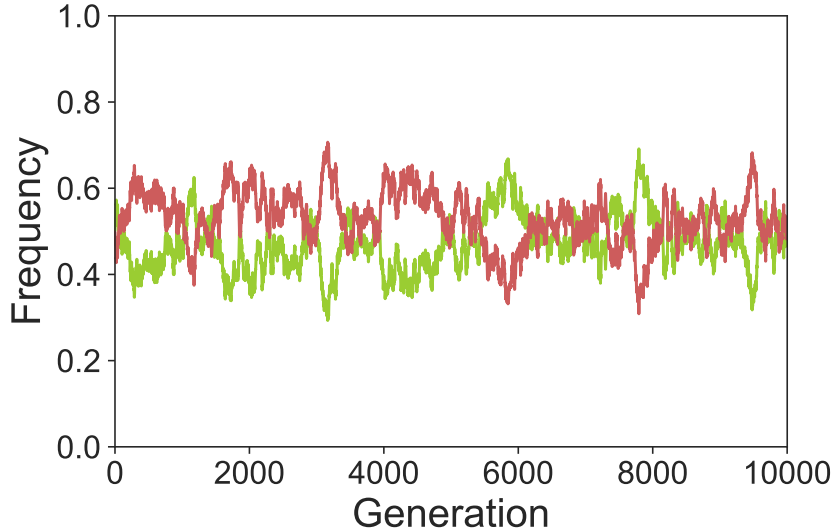




**Figure 6: Evolution of cooperation in a spatial model.** The expected frequency of cooperators in a structured population after 10,000 generations is shown (red for 0%, green for 100%) as function of both the cost of cooperation ( $c$ ) on the y-axis, and the symmetric horizontal transmission rate ( $T = T_A = T_B$ ) on the x-axis of the left panel, or the transmission bias  $T_A - T_B$  on the x-axis of the right panel. The population evolves on a 100-by-100 grid. Cooperation and horizontal transmission are both local between adjacent sites, and each site had 8 neighbors. Selection operates globally (see Figure 7 for results from a model with local selection). The black curves represent the cost boundaries for the evolution of cooperation in a well-mixed population with social association where  $\alpha = 1/8$  in **(a)** Eq. 24 and **(b)** Eq. 23. Simulations were stopped at generation 10,000 or if one of the phenotypes fixed and 50 simulations were executed for each parameter set. Here, population size is 10,000 (100-by-100 grid), benefit of cooperation,  $b = 1.3$ , perfect vertical transmission  $v = 1$ . **(a)** Symmetric horizontal transmission,  $T = T_A = T_B$ . **(b)** Horizontal transmission rates  $T_A = 0.4$ ,  $0.3 < T_B < 0.5$ .



**Figure 7: Evolution of cooperation in a spatial model and local selection.** The expected frequency of cooperators in a structured population after 10,000 generations is shown (red for 0%, green for 100%) as function of both the cost of cooperation ( $c$ ) on the y-axis, and the symmetric horizontal transmission rate ( $T = T_A = T_B$ ) on the x-axis of the left panel, or the transmission bias  $T_A - T_B$  on the x-axis of the right panel. The population evolves on a 100-by-100 grid. Cooperation and horizontal transmission are both local between adjacent sites, and each site had 8 neighbors. Selection operates locally (see Figure 6 for results from a model with global selection). The black curves represent the cost boundaries for the evolution of cooperation in a well-mixed population with social association where  $\alpha = 1/8$  in (a) Eq. 24 and (b) Eq. 23. Simulations were stopped at generation 10,000 or if one of the phenotypes fixed and 50 simulations were executed for each parameter set. Here, population size is 10,000 (100-by-100 grid), benefit of cooperation,  $b = 1.3$ , perfect vertical transmission  $v = 1$ . (a) Symmetric horizontal transmission,  $T = T_A = T_B$ . (b) Horizontal transmission rates  $T_A = 0.4$ ,  $0.3 < T_B < 0.5$ .



**Figure 8: Stable coexistence of both phenotypes in spatial model.** The frequency of cooperators (green) and defectors (red) in the spatial model. Both phenotypes have initial frequency of 50 percent. The figure shows that there are no fixation of neither phenotype through out the simulation. The frequency of both cooperators and defectors oscillates around the initial frequency. Here, population size is 10,000 (100-by-100 grid), selection operates globally, benefit of cooperation,  $b = 1.3$ , perfect vertical transmission  $v = 1$ , horizontal transmission of cooperators  $T_A = 0.4$ , horizontal transmission of defectors  $T_B = 0.435$  and cost  $c = 0.02$ .