

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

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Abstract

We construct models for the cultural evolution of cooperation in a well-mixed population with vertical, horizontal, and oblique transmission. Conditions are found for fixation and coexistence of cooperation and defection. The results show that association between cooperation and horizontal transmission facilitates the evolution of cooperation. A spatial model is constructed and its results are compared to the well-mixed 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 relatedness coefficient r measures a probability that an allele sampled from the cooperator is identical by descent to one at the same locus in the recipient. This condition is known as *Hamilton's rule*:

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

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 r in inequality 1.

The role of assortment in the evolution of altruism was studied by Fletcher and Doebeli (2009) in a *public goods* game. They found that for altruism to evolve, cooperative individuals must 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.” This condition can be summarized by (Fletcher and Doebeli, 2009, eq. 2.3)

$$c < b \cdot (e_C - e_D), \quad (3)$$

where e_C is the probability that a cooperator receives help, and e_D is the probability that a defector receives help.²

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 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)

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

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 $e_C = r + p$, $e_D = p$ and $e_C = m + (1 - m)p$, $e_D = (1 - m)p$, respectively, where p is the frequency of cooperators.

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

62 Cultural transmission may be either viewed as vertical, horizontal or oblique: vertical transmission
 occurs between parents and offspring, horizontal transmission occurs between individuals from the
 64 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
 66 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)
 68 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
 70 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
 72 mathematically similar to those for transmission of infectious diseases (Cavalli-Sforza and Feldman,
 1981).

74 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
 76 models behavioral changes are mediated by cultural transmission that can occur specifically during
 social interactions. For instance, when there is an association between the choice of partner for social
 78 interaction and the choice of partner for cultural transmission. As another example, when an individual
 interacts with an individual of a different phenotype, this exposure to a different phenotype may lead
 80 it to learn or 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
 82 generation of assortment in the sense of Fletcher and Doebeli (2009)). This further emphasizes that
 treatment of cooperation as a cultural trait, rather than a genetic one, can lead to a better understanding
 84 of its evolutionary dynamics.

Models

86 Consider a very large population whose members are characterized by their phenotype ϕ , which can
 be of two types, $\phi = A$ for cooperators or $\phi = B$ for defectors. An offspring inherits its phenotype
 88 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
 90 the parent phenotype is ϕ and assuming uni-parental inheritance, the conditional probability that the
 phenotype ϕ' of the offspring is A is

$$92 \quad P(\phi' = A \mid \phi) = \begin{cases} v + (1 - v)p, & \text{if } \phi = A \\ (1 - v)p, & \text{if } \phi = B \end{cases}, \quad (5)$$

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

94 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
 96 vertical and oblique transmission) is

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

98 Individuals are assumed to interact according to a *prisoner's dilemma*. Specifically, individuals
 100 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 .

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

Table 1: Payoff matrix for prisoner's dilemma. The fitness of phenotype ϕ_1 when interacting with phenotype ϕ_2 . A is a cooperative phenotype, B is a defector phenotype, b is the benefit gained by an individual interacting with a cooperator, and c is the cost of cooperation. $b > c > 0$.

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

Horizontal cultural transmission occurs between pairs of individuals from the same generation. It
 106 occurs between social partners with probability α , or between a random pair with probability $1 - \alpha$
 (see Figure 1). The social association α is therefore the fraction of population that receives (horizontal
 108 transmission) from the social interaction partner, and $1 - \alpha$ receives randomly. Horizontal transmission
 is not always successful, as one partner may reject the other's phenotype. The probability for successful
 110 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
 112 transmission, is

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

114 which simplifies to

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

116 The frequency of A among parents (i.e. after selection) follows a similar dynamic, but also includes

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

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

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

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

Eq. 9 can be simplified to

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

where $\hat{p} = v\tilde{p} + (1-v)p$.

124 Results

Oblique and Horizontal Transmission

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

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

which gives the following result.

130

Result 1 (Oblique and horizontal transmission of cooperation). *Without vertical transmission ($v = 0$),
132 if there is a horizontal transmission bias in favor of cooperation, namely*

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

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

If $T_A = T_B$, then $p' = p$ and the population is static. Therefore, in the absence of vertical transmission,
136 selection plays no role in the evolution of cooperation. Hence, cooperation will evolve if the cooperator
phenotype has a horizontal transmission bias (see Figure 5c).

138 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
140 the frequency of the cooperative phenotype among parents in the next generation \tilde{p}' can be written
as

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

Fixation of either cooperation, $\tilde{p} = 1$, or defection, $\tilde{p} = 0$, are equilibria of Eq. 14, that is, they solve
144 $\tilde{p}' = \tilde{p}$. We therefore assume for the remainder of the analysis that $0 < \tilde{p} < 1$.

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

$$146 \quad \tilde{p}(1 - \tilde{p})[(1 + b)T_A + (1 - c)(1 - T_B) - 1] = 0, \quad (15)$$

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

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

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

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

152

154 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

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

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

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

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

$$160 \quad \tilde{p}^* = \frac{c(1 - T_B) - b\alpha T_A - (T_A - T_B)}{b(1 - \alpha)(T_A - T_B)}, \quad (20)$$

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

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

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

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

162 We define the initial frequency of the cooperator phenotype among parents, \tilde{p}_0 , and the *cost bound-*
aries,

$$164 \quad \gamma_1 = \frac{b\alpha T_A + (T_A - T_B)}{1 - T_B}, \quad \gamma_2 = \frac{b\alpha T_B + (1 + b)(T_A - T_B)}{1 - T_B}. \quad (23)$$

Then, applying Eqs. 20, 21, and 22, we summarize the possible outcomes in following result and
166 corollaries.

168 **Result 2** (Vertical and horizontal transmission of cooperation). *With vertical and horizontal but*
without oblique transmission ($v = 1$), the cultural evolution of a cooperator phenotype will follow one
170 *of the following scenarios, depending on the cost boundaries γ_1 and γ_2 (Eq. 23):*

1. Fixation of cooperation: if (i) $T = T_A = T_B$ and $c < b \cdot \alpha \frac{T}{1-T}$; or if (ii) $T_A > T_B$ and $c < \gamma_1$; or
 172 if (iii) $T_A < T_B$ and $c < \gamma_2$.

2. Fixation of defection: if (iv) $T = T_A = T_B$ and $c > b \cdot \alpha \frac{T}{1-T}$; or if (v) $T_A > T_B$ and $\gamma_2 < c$; or if
 174 (vi) $T_A < T_B$ and $\gamma_1 < c$.

3. Stable coexistence of both phenotypes at \tilde{p}^* : if (vii) $T_A < T_B$ and $\gamma_2 < c < \gamma_1$.

4. Unstable coexistence and fixation of either phenotype depending on initial frequency: if (viii)
 176 $T_A > T_B$ and $\gamma_1 < c < \gamma_2$.

178 These conditions are illustrated in Figure 3. Note that cooperation and defection can coexist stably
 if there is horizontal bias for defection and the cost of cooperation is large but not too large. The
 180 recursion dynamic for this case is illustrated in Figure 2.

Much of the literature on evolution of cooperation focuses on conditions for an initially rare cooper-
 182 ative phenotype to invade a population of defectors. The next corollary deals with such a condition,
 followed by a corollary that deals with symmetric horizontal transmission, i.e. $T_A = T_B$.

Corollary 1 (Condition for cooperation to increase when initially rare). *If the initial frequency of the*
 186 *cooperative phenotype is very close to zero, $\tilde{p}_0 \approx 0$, then this frequency will increase if*

$$T_A > T_B \text{ and } c < \gamma_1, \quad \text{or} \quad T_A < T_B \text{ and } \gamma_2 < c < \gamma_1. \quad (24)$$

188 In general, these conditions cannot be formulated in the form of Hamilton's rule ($c < b \cdot r$) due to the
 horizontal transmission bias $T_A - T_B$. Without horizontal transmission bias, i.e., with $T = T_A = T_B$,
 190 these conditions reduce to a form of Hamilton's rule.

Corollary 2 (Symmetric horizontal transmission). *If $T = T_A = T_B$, then cooperation will take over*
 192 *the population if*

$$c < b \cdot \alpha \frac{T}{1-T}. \quad (25)$$

196 Inequality 25 is obtained by setting $T = T_A = T_B$ in inequality 19 and can be interpreted as a version
 of Hamilton's rule (inequality 1) or as a version of inequality 3, where $\alpha T / (1 - T)$ can be regarded as
 the 'effective relatedness' or 'effective assortment', respectively. Figure 5a demonstrates this condition.

Corollary 3 (No social association of transmission and cooperation). *Without association ($\alpha = 0$)*
 200 *and with horizontal bias for cooperation ($T_A > T_B$), then (1) if the cost is low compared to the bias*
($c < (T_A - T_B) / (1 - T_B)$), then cooperation will fix from any positive frequency; (2) if the cost is low
 202 *compared to the benefit ($c < (1 + b)(T_A - T_B)(1 - T_B)$), then cooperation will fix if the initial frequency*
is high enough ($\tilde{p}_0 > \tilde{p}^$).*

204 Figure 3a illustrates these conditions, where the third equilibrium given by Eq. 20 becomes

$$\tilde{p}^*(\alpha = 0) = \frac{c(1 - T_B) - (T_A - T_B)}{b(T_A - T_B)}, \quad (26)$$

206 and the cost boundaries are

$$\gamma_1(\alpha = 0) = \frac{T_A - T_B}{1 - T_B}, \quad \gamma_2(\alpha = 0) = (1 + b) \frac{T_A - T_B}{1 - T_B}. \quad (27)$$

208 If $T_A > T_B$ then $0 < \gamma_1(\alpha = 0) < \gamma_2(\alpha = 0)$. So either $c < \gamma_1(\alpha = 0)$ or $\gamma_1(\alpha = 0) < c < \gamma_2(\alpha = 0)$
 will allow fixation of cooperation, the latter only if the initial frequency is high enough. If $T_A < T_B$

210 then $\gamma_2(\alpha = 0) < \gamma_1(\alpha = 0) < 0 < c$, and defection will fix.

212 **Corollary 4** (Perfect social association of transmission and cooperation). *With perfect social asso-*
ciation ($\alpha = 1$), there are only two equilibria, $\tilde{p} = 0$ and $\tilde{p} = 1$. The condition for evolution of
 214 *cooperation (i.e. global stability of $\tilde{p} = 1$) is found from inequality 17, namely*

$$c < \frac{b \cdot T_A + (T_A - T_B)}{1 - T_B}. \quad (28)$$

216 With perfect social association horizontal transmission always co-occurs with the cooperative inter-
 action. The same occurs in Lewin-Epstein et al. (2017), and therefore this corollary is equivalent to
 218 their result (see their eq. 1).

In terms of the cost boundaries, inequality 28 is equivalent to $c < \gamma_1$, and if $T_A > T_B$ then that suffices
 220 for fixation of cooperation. If $T_B > T_A$ then $\gamma_2(\alpha = 1) < 0$ and again, inequality 28 is sufficient for
 increase in the frequency of A. Inequality 28 can be written as

$$222 \quad 1 - (1 - c)(1 - T_B) < (1 + b)T_A, \quad (29)$$

which provides an interesting interpretation for the success of cooperation. In the interaction between
 224 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
 226 a defector, or that it fails to reproduce. This is the *effective cost of cooperation* from this interaction,
 while $(1 + b)T_A$ is the probability that the defector becomes cooperative and reproduces, which is the
 228 *effective benefit of cooperation* from this interaction. Thus, inequality 28 entails that cooperation can
 evolve if the effective cost of cooperation is less than the effective benefit.

230 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
 232 denote the social association boundaries by

$$a_1 = \frac{c(1 - T_B) - (1 + b)(T_A - T_B)}{b \cdot T_B}, \quad a_2 = \frac{c(1 - T_B) - (T_A - T_B)}{b \cdot T_A}. \quad (30)$$

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

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

$$238 \quad \begin{aligned} &T_A > T_B \text{ and } a_2 < \alpha, \quad \text{or} \\ &T_A < T_B \text{ and } a_1 < \alpha. \end{aligned} \quad (31)$$

Figure 3c demonstrates these conditions. With horizontal bias for cooperation ($T_A > T_B$; positive
 240 x-axis) cooperation fixes in the population from any initial positive frequency (green) if α (y-axis) is
 above the orange line (a_1), or if initially present at a high enough frequency (blue) if α is above the
 242 blue line (a_2). With horizontal bias for defection ($T_B > T_A$; negative x-axis) cooperation fixes if α is
 above the blue line (a_2), but can be maintained in coexistence with defection (yellow) if α is above
 244 the orange line (a_1). Without horizontal bias ($T_A = T_B$) fixation occurs if the assortment rate is high
 enough, $\alpha > \frac{c}{b} \cdot \frac{1-T}{T}$ (inequality 25).

246 With Vertical and Oblique Transmission

With both vertical and oblique transmission, $0 < \nu < 1$, the recursion system is more complex, and we focus on local rather than on global stability. To proceed, we note that Eq. 6 can give \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). We then determine the equilibria, namely, solutions of $\hat{p}' = \hat{p}$, and analyse their local stability.

We apply Eqs. 6, 8, and 11 to obtain the function $f(\hat{p})$ (see Appendix Appendix A):

$$254 \quad f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = \beta_1 \hat{p}^3 + \beta_2 \hat{p}^2 + \beta_3 \hat{p}, \quad (32)$$

where

$$\begin{aligned} \beta_1 &= [c(1 - \nu) - b(1 - \alpha\nu)](T_A - T_B), \\ \beta_2 &= -\beta_1 - \beta_3, \\ \beta_3 &= \alpha b \nu T_A - c \nu(1 - T_B) + (T_A - T_B). \end{aligned} \quad (33)$$

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

$$258 \quad f(\hat{p}) = \hat{p}(1 - \hat{p})[\alpha b \nu T - c \nu(1 - T)]. \quad (34)$$

Clearly the only two equilibria are the fixations $\hat{p} = 0$ and $\hat{p} = 1$. These equilibria are locally stable if $f'(\hat{p}) < 0$ near the equilibrium (Appendix Appendix B), and

$$262 \quad f'(\hat{p}) = (1 - 2\hat{p})[\alpha b \nu T - c \nu(1 - T)], \quad (35)$$

with

$$\begin{aligned} f'(0) &= \alpha b \nu T - c \nu(1 - T), \\ f'(1) &= -\alpha b \nu T + c \nu(1 - T). \end{aligned} \quad (36)$$

Therefore with symmetric horizontal transmission, fixation of the cooperative phenotype ($\hat{p} = 1$) occurs under the same condition as Corollary 1.1, namely Eq. 25.

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

$$270 \quad \hat{p}^* = \frac{\beta_3}{\beta_1}. \quad (37)$$

Note that the sign of the cubic (Eq. 32) at positive (negative) infinity is equal (opposite) to the sign of β_1 . If $T_A > T_B$, then

$$\beta_1 < [c(1 - \alpha\nu) - b(1 - \alpha\nu)](T_A - T_B) = (1 - \alpha\nu)(c - b)(T_A - T_B) < 0, \quad (38)$$

since $c < b$ and $1 > \alpha\nu$. Hence the signs of the cubic at positive and negative infinity are negative and positive, respectively. First, if $\beta_3 < \beta_1$ then $1 < \hat{p}^*$ and therefore $f'(0) < 0$ and $f'(1) > 0$; that is, fixation of the defector phenotype B is the only locally stable legitimate (i.e. between 0 and 1) equilibrium. Second, if $\beta_1 < \beta_3 < 0$ then $0 < \hat{p}^* < 1$ and therefore $f'(0) < 0$ and $f'(1) < 0$, that is, both fixations are locally stable and \hat{p}^* separates the domains of attraction. Third, if $0 < \beta_3$ then $\hat{p}^* < 0$ and therefore $f'(0) > 0$ and $f'(1) < 0$; that is, fixation of the cooperator phenotype A is the only locally stable legitimate equilibrium.

Similarly, if $T_B > T_A$, then

$$282 \quad \beta_1 > [c(1 - \alpha\nu) - b(1 - \alpha\nu)](T_A - T_B) = (1 - \alpha\nu)(c - b)(T_A - T_B) > 0, \quad (39)$$

since $c < b$ and $1 > \alpha v$, and the signs of the cubic at positive and negative infinity are positive and negative, respectively. First, if $\beta_3 < 0$ then $\hat{p}^* < 0$ and therefore $f'(0) < 0$ and $f'(1) > 0$; that is, fixation of the defector phenotype $A = B$ is the only locally stable legitimate equilibrium. Second, if $0 < \beta_3 < \beta_1$ then $0 < \hat{p}^* < 1$ and therefore $f'(0) > 0$ and $f'(1) > 0$; that is, both fixations are locally unstable and \hat{p}^* is a stable polymorphic equilibrium. Third, if $\beta_1 < \beta_3$ then $\hat{p}^* > 1$ and therefore $f'(0) > 0$ and $f'(1) < 0$, and fixation of the cooperator phenotype A is the only locally stable legitimate equilibrium.

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

$$\hat{\gamma}_1 = \frac{bv\alpha T_A + (T_A - T_B)}{v(1 - T_B)}, \quad \hat{\gamma}_2 = \frac{bv\alpha T_B + (1 + b)(T_A - T_B)}{v(1 - T_B) + (1 - v)(T_A - T_B)}, \quad (40)$$

and define a vertical transmission threshold,

$$\hat{v} = \frac{T_B - T_A}{1 - T_A}. \quad (41)$$

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. 40) and the vertical threshold \hat{v} (Eq. 41) :*

1. Fixation of cooperation: if (i) $T = T_A = T_B$ and $c < b \cdot \alpha \frac{T}{1-T}$; or if (ii) $T_A > T_B$ and $c < \hat{\gamma}_1$; or if (iii.a) $T_A < T_B$ and $v > \hat{v}$ and $c < \hat{\gamma}_2$; or if (iii.b) $T_A < T_B$ and $v < \hat{v}$ and $\hat{\gamma}_2 < c$.
2. Fixation of defection: if (iv) $T = T_A = T_B$ and $c > b \cdot \alpha \frac{T}{1-T}$; or if (v) $T_A > T_B$ and $\hat{\gamma}_2 < c$; or if (vi) $T_A < T_B$ and $\hat{\gamma}_1 < c$.
3. Stable Coexistence of both phenotypes at \hat{p}^* : if (vii.a) $T_A < T_B$ and $v < \hat{v}$ and $c < \hat{\gamma}_2$ and $c < \hat{\gamma}_1$; or if (vii.b) $T_A < T_B$ and $v > \hat{v}$ and $\hat{\gamma}_2 < c < \hat{\gamma}_1$.
4. Unstable coexistence and fixation of either phenotype depending on initial frequency: if (viii) $T_A > T_B$ and $\hat{\gamma}_1 < c < \hat{\gamma}_2$.

With population structure

We constructed an additional model in which partner association emerges from the population structure. We model a non-overlapping 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 which is either a cooperator, A , or a defector B . In each generation individuals interact with their neighbors, i.e. individuals that inhabit adjacent sites, in a prisoner's dilemma game (Table 1) and in horizontal cultural transmission. As before, T_A and T_B are the probabilities to transmit the phenotypes A and B during horizontal transmission. At each generation, each individual is chosen to "initiate" interactions with probability 1/2. Initiators then interact with a random neighbor for 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 partner 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 on each generation is random. After all interactions take place, 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 of that individual ($n_b \leq n_c$). Then a new generation is generated. Each site is colonized by an offspring of one of the individuals that inhabit either this site or one of the neighboring sites. The parent is randomly drawn with probability proportional to its fitness, divided by the average fitness in his neighborhood. Offspring then have the same phenotype as their parents.

Figure 6 shows that the highest cooperation cost to benefit ratio (c/b) that permits the evolution of cooperation in simulations of the spatial model is roughly $\alpha \cdot T/(1 - T)$, where $T = T_A = T_B$ is the horizontal transmission rate. This agrees with the condition we derived in Corollary 2 for a population without population structure. This demonstrates that the partner association parameter 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, a horizontal transmission bias for the cooperative phenotype was found to be sufficient and necessary 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). Remarkably, stable coexistence between cooperation and defection can be maintained if horizontal transmission is biased for defection ($T_B > T_A$) and both the cost of cooperation and social association are intermediate (yellow areas in Figure 3).

We tested the applicability of our analytic results to a complex spatial stochastic model (Figure 6). Indeed, our derived condition provide a good approximation to simulation results, demonstrating that association between cooperation and transmission can arise in a structured population simply because the choice of individuals for social interactions is small.

Feldman et al. (1985) studied the dynamics of an altruistic phenotype with vertical cultural transmission and a gene that modifies the transmission of the phenotype. Their results are very sensitive to this genetic modification: without it, the conditions for invasion of the altruistic phenotype reduce to Hamilton's rule. Further work is needed to include such genetic modification of cultural transmission to our model.

Woodcock (2006) has previously argued 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 significant duration of time. Our results provide strong evidence for his hypothesis that horizontal transmission could 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) have 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. They therefore suggested that to explain the evolution of altruism, we should seek mechanisms that generate such assortment, like 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 ($\alpha > (c(1 - T_B) + (T_B - T_A))/bT_A$), cooperation can increase in frequency when initially rare even when there is horizontal transmission bias against it ($T_B > T_A$, see Result 2).

How does non-vertical transmission generate assortment? Lewin-Epstein et al. (2017) and Lewin-Epstein and Hadany (2020), who suggested that microbes that manipulate their hosts to act altruistically can be favored by selection, and may help 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 the microbes of the donor host, even when the two hosts are (genetically) unrelated. However, we are more interested in the assortment point-of-view: infection by behavior-determining microbes during interactions effectively generates assortment because recipient of help may be infected by the behavior-determining microbe and therefore 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 for explaining complex evolutionary phenomena, and furthers our understating of the cultural evolution of cooperation.

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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,

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

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

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

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

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

404 Using *SymPy* (Meurer et al., 2017), a Python library for symbolic mathematics, we simplify Eq. A3 to eqs. 32-33.

406 Appendix B

Denote $f(p) = \lambda(p' - p)$, where $\lambda > 0$, and assume $f(p^*) = 0$; i.e., p^* is an equilibrium. We want a
408 condition for $|p' - p^*| < |p - p^*|$.

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

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

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

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

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

Therefore, if $f'(1) < 0$ then there exists $\epsilon > 0$ such that for any $1 - \epsilon < 1 - p < 1$ it is guaranteed that
418 $1 - p' < 1 - p$, that is, p' is closer than p to one.

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Figures

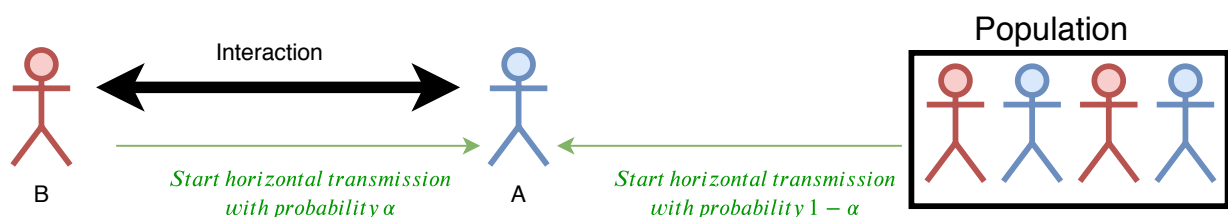


Figure 1: Cultural horizontal transmission with assortment. Transmission occurs between interacting partners with probability α (left) or between two random peers with probability $1 - \alpha$.

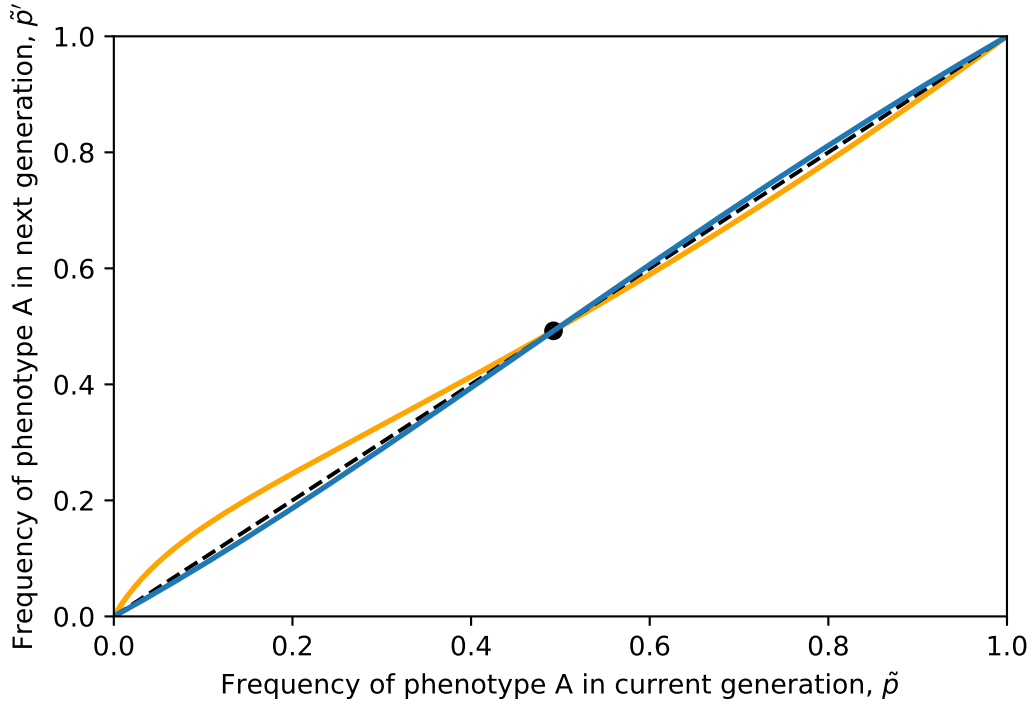


Figure 2: Stable and unstable coexistence between cooperation and defection without oblique transmission. The curves show the frequency of the cooperative phenotype A among parents in the next generation \tilde{p}' vs. the current generation \tilde{p} (Eq. 14). The dashed black line is $\tilde{p}' = \tilde{p}$. The curves and the dashed line intersect at the polymorphic equilibrium \tilde{p}^* (black circle). When the curves are above the dashed line, $\tilde{p}' > \tilde{p}$, then \tilde{p} increase. When the curves are below the dashed line, $\tilde{p}' < \tilde{p}$, then \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 $\gamma_2 < c < \gamma_1$ (Eq. 23). The blue curve, for which the equilibrium is unstable, is given by $T_A = 0.5$, $T_B = 0.1$, $b = 1.3$, $c = 0.904$, and $\alpha = 0.4$, which give $\gamma_1 < c < \gamma_2$. In both cases there is no oblique transmission, $\nu = 1$; see Figure 4 for $\nu < 1$.

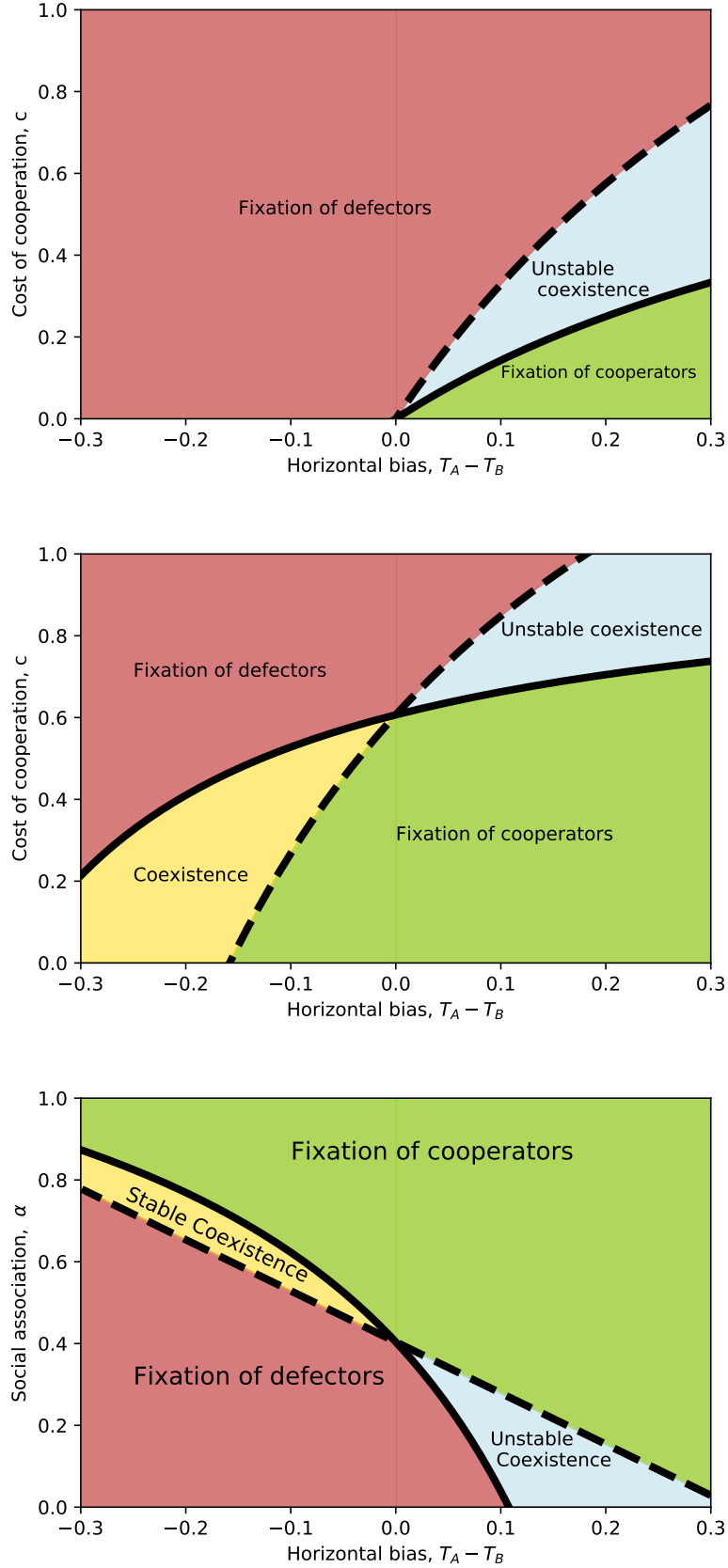


Figure 3: Evolution of cooperation under vertical and horizontal cultural transmission. The figure shows the global fixation of cooperation (green), global fixation of defection (red), fixation of either cooperation or defection depending on the initial conditions, i.e. unstable coexistence (blue), and 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 (Eq. 23) are the solid and dashed lines. **(c)** the social association α is on the y-axis; the social association boundaries a_1 and a_2 (Eq. 30) are the solid and dashed lines. Here, $b = 1.3$, $T_A = 0.4$. **(a)** $\alpha = 0$. **(b)** $\alpha = 0.7$. **(c)** $c = 0.35$.

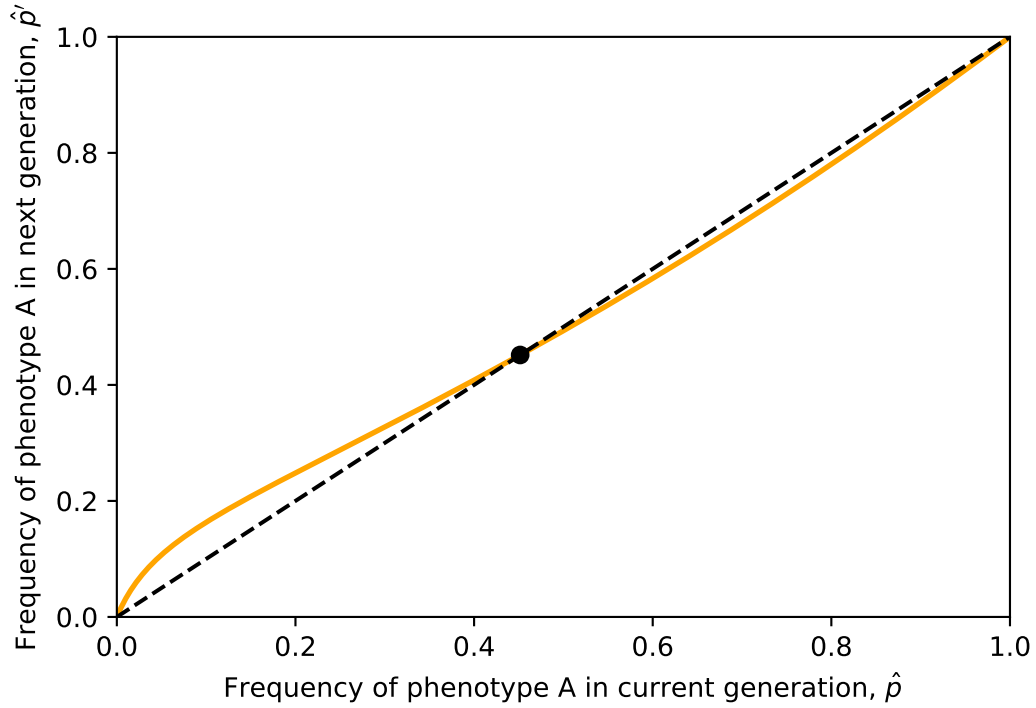


Figure 4: Stable coexistence between cooperation and defection with oblique transmission. The curve shows the frequency of the cooperative phenotype A among juveniles in the next generation \hat{p}' vs. the current generation \hat{p} (Eq. 6). The dashed black line is $\hat{p}' = \hat{p}$. The curve and the dashed line intersect at the stable equilibrium \hat{p}^* (black circle). When $\hat{p} < \hat{p}^*$ then the curve is above the dashed line, $\hat{p}' > \hat{p}$, and \hat{p} increases towards \hat{p}^* . When $\hat{p} > \hat{p}^*$ then the curve is below the dashed line, $\hat{p}' < \hat{p}$, and \hat{p} decreases towards \hat{p}^* . Here, $T_A = 0.4$, $T_B = 0.9$, $b = 20$, $c = 0.1$, $\alpha = 1$, and $\nu = 0.4$, which give $0 < \beta_3 < \beta_1$ (Eq. 33).

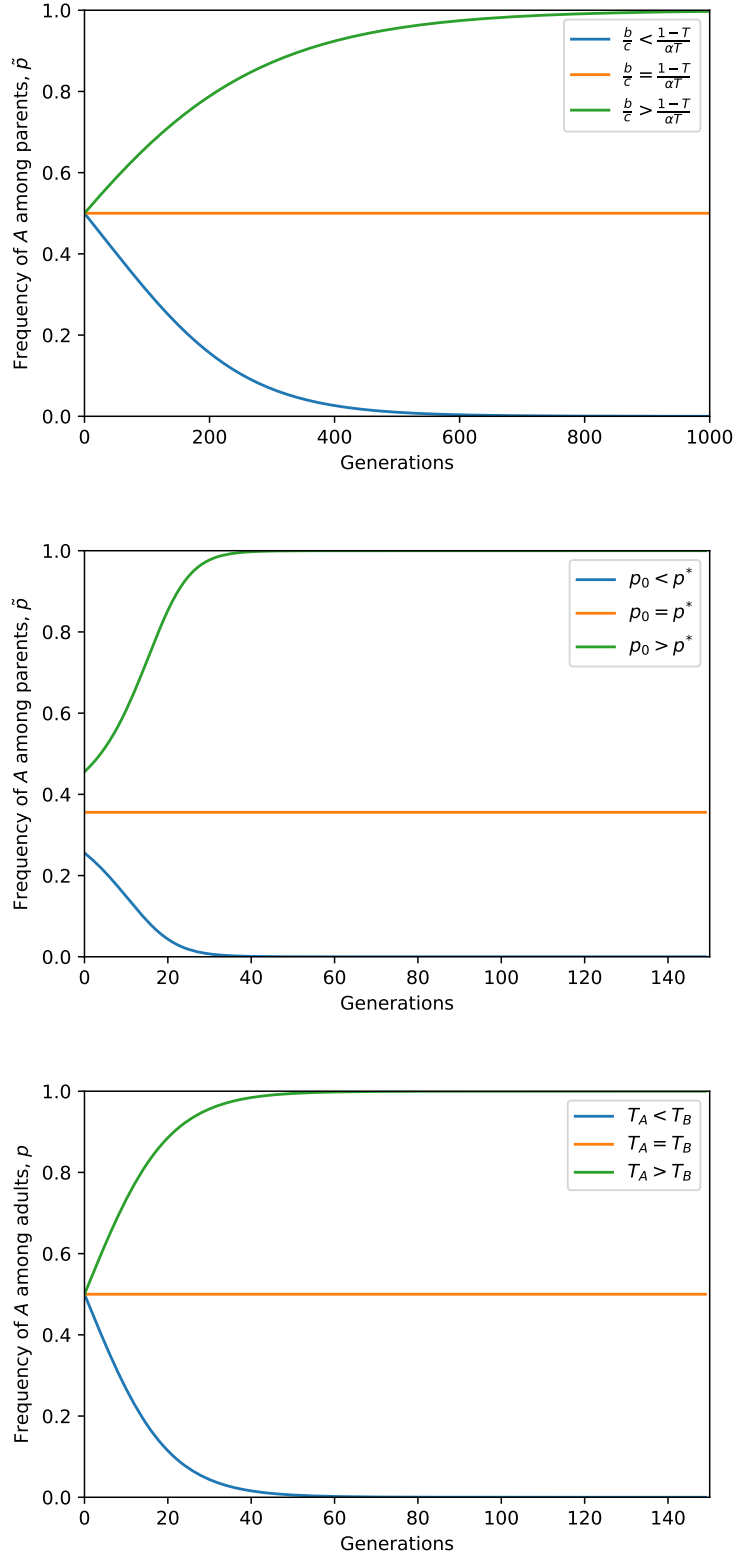


Figure 5: Dynamics of the frequency of cooperation. The frequency \tilde{p} of parents with cooperative phenotype A in (a-b) and the frequency p of adults with cooperative phenotype A in (c). The different lines correspond to parameter values that lead to fixation of cooperation (green), extinction of cooperation (red), or stable coexistence of cooperators and defectors (yellow). (a) $v = 1$, $T_A = T_B = T = 0.2$, $\alpha = 0.5 \neq 0$, $\tilde{p}_0 = 0.5$ and $c = 0.1$; (b) $v = 1$, $\alpha = 0$, $\tilde{p}^* \approx 0.35$, $T_A = 0.65$, $T_B = 0.1$, $b = 1.3$ and $c = 0.65$; (c) $v = 0$, $\alpha = 0.5$, $p_0 = 0.5$, $T_A = 0.5$, $b = 1.3$ and $c = 0.5$.

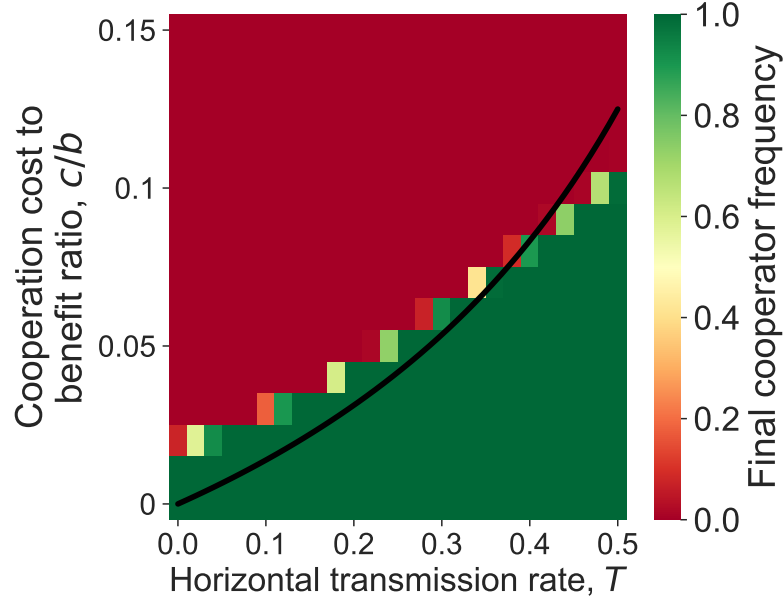


Figure 6: Evolution of cooperation in a spatial model. The expected frequency of cooperators in a structured population after 10,000 generations is shown (red for 0%, green for 100%) as function of both the ratio between the cost and benefit of cooperation (c/b) on the y-axis, and the horizontal transmission rate (without transmission bias, $T = T_A = T_B$) on the x-axis. The population evolves on a 100-by-100 grid. Selection, cooperation, and horizontal cultural transmission are all local between adjacent sites. The black curve represents the condition for the evolution of cooperation in a well-mixed population with partner association, $c/b < \alpha T / (1 - T)$, where $\alpha = 1/8$; see Eq. 25. Note that in the structured population, selection is local, whereas in the unstructured population, selection is global. This can explain the small difference in the results. Here, population size is 10,000 (100-by-100 grid); cost of cooperation, $c = 0.05$. 50 simulations were executed per parameter set. Simulations were stopped at generation 10,000 or if one of the phenotypes fixed.