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.

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*:

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

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[1] (Eshel and Cavalli-Sforza, 1982, eq. 3.2)

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

where b and c are the benefit and cost of cooperation. Here m in 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)

$$c < b \cdot (p_C - p_D)\,, \tag{3}$$

where p_C is the probability that a cooperator receives help, and p_D is the probability that a defector receives help.[2] 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

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

[2]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 φ, then the condition for evolution of altruism in the case of sib-to-sib altruism is (Feldman et al., 1985, Eq. 16)

$$c < b \cdot \varphi - \frac{1-\varphi}{\varphi}. \tag{4}$$

In inequality 4, φ 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 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 ϕ and assuming uni-parental inheritance, the conditional probability that the phenotype ϕ' of the offspring is A is

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

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

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

Individuals are assumed to interact according to a *prisoner's dilemma*. Specifically, individuals interact in pairs; a cooperator suffers a fitness cost $0 < c < 1$, and its partner gains a fitness benefit b, where we assume $c < b$. Table 1 shows the payoff matrix, i.e. the fitness of an individual with phenotype ϕ_1 when interacting with a partner of phenotype ϕ_2.

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

Horizontal cultural transmission occurs between pairs of individuals from the same generation. It occurs between socially interacting partners with probability α, or between a random pair with probability $1-\alpha$ (see Figure 1). However, horizontal transmission is not always successful, as one partner may reject the other's phenotype. The probability for successful horizontal transmission of phenotypes A and B are T_A and T_B, respectively (Table 2).

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

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

which simplifies to

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

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

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

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

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

Eq. 9 can be simplified to

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

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

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

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*

$$T_A > T_B \ , \tag{13}$$

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 6c). 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

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

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

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

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,

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

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

$$(1 - c)(1 - T_B) + (1 + b)T_A > 1 \ . \tag{17}$$

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 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 γ_1 and γ_2 (Figure 8):*

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 3.

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 3b. 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 2 shows the mapping $\tilde{p} \to \tilde{p}'$; see blue areas in Figure 3a and Figure 3b.

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

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

Note that the right-hand side equals γ_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 6a illustrates this condition.

The condition in inequality 24 demonstrates the importance of the social association α. 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*

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

Figure 3a illustrates these conditions, which are obtained by setting $\alpha = 0$ in Eqs. 20 and 8. 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*

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

This condition is obtained from inequality 17, and the right-hand side equals γ_1 when $\alpha = 1$ (Figure 8). 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

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

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 3c 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):

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

where

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

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

$$f(\hat{p}) = \hat{p}(1-\hat{p})\big[\alpha bvT - cv(1-T)\big]. \tag{30}$$

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

$$f'(\hat{p}) = (1-2\hat{p})\big[\alpha bvT - cv(1-T)\big], \tag{31}$$

with

$$f'(0) = \alpha bvT - cv(1-T),$$
$$f'(1) = -\alpha bvT + cv(1-T). \tag{32}$$

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 β_1 is not necessarily zero, and $f(\hat{p})$ is a cubic polynomial. Therefore, three equilibria may exist, two of which are $\hat{p} = 0$ and $\hat{p} = 1$, and the third is

$$\hat{p}^* = \frac{\beta_3}{\beta_1}. \tag{33}$$

Note that the sign of the cubic (Eq. 28) at positive (negative) infinity is equal (opposite) to the sign of β_1. If $T_A > T_B$, then

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

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

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

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 $\hat{\gamma}_2$,

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

and a vertical transmission threshold,

$$\hat{v} = \frac{T_B - T_A}{1 - T_A}. \tag{37}$$

First, assume $T_A < T_B$. $\beta_3 < 0$ requires $\hat{\gamma}_1 < c$, and for $\beta_3 < \beta_1$ we need $c\big[v(1-T_B)+(1-v)(T_A-T_B)\big] > bv\alpha T_B + (1+b)(T_A - T_B)$. 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 $c\big[v(1-T_B)+(1-v)(T_A-T_B)\big] < bv\alpha T_B + (1+b)(T_A - T_B)$. 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 $c > \hat{\gamma}_2$.

The following result summarizes the possible outcomes.

Result 3 (Vertical, oblique, and horizontal transmission of cooperation)**.** *With vertical, horizontal, and oblique transmission, the cultural evolution of a cooperator phenotype will follow one of the following scenarios depending on the cost boundaries $\hat{\gamma}_1$ and $\hat{\gamma}_2$ (Eq. 36) and the vertical transmission threshold $\hat{v}$ (Eq. 37) :*

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* $c < \hat{\gamma}_2$.
2. Fixation of defection*: if* (iii) $T_A \geq T_B$ *and* $\hat{\gamma}_2 < c$*; or if* (iv) $T_A < T_B$ *and* $\hat{\gamma}_1 < c$.
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* $\hat{\gamma}_2 < c < \hat{\gamma}_1$.
4. Unstable coexistence*: if* (vii) $T_A > T_B$ *and* $\hat{\gamma}_1 < c < \hat{\gamma}_2$.

These conditions are illustrated in Figure 4ab.

Much of the literature on evolution of cooperation focuses on conditions for initially rare cooperative 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 is very close to zero, $\hat{p}_0 \approx 0$, then its frequency will increase if*

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

This condition merges the conditions for fixation of cooperation and for stable coexistence, which both lead to the instability of $\hat{p} = 0$, the fixation of defection. Importantly, increasing social association α increases the boundary cost ($\partial\hat{\gamma}_1/\partial\alpha > 0$), making it easier for cooperation to increase from rarity. Similarly, increasing the horizontal transmission of cooperation increases the boundary ($\partial\hat{\gamma}_1/\partial T_A > 0$), making it easier for cooperation to evolve. However, increasing the horizontal transmission of defection can either increase or decrease the boundary depending on $sign(\partial\gamma_1/\partial T_B) = sign(vb\alpha T_A + T_A - 1)$. Therefore, increasing T_B increases the boundary when $T_A > \frac{1}{1+\alpha bv}$ but when this applies we get that $\hat{\gamma}_1 > 1$ which guarantees cooperation will evolve from rairty since $c < 1$. When $T_A < \frac{1}{1+\alpha bv}$ increasing T_B decreases the boundary.

Increasing the vertical transmission v can either increase or decrease the boundary, depending on the 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 get $\partial\hat{\gamma}_1/\partial v > 0$ and therefore, as the vertical transmission increases the boundary on the cost increases 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 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 rairty.

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

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

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

Then the following applies.

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 4cd illustrates this conditions.

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 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.

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

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

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 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: in this case oblique transmission can prevent fixation of cooperation, see Figure 4bd.

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 α 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 7 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. 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 (α) can emerge from local interactions between individuals in a structured population.

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),

$$c \cdot v(1 - T_B) < b \cdot v\alpha T_A + (T_A - T_B) \ , \tag{41}$$

that is, if the effective cost of cooperation (left-hand side) is smaller then 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 3-4).

We find that increasing social association (α) increases the opportunity for evolution of cooperation (Corollaries 4 and 6, Figures 3c and 4cd). 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 3). 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 4ac). 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 4bd) 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 7). 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*: the correlation between individuals that carry an altruistic trait and the amount of altruistic behavior 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 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 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 cooperation (Figure 3). With enough social association ($\alpha > \big(c(1-T_B)+(T_B-T_A)\big)/bT_A$), cooperation can increase in frequency when initially rare even when there is horizontal transmission bias against it ($T_A < T_B$, see Result 2).

How does non-vertical transmission generate assortment? Lewin-Epstein et al. (2017) and Lewin-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 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 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 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 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 α.

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 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 phenomena, and furthers our understating of the cultural evolution of cooperation.

Acknowledgements

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Appendices

Appendix A

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

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

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

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

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

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

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

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.

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

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

Therefore, by definition of big-O notation, if $f'(0) < 0$ then there exists $\epsilon > 0$ such that for any $0 < p < \epsilon$, it is guaranteed that $0 < p' < p$; that is, p' is closer to zero than p.

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

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

Therefore, if $f'(1) < 0$ then there exists $\epsilon > 0$ such that for any $1-\epsilon < 1-p < 1$ 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 ϕ_1 when interacting with phenotype ϕ_2. A is a cooperative phenotype, B is a defector phenotype, b is the benefit gained by an individual interacting with a cooperator, and c is the cost of cooperation. $0 < b < c$.

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

Phenotype ϕ_1	Phenotype ϕ_2	Frequency	Fitness of ϕ_1	$P(\phi_1 = A)$ via horizontal transmission:	
				from partner, α	from population, $(1 - \alpha)$
A	A	$\hat{p}^2$	$1 + b - c$	1	$\hat{p} + (1 - \hat{p})(1 - T_B)$
A	B	$\hat{p}(1 - \hat{p})$	$1 - c$	$1 - T_B$	$\hat{p} + (1 - \hat{p})(1 - T_B)$
B	A	$\hat{p}(1 - \hat{p})$	$1 + b$	T_A	$\hat{p}T_A$
B	B	$(1 - \hat{p})^2$	1	0	$\hat{p}T_A$

Table 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	$c < b$
α	Probability of social association	$[0, 1]$
T_A, T_B	Horizontal transmission rates of phenotype A and B	$[0, 1]$

Figures

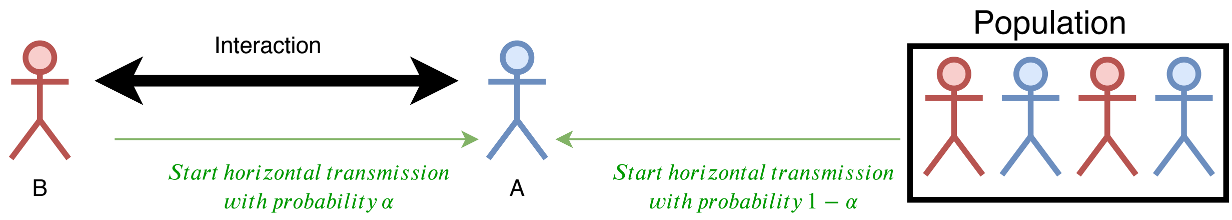

Figure 1: Cultural horizontal transmission with assortment. Transmission occurs between interacting partners with probability α (left) or between two random peers with probability $1-\alpha$, where α is the *social association* parameter.

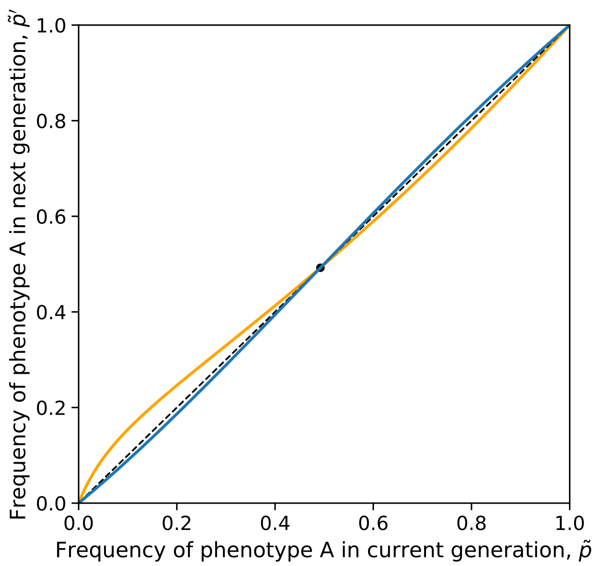

Figure 2: Stable and unstable coexistence between cooperation and defection without oblique transmission. The curves show the frequency of the cooperative phenotype A among parents in the next generation, $\tilde{p}'$, vs. that in the current generation $\tilde{p}$ (Eq. 14). The dashed black line is $\tilde{p}' = \tilde{p}$. The curves and the dashed line intersect at the polymorphic equilibrium $\tilde{p}^*$ (black circle). When the curves are above the dashed line, $\tilde{p}' > \tilde{p}$, and $\tilde{p}$ increases. When the curves are below the dashed line, $\tilde{p}' < \tilde{p}$, and $\tilde{p}$ decreases. 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 $\gamma_2 < c < \gamma_1$ (Figure 8) The blue curve, for which the equilibrium is unstable, is given by $T_A = 0.5$, $T_B = 0.1$, $b = 1.3$, $c = 0.904$, and $\alpha = 0.4$, which give $\gamma_1 < c < \gamma_2$. In both cases there is no oblique transmission, $v = 1$; see Figure 5 for $v < 1$.

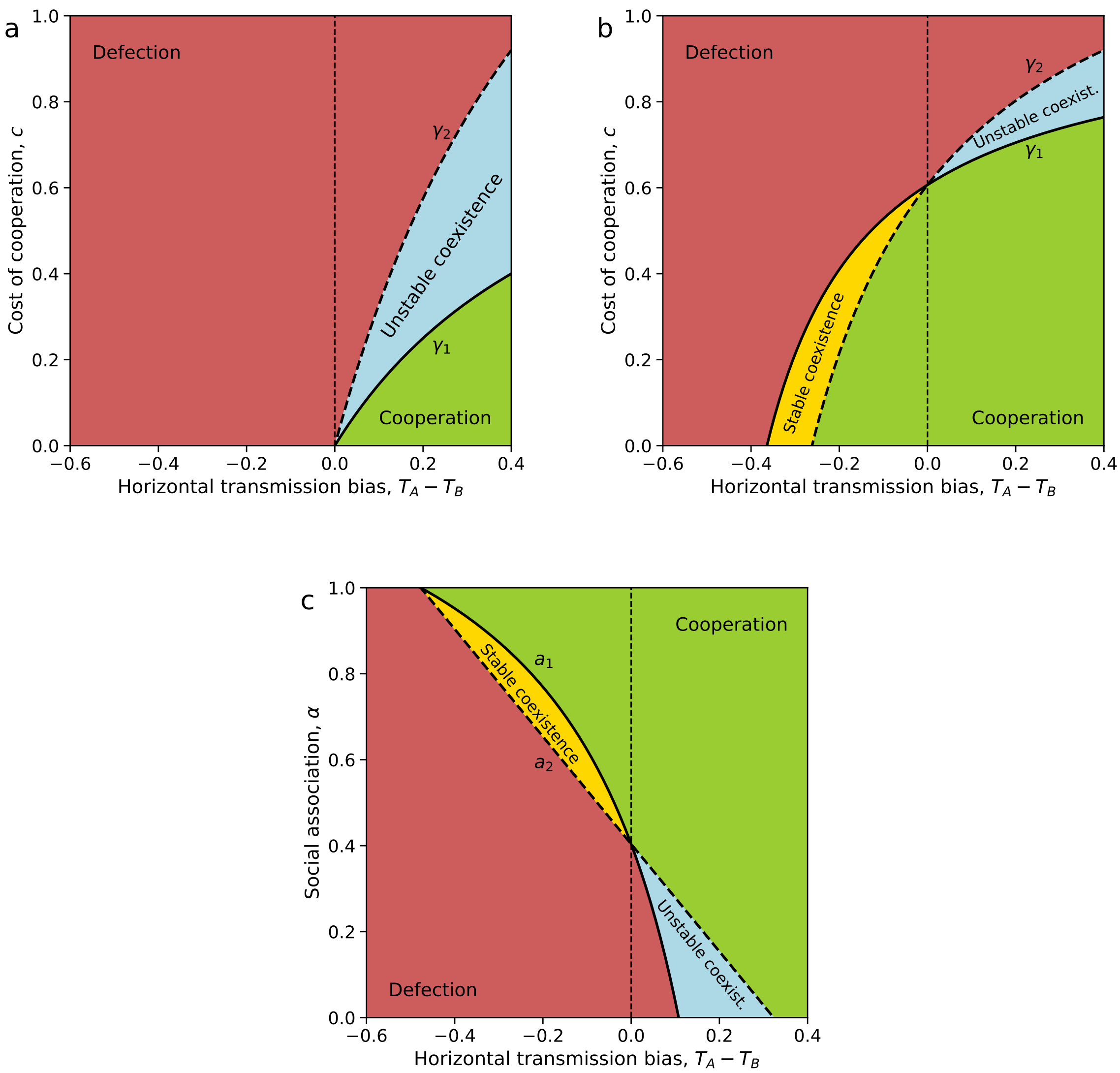

Figure 3: Evolution of cooperation under vertical and horizontal cultural transmission. The figure shows the global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial conditions, i.e. unstable coexistence (blue), and stable coexistence of cooperation and defection (yellow). In all cases the horizontal bias $(T_A - T_B)$ is on the x-axis. (**a-b**) The cost of cooperation c is on the y-axis; the cost boundaries γ_1 and γ_2 (Figure 8) are the solid and dashed lines, respectively. (**c**) social association α 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**) $c = 0.35$.

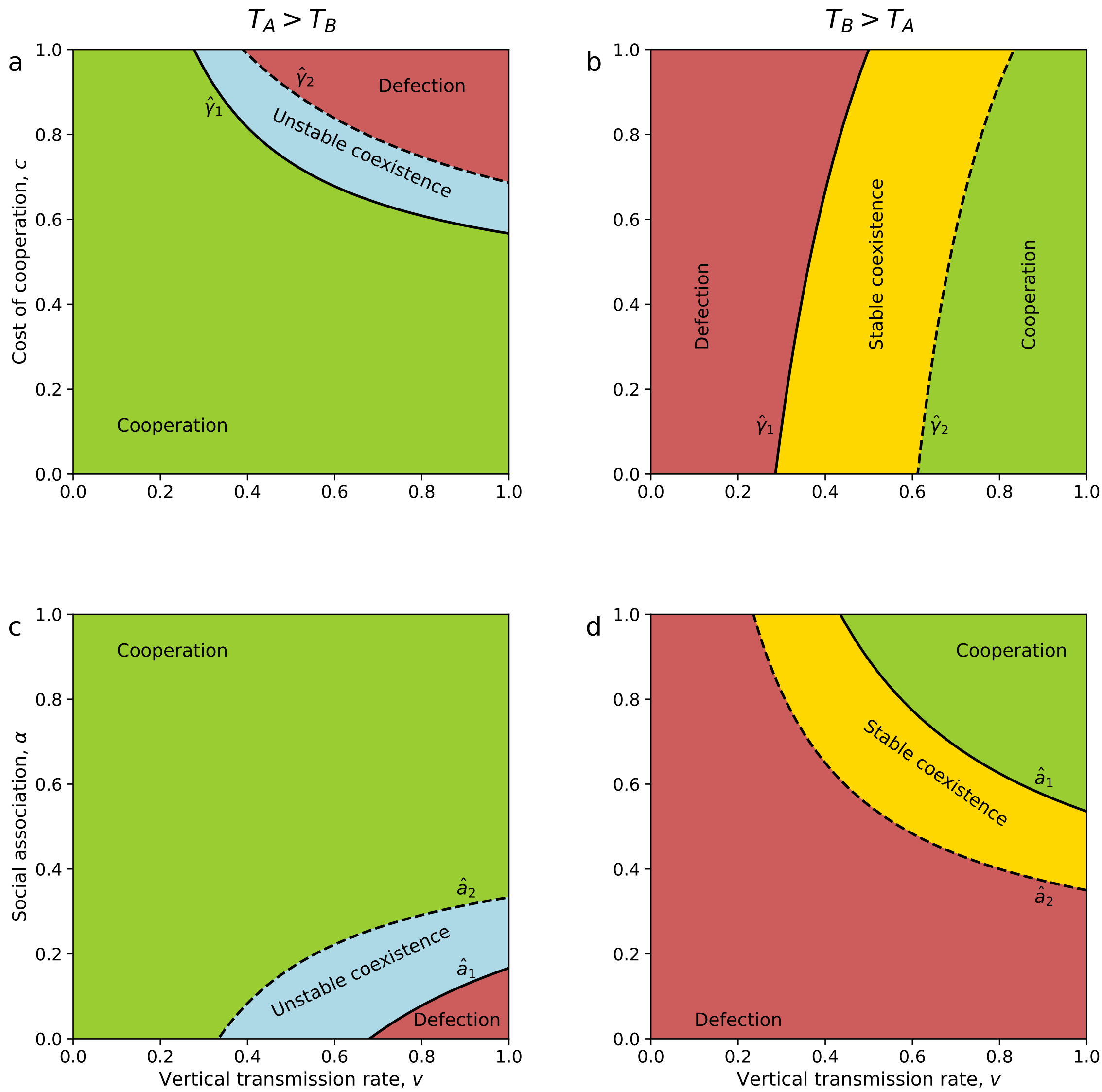

Figure 4: Evolution of cooperation under vertical, oblique, and horizontal cultural transmission. The figure shows the global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial conditions, i.e. unstable coexistence (blue), and stable coexistence of cooperation and defection (yellow). In all cases the vertical transmission rate v 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 α 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**) $b = 2$, $T_B = 0.7$, $c = 0.5$.

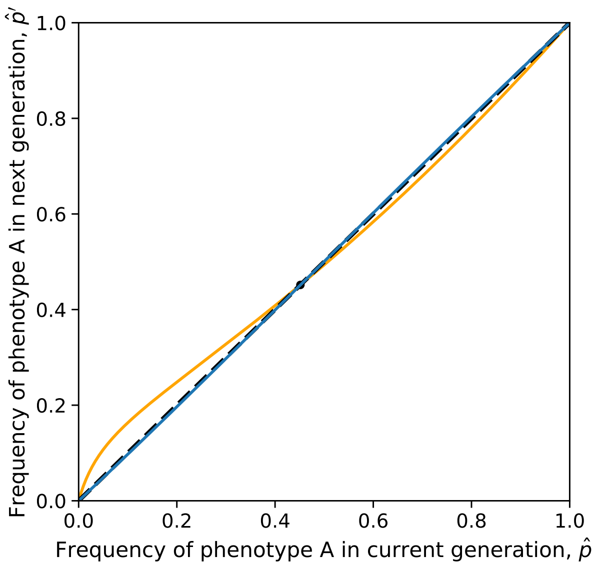

Figure 5: Stable and unstable coexistence between cooperation and defection with oblique transmission. The curves show the frequency $\hat{p}'$ of the cooperative phenotype A among juveniles in the next generation vs. that in current generation $\hat{p}$ (Eq. 6). The dashed black line is $\hat{p}' = \hat{p}$. 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 $\hat{p}^*$. The orange curve is parameterized by $T_A = 0.4$, $T_B = 0.9$, $b = 20$, $c = 0.1$, $\alpha = 1$, and $v = 0.4$, which give $0 < \beta_3 < \beta_1$ (Eq. 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 $v = 0.6$, which give $\beta_1 < \beta_3 < 0$.

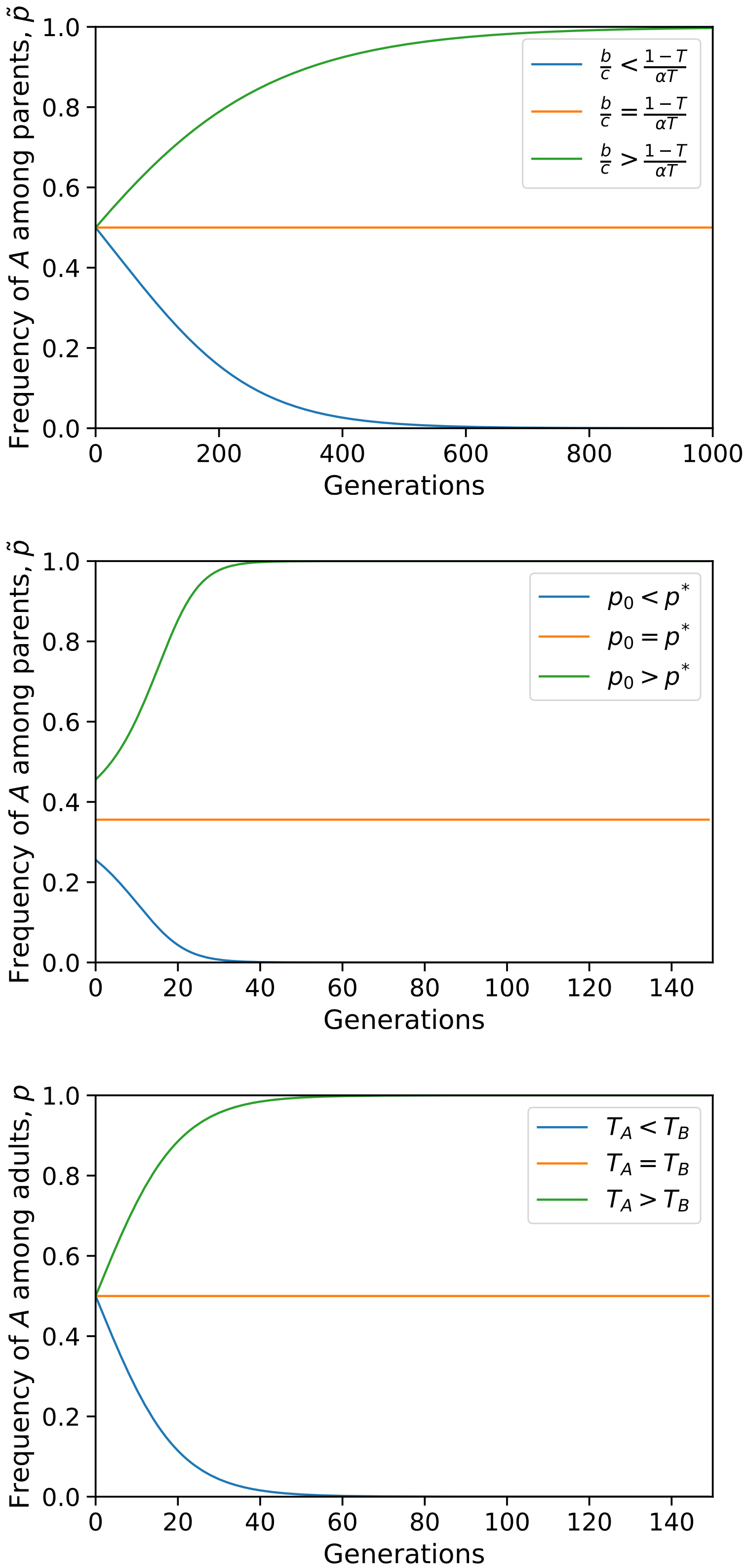

Figure 6: Dynamics of the frequency of cooperation. The frequency $\tilde{p}$ of parents with cooperative phenotype A in **(a-b)** and the frequency p of adults with cooperative phenotype A in **(c)**. The different lines correspond to parameter values that lead to fixation of cooperation (green), extinction 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 $c = 0.5$.

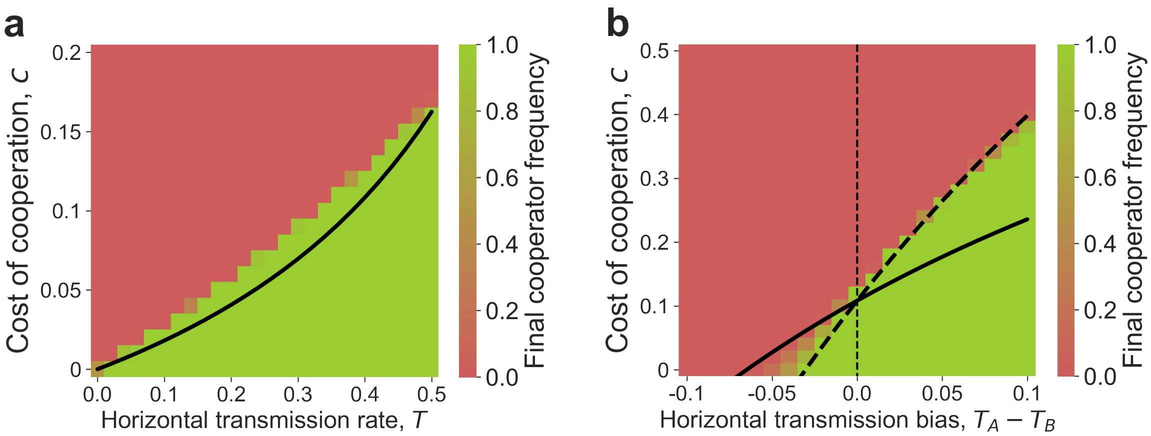

Figure 7: Evolution of cooperation in a spatial model. The expected frequency of cooperators in a structured population after 10,000 generations is shown (red for 0%, green for 100%) as function of both the cost of cooperation (c) on the y-axis, and the symmetric horizontal transmission rate ($T = T_A = T_B$) 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 8 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 (left) Eq. 24 and (right) . 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 $v = 1$. **(left)** Symmetric horizontal transmission, $T = T_A = T_B$. **(right)** Horizontal transmission rates $T_A = 0.4$, $0.3 < T_B < 0.5$.

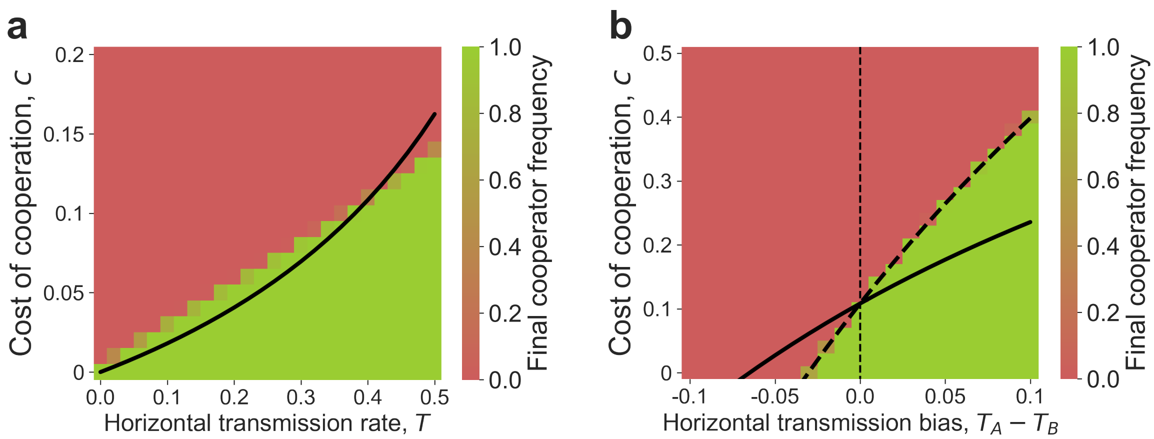

Figure 8: Evolution of cooperation in a spatial model and local selection. The expected frequency of cooperators in a structured population after 10,000 generations is shown (red for 0%, green for 100%) as function of both the cost of cooperation (c) on the y-axis, and the symmetric horizontal transmission 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 7 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 (left) Eq. 24 and (right) . 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 $v = 1$. **(left)** Symmetric horizontal transmission, $T = T_A = T_B$. **(right)** Horizontal transmission rates $T_A = 0.4$, $0.3 < T_B < 0.5$.