

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

Dor Cohen¹, Ohad Lewin-Epstein², Marcus W. Feldman³, and Yoav Ram^{1,4,5,*}

¹School of Computer Science, Interdisciplinary Center Herzliya, Herzliya, Israel

²School of Plant Sciences and Food Security, Tel Aviv University, Tel Aviv, Israel

³Department of Biology, Stanford University, Stanford, CA

⁴School of Zoology, Tel Aviv University, Tel Aviv, Israel

⁵Sagol School of Neuroscience, Tel Aviv University, Tel Aviv, Israel

*Corresponding author: yoav@yoavram.com

November 8, 2020

Abstract

We study the cultural evolution of cooperation under vertical and non-vertical cultural transmission. Conditions are found for fixation and coexistence of cooperation and defection. The evolution of cooperation is facilitated by horizontal transmission and by an association between social interactions and horizontal transmission. The effect of oblique transmission depends on the horizontal transmission bias. A stable coexistence between cooperation and defection can occur. When it does, selection favors the evolution of higher association between social interactions and horizontal transmission, which leads to an increased frequency of cooperation and higher population mean fitness. The derived conditions are compared to outcomes of stochastic simulations of structured populations. Comparisons are drawn with Hamilton's rule and the concepts of relatedness and assortment.

22 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 (Haldane, 1932, Appendix).

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 if¹ (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.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

¹In 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).

²Inequality 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)

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

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 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 diminish 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 (Zefferman, 2016), the conditional probability that the phenotype ϕ' of the offspring is A is

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

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

106

$$\hat{p} = \tilde{p}[v + (1 - v)p] + (1 - \tilde{p})[(1 - v)p] = v\tilde{p} + (1 - v)p . \quad (6)$$

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

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

which simplifies to

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

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

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

where fitness values are taken from Table 1 and Table 2, and the population mean fitness is $\bar{w} = 1 + \hat{p}(b - c)$. Eq. 9 can be simplified to

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

Finally, we find an equation for the frequency of phenotype A among juveniles in the next generation \hat{p}' as a function of the frequency in the current generation. Starting from Eq. 6, we substitute Eq. 8

132 for p' and Eq. 10 for \tilde{p}' . We therefore have

$$\begin{aligned} \hat{p}' = & \frac{v}{\bar{w}} \left[\hat{p}^2 (1 + b - c) \left[1 - (1 - \hat{p})(1 - \alpha)T_B \right] \right] + \\ & \frac{v}{\bar{w}} \left[\hat{p}(1 - \hat{p})(1 - c)(\hat{p}(1 - \alpha)T_B + 1 - T_B) \right] + \\ & \frac{v}{\bar{w}} \left[\hat{p}(1 - \hat{p})(1 + b)(\hat{p}(1 - \alpha) + \alpha)T_A \right] + \\ & \frac{v}{\bar{w}} (1 - \hat{p})^2 \hat{p}(1 - \alpha)T_A + \\ & (1 - v)\hat{p}^2(T_B - T_A) + (1 - v)\hat{p}(1 + T_A - T_B) . \end{aligned} \quad (11)$$

134 Table 3 summarizes the model variables and parameters.

Results

136 In the following sections, we determine the equilibria of the model in Eq. 11, namely, solutions
of $\hat{p}' = \hat{p}$, and analyze their local stability. We then analyze the evolution of a modifier of social
138 association. Finally, we compare derived conditions to outcomes of stochastic simulations with a
structured population.

140 Evolution of cooperation

We determined the equilibria of our model, i.e. the fixed points of Eq. 11, and their local stability.
142 The equilibria are $\hat{p} = 0$, $\hat{p} = 1$, and (see Eq. B5)

$$\hat{p}^* = \frac{\alpha b v T_A - c v (1 - T_B) + (T_A - T_B)}{[c(1 - v) - b(1 - \alpha v)](T_A - T_B)} . \quad (12)$$

144 To find conditions on the cost of cooperation, c , we define the following cost boundaries, γ_1 and γ_2 ,
vertical transmission threshold, \hat{v} ,

$$146 \quad \gamma_1 = \frac{b v \alpha T_A + (T_A - T_B)}{v(1 - T_B)}, \quad \gamma_2 = \frac{b v \alpha T_B + (1 + b)(T_A - T_B)}{v(1 - T_B) + (1 - v)(T_A - T_B)}, \quad \hat{v} = \frac{T_B - T_A}{1 - T_A} . \quad (13)$$

The full analysis is given in Appendix B. The following result summarizes the possible outcomes.

148

Result 1 (Equilibria and stability). *With vertical, horizontal, and oblique transmission, the cultural
150 evolution of a cooperator phenotype will follow one of the following scenarios depending on the cost
boundaries γ_1 and γ_2 and the vertical transmission threshold \hat{v} (Eq. 13) :*

- 152 1. Fixation of cooperation: if (i) $T_A \geq T_B$ and $c < \gamma_1$; or if (ii) $T_A < T_B$ and $v > \hat{v}$ 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 $\gamma_1 < c$.
- 154 3. Stable coexistence: if (v) $T_A < T_B$ and $v < \hat{v}$ and $c < \gamma_1$; or if (vi) $T_A < T_B$ and $v > \hat{v}$ and
 $\gamma_2 < c < \gamma_1$.
- 156 4. Unstable coexistence: if (vii) $T_A > T_B$ and $\gamma_1 < c < \gamma_2$.

These conditions are illustrated in Figure 3ab.

158 Much of the literature on evolution of cooperation focuses on conditions for an initially rare coopera-
tive phenotype to invade a population of defectors. The following remarks on such a condition.

160

Remark 1 (Condition for cooperation to increase from rarity: cost of cooperation). *If the initial frequency of cooperation is very close to zero, then its frequency will increase if the cost of cooperation is low enough,*

$$c < \gamma_1 = \frac{bv\alpha T_A + (T_A - T_B)}{v(1 - T_B)} . \quad (14)$$

This unites the conditions for fixation of cooperation and for stable coexistence, which both lead to instability of the fixation state associated with defection, $\hat{p} = 0$.

Importantly, increasing social association α increases the boundary cost ($\partial\gamma_1/\partial\alpha > 0$), making it easier for cooperation to increase from rarity. Similarly, increasing the horizontal transmission of cooperation, T_A , increases the boundary ($\partial\gamma_1/\partial T_A > 0$), facilitating the evolution of cooperation. However, increasing the horizontal transmission of defection, T_B , can increase or decrease the cost boundary, but it increases the cost boundary when it is already above one ($c < 1 < \gamma_1$): $\partial\gamma_1/\partial T_B$ is positive when $T_A > \frac{1}{1+\alpha bv}$, which gives $\gamma_1 > 1/v$. Therefore, increasing T_B decreases the cost boundary and limits the evolution of cooperation, but only if $T_A < \frac{1}{1+\alpha bv}$.

Increasing the vertical transmission rate, v , can either increase or decrease the boundary, depending on the horizontal transmission bias, $T_A - T_B$, because $\text{sign}(\partial\gamma_1/\partial v) = -\text{sign}(T_A - T_B)$. When $T_A < T_B$ we get $\partial\gamma_1/\partial v > 0$, and therefore as the vertical transmission rate increases, the cost boundary increases, making it easier for cooperation to evolve from rarity. In contrast, when $T_A > T_B$ we get $\partial\gamma_1/\partial v < 0$, and therefore as the vertical transmission rate increases, the cost boundary decreases, making it harder for cooperation to evolve from rarity.

In general, this condition cannot be formulated in the form of Hamilton's rule due to the horizontal transmission bias term, $T_A - T_B$. When there is no horizontal transmission bias, $T_A = T_B$, the next remark applies.

Remark 2 (Unbiased horizontal transmission). *If horizontal transmission is unbiased, $T = T_A = T_B$, then cooperation will take over the population from any initial frequency if the cost is low enough,*

$$c < b \cdot \frac{v\alpha T}{1 - T} . \quad (15)$$

This condition is obtained by setting $T = T_A = T_B$ in inequality 14 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 $v\alpha T/(1 - T)$ can be regarded as the *effective relatedness* or *effective assortment*, respectively. Figure S3a illustrates this condition for $v = 1$. Note that the right-hand side equals γ_1 when $T = T_A = T_B$.

In the next remarks we examine the effect of social association on the evolution of cooperation.

Remark 3 (No social association). *Without social association ($\alpha = 0$), cooperation will increase from rarity if there is horizontal transmission bias for cooperation, $T_A > T_B$, and*

$$c < \frac{T_A - T_B}{v(1 - T_B)} . \quad (16)$$

Figure 2a illustrates this condition, which is obtained by setting $\alpha = 0$ in inequality 14. Importantly, the benefit of cooperation, b , does not affect the evolution of cooperation in the absence of social association, and the outcome is determined only by cultural transmission.

200 **Remark 4** (Perfect social association). *With perfect social association ($\alpha = 1$), cooperation will increase from rarity if*

$$202 \quad c < \frac{bvT_A + (T_A - T_B)}{v(1 - T_B)}. \quad (17)$$

This condition is obtained by setting $\alpha = 1$ in inequality 14.

204 Moreover, without oblique transmission, $v = 1$, 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 inequality 17 applies.
206 This is similar to case of microbe-associated cooperation studied by Lewin-Epstein et al. (2017), and therefore when $v = 1$, this remark is equivalent to their eq. 1.

208 Given the previous two remarks 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. Consider
210 the social association boundaries, a_1 and a_2 ,

$$a_1 = \frac{c \cdot v(1 - T_A) - (T_A - T_B)(1 + b - c)}{b \cdot v \cdot T_B}, \quad a_2 = \frac{c \cdot v(1 - T_B) - (T_A - T_B)}{b \cdot v \cdot T_A}. \quad (18)$$

212 Then the following applies.

214 **Remark 5** (Condition for cooperation to increase from rarity: social association). *Cooperation will increase from rarity if social association is high enough, specifically if $a_2 < \alpha$.*

216 Figures 2c and 3cd illustrate this condition. 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
218 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
220 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, $\frac{c}{b \cdot v} \cdot \frac{1-T}{T} < \alpha$ (inequality 15; in this
222 case $a_1 = a_2$).

Interestingly, because $\text{sign}(\partial a_2 / \partial v) = \text{sign}(T_A - T_B)$, the effect of the vertical transmission rate
224 v on this condition depends on the horizontal transmission bias. That is, with horizontal bias for cooperation, $T_A > T_B$, evolution of cooperation is facilitated by oblique transmission, whereas with
226 horizontal bias for defection, $T_A < T_B$, evolution of cooperation is facilitated by vertical transmission. This is demonstrated in Figure 3cd.

228 The next remarks further inspect the roles of vertical and oblique transmission in the evolution of cooperation.

230

Remark 6 (Necessary condition for fixation of cooperation: vertical transmission rate). *Fixation of cooperation is possible only if the vertical transmission rate is high enough,*

$$v > \hat{v} = \frac{T_B - T_A}{1 - T_A}. \quad (19)$$

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

Without oblique transmission, the following applies.

240

Remark 7 (Condition for cooperation to increase from rarity: vertical and horizontal transmission).

Without oblique transmission ($v = 1$) cooperation will increase from rarity if

$$c < \frac{b\alpha T_A + (T_A - T_B)}{1 - T_B}, \quad (20)$$

which can also be written as

$$\frac{c(1 - T_B) - (T_A - T_B)}{bT_A} < \alpha. \quad (21)$$

These conditions is obtained by setting $v = 1$ in inequalities 14 and 18

Without vertical transmission we have the following result.

Remark 8 (Condition for global fixation of cooperation: oblique and horizontal transmission). Without vertical transmission ($v = 0$), the frequency of the cooperator phenotype among adults increases every generation, $p' > p$ if there is a horizontal transmission bias in favor of cooperation, namely

$$T_A > T_B. \quad (22)$$

This condition is found by setting $v = 0$ in Eq. 6, which becomes $\hat{p} = p$, and then Eq. 8 becomes $p' = p^2(T_B - T_A) + p(1 + T_A - T_B)$. That is, in the absence of vertical transmission, selection plays no role in the evolution of cooperation (i.e. b and c do not affect p'). 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. Note that without bias in horizontal transmission, $T_A = T_B$, phenotype frequencies are static, $p' = p$.

Finally, the last remark focuses on the coexistence of cooperation and defection.

Remark 9 (Coexistence of cooperation and defection). Cooperation and defection can coexist at frequencies \tilde{p}^* and $1 - \tilde{p}^*$ (Eq. 12). When it occurs, the coexistence is stable if there is horizontal transmission bias for defection, $T_A < T_B$, and unstable if there is horizontal bias for cooperation, $T_A > T_B$.

See yellow and blue area in Figure 2 and Figure 3 for cases of stable and unstable coexistence, respectively. When unstable coexistence occurs, cooperation will fix if its initial frequency is $p > \tilde{p}^*$, and defection 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 S2a shows the mapping $\tilde{p} \rightarrow \tilde{p}'$.

Evolution of social association

We now analyze the evolution of social association under perfect vertical transmission, $v = 1$. We assume a population at a stable coexistence of the two phenotypes, cooperation A , and defection B , such that the frequency of A among juveniles is \hat{p}^* (Eq. 12). Note that for stable coexistence to occur, we assume horizontal bias for defection, $T_A < T_B$, and an intermediate cost of cooperation, $\gamma_2 < c < \gamma_1$ (Eq. 13)

The stable population mean fitness is $\bar{w}^* = 1 + \hat{p}^*(b - c)$, which is increasing in \hat{p}^* . In turn, \hat{p}^* is also increasing in α (Appendix C). Therefore, if social association increases, the population mean fitness also increases. But can an allele that increases social association evolve? To answer this question, we extend our model to include a “modifier locus” (Lieberman and Feldman, 1986; Lieberman, 1988) that determines social association, but has no direct effect on fitness. Assume that the modifier locus

has two alleles, M and m , which induce social associations α_1 and α_2 , respectively. Suppose that the
 282 population evolves to a stable equilibrium when only allele M is present. We check the local stability
 of this equilibrium to the invasion of the modifier allele m ; this stability is called “external stability”,
 284 see Altenberg et al. (2017).

The full analysis is given in Appendix D, and following result summarizes the outcomes of such
 286 invasions.

Result 2 (Evolution of social association). *In a population at a stable coexistence between cooperation
 288 and defection, a modifier allele can successfully invade the population if it increases the social
 association. Such an invasion will, in turn, increase the frequency of cooperator as well as the
 290 population mean fitness.*

Let us assume that modifier alleles with increased and decreased social association can appear in
 292 the population from time to time. Then, this results suggests that social association will continue to
 (slowly) increase as long as cooperation and defection coexist. This coexistence requires $a_2 < \alpha < a_1$
 294 (Figure 2c), and so this process will proceed until $\alpha = a_1$ and cooperation takes over the population.
 296

Population structure

Social association may also emerge from population structure. Consider a population colonizing a 2D
 298 grid of size 100-by-100, where each site is inhabited by one individual, similarly to Lewin-Epstein and
 300 Hadany (2020). Each individual is characterized by its phenotype: either cooperator, A , or defector, B .
 Initially, each site in the grid is randomly colonized with either a cooperator or a defector, with equal
 302 probability. In each generation, half of the individuals are randomly chosen to “initiate” interactions.
 Initiators then interact with a random neighbor (i.e. individual in an adjacent site) in a prisoners’
 304 dilemma game (Table 1) and a random neighbor (with replacement) in horizontal cultural transmission
 (Figure 1). The expected number of each of these interactions per individual per generation is one.
 306 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
 308 a finite grid m can be lower in edge neighborhoods close to the grid border. As before, T_A and T_B are
 the probability for successful horizontal transmission of phenotypes A and B , respectively.

The order the interactions across the grid at each generation is random. After all interactions take
 310 place, individual fitness is determined by $w = 1 + b \cdot n_b - c \cdot n_c$, where n_b is the number interactions
 312 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
 314 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,
 316 divided by the average fitness of all potential parents. Offspring then have the same phenotype as their
 parents (i.e. $v = 1$).

The outcomes of stochastic simulations with a structured population are shown in Figure 4. The
 318 figure demonstrates that the highest cost of cooperation c that permits the evolution of cooperation
 320 agrees with the conditions derived above for a model without population structure or stochasticity. An
 example for stable coexistence is shown in Figure 4c. Simulating a structured population with local
 322 selection (i.e. sites can only be settled by offspring of neighbor parents) had only a minor effect on
 the agreement with the derived conditions (Figure S1).

These comparisons between the deterministic unstructured model and the stochastic structured model
 324 show that the derived conditions can be useful for predicting the dynamics of complex scenarios.

Moreover, our structured populations demonstrate how social association (α) can emerge from local interactions between individuals.

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 a combination of vertical, oblique, and horizontal transmission, cooperation or defection can either fix or coexist, depending on the relationship between the cost and benefit of cooperation, the horizontal transmission bias, and the association between social interaction and horizontal transmission (Result 1). Importantly, cooperation can increase from rarity (i.e. invade a population of defectors) if and only if (inequality 14),

$$c \cdot v(1 - T_B) < b \cdot v\alpha T_A + (T_A - T_B) . \quad (23)$$

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). This condition cannot be formulated in the form of Hamilton's rule, $c < b \cdot r$, due to the effect of biased horizontal transmission.

Remarkably, stable coexistence between cooperation and defection can be stable 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 higher social association α leads to evolution of higher frequencies of cooperation (Remark 5, Figures 2c and 3cd), and that when both cooperation and defection coexist, higher social association is expected to evolve (Result 2). Without social association, the benefit of cooperation cannot facilitate its evolution; cooperation can only succeed under horizontal transmission bias ($T_A > T_B$, Remark 3).

Indeed, horizontal transmission plays a major role in the evolution of cooperation: increasing the transmission of cooperation, T_A , or decreasing the transmission of defection, T_B , facilitates the evolution of cooperation (Remarks 1 and 5, Figures 2-3). The effect of oblique transmission is more complex (Corollary 5). 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 for cooperation to fix in the population ($v > \hat{v}$, see Remark 6, Figure 3bd).

The conditions derived from our deterministic model provide a good approximation to outcomes of simulations of a complex stochastic model with structured populations, in which individuals can only interact with and transmit to their neighbors (Figure 4). In these structured populations social association arises due to both social interactions and horizontal cultural transmission being 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 review 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 (Figures 2-3). With enough social association, cooperation can increase in frequency when initially rare even when there is horizontal transmission bias against it ($T_A < T_B$, see Remark 5).

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, i.e. when there is social association, because the recipient of help may be also the recipient of the cultural trait for cooperation. 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

We thank Lilach Hadany, Ayelet Shavit, and Kaleda Krebs Denton for discussions and comments. This work was supported in part by the Israel Science Foundation 552/19 (YR), and Minerva Stiftung Center for Lab Evolution (YR).

Appendices

Appendix A Local stability criterion

Let $f(p) = \lambda \cdot (p' - p)$, where $\lambda > 0$, and 0 and 1 are equilibria, that is, $f(0) = 0$ and $f(1) = 0$.

Set $p > p^* = 0$. Using a linear approximation for $f(p)$ near 0, we have

$$p' < p \Leftrightarrow f(p)/p < 0 \Leftrightarrow \frac{f'(0) \cdot p + O(p^2)}{p} < 0 \Leftrightarrow f'(0) + O(p) < 0. \quad (\text{A1})$$

Therefore, by definition of big-O notation, if $f'(0) < 0$ then there exists $\epsilon > 0$ such that for any
412 $0 < p < \epsilon$, it is guaranteed that $0 < p' < p$; that is, p' is closer to zero than p .

Set $p < p^* = 1$ Using a linear approximation for $f(p)$ near 1, we have

$$414 \quad 1 - p' < 1 - p \Leftrightarrow -\frac{f(p)}{1 - p} < 0 \Leftrightarrow \frac{f'(1)(p - 1) + O((p - 1)^2)}{p - 1} < 0 \Leftrightarrow f'(1) - O(1 - p) < 0. \quad (\text{A2})$$

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

Appendix B Equilibria and stability

418 We define $f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p})$. Then, using *SymPy* (Meurer et al., 2017), a Python library for symbolic mathematics, this simplifies to

$$420 \quad f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = \beta_1 \hat{p}^3 + \beta_2 \hat{p}^2 + \beta_3 \hat{p}, \quad (\text{B1})$$

where

$$\begin{aligned} \beta_1 &= [c(1 - v) - b(1 - \alpha v)](T_A - T_B), \\ 422 \quad \beta_2 &= -\beta_1 - \beta_3, \\ \beta_3 &= \alpha b v T_A - c v(1 - T_B) + (T_A - T_B). \end{aligned} \quad (\text{B2})$$

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

$$f(\hat{p}) = \hat{p}(1 - \hat{p})[\alpha b v T - c v(1 - T)]. \quad (\text{B3})$$

426 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 A), where $f'(\hat{p}) = (1 - 2\hat{p})[\alpha b v T - c v(1 -$
428 $T)]$, so that

$$\begin{aligned} f'(0) &= \alpha b v T - c v(1 - T), \\ f'(1) &= -\alpha b v T + c v(1 - T). \end{aligned} \quad (\text{B4})$$

430 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
432 is

$$\hat{p}^* = \frac{\beta_3}{\beta_1} = \frac{\alpha b v T_A - c v(1 - T_B) + (T_A - T_B)}{[c(1 - v) - b(1 - \alpha v)](T_A - T_B)}. \quad (\text{B5})$$

434 Note that the sign of the cubic (Eq. B1) at positive (negative) infinity is equal (opposite) to the sign of
 β_1 . If $T_A > T_B$, then

$$436 \quad \beta_1 < [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) < 0, \quad (\text{B6})$$

since $c < b$ and $\alpha v < 1$. Hence the signs of the cubic at positive and negative infinity are negative
438 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)
440 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
442 $\hat{p}^* < 0$ and therefore $f'(0) > 0$ and $f'(1) < 0$; that is, fixation of the cooperator phenotype A is the
only locally stable legitimate equilibrium.

444 Similarly, if $T_A < T_B$, then

$$\beta_1 > [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) > 0, \quad (\text{B7})$$

446 since $c < b$ and $\alpha v < 1$, and the signs of the cubic at positive and negative infinity are positive and
 448 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
 450 $0 < \beta_3 < \beta_1$ 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
 452 therefore $f'(0) > 0$ and $f'(1) < 0$, and fixation of the cooperator phenotype A is the only locally
 stable legitimate equilibrium.

This analysis can be summarized with the following conditions:

- 454 1. *Fixation of cooperation*: if (i) $T = T_A = T_B$ and $c < b \cdot \frac{\alpha T}{1-T}$; or if (ii) $T_A > T_B$ and $0 < \beta_3$; or if
 (iii) $T_A < T_B$ and $\beta_1 < \beta_3$.
- 456 2. *Fixation of the defection*: if (iv) $T = T_A = T_B$ and $c > b \cdot \frac{\alpha T}{1-T}$; or if (v) $T_A > T_B$ and $\beta_3 < \beta_1 < 0$;
 or if (vi) $T_A < T_B$ and $\beta_3 < 0$.
- 458 3. *Coexistence of both phenotypes at \hat{p}^** : if (vii) $T_A < T_B$ and $0 < \beta_3 < \beta_1$.
4. *Fixation of either phenotype depending on initial frequency*: if (viii) $T_A > T_B$ and $\beta_1 < \beta_3 < 0$.

460 We now proceed to use the cost boundaries, γ_1 and γ_2 , and the vertical transmission threshold, \hat{v}
 (Eq. 13). First, assume $T_A < T_B$. $\beta_3 < 0$ requires $\gamma_1 < c$. For $\beta_3 < \beta_1$ we need $c[v(1 - T_B) + (1 -$
 462 $v)(T_A - T_B)] > bv\alpha T_B + (1 + b)(T_A - T_B)$. 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 $\gamma_2 < c$ or $v < \hat{v}$ and $c < \gamma_2$, and for
 464 $0 < \beta_3 < \beta_1$ we need $v > \hat{v}$ and $\gamma_2 < c < \gamma_1$, or $v < \hat{v}$ and $c < \min(\gamma_1, \gamma_2)$. For $\beta_1 < \beta_3$ we need
 $v > \hat{v}$ and $c < \gamma_2$ or $v < \hat{v}$ and $\gamma_2 < c$. However, some of these conditions cannot be met, since $v < \hat{v}$
 466 implies $c < 1 < \gamma_2$.

Second, assume $T_A > T_B$. $\beta_3 > 0$ requires $\gamma_1 > c$. For $\beta_1 < \beta_3$ we need $c[v(1 - T_B) + (1 - v)(T_A - T_B)] <$
 468 $bv\alpha T_B + (1 + b)(T_A - T_B)$. Thus for $\beta_1 < \beta_3$ we need $v > \hat{v}$ and $c < \gamma_2$ or $v < \hat{v}$ and $c > \gamma_2$. But $\hat{v} < 0$
 when $T_A > T_B$, and therefore we have $\beta_1 < \beta_3$ if $c < \gamma_2$. Similarly, we have $\beta_3 < \beta_1$ if $c > \gamma_2$.

470 This analysis is summarized in Result 1.

Appendix C Effect of social association on mean fitness

472 To determine the effect of increasing α on the stable population mean fitness, $\bar{w}^* = 1 + (b - c)\hat{p}^*$, we
 must analyze its effect on \hat{p}^* ,

$$474 \quad \frac{\partial \hat{p}^*}{\partial \alpha} = \frac{bT_A - c(1 - T_B) + (T_A - T_B)}{b(1 - \alpha)^2(T_B - T_A)}. \quad (C1)$$

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

$$476 \quad c < \gamma_1 = \frac{b\alpha T_A + (T_A - T_B)}{1 - T_B} < \frac{bT_A + (T_A - T_B)}{1 - T_B}. \quad (C2)$$

Therefore, the numerator in Eq. C1 is positive. Since $T_A < T_B$, the denominator in Eq. C1 is also
 478 positive, and hence the derivative $\partial \hat{p}^* / \partial \alpha$ is positive. Thus, the population mean fitness increases as
 social association α increases.

480 Appendix D External stability of \tilde{p}^*

We assume here that $v = 1$, i.e. no oblique transmission, and therefore $\hat{p} = \tilde{p}$. We define the
 482 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 frequencies

of the pheno-genotypes in the next generation are defined by the recursion system,

$$\begin{aligned}
\bar{w}\tilde{p}'_1 &= \tilde{p}_1x(1+b-c)(1-(1-\alpha_1)(1-x)T_B)+ \\
&\quad \tilde{p}_1(1-x)(1-c)(1-\alpha_1T_Bx-T_B(1-x))+ \\
&\quad \tilde{p}_2x(1+b)T_A(x+\alpha_1(1-x))+ \\
&\quad \tilde{p}_2(1-x)x(1-\alpha_1)T_A, \\
\bar{w}\tilde{p}'_2 &= \tilde{p}_1x(1+b-c)(1-\alpha_1)(1-x)T_B \\
&\quad \tilde{p}_1(1-x)(1-c)(\alpha_1T_B+(1-\alpha_1)(1-x)T_B)+ \\
&\quad \tilde{p}_2x(1+b)(1-\alpha_1T_A(1-x)-T_Ax)+ \\
&\quad \tilde{p}_2(1-x)(1-(1-\alpha_1)xT_A), \\
\bar{w}\tilde{p}'_3 &= \tilde{p}_3x(1+b-c)(1-(1-\alpha_2)(1-x)T_B)+ \\
&\quad \tilde{p}_3(1-x)(1-c)(1-\alpha_2T_Bx-T_B(1-x))+ \\
&\quad \tilde{p}_4x(1+b)T_A(x+\alpha_2(1-x))+ \\
&\quad \tilde{p}_4(1-x)x(1-\alpha_2)T_A, \\
\bar{w}\tilde{p}'_4 &= \tilde{p}_3x(1+b-c)(1-\alpha_2)(1-x)T_B+ \\
&\quad \tilde{p}_3(1-x)(1-c)(\alpha_2T_B+(1-\alpha_2)(1-x)T_B)+ \\
&\quad \tilde{p}_4x(1+b)(1-\alpha_2T_A(1-x)-T_Ax)+ \\
&\quad \tilde{p}_4(1-x)(1-(1-\alpha_2)xT_A),
\end{aligned} \tag{D1}$$

where $x = \tilde{p}_1 + \tilde{p}_3$ is the cooperator frequency, and $\bar{w} = 1 + (b-c)x$ is the population mean fitness.

The equilibrium when only allele M is present is $\tilde{\mathbf{p}}^* = (\tilde{p}^*, 1 - \tilde{p}^*, 0, 0)$, where

$$\tilde{p}^* = \frac{c(1-T_B) - b\alpha_1T_A - (T_A - T_B)}{b(1-\alpha_1)(T_A - T_B)}, \tag{D2}$$

which we get by setting $\alpha = \alpha_1$ and $v = 1$ in Eq. 12. The local stability of $\tilde{\mathbf{p}}^*$ to the introduction of allele m is determined by the linear approximation \mathbf{L}^* of the transformation in Eq. D1 near $\tilde{\mathbf{p}}^*$ (i.e., the Jacobian of the transformation at the equilibrium). \mathbf{L}^* is known to have 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 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 eigenvalues of the external stability matrix \mathbf{L}_{ex}^* ,

$$\begin{aligned}
\mathbf{L}_{ex}^* &= \frac{1}{\bar{w}^*} \begin{bmatrix} X & Y \\ Z & Q \end{bmatrix} = \\
&\frac{1}{\bar{w}^*} \begin{bmatrix} \frac{\partial \bar{w}\tilde{p}'_3}{\partial \tilde{p}_3}(\tilde{\mathbf{p}}^*) & \frac{\partial \bar{w}\tilde{p}'_4}{\partial \tilde{p}_3}(\tilde{\mathbf{p}}^*) \\ \frac{\partial \bar{w}\tilde{p}'_3}{\partial \tilde{p}_4}(\tilde{\mathbf{p}}^*) & \frac{\partial \bar{w}\tilde{p}'_4}{\partial \tilde{p}_4}(\tilde{\mathbf{p}}^*) \end{bmatrix} = \\
&\frac{1}{\bar{w}^*} \begin{bmatrix} (1+b\tilde{p}^*-c)(1-T_B(1-\tilde{p}^*)) + b\tilde{p}^*\alpha_2T_B(1-\tilde{p}^*) & (1+b\tilde{p}^*)T_A\tilde{p}^* + b\tilde{p}^*\alpha_2T_A(1-\tilde{p}^*) \\ (1+b\tilde{p}^*-c)T_B(1-\tilde{p}^*) - b\tilde{p}^*\alpha_2T_B(1-\tilde{p}^*) & (1+b\tilde{p}^*)(1-T_A\tilde{p}^*) - b\tilde{p}^*\alpha_2T_A(1-\tilde{p}^*) \end{bmatrix},
\end{aligned} \tag{D3}$$

where the elements of \mathbf{L}_{ex}^* are derived from Eq. D1.

Note that \mathbf{L}_{ex}^* is positive, and due to the Perron-Frobenius theorem, its leading eigenvalue is real and positive. If the leading eigenvalue is less than 1, then the equilibrium $\tilde{\mathbf{p}}^*$ is externally stable and allele m cannot invade the population of allele M . The eigenvalues of \mathbf{L}_{ex}^* are the roots of the characteristic polynomial

$$R(\lambda) = \lambda^2 - \lambda \frac{(X+Q)}{\bar{w}^*} + \frac{XQ - YZ}{\bar{w}^{*2}}. \tag{D4}$$

The characteristic polynomial $R(\lambda)$ is a quadratic with a positive leading coefficient. Therefore,
 504 $R(\infty) = R(-\infty) > 0$. Hence, the leading eigenvalue is greater than one, implying external stability, if
 and only if $R(1) > 0$ and $R'(1) > 0$. Thus, a sufficient condition for instability is $R(1) < 0$. Using
 506 *SymPy* (Meurer et al., 2017), a Python library for symbolic mathematics, we find that $R(1) < 0$ if and
 only if $\alpha_2 < \alpha_1$. That is, if the social association α_2 of the invading modifier allele m is less than α_1
 508 of the resident M , then invasion will be successful.

Determining a necessary and sufficient condition for successful invasion is more complicated, requiring
 510 analysis of the sign of $R'(1)$.

References

- 512 Lee Altenberg, Uri Liberman, and Marcus W. Feldman. Unified reduction principle for the evolution
 of mutation, migration, and recombination. *Proc. Natl. Acad. Sci. U. S. A.*, 114(12):E2392–E2400,
 514 mar 2017. ISSN 0027-8424. doi: 10.1073/pnas.1619655114.
- Robert Axelrod and William D Hamilton. The evolution of cooperation. *Science*, 211(4489):1390–
 516 1396, 1981.
- Piter Bijma and Duur K. Aanen. Assortment, Hamilton’s rule and multilevel selection. *Proc. R. Soc.
 518 B Biol. Sci.*, 277(1682):673–675, 2010. ISSN 14712970. doi: 10.1098/rspb.2009.1093.
- Luigi Luca Cavalli-Sforza and Marcus W Feldman. *Cultural transmission and evolution: A quantita-
 520 tive approach*. Number 16. Princeton University Press, 1981.
- Lee Alan Dugatkin. *Cooperation among Animals: An Evolutionary Perspective*. Oxford University
 522 Press on Demand, 1997.
- Ilan Eshel and Luigi Luca Cavalli-Sforza. Assortment of encounters and evolution of cooperativeness.
 524 *Proceedings of the National Academy of Sciences*, 79(4):1331–1335, 1982.
- Marcus W Feldman, Luca L Cavalli-Sforza, and Joel R Peck. Gene-culture coevolution: models
 526 for the evolution of altruism with cultural transmission. *Proceedings of the National Academy of
 Sciences*, 82(17):5814–5818, 1985.
- 528 Jeffrey A. Fletcher and Michael Doebeli. A simple and general explanation for the evolution of altruism.
Proc. R. Soc. B Biol. Sci., 276(1654):13–19, 2009. ISSN 14712970. doi: 10.1098/rspb.2008.0829.
- 530 J. B. S. Haldane. *The Causes of Evolution*. London, 1932.
- William D Hamilton. The genetical evolution of social behaviour. ii. *Journal of Theoretical Biology*,
 532 7(1):17–52, 1964.
- Adrian V Jaeggi and Michael Gurven. Natural cooperators: food sharing in humans and other primates.
 534 *Evolutionary Anthropology: Issues, News, and Reviews*, 22(4):186–195, 2013.
- Indrikis Krams, Tatjana Krama, Kristine Igaune, and Raivo Mänd. Experimental evidence of reciprocal
 536 altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, 62(4):599–605, 2008.
- Ohad Lewin-Epstein and Lilach Hadany. Host-microbiome coevolution can promote cooperation in
 538 a rock-paper-scissors dynamics. *Proc. R. Soc. B Biol. Sci.*, 287(1920):20192754, feb 2020. ISSN
 0962-8452. doi: 10.1098/rspb.2019.2754.
- 540 Ohad Lewin-Epstein, Ranit Aharonov, and Lilach Hadany. Microbes can help explain the evolution
 of host altruism. *Nature Communications*, 8:14040, 2017.
- 542 Uri Liberman. External stability and ESS: criteria for initial increase of new mutant allele. *J. Math.
 Biol.*, 26(4):477–485, 1988. ISSN 03036812. doi: 10.1007/BF00276375.

- 544 Uri Liberman and Marcus W. Feldman. A general reduction principle for genetic modifiers of recombination. *Theor. Popul. Biol.*, 30(3):341–71, dec 1986. ISSN 0040-5809.
- 546 Stephen J Lycett and John AJ Gowlett. On questions surrounding the acheulean ‘tradition’. *World Archaeology*, 40(3):295–315, 2008.
- 548 Aaron Meurer, Christopher P Smith, Mateusz Paprocki, Ondřej Čertík, Sergey B Kirpichev, Matthew Rocklin, AMiT Kumar, Sergiu Ivanov, Jason K Moore, Sartaj Singh, et al. Sympy: symbolic
550 computing in python. *PeerJ Computer Science*, 3:e103, 2017.
- Yoav Ram, Uri Liberman, and Marcus W Feldman. Evolution of vertical and oblique transmission
552 under fluctuating selection. *Proceedings of the National Academy of Sciences*, 115(6):E1174–E1183, 2018.
- 554 George E Rice and Priscilla Gainer. “Altruism” in the albino rat. *Journal of Comparative and Physiological Psychology*, 55(1):123, 1962.
- 556 Peter J Richerson and Robert Boyd. *Not by Genes Alone: How Culture Transformed Human Evolution*. University of Chicago Press, 2008.
- 558 Barry Sinervo, Alexis Chaine, Jean Clobert, Ryan Calsbeek, Lisa Hazard, Lesley Lancaster, Andrew G McAdam, Suzanne Alonzo, Gwynne Corrigan, and Michael E Hochberg. Self-recognition, color
560 signals, and cycles of greenbeard mutualism and altruism. *Proceedings of the National Academy of Sciences*, 103(19):7372–7377, 2006.
- 562 Peter B Stacey and Walter D Koenig, editors. *Cooperative breeding in birds: long term studies of ecology and behaviour*. Cambridge University Press, 1990.
- 564 Scott Woodcock. The significance of non-vertical transmission of phenotype for the evolution of altruism. *Biology and Philosophy*, 21(2):213–234, 2006.
- 566 Matthew R. Zefferman. Mothers teach daughters because daughters teach granddaughters: the evolution of sex-biased transmission. *Behav. Ecol.*, 27(4):1172–1181, 2016. ISSN 1045-2249. doi:
568 10.1093/beheco/arw022.

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. $0 < c < 1$ and $c < b$.

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 | $[0, 1]$ |

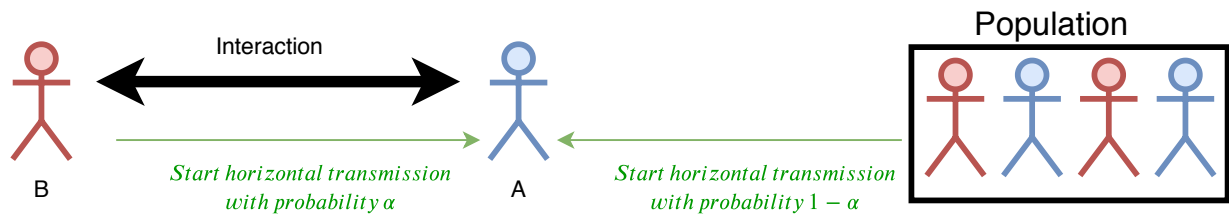


Figure 1: Cultural horizontal transmission with assortment. Transmission occurs between interacting partners with probability α (left) or between two random peers with probability $1 - \alpha$, where α is the *social association* parameter.

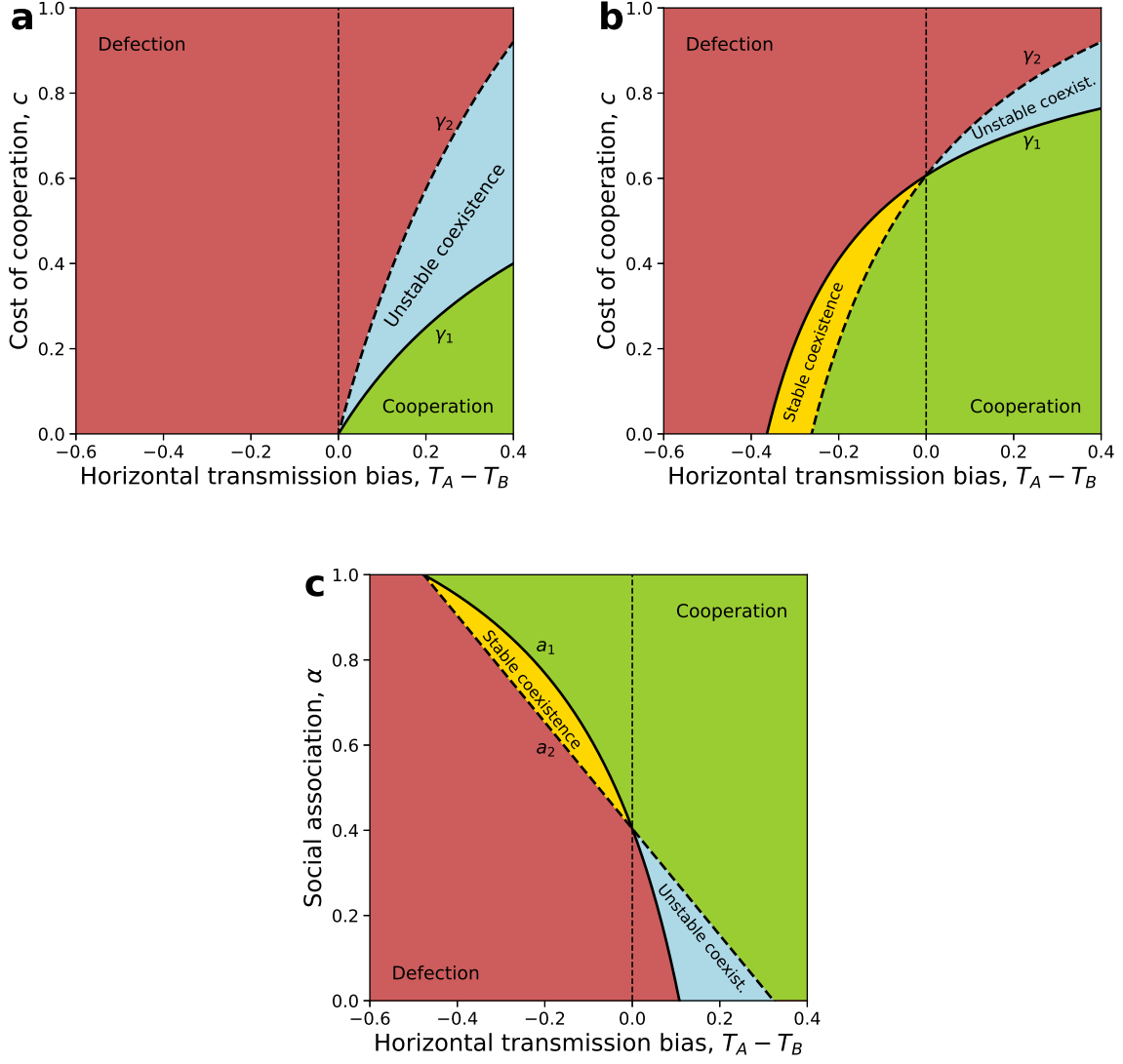


Figure 2: Evolution of cooperation under vertical and horizontal cultural transmission. The figure shows the global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial conditions, i.e. unstable coexistence (blue), and stable coexistence of cooperation and defection (yellow). In all cases the horizontal bias ($T_A - T_B$) is on the x-axis. **(a-b)** The cost of cooperation c is on the y-axis; the cost boundaries γ_1 and γ_2 (Eq. 13) 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. 18) are the solid and dashed lines, respectively. Here, $b = 1.3$, $T_A = 0.4$. **(a)** $\alpha = 0$. **(b)** $\alpha = 0.7$. **(c)** $c = 0.35$.

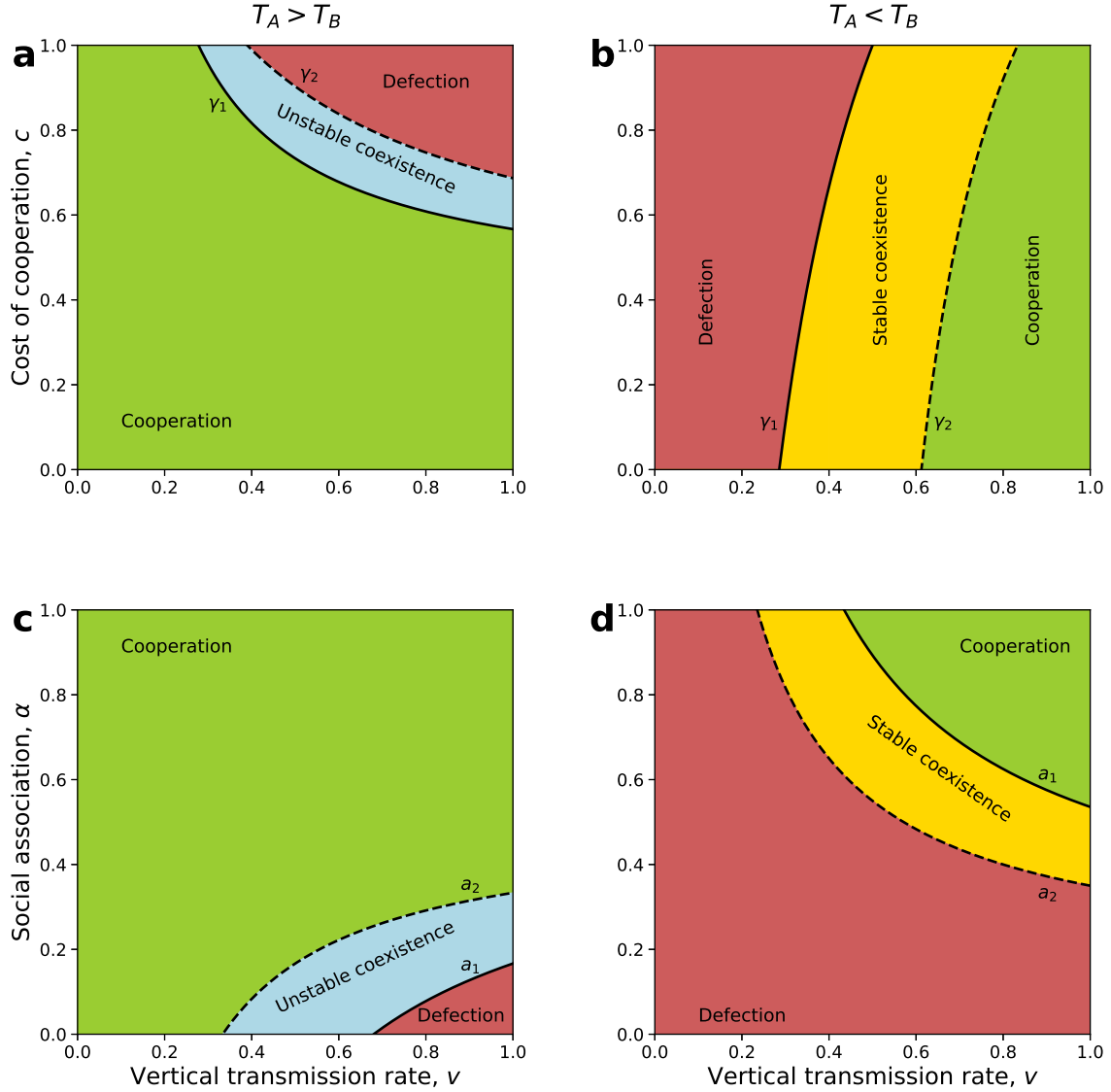


Figure 3: Evolution of cooperation under vertical, oblique, and horizontal cultural transmission.

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 v is on the x-axis. **(a-b)** The cost of cooperation c is on the y-axis and the cost boundaries γ_1 and γ_2 (Eq. 13) 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 a_1 and a_2 (Eq. 18) 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)** $b = 2$, $T_B = 0.7$, $c = 0.5$.

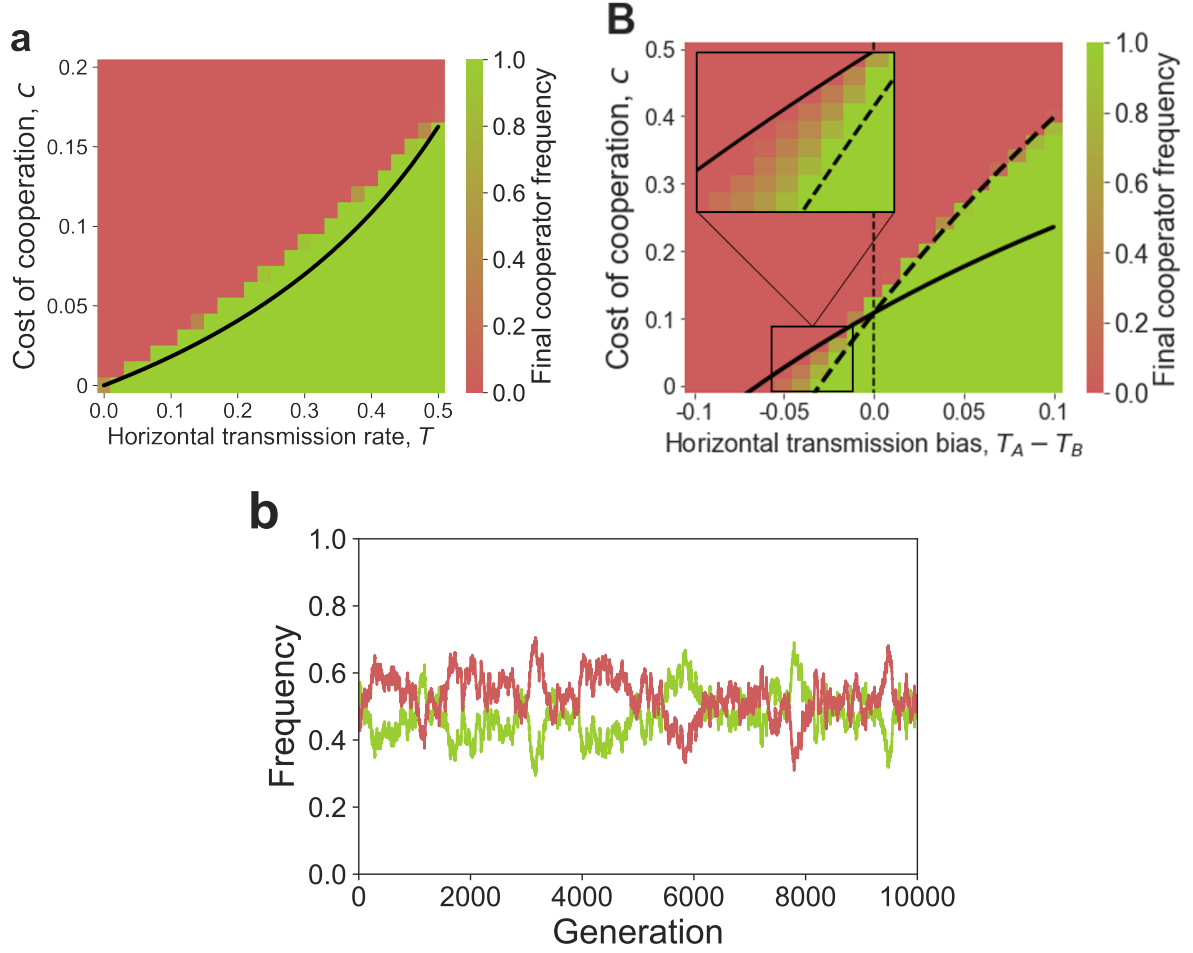


Figure 4: Evolution of cooperation in a structured population. The expected frequency of cooperators in a structured population after 10,000 generations is shown (red for 0%, green for 100%) as function of both the cost of cooperation (c) on the y-axis, and the symmetric horizontal transmission rate ($T = T_A = T_B$) 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 S1 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. 15 and **(b)** Eq. 13. 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 $T_A = 0.4$, $0.3 < T_B < 0.5$.

Supplementary Material

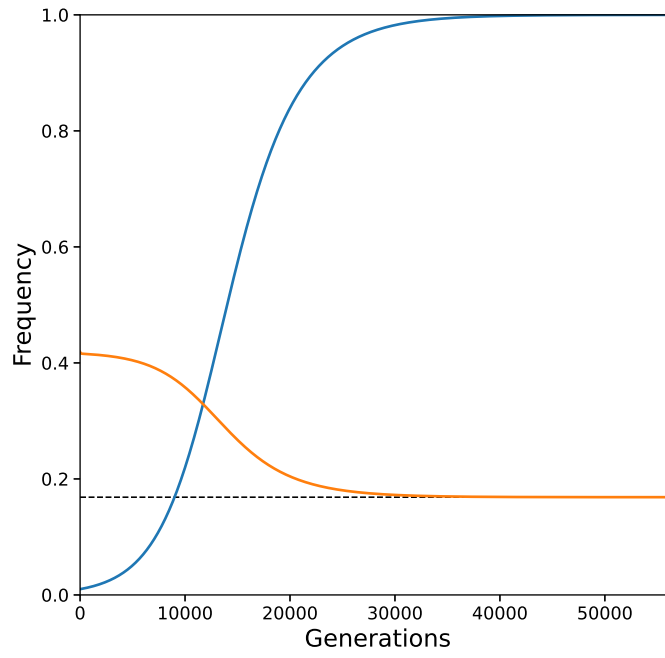


Figure 5: Evolution of social association. successful invasion of new modifier allele m ; starting from stable coexistence of cooperators and defectors with social association α_1 . The invaders have modifier allele m which cause different social association value, α_2 where $\alpha_2 < \alpha_1$. The blue curve describes the frequency of the invaders, starting from initial frequency of 1%. The orange curve describes the frequency of cooperators after invasion. The frequency of cooperators decreases towards new stable frequency which is described by the black dashed line. The frequency of cooperators after the fixation of the invaders is the equilibrium described in Eq. 12 with social association $\alpha = \alpha_2$. In this case $T_A = 0.4$, $T_B = 0.7$, $b = 1.3$, $c = 0.05$, $\alpha_1 = 0.7$ and $\alpha_2 = 0.65$.

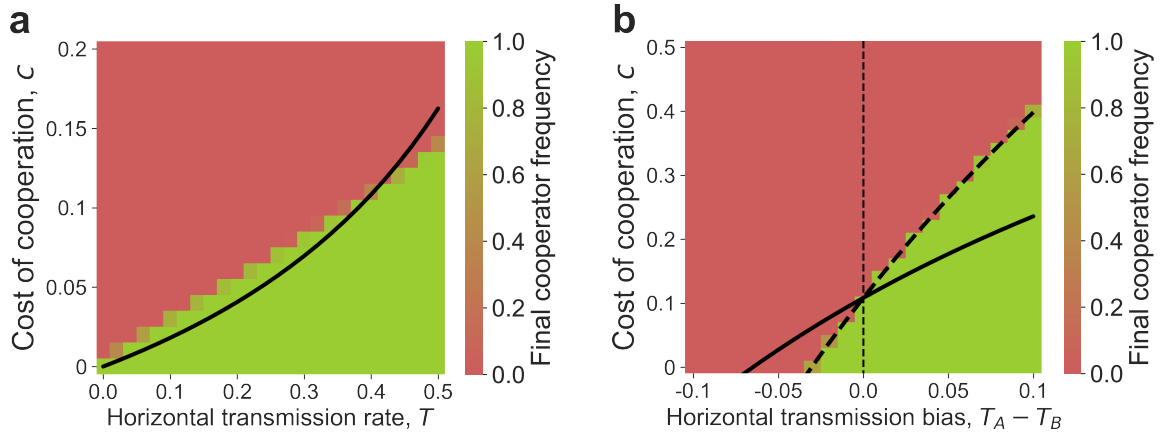


Figure S1: Evolution of cooperation in a structured population with local selection. The expected frequency of cooperators in a structured population after 10,000 generations is shown (red for 0%, green for 100%) as function of both the cost of cooperation (c) on the y-axis, and the symmetric horizontal 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 4 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. 15 and (b) Eq. 13. 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 $\nu = 1$. (a) Symmetric horizontal transmission, $T = T_A = T_B$. (b) Horizontal transmission rates $T_A = 0.4$, $0.3 < T_B < 0.5$.

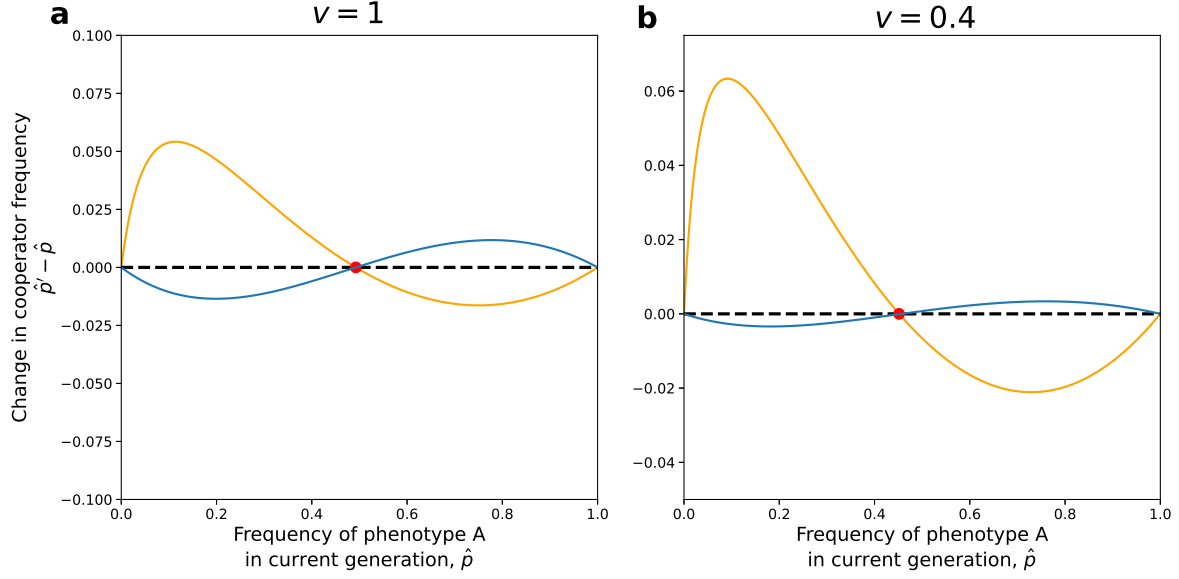


Figure S2: Stable and unstable coexistence between cooperation and defection. The curves show the difference of $\hat{p}' - \hat{p}$ vs \hat{p} where \hat{p}' and \hat{p} are the frequency of the cooperative phenotype A among juveniles in the next generation and current generations (Eq. 6). The dashed black line is $\hat{p}' - \hat{p} = 0$. The curves and the dashed line intersect at the stable equilibrium \hat{p}^* (red circle). When $\hat{p}' - \hat{p} > 0$, \hat{p} increases towards \hat{p}^* . When $\hat{p}' - \hat{p} < 0$, \hat{p} decreases towards \hat{p}^* . **(a)** There is no oblique transmission, $v = 1$. 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. 13). 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 $v = 0.4$, which give $0 < \beta_3 < \beta_1$ (Eq. B2). 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 $\beta_1 < \beta_3 < 0$.

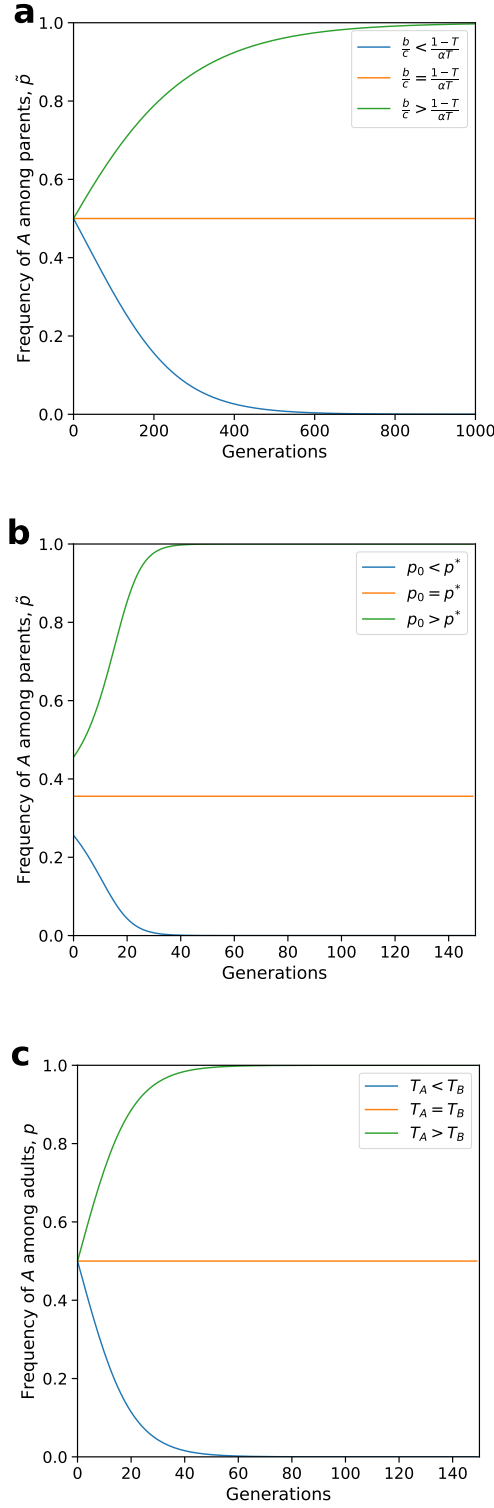


Figure S3: Dynamics of the frequency of cooperation. The frequency \tilde{p} of parents with cooperative phenotype A in (a-b) and the frequency p of adults with cooperative phenotype A in (c). The different lines correspond to parameter values that lead to fixation of cooperation (green), extinction 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 $c = 0.5$.