

Conditions for Cooperation to be More Abundant than Defection in a Hierarchically Structured Population

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Abstract We study conditions for weak selection to favor tit-for-tat (TFT) over AllD in a repeated Prisoner's Dilemma game played in a finite population subdivided into three subpopulations under the assumption of cyclic dominance in asymmetric interactions. Assuming parent-independent mutation and uniform migration, we show that TFT is more abundant than AllD in the stationary state if the defection cost incurred by individuals in interaction with dominant defecting individuals exceeds some threshold value. This threshold value decreases as the number of repetitions of the game, the population size, or the mutation rate increases, but increases as the migration rate increases. The same conclusions hold in the case of linear dominance.

Keywords Evolution of cooperation · Cyclic dominance · Linear dominance · Prisoner's Dilemma · Abundance in frequency

1 Introduction

Classical game theory is used to understand economic equilibrium states resulting from strategic decisions of rational agents, individuals or firms, to optimize some expected payoffs (see, e.g., Von Neumann and Morgenstern [51]; Fudenberg and Tirole [9]; Osborne and Rubinstein [39]). The most important concept in game theory is that of a Nash equilibrium in which no player has anything to gain by changing only its own strategy (Nash [28]). In evolutionary game theory, this has been extended to a stronger concept known as an evolutionarily stable strategy, which is such that once fixed in the population, no mutant strategy can initially invade the population under the influence of natural selection (Maynard Smith and Price [27]; Maynard Smith [26]; see, e.g., Hofbauer and Sigmund [14, 15] for a

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review). A related concept is that of a convergence stable strategy (CSS), which is such that a close-by resident strategy is invaded by a mutant strategy if and only if the mutant strategy is closer to the CSS (Eshel [6]). Conditions for initial increase in the frequency of a mutant strategy is then of prime interest. An underlying assumption is that strategies replicate at rates according to expected payoffs. This leads to models of frequency-dependent dynamics that make room for a trial-and-error learning process when mutant strategies are introduced into a population one at a time.

The main theoretical framework in evolutionary game theory is the replicator equation (Taylor and Jonker [50]; Hofbauer et al. [16]; Zeeman [52]). It is a differential equation that describes the deterministic dynamics of strategy frequencies in a well-mixed, infinitely large population. Suppose an infinite population in which each individual adopts one strategy chosen in a finite set of strategies. The expected payoff to each strategy is given by a function of the relative frequencies of all strategies in use in the population. This expected payoff is interpreted as a rate of reproduction. Under the assumption of random pairwise interactions among individuals, this expected payoff is a linear function with respect to the strategy frequencies whose coefficients are the entries of some payoff matrix.

More precisely, consider a game with n possible strategies in an infinite population. Let $A = [a_{i,j}]$ be the $n \times n$ payoff matrix. The entry $a_{i,j}$ represents the payoff received by an individual that adopts strategy i when it interacts with an individual that uses strategy j , for $i, j = 1, \dots, n$. Let x_i be the frequency of strategy i in the whole population, for $i = 1, \dots, n$. Under the assumption of random pairwise interactions, the expected payoff to strategy i is

$$w_i(\mathbf{x}) = \sum_{j=1}^N a_{i,j} x_j,$$

for $i = 1, \dots, n$, where $\mathbf{x} = (x_1, \dots, x_n)$. The replicator equation is then given by

$$\frac{dx_i}{dt} = x_i (w_i(\mathbf{x}) - \bar{w}(\mathbf{x})),$$

for $i = 1, \dots, n$, where $\bar{w}(\mathbf{x}) = \sum_{i=1}^N x_i w_i(\mathbf{x})$ is the average payoff in the population. A discrete-time version is described by the difference equation:

$$\Delta x_i = \frac{\delta x_i (w_i(\mathbf{x}) - \bar{w}(\mathbf{x}))}{1 + \delta \bar{w}(\mathbf{x})},$$

for $i = 1, \dots, n$ and some scaling factor $\delta > 0$ small enough. This equation is obtained by taking the quantity $1 + \delta w_i(\mathbf{x})$ whose mean is $1 + \delta \bar{w}(\mathbf{x})$ as the reproductive success, or fitness, of an individual using strategy i from one time step to the next, for $i = 1, \dots, n$.

Recent advances in evolutionary game theory take into account the fact that real populations are limited in size. In a finite population, whatever be the updating rule for the state of the population from one time step to the next, the dynamics is described by a stochastic process which is often a Markov chain. In the absence of mutation, a strategy is said to be favored by selection if its fixation probability is higher than what it would be in the absence of selection (Rousset and Billiard [42], Nowak et al. [32]). In the presence of symmetric mutation, a strategy is favored by selection if its abundance in the stationary state is higher than what it would be in the absence of selection (Antal et al. [1]). There is a connection between this definition in the limit of a small mutation rate and fixation probabilities of single strategies in the absence of mutation (Rousset and Billiard [42], Rousset [40], Fudenberg and Imhof [7]).

Two strategies in well-mixed and finite populations are considered in Nowak et al. [32], Taylor et al. [48], and Antal et al. [1] under the assumption that one individual is replaced

at a time as in a Moran model or a pairwise comparison process; in Lessard [20] and Imhof [17] in the case where all individuals are replaced independently at a time as in a Wright-Fisher model; and in Lessard and Ladret [24] and Lessard [21, 23] in the case of individuals replaced at a time according to a general exchangeable scheme extending the Cannings model. Multiple strategies in the same context are studied in Antal et al. [2], Lessard and Lahaie [25], and Tarnita et al. [44, 47]. A connection between a game in groups of finite size chosen at random in an infinite population and a game in a finite population is made in Hilbe [13].

Further advances in evolutionary game theory include extensions to populations that are structured by geography or some other factors to take into account that real populations are subdivided into groups, small or large, overlapping or not. For a population subdivided into two subpopulations and any migration rates: see, e.g., Ladret and Lessard [19], and for a large number of subpopulations with uniform or proportional dispersal of migrants known as the island model, e.g., Rousset and Billiard [42], Ladret and Lessard [18], and Lessard [22, 23]. The case of isolation by distance with demes on a lattice and migration to neighboring demes is considered in Rousset and Billiard [42] and Rousset [41]. Demes may not always correspond to geographic locations. Often, individuals exhibit other phenotypic traits, for instance, in addition to their behavioral strategies like size, height, or other aspects of physical appearance. A particular setting is studied in Antal et al. [3]: every individual from a finite population has a phenotype represented by an integer and can interact with every individual that has the same phenotype. A different setting is considered in Tarnita et al. [45]: a population of N individuals is distributed over M sets, each individual belonging to exactly K sets, and pairwise interactions occur within each set. There is also the case of single individuals arranged on a regular lattice and interacting with nearest neighbours (Nowak and May [31], Hauert and Doebeli [12]), and more generally single individuals occupying the vertices of a graph and interacting with the individuals to which they are connected by edges (Ohtsuki and Nowak [35, 36], Ohtsuki et al. [37, 38], Taylor et al. [49]). See, e.g., Nowak et al. [34], for a review of evolutionary dynamics in structured populations.

An important question in evolutionary biology is the emergence of cooperative behaviors by natural selection. To understand this biological phenomenon, a theoretical framework widely used is the Prisoner’s Dilemma (Axelrod and Hamilton [5]): cooperation and defection denoted by C and D , respectively, are considered as strategies, and the payoff matrix is given by

$$\begin{matrix} & C & D \\ C & (R & S) \\ D & (T & P) \end{matrix}$$

where $T > R > P > S$. This is the case, for instance, when the payoff matrix is in the form:

$$\begin{matrix} & C & D \\ C & (b - c & -c) \\ D & (b & 0) \end{matrix}$$

where $b > c > 0$. The interpretation is that a donor pays a cost c for a recipient to get a benefit b in a pairwise interaction. In this situation, it is always advantageous for a player to defect since the payoff to a defector is larger than the payoff to a cooperator whatever be the strategy of the opponent.

It has been proposed to extend the Prisoner’s Dilemma by allowing repetitions of the game, which is known as the iterated Prisoner’s Dilemma. Simulations in this setting have shown that a very successful strategy is tit-for-tat (TFT) (see Axelrod and Hamilton [5]),

in which the player cooperates in the first round and then does whatever the opponent did in the previous round. If the alternative strategy is always defect (AllD) and the number of repetitions of the game between two individuals is fixed to m , then the payoff matrix becomes

$$\begin{matrix} & \text{TFT} & \text{AllD} \\ \text{TFT} & (m(b-c), b) & (-c, 0) \\ \text{AllD} & (m(b-c), b) & (-c, 0) \end{matrix}$$

If m is large enough, then the payoff to TFT against TFT becomes larger than the payoff to AllD against TFT. Therefore, if the frequency of TFT exceeds some threshold value and pairwise interactions occur at random, then the expected payoff to TFT becomes larger than the expected payoff to AllD. In a large population, however, TFT cannot evolve from any initial frequency below that threshold value. This is not the case in a finite population because of stochastic effects. In a population of fixed size N —under an updating Moran process, for instance—weak selection favors a single TFT replacing AllD if (Nowak et al. [32])

$$m(b-c)(N-2) - c(2N-1) - b(N+1) > 0.$$

In the presence of symmetric mutation, TFT is more abundant than AllD in the mutation–selection balance if (Antal et al. [1])

$$m(b-c)(N-2) - cN - bN > 0.$$

Both conditions are satisfied if m is large enough.

Many studies to understand the evolution of cooperation based on the Prisoner’s Dilemma or its iterated form can be found in the literature (Axelrod [4]; Hamilton [10]; Nowak and Sigmund [33]; Nowak [29]; Nowak [30]). In most studies, however, symmetric interactions between individuals are assumed, which means that the payoffs depend only on the strategies used by the individuals, which are undistinguishable otherwise.

Differences in strength or fighting ability, gender, age, size, etc. make asymmetric interactions common in nature (see, e.g., Hammerstein [11]). Tao et al. [43] consider a case of dominance hierarchy induced by differences in resource holding power. They study the evolution of cooperation in the case of two infinite, isolated subpopulations with the assumption that the individuals in one subpopulation dominate the individuals of the other in random pairwise interactions. Moreover, they introduce the concept of a defection cost of inferior individuals. If, for instance, the two subpopulations are represented by S_1 and S_2 with individuals in S_1 dominating the individuals in S_2 , then a defector in S_2 is assumed to incur a cost, $\beta > 0$, when it interacts with a defector in S_1 . In the case of an iterated game, the defection cost is added as many times as both individuals defect. It is shown that subdued cooperation of individuals in S_2 may induce a globally stable equilibrium exhibiting full cooperation in both subpopulations when the defection cost $\beta > 0$ is large enough compared to the cooperation cost c , and the number of repetitions of the game m exceeds some threshold value. Similar results are obtained in the case of three infinite subpopulations under the assumption of linear dominance with S_i -individuals dominating S_j -individuals whenever $j > i$ and the assumption of cyclic dominance as described below. In this case, however, there is no condition on the number of repetitions of the game.

In this paper, a model of cyclic dominance for three finite subpopulations reproducing according to a Moran process and allowing for migration is considered. A mutation–selection equilibrium in the case of weak selection is studied using a perturbation method as in Antal et al. [3]. The population is subdivided into three subpopulations, represented by S_1 , S_2 , and

S_3 . Each subpopulation is made of a finite number N of individuals. Each individual adopts one of two strategies: TFT or always defect (AllD). Pairwise interactions between individuals within as well as between subpopulations occur at random. A triangular dominance hierarchy relationship is assumed: the individuals in S_1 dominate the individuals in S_2 which dominate the individuals in S_3 which in turn dominate the individuals in S_1 . The random pairwise interactions determine the fitness of each individual given in the form $f = 1 + \delta w$, where w is the expected payoff associated to the strategy used by the individual, and $\delta > 0$ is an intensity of selection. Time is discrete and at every time step, one offspring is produced by an individual chosen with probability proportional to fitness. Selection is weak if the intensity of selection is small enough, actually $\delta \ll \frac{1}{N}$, while neutrality corresponds to the case $\delta = 0$. The offspring produced inherits the strategy used by its parent unless there is mutation, which occurs with probability $u > 0$. In this case, the offspring adopts one strategy chosen at random among TFT and AllD. Therefore, mutation is parent independent. Finally, the offspring replaces an individual chosen at random in the same subpopulation unless there is migration, which occurs with probability $v > 0$. In this case, the individual replaced is chosen at random in one of the two other subpopulations chosen at random. Therefore, migration is uniform.

In the neutral case, the expected frequency of TFT at equilibrium is equal to $1/2$. In this paper, we are interested in the effect of weak selection on this equilibrium frequency. We recall that weak selection will favor TFT if its abundance (expected frequency at equilibrium) exceeds $1/2$ (Antal et al. [2,3]). In Sect. 2, the details of the model are presented. In Sect. 3, the transition probabilities from one population state to the next are given. In Sect. 4, a condition for weak selection to favor TFT is deduced by using a perturbation method as in Antal et al. [3]. Calculations in terms of probabilities of identity by strategy in the stationary state are done in Sect. 5. The results are discussed in Sect. 6. Finally, the same results under the assumption of linear dominance are given in an appendix (Sect. 7).

2 Model of Cyclic Dominance for the Iterated Prisoner’s Dilemma in Three Finite Subpopulations

Consider a population consisting of three subpopulations represented by S_1 , S_2 , and S_3 . Every subpopulation is of the same finite size N . In pairwise interactions, in the context of an iterated Prisoner’s Dilemma, each individual in the population adopts one of two strategies, namely TFT (labeled 1) or AllD (labeled 2). Pairwise interactions are symmetric between individuals in the same subpopulation but asymmetric between individuals in different subpopulations. Cyclic dominance is assumed so that an individual in S_1 dominates an individual in S_2 which dominates an individual in S_3 which in turn dominates an individual in S_1 .

Assuming m rounds of the Prisoner’s Dilemma with a cost $c > 0$ incurred by a player for cooperation but a benefit $b > c$ provided to its opponent in each round of the game, the payoff matrix for symmetric interactions in subpopulation S_1 , S_2 , or S_3 with TFT and AllD in this order as strategies is given by

$$A_{1,1} = A_{2,2} = A_{3,3} = \begin{pmatrix} m(b-c) & -c \\ b & 0 \end{pmatrix}.$$

In asymmetric interactions, there is also a cost $\beta > 0$ incurred by a player for defection when the opponent is dominant and defects in the same round. The parameter β is called a defection cost. Note that there is no defection cost when the opponent cooperates. Thus, the

payoff matrix for individuals in S_1 , S_2 , or S_3 in interaction with dominant individuals in S_3 , S_1 , or S_2 , respectively, is

$$A_{1,3} = A_{2,1} = A_{3,2} = \begin{pmatrix} m(b - c) & -c - (m - 1)\beta \\ b - (m - 1)\beta & -m\beta \end{pmatrix}.$$

Note that the corresponding payoff matrix for the dominant individuals in S_3 , S_1 , or S_2 in interaction with individuals in S_1 , S_2 , or S_3 , respectively, is the same as the payoff matrix for symmetric interactions:

$$A_{3,1} = A_{1,2} = A_{2,3} = \begin{pmatrix} m(b - c) & -c \\ b & 0 \end{pmatrix}.$$

Pairwise interactions are assumed to occur at random in the whole population. Note that an individual cannot interact with itself. The expected payoff to an individual according to its strategy and the frequencies of the two strategies in the three subpopulations will affect its fitness for reproduction by a small additive amount.

Let n_i denote the number of individuals using TFT in subpopulation S_i , for $i = 1, 2, 3$. Then the state of the whole population is given by the vector $\mathbf{n} = (n_1, n_2, n_3)$. The state of the whole population can alternatively be described by the vector $\mathbf{x} = (x_1, x_2, x_3)$, where

$$x_i = \frac{n_i}{N}$$

represents the frequency of TFT in subpopulation S_i , for $i = 1, 2, 3$. Note that

$$x = \frac{1}{3}(x_1 + x_2 + x_3)$$

is the frequency of TFT in the whole population.

Let $w_1^{(i)}$ and $w_2^{(i)}$ be the expected payoffs to TFT (strategy 1) and AllD (strategy 2), respectively, in subpopulation S_i , for $i = 1, 2, 3$. Assuming random pairwise interactions in the whole population and recalling that an individual cannot interact with itself, an individual in S_i that plays TFT interacts with an individual in S_i that plays TFT with probability $\frac{n_i-1}{3N-1}$ and AllD with probability $\frac{N-n_i}{3N-1}$, for $i = 1, 2, 3$. On the other hand, the individual interacts with an individual in S_j that plays TFT with probability $\frac{n_j}{3N-1}$ and AllD with probability $\frac{N-n_j}{3N-1}$, for $j \neq i$. Using the payoff matrices for symmetric and asymmetric interactions, the expected payoffs to TFT in the three subpopulations are found to be as follows:

$$\begin{aligned} w_1^{(1)} &= \frac{3N}{3N-1} \left[mx(b-c) - \frac{m(b-c)}{3N} - (1-x)c - \frac{1}{3}(1-x_3)(m-1)\beta \right], \\ w_1^{(2)} &= \frac{3N}{3N-1} \left[mx(b-c) - \frac{m(b-c)}{3N} - (1-x)c - \frac{1}{3}(1-x_1)(m-1)\beta \right], \\ w_1^{(3)} &= \frac{3N}{3N-1} \left[mx(b-c) - \frac{m(b-c)}{3N} - (1-x)c - \frac{1}{3}(1-x_2)(m-1)\beta \right]. \end{aligned}$$

For ALLD, the corresponding expressions are given by

$$\begin{aligned}
 w_2^{(1)} &= \frac{3N}{3N-1} \left[xb - \frac{1}{3}(m-x_3)\beta \right], \\
 w_2^{(2)} &= \frac{3N}{3N-1} \left[xb - \frac{1}{3}(m-x_1)\beta \right], \\
 w_2^{(3)} &= \frac{3N}{3N-1} \left[xb - \frac{1}{3}(m-x_2)\beta \right].
 \end{aligned}$$

With the convention that $x_4 = x_1$ and $x_5 = x_2$, the expected payoffs to TFT and ALLD in subpopulation S_i can be expressed as

$$w_1^{(i)} = \frac{3N}{3N-1} \left[mx(b-c) - \frac{m(b-c)}{3N} - (1-x)c - \frac{1}{3}(1-x_{i+2})(m-1)\beta \right] \tag{1}$$

and

$$w_2^{(i)} = \frac{3N}{3N-1} \left[xb - \frac{1}{3}(m-x_{i+2})\beta \right], \tag{2}$$

respectively, for $i = 1, 2, 3$.

Time is discrete, and at each time step, an individual from the whole population is chosen with probability proportional to its fitness to produce an offspring. The fitness of an individual is assumed to be in the form:

$$f = 1 + \delta w,$$

where $\delta > 0$ represents a strength of selection, and w is the expected payoff to the individual. The neutral case discussed in Sect. 5 corresponds to $\delta = 0$. Note that δ is assumed to be sufficiently small so that all fitness values are positive.

The fitnesses of TFT and ALLD in subpopulation S_i are given by

$$f_1^{(i)} = 1 + \delta w_1^{(i)}, \quad f_2^{(i)} = 1 + \delta w_2^{(i)}, \tag{3}$$

respectively, for $i = 1, 2, 3$. The average fitness in the whole population is given by

$$\bar{f} = 1 + \delta \bar{w}, \tag{4}$$

where

$$\bar{w} = \frac{1}{3} \left(\sum_{i=1}^3 x_i w_1^{(i)} + \sum_{i=1}^3 (1-x_i) w_2^{(i)} \right) \tag{5}$$

is the average payoff in the whole population.

The strategy adopted by the offspring produced is subject to mutation: with probability $1-u < 1$ it is necessarily the same as the parental strategy but with the complementary probability $u > 0$ it is a strategy chosen at random among the two available strategies. Finally, the offspring replaces an individual chosen at random either in the same subpopulation with probability $1-v < 1$ or in another subpopulation chosen at random with the complementary probability $v > 0$.

3 Transition Probabilities

In this section, we calculate the probability of transition from one population state to the next. Let $\mathbf{n} = (n_1, n_2, n_3)$ be the current state of the population, and \mathbf{n}' be the population

state after one time step. Given that one individual is replaced at a time in the whole population and that this individual can be in one of the three subpopulations, the probability of transition from \mathbf{n} to \mathbf{n}' , denoted by $p_{\mathbf{n},\mathbf{n}'}$, is positive in seven cases: $\mathbf{n} + \mathbf{e}_1$, $\mathbf{n} + \mathbf{e}_2$, $\mathbf{n} + \mathbf{e}_3$, $\mathbf{n} - \mathbf{e}_1$, $\mathbf{n} - \mathbf{e}_2$, $\mathbf{n} - \mathbf{e}_3$ and \mathbf{n} , where $\mathbf{e}_1 = (1, 0, 0)$, $\mathbf{e}_2 = (0, 1, 0)$, and $\mathbf{e}_3 = (0, 0, 1)$.

The probability of transition from \mathbf{n} to $\mathbf{n} \pm \mathbf{e}_i$ can be expressed as a sum of two terms: the first corresponds to a transition in the case of mutation, which occurs with probability u ; and the second describes a transition under the effect of selection in the absence of mutation, which occurs with probability $1 - u$. More precisely, we have

$$p_{\mathbf{n},\mathbf{n}\pm\mathbf{e}_i} = up_{\mathbf{n},\mathbf{n}\pm\mathbf{e}_i}^{\text{mut}} + (1 - u)p_{\mathbf{n},\mathbf{n}\pm\mathbf{e}_i}^{\text{sel}},$$

for $i = 1, 2, 3$, where $p_{\mathbf{n},\mathbf{n}\pm\mathbf{e}_i}^{\text{mut}}$ and $p_{\mathbf{n},\mathbf{n}\pm\mathbf{e}_i}^{\text{sel}}$ designate conditional transition probabilities, given mutation and given no mutation, respectively. Given mutation, a transition from \mathbf{n} to $\mathbf{n} + \mathbf{e}_i$ takes place if the offspring produced chooses strategy TFT, which occurs with probability $1/2$, and replaces an individual that plays strategy AIID in subpopulation S_i , which occurs with probability $(1 - x_i)/3$, for $i = 1, 2, 3$. Then we have

$$p_{\mathbf{n},\mathbf{n}+\mathbf{e}_i}^{\text{mut}} = \frac{1 - x_i}{6},$$

for $i = 1, 2, 3$. Similarly, the individual replaced is in subpopulation S_i and plays strategy TFT with probability $x_i/3$, and therefore

$$p_{\mathbf{n},\mathbf{n}-\mathbf{e}_i}^{\text{mut}} = \frac{x_i}{6},$$

for $i = 1, 2, 3$. Note that the probability to stay in the same population state ($\mathbf{n}' = \mathbf{n}$) is given by

$$p_{\mathbf{n},\mathbf{n}} = 1 - \sum_{i=1}^3 (p_{\mathbf{n},\mathbf{n}+\mathbf{e}_i} + p_{\mathbf{n},\mathbf{n}-\mathbf{e}_i}).$$

In the remainder of this section, we calculate the conditional transition probabilities given no mutation. Under this condition, the transition from \mathbf{n} to $\mathbf{n} + \mathbf{e}_1$ takes place when a TFT strategist from the whole population is selected to produce an offspring, and that this offspring replaces an AIID strategist from subpopulation S_1 . A reproducing TFT strategist is selected from subpopulation S_1 with probability proportional to $x_1 f_1^{(1)}$. Its offspring replaces an individual in S_1 with probability $1 - v$, and this individual is an AIID strategist with probability $1 - x_1$. On the other hand, with probability proportional to $x_i f_1^{(i)}$, the offspring is produced by a TFT strategist selected from subpopulation S_i , for $i = 2, 3$. With probability $v/2$, this offspring replaces an individual in S_1 , which is an AIID strategist with probability $1 - x_1$. Then the conditional probability of this transition can be expressed as

$$p_{\mathbf{n},\mathbf{n}+\mathbf{e}_1}^{\text{sel}} = (1 - v) \frac{x_1 f_1^{(1)}}{3f} (1 - x_1) + \frac{v}{2} \left\{ \frac{x_2 f_1^{(2)}}{3f} (1 - x_1) + \frac{x_3 f_1^{(3)}}{3f} (1 - x_1) \right\}.$$

Analogously we have

$$p_{\mathbf{n},\mathbf{n}+\mathbf{e}_2}^{\text{sel}} = (1 - v) \frac{x_2 f_1^{(2)}}{3f} (1 - x_2) + \frac{v}{2} \left\{ \frac{x_1 f_1^{(1)}}{3f} (1 - x_2) + \frac{x_3 f_1^{(3)}}{3f} (1 - x_2) \right\},$$

$$p_{\mathbf{n}, \mathbf{n} + \mathbf{e}_3}^{\text{sel}} = (1 - v) \frac{x_3 f_1^{(3)}}{3\bar{f}} (1 - x_3) + \frac{v}{2} \left\{ \frac{x_1 f_1^{(1)}}{3\bar{f}} (1 - x_3) + \frac{x_2 f_1^{(2)}}{3\bar{f}} (1 - x_3) \right\}.$$

Still given no mutation, the transition from \mathbf{n} to $\mathbf{n} - \mathbf{e}_i$ occurs if an AIID strategist from the whole population is selected to produce an offspring, and that this offspring replaces a TFT strategist from subpopulation S_i , for $i = 1, 2, 3$. Proceeding as previously, the transition probabilities are found to be

$$p_{\mathbf{n}, \mathbf{n} - \mathbf{e}_1}^{\text{sel}} = (1 - v) \frac{(1 - x_1) f_2^{(1)}}{3\bar{f}} x_1 + \frac{v}{2} \left\{ \frac{(1 - x_2) f_2^{(2)}}{3\bar{f}} x_1 + \frac{(1 - x_3) f_2^{(3)}}{3\bar{f}} x_1 \right\},$$

$$p_{\mathbf{n}, \mathbf{n} - \mathbf{e}_2}^{\text{sel}} = (1 - v) \frac{(1 - x_2) f_2^{(2)}}{3\bar{f}} x_2 + \frac{v}{2} \left\{ \frac{(1 - x_1) f_2^{(1)}}{3\bar{f}} x_2 + \frac{(1 - x_3) f_2^{(3)}}{3\bar{f}} x_2 \right\},$$

$$p_{\mathbf{n}, \mathbf{n} - \mathbf{e}_3}^{\text{sel}} = (1 - v) \frac{(1 - x_3) f_2^{(3)}}{3\bar{f}} x_3 + \frac{v}{2} \left\{ \frac{(1 - x_1) f_2^{(1)}}{3\bar{f}} x_3 + \frac{(1 - x_2) f_2^{(2)}}{3\bar{f}} x_3 \right\}.$$

Finally, the conditional probability to stay in the same state ($\mathbf{n}' = \mathbf{n}$) is given by

$$p_{\mathbf{n}, \mathbf{n}}^{\text{sel}} = 1 - \sum_{i=1}^3 (p_{\mathbf{n}, \mathbf{n} + \mathbf{e}_i}^{\text{sel}} + p_{\mathbf{n}, \mathbf{n} - \mathbf{e}_i}^{\text{sel}}).$$

Note that the conditional probability of all transitions with an increase of 1 in the total number of TFT strategists and the conditional probability of all transitions with a decrease of 1 in this number, given no mutation, are given by

$$p_+^{\text{sel}}(\mathbf{n}) = \sum_{i=1}^3 p_{\mathbf{n}, \mathbf{n} + \mathbf{e}_i}^{\text{sel}} = (1 - v) \sum_{i=1}^3 \frac{x_i f_1^{(i)}}{3\bar{f}} (1 - x_i) + \frac{v}{2} \sum_{i \neq j=1}^3 \frac{x_i f_1^{(i)}}{3\bar{f}} (1 - x_j) \quad (6)$$

and

$$p_-^{\text{sel}}(\mathbf{n}) = \sum_{i=1}^3 p_{\mathbf{n}, \mathbf{n} - \mathbf{e}_i}^{\text{sel}} = (1 - v) \sum_{i=1}^3 \frac{(1 - x_i) f_2^{(i)}}{3\bar{f}} x_i + \frac{v}{2} \sum_{i \neq j=1}^3 \frac{(1 - x_i) f_2^{(i)}}{3\bar{f}} x_j, \quad (7)$$

respectively, where $i \neq j$ means two different integers. The second summation in these equations is over $i, j = 1, 2, 3$ such that $i \neq j$.

4 Condition for Weak Selection to Favor Cooperation

Selection is said to favor TFT over AIID if the expected frequency of TFT strictly exceeds 1/2 in the stationary state (Antal et al. [2,3]). The frequency of TFT in the whole population, represented by X , changes over one time step under selection and mutation by a quantity represented by ΔX_{tot} . Like the transition probabilities for the population states, the expected value of this total change can be expressed as a sum of two components. The first component corresponds to the expected change in the case of mutation, which occurs with probability

u and which does not depend on selection. The second component describes the expected change in the case of no mutation, which occurs with probability $1 - u$ and which depends on selection. More precisely, we have

$$\mathbb{E}_\delta [\Delta X_{\text{tot}}|\mathbf{X}] = u\mathbb{E}_\delta [\Delta X_{\text{mut}}|\mathbf{X}] + (1 - u)\mathbb{E}_\delta [\Delta X_{\text{sel}}|\mathbf{X}], \tag{8}$$

where $\mathbf{X} = (X_1, X_2, X_3)$ represents the current population state, and ΔX_{tot} is the total change in the frequency of TFT over one time step, while ΔX_{mut} and ΔX_{sel} denote the conditional changes, given mutation and given no mutation, respectively. In the stationary state, the expected frequency of strategy TFT is constant. Hence, the total expected change vanishes. Conditioning on the current population state, this entails

$$0 = \mathbb{E}_\delta [\Delta X_{\text{tot}}] = \mathbb{E}_\delta \left(\mathbb{E}_\delta [\Delta X_{\text{tot}}|\mathbf{X}] \right) = u\mathbb{E}_\delta [\Delta X_{\text{mut}}] + (1 - u)\mathbb{E}_\delta [\Delta X_{\text{sel}}]. \tag{9}$$

Given a population state $\mathbf{X} = (X_1, X_2, X_3)$ and mutation of the offspring produced, this offspring chooses TFT as strategy with probability $1/2$ whatever be the strategy of its parent. On the other hand, the individual replaced is a TFT strategist with probability

$$X = \frac{X_1 + X_2 + X_3}{3}.$$

Therefore,

$$\mathbb{E}_\delta [\Delta X_{\text{mut}}|\mathbf{X}] = \frac{1}{3N} \left(\frac{1}{2} - X \right),$$

from which

$$\mathbb{E}_\delta [\Delta X_{\text{mut}}] = \frac{1}{3N} \left(\frac{1}{2} - E_\delta(X) \right).$$

Then the expected frequency of TFT at stationarity is given by

$$\mathbb{E}_\delta[X] = \frac{1}{2} - 3N\mathbb{E}_\delta [\Delta X_{\text{mut}}] = \frac{1}{2} + \frac{3N(1 - u)}{u}\mathbb{E}_\delta[\Delta X_{\text{sel}}]. \tag{10}$$

We conclude that TFT is favored by selection if the expected change in the frequency of TFT under selection but without mutation is positive in the stationary state, that is,

$$\mathbb{E}_\delta[\Delta X_{\text{sel}}] > 0. \tag{11}$$

Given a population state $\mathbf{X} = \mathbf{x} = \mathbf{n}/N$ and no mutation, the change in the frequency of TFT is $\frac{1}{3N}$ with probability $\mathbf{p}_+^{\text{sel}}(\mathbf{n})$, $-\frac{1}{3N}$ with probability $\mathbf{p}_-^{\text{sel}}(\mathbf{n})$, and 0 otherwise. Therefore, the conditional expected change is

$$\mathbb{E}_\delta[\Delta X_{\text{sel}}|\mathbf{X} = \mathbf{x}] = \frac{1}{3N} \left(\mathbf{p}_+^{\text{sel}}(\mathbf{n}) - \mathbf{p}_-^{\text{sel}}(\mathbf{n}) \right). \tag{12}$$

Using Eqs. (6) and (7), we find that

$$\begin{aligned} \mathbb{E}_\delta[\Delta X_{\text{sel}}|\mathbf{X} = \mathbf{x}] &= \frac{1 - v}{9N} \sum_{i=1}^3 x_i(1 - x_i) \left(\frac{f_1^{(i)}}{f} - \frac{f_2^{(i)}}{f} \right) \\ &+ \frac{v}{18N} \sum_{i \neq j=1}^3 x_i(1 - x_j) \left(\frac{f_1^{(i)}}{f} - \frac{f_2^{(j)}}{f} \right). \end{aligned}$$

Expressing the fitnesses of the two strategies in the three subpopulations in terms of expected payoffs as in (3) and developing with respect to the intensity of selection δ yield the first-order approximation:

$$\begin{aligned} \mathbb{E}_\delta[\Delta X_{\text{sel}}|\mathbf{X} = \mathbf{x}] &= \frac{(1-v)\delta}{9N} \sum_{i=1}^3 x_i(1-x_i) \left(w_1^{(i)} - w_2^{(i)} \right) \\ &+ \frac{v\delta}{18N} \sum_{i \neq j=1}^3 x_i(1-x_j) \left(w_1^{(i)} - w_2^{(j)} \right) + o(\delta). \end{aligned} \tag{13}$$

Using Eqs. (1) and (2), the difference between the expected payoff to a TFT strategist in subpopulation S_i and the expected payoff to an *AIID* strategist in subpopulation S_j is given by

$$\begin{aligned} w_1^{(i)} - w_2^{(j)} &= \frac{3N}{3N-1} \\ &\times \left\{ (m-1)x(b-c) - \left[\frac{m}{3N}(b-c) + c \right] + \frac{1}{3}(m-x_{j+2})\beta - \frac{1}{3}(m-1)(1-x_{i+2})\beta \right\}, \end{aligned}$$

for $i, j = 1, 2, 3$. Plugging this expression in Eq. (13) leads to

$$\begin{aligned} \mathbb{E}_\delta[\Delta X_{\text{sel}}|\mathbf{X} = \mathbf{x}] &= \frac{\delta(m-1)}{3(3N-1)} \left\{ (1-v) \sum_{i=1}^3 x_i(1-x_i)x + \frac{v}{2} \sum_{i \neq j=1}^3 x_i(1-x_j)x \right\} (b-c) \\ &- \frac{\delta}{3(3N-1)} \left\{ (1-v) \sum_{i=1}^3 x_i(1-x_i) + \frac{v}{2} \sum_{i \neq j=1}^3 x_i(1-x_j) \right\} \left[\frac{m}{3N}(b-c) + c \right] \\ &+ \frac{\delta}{9(3N-1)} \left\{ (1-v) \sum_{i=1}^3 x_i(1-x_i)(m-x_{i+2}) \right. \\ &+ \frac{v}{2} \sum_{i \neq j=1}^3 x_i(1-x_j)(m-x_{j+2}) \\ &- (1-v) \sum_{i=1}^3 x_i(1-x_i)(m-1)(1-x_{i+2}) \\ &\left. - \frac{v}{2} \sum_{i \neq j=1}^3 x_i(1-x_j)(m-1)(1-x_{i+2}) \right\} \beta + o(\delta). \end{aligned}$$

Taking the expected value in the stationary state and developing with respect to the intensity of selection yield,

$$(3N-1)\mathbb{E}_\delta[\Delta X_{\text{sel}}] = \frac{\delta}{3} \left\{ \left(M_1 - \frac{mM_2}{3N} \right) (b-c) - M_2c + M_3\beta \right\} + o(\delta), \tag{14}$$

where

$$M_1 = (m - 1) \left\{ (1 - v) \sum_{i=1}^3 \mathbb{E}_0 [x_i(1 - x_i)x] + \frac{v}{2} \sum_{i \neq j=1}^3 \mathbb{E}_0 [x_i(1 - x_j)x] \right\}, \tag{15}$$

$$M_2 = (1 - v) \sum_{i=1}^3 \mathbb{E}_0 [x_i(1 - x_i)] + \frac{v}{2} \sum_{i \neq j=1}^3 \mathbb{E}_0 [x_i(1 - x_j)], \tag{16}$$

$$\begin{aligned} M_3 &= \frac{(1 - v)}{3} \sum_{i=1}^3 \mathbb{E}_0 [x_i(1 - x_i)(m - x_{i+2})] \\ &\quad + \frac{v}{6} \sum_{i \neq j=1}^3 \mathbb{E}_0 [x_i(1 - x_j)(m - x_{j+2})] \\ &\quad - \frac{(m - 1)}{3} \left\{ (1 - v) \sum_{i=1}^3 \mathbb{E}_0 [x_i(1 - x_i)(1 - x_{i+2})] \right. \\ &\quad \left. + \frac{v}{2} \sum_{i \neq j=1}^3 \mathbb{E}_0 [x_i(1 - x_j)(1 - x_{i+2})] \right\}. \end{aligned} \tag{17}$$

Here, \mathbb{E}_0 denotes expectation in the stationary state under neutrality ($\delta = 0$). Let us introduce the following probabilities of identity by strategy in the stationary state under neutrality:

- $\phi_{2,1} = \mathbb{P}_0[2 \text{ individuals in the same subpopulation have the same strategy}],$
- $\phi_{2,2} = \mathbb{P}_0[2 \text{ individuals in 2 different subpopulations have the same strategy}],$
- $\phi_{3,1} = \mathbb{P}_0[3 \text{ individuals in the same subpopulation have the same strategy}],$
- $\phi_{3,2} = \mathbb{P}_0[3 \text{ individuals in 2 different subpopulations have the same strategy}],$
- $\phi_{3,3} = \mathbb{P}_0[3 \text{ individuals in 3 different subpopulations have the same strategy}].$

In these probabilities, the individuals and the subpopulations are chosen at random. In the case of $\phi_{3,2}$, two individuals are chosen at random in one subpopulation chosen at random, and one individual is chosen at random in one of the two other subpopulations chosen at random. Using these probabilities, the above quantities take the following expressions (see Sect. 5 for details):

$$\begin{aligned} M_1 &= (m - 1)(1 - v) \frac{N - 1}{2N^2} \left[1 - \phi_{2,1} + (N - 2)(\phi_{2,1} - \phi_{3,1}) + 2N(\phi_{2,2} - \phi_{3,2}) \right] \\ &\quad + \frac{v(m - 1)}{2N} \left[1 - \phi_{2,1} + 2(N - 1)(\phi_{2,2} - \phi_{3,2}) + N(\phi_{2,1} - \phi_{3,3}) \right], \end{aligned} \tag{18}$$

$$M_2 = (1 - v) \frac{3(N - 1)}{2N} (1 - \phi_{2,1}) + \frac{3v}{2} (1 - \phi_{2,2}), \tag{19}$$

$$\begin{aligned} M_3 &= \frac{N - 1}{2N} (1 - v) \left[1 - \phi_{2,1} + (m - 2)(\phi_{2,2} - \phi_{3,2}) \right] \\ &\quad + \frac{v}{2} \left(\frac{2N - 1}{2N} (1 - \phi_{2,2}) + \frac{N - 1}{2N} [\phi_{3,2} - \phi_{2,1} + (m - 1)(\phi_{2,2} - \phi_{3,2})] \right) \\ &\quad + \frac{m - 2}{2} (\phi_{2,2} - \phi_{3,3}). \end{aligned} \tag{20}$$

Then a sufficient condition for TFT to be favored by weak selection ($\delta > 0$ small enough) is that

$$\left(M_1 - \frac{mM_2}{3N}\right)(b - c) - M_2c + M_3\beta > 0. \tag{21}$$

In the limit of a large subpopulation size ($N \rightarrow \infty$), we have

$$\begin{aligned} \lim_{N \rightarrow \infty} M_1 &= (m - 1) \left\{ \frac{(1 - v)}{2} [\phi_{2,1} + 2\phi_{2,2} - \phi_{3,1} - 2\phi_{3,2}] \right. \\ &\quad \left. + \frac{v}{2} [\phi_{2,1} + 2\phi_{2,2} - 2\phi_{3,2} - \phi_{3,3}] \right\}, \\ \lim_{N \rightarrow \infty} M_2 &= \frac{3}{2} [1 - \phi_{2,1} + v(\phi_{2,1} - \phi_{2,2})], \\ \lim_{N \rightarrow \infty} M_3 &= \frac{1 - v}{2} [1 - \phi_{2,1} + (m - 2)(\phi_{2,2} - \phi_{3,2})] \\ &\quad + \frac{v}{2} \left(1 - \phi_{2,2} + \frac{\phi_{3,2} - \phi_{2,1} + (m - 1)(\phi_{2,2} - \phi_{3,2}) + (m - 2)(\phi_{2,2} - \phi_{3,3})}{2} \right), \end{aligned}$$

where $\phi_{2,1} = \phi_{2,2} = \frac{1}{2}$ and $\phi_{3,1} = \phi_{3,2} = \phi_{3,3} = \frac{1}{4}$. Therefore, we have

$$\lim_{N \rightarrow \infty} M_1 = \frac{3}{8}(m - 1), \quad \lim_{N \rightarrow \infty} M_2 = \frac{3}{4}, \quad \lim_{N \rightarrow \infty} M_3 = \frac{m}{8}.$$

In this case, the sufficient condition (21) for weak selection to favor TFT becomes

$$\beta > \beta^* = \frac{3(b + c)}{m} - 3(b - c). \tag{22}$$

Note that this condition does not depend on the migration parameter v . When $m = 1$, which corresponds to the case of the Prisoner’s Dilemma played only once, the condition reduces to

$$\beta > 6c. \tag{23}$$

As the number of repetitions of the game increases, the condition becomes less stringent since β^* decreases as m increases. If $\beta = 0$, then TFT is more abundant than ALLD in the stationary state under weak selection when

$$m > \frac{b + c}{b - c} = 1 + \frac{2c}{b - c}.$$

5 Calculations in the Stationary State under Neutrality

In this section, we consider the neutral case, that is, the case where all players have the same fitness equal to 1. We suppose that the population has reached its stationary state under the effects of mutation and migration. By symmetry, the frequencies of TFT in the three

subpopulations satisfy

$$\begin{aligned} \mathbb{E}_0[x_i] &= \mathbb{E}_0[x_1], \\ \mathbb{E}_0[x_i^2] &= \mathbb{E}_0[x_1^2], \\ \mathbb{E}_0[x_i^3] &= \mathbb{E}_0[x_1^3], \\ \mathbb{E}_0[x_i x_j] &= \mathbb{E}_0[x_1 x_2], \\ \mathbb{E}_0[x_i^2 x_j] &= \mathbb{E}_0[x_1^2 x_2], \end{aligned}$$

for $i, j = 1, 2, 3$ with $i \neq j$. Using these equalities and recalling that $x = (x_1 + x_2 + x_3)/3$, the quantities in Eqs. (15), (16), and (17) can be expressed as

$$\begin{aligned} M_1 &= (1 - v)(m - 1) \left(\mathbb{E}_0[x_1^2] + 2\mathbb{E}_0[x_1 x_2] - \mathbb{E}_0[x_1^3] - 2\mathbb{E}_0[x_1^2 x_2] \right) \\ &\quad + v(m - 1) \left(\mathbb{E}_0[x_1^2] - 2\mathbb{E}_0[x_1^2 x_2] + 2\mathbb{E}_0[x_1 x_2] - \mathbb{E}_0[x_1 x_2 x_3] \right), \\ M_2 &= 3(1 - v) \left(\mathbb{E}_0[x_1] - \mathbb{E}_0[x_1^2] \right) + 3v \left(\mathbb{E}_0[x_1] - \mathbb{E}_0[x_1 x_2] \right), \\ M_3 &= (1 - v) \left(m\mathbb{E}_0[x_1] - m\mathbb{E}_0[x_1^2] - \mathbb{E}_0[x_1 x_2] + \mathbb{E}_0[x_1^2 x_2] \right) \\ &\quad + \frac{v}{2} \left(2m\mathbb{E}_0[x_1] - (2m + 1)\mathbb{E}_0[x_1 x_2] - \mathbb{E}_0[x_1^2] + \mathbb{E}_0[x_1^2 x_2] + \mathbb{E}_0[x_1 x_2 x_3] \right) \\ &\quad - (1 - v)(m - 1) \left(\mathbb{E}_0[x_1] + \mathbb{E}_0[x_1^2] - \mathbb{E}_0[x_1 x_2] + \mathbb{E}_0[x_1^2 x_2] \right) \\ &\quad - \frac{v}{2}(m - 1) \left(2\mathbb{E}_0[x_1] - 4\mathbb{E}_0[x_1 x_2] + \mathbb{E}_0[x_1^2 x_2] + \mathbb{E}_0[x_1 x_2 x_3] \right). \end{aligned}$$

It remains to calculate the expected values $\mathbb{E}_0[x_1]$, $\mathbb{E}_0[x_1^2]$, $\mathbb{E}_0[x_1^3]$, $\mathbb{E}_0[x_1 x_2]$, $\mathbb{E}_0[x_1^2 x_2]$, and $\mathbb{E}_0[x_1 x_2 x_3]$.

Let the N individuals in subpopulation S_i be denoted by $I_1^{(i)}, \dots, I_N^{(i)}$, for $i = 1, 2, 3$. The strategy of each individual is represented by an indicator variable, namely,

$$\chi_l^{(i)} = \begin{cases} 1 & \text{if } I_l^{(i)} \text{ is a TFT strategist,} \\ 0 & \text{if } I_l^{(i)} \text{ is an AIID strategist,} \end{cases}$$

for $l = 1, \dots, N$ and $i = 1, 2, 3$. Then the frequency of TFT in subpopulation S_1 can be expressed as

$$x_1 = \frac{1}{N} \sum_{l=1}^N \chi_l^{(1)}. \tag{24}$$

Similarly, the square and the cube of this frequency can be written as

$$\begin{aligned} x_1^2 &= \frac{1}{N^2} \sum_{l,l'=1}^N \chi_l^{(1)} \chi_{l'}^{(1)}, \\ x_1^3 &= \frac{1}{N^3} \sum_{l,l',l''=1}^N \chi_l^{(1)} \chi_{l'}^{(1)} \chi_{l''}^{(1)}, \end{aligned}$$

respectively. Since the square and the cube of an indicator variable are the same indicator variable and an expectation is a linear operator, we have

$$\mathbb{E}_0[x_1^2] = \frac{1}{N^2} \sum_{l=1}^N \mathbb{E}_0[\chi_l^{(1)}] + \frac{1}{N^2} \sum_{l \neq l'=1}^N \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)}],$$

$$\mathbb{E}_0[x_1^3] = \frac{1}{N^3} \sum_{l=1}^N \mathbb{E}_0[\chi_l^{(1)}] + \frac{3}{N^3} \sum_{l \neq l'=1}^N \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)}] + \frac{1}{N^3} \sum_{l \neq l' \neq l''=1}^N \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)} \chi_{l''}^{(1)}],$$

where $l \neq l'$ means two different integers in $\{1, 2, \dots, N\}$, and $l \neq l' \neq l''$ stands for three different integers in $\{1, 2, \dots, N\}$. Using the symmetry of the two strategies in the neutral model and the notation for the probabilities introduced in the previous section, we get the following equalities:

$$\mathbb{E}_0[\chi_l^{(1)}] = \frac{1}{2} \mathbb{E}_0[\chi_l^{(1)} + (1 - \chi_l^{(1)})] = \frac{1}{2},$$

$$\mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)}] = \frac{1}{2} \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)} + (1 - \chi_l^{(1)}) (1 - \chi_{l'}^{(1)})] = \frac{1}{2} \phi_{2,1},$$

$$\mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)} \chi_{l''}^{(1)}] = \frac{1}{2} \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)} \chi_{l''}^{(1)} + (1 - \chi_l^{(1)}) (1 - \chi_{l'}^{(1)}) (1 - \chi_{l''}^{(1)})] = \frac{1}{2} \phi_{3,1},$$

for three different integers l, l', l'' in $\{1, 2, \dots, N\}$. Therefore, we have

$$\mathbb{E}_0[x_1^2] = \frac{1}{2N} + \frac{(N - 1)}{2N} \phi_{2,1}, \tag{25}$$

$$\mathbb{E}_0[x_1^3] = \frac{1}{2N^2} + \frac{3(N - 1)}{2N^2} \phi_{2,1} + \frac{(N - 1)(N - 2)}{2N^2} \phi_{3,1}. \tag{26}$$

Similarly, we find that

$$\mathbb{E}_0[x_1 x_2] = \frac{1}{N^2} \sum_{l, l'=1}^N \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(2)}] = \frac{1}{2} \phi_{2,2} \tag{27}$$

and

$$\begin{aligned} \mathbb{E}_0[x_1^2 x_2] &= \frac{1}{N^3} \sum_{l, l', l''=1}^N \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)} \chi_{l''}^{(2)}] \\ &= \frac{1}{N^3} \sum_{l, l''=1}^N \mathbb{E}_0[\chi_l^{(1)} \chi_{l''}^{(2)}] + \frac{1}{N^3} \sum_{l \neq l'=1}^N \sum_{l''=1}^N \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)} \chi_{l''}^{(2)}] \\ &= \frac{1}{2N} \phi_{2,2} + \frac{N - 1}{2N} \phi_{3,2}, \end{aligned}$$

where

$$\begin{aligned} \phi_{2,2} &= \mathbb{E}_0[\chi_l^{(1)} \chi_{l''}^{(2)} + (1 - \chi_l^{(1)}) (1 - \chi_{l''}^{(2)})], \\ \phi_{3,2} &= \mathbb{E}_0[\chi_l^{(1)} \chi_{l'}^{(1)} \chi_{l''}^{(2)} + (1 - \chi_l^{(1)}) (1 - \chi_{l'}^{(1)}) (1 - \chi_{l''}^{(2)})], \end{aligned}$$

for three integers l, l', l'' in $\{1, 2, \dots, N\}$ such that $l \neq l'$. Finally, we have the following equation:

$$\mathbb{E}_0[x_1 x_2 x_3] = \frac{1}{N^3} \sum_{l, l', l''=1}^N \mathbb{E}_0 \left[\chi_l^1 \chi_{l'}^2 \chi_{l''}^3 \right] \tag{28}$$

$$= \frac{1}{2N^3} \sum_{l, l', l''=1}^N \mathbb{E}_0 \left[\chi_l^1 \chi_{l'}^2 \chi_{l''}^3 + (1 - \chi_l^1) (1 - \chi_{l'}^2) (1 - \chi_{l''}^3) \right] \tag{29}$$

$$= \frac{\phi_{3,3}}{2}, \tag{30}$$

where

$$\phi_{3,3} = \mathbb{E}_0 \left[\chi_l^{(1)} \chi_{l'}^2 \chi_{l''}^3 + \left(1 - \chi_l^{(1)} \right) \left(1 - \chi_{l'}^2 \right) \left(1 - \chi_{l''}^3 \right) \right],$$

for three integers l, l', l'' in $\{1, 2, \dots, N\}$.

The above expressions for the expected values lead to the expressions for the quantities $M_1, M_2,$ and M_3 in Eqs. (18), (19) and (20) in terms of

$$\phi_{k,n} = \mathbb{P}_0[k \text{ individuals in } n \text{ subpopulations have the same strategy}],$$

for $k = 2, 3$ and $n = 1, 2, 3$, where individuals and subpopulations are chosen at random without replacement. What remains is the calculation of these probabilities.

Consider first two individuals chosen at random without replacement in the same subpopulation. Looking one time step back, there are four possibilities for the lineages of the two individuals. The first possibility is that one of the individuals is the offspring of the other, which occurs with the probability:

$$p_1 = 2 \times \frac{1}{3N} \times \frac{1}{N} \times (1 - v) = \frac{2(1 - v)}{3N^2}.$$

The second is that one of the individuals is the offspring of an individual chosen at random in the same subpopulation as the other individual, but different from this individual. This event has the probability:

$$p_2 = 2 \times \frac{N - 1}{3N} \times \frac{1}{N} \times (1 - v) = \frac{2(N - 1)(1 - v)}{3N^2}.$$

The third is that one of the individuals is the offspring of an individual chosen at random in a subpopulation different from the subpopulation of the other individual, which has the probability:

$$p_3 = 2 \times \frac{2N}{3N} \times \frac{v}{2} \times \frac{1}{N} = \frac{2Nv}{3N^2}.$$

The last possibility is that none of two individuals is an offspring of an individual in the population one time step back. The probability of this event is given by

$$p_3 = 1 - (p_1 + p_2 + p_4) = 1 - \frac{2}{3N}.$$

Then, conditioning on the event affecting the lineages of the two individuals one time step back, we arrive at the equation:

$$\phi_{2,1} = p_1 \left[(1 - u) + \frac{u}{2} \right] + p_2 \left[(1 - u)y + \frac{u}{2} \right] + p_3 \left[(1 - u)\phi_{2,2} + \frac{u}{2} \right] + p_4 \phi_{2,1}.$$

This yields

$$\phi_{2,1} = a_1 + a_2\phi_{2,2}, \tag{31}$$

where

$$a_1 = \frac{\frac{u}{2}(p_1 + p_2 + p_3) + (1-u)p_1}{1 - (1-u)p_2 - p_4} = \frac{uN + 2(1-u)(1-v)}{2N - 2(N-1)(1-u)(1-v)},$$

$$a_2 = \frac{(1-u)p_3}{1 - (1-u)p_2 - p_4} = \frac{2(1-u)Nv}{2N - 2(N-1)(1-u)(1-v)}.$$

Now for two individuals chosen at random from two different subpopulations, the events described above have the probabilities given by

$$q_1 = 2 \times \frac{1}{3N} \times \frac{1}{N} \times \frac{v}{2} = \frac{v}{3N^2},$$

$$q_2 = 2 \times \frac{N-1}{3N} \times \frac{1}{N} \times \frac{v}{2} = \frac{(N-1)v}{3N^2},$$

$$q_3 = 2 \left[\frac{N}{3N} \times \frac{1}{N} \times \frac{v}{2} + \frac{N}{3N} \times \frac{1}{N} \times (1-v) \right] = \frac{N(2-v)}{3N^2},$$

$$q_4 = 1 - (q_1 + q_2 + q_3) = 1 - \frac{2}{3N},$$

respectively. Therefore

$$\phi_{2,2} = q_1 \left[(1-u) + \frac{u}{2} \right] + q_2 \left[(1-u)\phi_{2,1} + \frac{u}{2} \right] + q_3 \left[(1-u)\phi_{2,2} + \frac{u}{2} \right] + q_4\phi_{2,2},$$

from which

$$\phi_{2,2} = b_1 + b_2\phi_{2,1}, \tag{32}$$

where

$$b_1 = \frac{\frac{u}{2}(q_1 + q_2 + q_3) + (1-u)q_1}{1 - (1-u)q_3 - q_4} = \frac{uN + (1-u)v}{2uN + vN(1-u)},$$

$$b_2 = \frac{(1-u)q_2}{1 - (1-u)q_3 - q_4} = \frac{(1-u)(N-1)v}{2uN + vN(1-u)}.$$

From Eqs. (31) and (32), we arrive at the solution:

$$\phi_{2,1} = \frac{a_1 + a_2b_1}{1 - a_2b_2}$$

$$= \frac{[uN + 2(1-u)(1-v)][2u + v(1-u)] + 2(1-u)v[uN + v(1-u)]}{[2u + v(1-u)][2N - 2(N-1)(1-u)(1-v)] - 2(N-1)v^2(1-u)^2}, \tag{33}$$

$$\phi_{2,2} = \frac{b_1 + b_2a_1}{1 - a_2b_2}$$

$$= \frac{2uN + 2v(1-u) - (N-1)(u-u^2)(2-3v)}{[2u + v(1-u)][2N - 2(N-1)(1-u)(1-v)] - 2(N-1)v^2(1-u)^2}. \tag{34}$$

Similarly, for three individuals chosen at random without replacement in the same subpopulation from one time step to the previous one, one of the individuals can be an offspring, and then it can be an offspring of anyone of the two others, or an offspring of an individual in the same subpopulation but different from the two others, or an offspring of an individual

in a different subpopulation. Otherwise, none of the individuals is an offspring. These events have probabilities given by

$$\begin{aligned} r_1 &= 6 \times \frac{1}{3N} \times (1-v) \times \frac{1}{N} = \frac{2(1-v)}{N^2}, \\ r_2 &= 3 \times \frac{N-2}{3N} \times (1-v) \times \frac{3}{3N} = \frac{(N-2)(1-v)}{N^2}, \\ r_3 &= 3 \times \frac{2N}{3N} \times \frac{v}{2} \times \frac{1}{N} = \frac{Nv}{N^2}, \\ r_4 &= 1 - \frac{1}{N} = \frac{N-1}{N}, \end{aligned}$$

respectively. Conditioning on these events, we find that

$$\phi_{3,1} = r_1 \left[(1-u) + \frac{u}{2} \right] \phi_{2,1} + r_2 \left[(1-u)\phi_{3,1} + \frac{u}{2}\phi_{2,1} \right] + r_3 \left[(1-u)\phi_{3,2} + \frac{u}{2}\phi_{2,1} \right] + r_4\phi_{3,1}.$$

Then we have

$$\phi_{3,1} = c_1\phi_{2,1} + c_2\phi_{3,2}, \tag{35}$$

where

$$\begin{aligned} c_1 &= \frac{\frac{u}{2}(r_1 + r_2 + r_3) + (1-u)r_1}{1 - r_2 - r_4 + ur_2} = \frac{\frac{Nu}{2} + 2(1-u)(1-v)}{N - (1-u)(N-2)(1-v)}, \\ c_2 &= \frac{(1-u)r_3}{1 - r_2 - r_4 + ur_2} = \frac{(1-u)Nv}{N - (1-u)(N-2)(1-v)}. \end{aligned}$$

Proceeding in the same way for two individuals in the same subpopulation and one in another population, we find that

$$\phi_{3,2} = d_1\phi_{2,1} + d_2\phi_{2,2} + d_3\phi_{3,1} + d_4\phi_{3,3}, \tag{36}$$

where

$$\begin{aligned} d_1 &= \frac{\frac{Nu}{2} + (1-u)v}{3N - (1-u)(2-v)\left(\frac{3N}{2} - 1\right)}, \\ d_2 &= \frac{Nu + (1-u)(2-v)}{3N - (1-u)(2-v)\left(\frac{3N}{2} - 1\right)}, \\ d_3 &= \frac{(1-u)(N-2)v}{6N - (1-u)(2-v)(3N-2)}, \\ d_4 &= \frac{(1-u)Nv}{3N - (1-u)(2-v)\left(\frac{3N}{2} - 1\right)}. \end{aligned}$$

Finally, for three individuals in three subpopulations, we have

$$\phi_{3,3} = e_1\phi_{2,2} + e_2\phi_{3,2}, \tag{37}$$

where

$$\begin{aligned} e_1 &= \frac{(1-u)v + \frac{uN}{2}}{N \left[1 - (1-u)(1-v) \right]}, \\ e_2 &= \frac{(1-u)(N-1)v}{N \left[1 - (1-u)(1-v) \right]}. \end{aligned}$$

From Eqs. (35), (36), and (37), we conclude that

$$\begin{aligned} \phi_{3,2} &= \frac{(d_1 + d_3c_1)\phi_{2,1} + (d_2 + d_4e_1)\phi_{2,2}}{1 - d_3c_2 - d_4e_2}, \\ \phi_{3,1} &= c_1\phi_{2,1} + c_2 \frac{(d_1 + d_3c_1)\phi_{2,1} + (d_2 + d_4e_1)\phi_{2,2}}{1 - d_3c_2 - d_4e_2}, \\ \phi_{3,3} &= e_1\phi_{2,2} + e_2 \frac{(d_1 + d_3c_1)\phi_{2,1} + (d_2 + d_4e_1)\phi_{2,2}}{1 - d_3c_2 - d_4e_2}. \end{aligned}$$

In the limit of a large subpopulation size, we have

$$\begin{aligned} \lim_{N \rightarrow \infty} \phi_{2,1} &= \lim_{N \rightarrow \infty} \frac{2u^2N + 3uNv(1 - u)}{4u^2N + 6uNv(1 - u)} = \frac{1}{2}, \\ \lim_{N \rightarrow \infty} \phi_{2,2} &= \lim_{N \rightarrow \infty} \frac{2uN - N(u - u^2)(2 - 3v)}{4u^2N + 6uNv(1 - u)} = \frac{1}{2}. \end{aligned}$$

We have also

$$\lim_{N \rightarrow \infty} \phi_{3,1} = \lim_{N \rightarrow \infty} \phi_{3,2} = \lim_{N \rightarrow \infty} \phi_{3,3} = \frac{1}{4}.$$

This means that the strategies of different individuals in the population at stationarity in the limit of a large subpopulation size are chosen independently at random. This is expected since this situation corresponds to a strong mutation limit.

6 Discussion

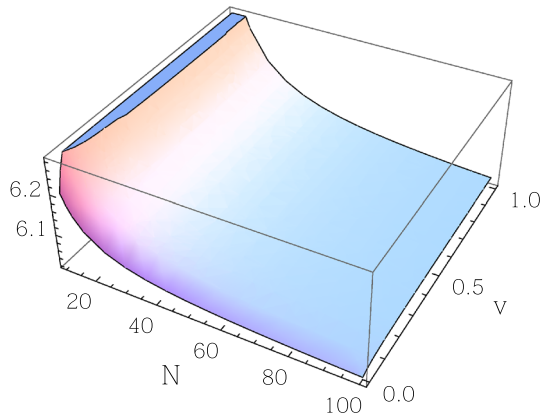
We have considered the repeated Prisoner’s Dilemma with TFT and ALLD as strategies played by individuals in a population made of three subpopulations of the same finite size N , updated by single birth–death events according to a Moran model with mutation, migration, and selection determined by expected payoffs, under the assumption of symmetric interactions between individuals within each subpopulation but asymmetric interactions between individuals in different subpopulations according to a cyclic dominance hierarchy scheme. Besides a cooperation cost c for a benefit $b > c$ to the opponent in each round of the Prisoner’s Dilemma, there is a defection cost β incurred by a defecting individual when the opponent is dominant and defecting.

In the limit of a large population size and with only one round of the game, we have shown that TFT is more abundant than ALLD in the stationary state under weak selection if $\beta > 6c$. The condition becomes less stringent as the number of rounds increases (see 22) and is always satisfied as soon as

$$m > \frac{3(b + c)}{3(b - c) + \beta}.$$

Note that the condition (22) in the limit of a large population size never depends on the migration rate. Moreover, as shown in the next section, this condition does not change with linear dominance. This is to be compared with the conditions for TFT to be globally asymptotically stable in an infinite population in the absence of migration in the case $m \geq 2$, which are $\beta > 3c$ with cyclic dominance and $\beta > 3c/2$ but for $m > \max\{(b + 2c - \beta)/(b - c), (2b + c)/(2b - 2c)\}$ with linear dominance (Tao et al. [43]).

Fig. 1 Threshold value that β must exceed for TFT to be more abundant than AllD in the stationary state under weak selection as a function of N and v for $m = 1, b = 2, c = 1, u = 0.1$



Note also that the condition (22) in the limit of a large population size can be written in the form (Tarnita et al. [46]):

$$\sigma R + S > T + \sigma P,$$

where $\sigma = 1$ represents a population structure coefficient and

$$R = m(b - c), \quad S = -c - \frac{(m - 1)\beta}{3}, \quad T = b - \frac{(m - 1)\beta}{3}, \quad P = -\frac{m\beta}{3},$$

represent payoffs. Therefore, the situation is equivalent to a model in a well-mixed population with a payoff matrix

$$\tilde{A} = \frac{A_{i,1} + A_{i,2} + A_{i,3}}{3} = \begin{pmatrix} m(b - c) & -c - \frac{(m-1)}{3}\beta \\ b - \frac{(m-1)}{3}\beta & -\frac{m}{3}\beta \end{pmatrix},$$

which can be called an effective game matrix (Lessard [22]). This is not the case, however, for a fixed finite population size (that is, $N < \infty$), since M_3 in (21) is not a linear function of m , while σ may depend on N and u , the mutation rate per birth event, but not on R, S, T , and P .

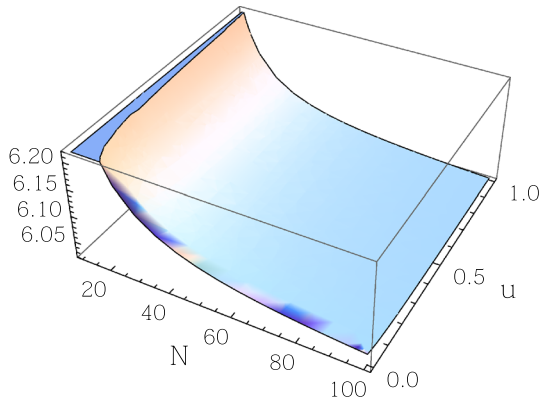
In the case of a low mutation rate, the assumption of weak selection could be relaxed at least in the limit of a large population size, since then conditions for a strategy to be more abundant in a well-mixed population (Fudenberg et al. [8]) can be applied using the effective game matrix.

The effects of the subpopulation size N along with the migration and mutation rates per birth event, v and u , on the general condition (21) for TFT to be more abundant than AllD in the stationary state under weak selection are illustrated in Figs. 1 and 2. For $m = 1, b = 2, c = 1$, the threshold value that the defection cost β must exceed increases as N or u decreases, for $v = 0.1$; or as v increases, for $u = 0.1$. This suggests that the evolution of cooperation in the case of dominance hierarchy is made easier if the population size or the mutation rate is larger or if the migration rate is smaller.

7 Appendix: Model of Linear Dominance

In this section, we consider m rounds of the Prisoner’s Dilemma played between individuals chosen at random in three subpopulations of the same finite size N represented by $S_1, S_2,$

Fig. 2 Threshold value that β must exceed for TFT to be more abundant than AllD in the stationary state under weak selection as a function of N and u for $m = 1, b = 2, c = 1, v = 0.1$



and S_3 under the assumption of linear hierarchy: an individual in S_1 dominates an individual in S_2 and in S_3 , while an individual in S_2 dominates an individual in S_3 . With respect to the strategies TFT and AllD, the payoff matrices $A_{i,j}$ for an individual in S_i in interaction with an individual in S_j , for $i, j = 1, 2, 3$, are given by

$$A_{1,1} = A_{2,2} = A_{3,3} = A_{1,2} = A_{1,3} = A_{2,3} = \begin{pmatrix} m(b-c) & -c \\ b & 0 \end{pmatrix},$$

$$A_{2,1} = A_{3,1} = A_{3,2} = \begin{pmatrix} m(b-c) & -c - (m-1)\beta \\ b - (m-1)\beta & -m\beta \end{pmatrix}.$$

The expected payoffs $w_1^{(i)}$ and $w_2^{(i)}$ to TFT and AllD, respectively, in subpopulation S_i , for $i = 1, 2, 3$, are then given by

$$\begin{aligned} w_1^{(1)} &= \frac{3N}{3N-1} \left[mx(b-c) - \frac{m(b-c)}{3N} - (1-x)c \right], \\ w_1^{(2)} &= \frac{3N}{3N-1} \left[mx(b-c) - \frac{m(b-c)}{3N} - (1-x)c - \frac{1}{3}(1-x_1)(m-1)\beta \right], \\ w_1^{(3)} &= \frac{3N}{3N-1} \left[mx(b-c) - \frac{m(b-c)}{3N} - (1-x)c - \frac{1}{3}(2-x_1-x_2)(m-1)\beta \right], \\ w_2^{(1)} &= \frac{3N}{3N-1} xb, \\ w_2^{(2)} &= \frac{3N}{3N-1} \left[xb - \frac{1}{3}(m-x_1)\beta \right], \\ w_2^{(3)} &= \frac{3N}{3N-1} \left[xb - \frac{1}{3}(m-x_1)\beta - \frac{1}{3}(m-x_2)\beta \right]. \end{aligned}$$

These expected payoffs can be expressed in the form:

$$w_1^{(i)} = \frac{3N}{3N-1} \left[mx(b-c) - \frac{m(b-c)}{3N} - (1-x)c - \frac{1}{3} \sum_{l<i} (1-x_l)(m-1)\beta \right], \quad (38)$$

and

$$w_2^{(i)} = \frac{3N}{3N-1} \left[xb - \frac{1}{3} \sum_{l < i} (m - x_l) \beta \right], \tag{39}$$

for $i = 1, 2, 3$. This yields differences in the form:

$$w_1^{(i)} - w_2^{(j)} = \frac{3N}{3N-1} \left\{ (m-1)x(b-c) - \left[\frac{m}{3N}(b-c) + c \right] + \frac{1}{3} \sum_{l < j} (m - x_l) \beta - \frac{1}{3} \sum_{l < i} (1 - x_l)(m - 1) \beta \right\},$$

for $i, j = 1, 2, 3$.

Plugging these expressions into (13) for the conditional expected change in frequency of TFT in the whole population given an intensity of selection $\delta > 0$ and no mutation, which remains valid under linear hierarchy, leads to

$$\begin{aligned} \mathbb{E}_\delta[\Delta X_{\text{sel}} | \mathbf{X} = \mathbf{x}] &= \frac{\delta(m-1)}{3(3N-1)} \left\{ (1-v) \sum_{i=1}^3 x_i(1-x_i)x + \frac{v}{2} \sum_{i \neq j=1}^3 x_i(1-x_j)x \right\} (b-c) \\ &- \frac{\delta}{3(3N-1)} \left\{ (1-v) \sum_{i=1}^3 x_i(1-x_i) + \frac{v}{2} \sum_{i \neq j=1}^3 x_i(1-x_j) \right\} \left[\frac{m}{3N}(b-c) + c \right] \\ &+ \frac{\delta}{9(3N-1)} \left\{ (1-v) \sum_{1 \leq l < i \leq 3} x_i(1-x_i)(m-x_l) \right. \\ &+ \frac{v}{2} \sum_{1 \leq l < j \leq 3} \sum_{\substack{i=1 \\ i \neq j}}^3 x_i(1-x_j)(m-x_l) - (1-v) \sum_{1 \leq l < i \leq 3} x_i(1-x_i)(m-1)(1-x_l) \\ &\left. - \frac{v}{2} \sum_{1 \leq l < i \leq 3} \sum_{\substack{j=1 \\ j \neq i}}^3 x_i(1-x_j)(m-1)(1-x_l) \right\} \beta + o(\delta). \end{aligned}$$

Taking the expected value in the stationary state gives

$$(3N-1)\mathbb{E}_\delta[\Delta X_{\text{sel}}] = \frac{\delta}{3} \left\{ \left(M'_1 - \frac{mM'_2}{3N} \right) (b-c) - M'_2c + M'_3\beta \right\} + o(\delta), \tag{40}$$

where

$$M'_1 = (m-1) \left\{ (1-v) \sum_{i=1}^3 \mathbb{E}_0[x_i(1-x_i)x] + \frac{v}{2} \sum_{i \neq j=1}^3 \mathbb{E}_0[x_i(1-x_j)x] \right\},$$

$$M'_2 = (1-v) \sum_{i=1}^3 \mathbb{E}_0[x_i(1-x_i)] + \frac{v}{2} \sum_{i \neq j=1}^3 \mathbb{E}_0[x_i(1-x_j)],$$

$$M'_3 = \frac{(1-v)}{3} \sum_{1 \leq l < i \leq 3} \mathbb{E}_0[x_i(1-x_i)(m-x_l)] + \frac{v}{6} \sum_{1 \leq l < j \leq 3} \sum_{\substack{i=1 \\ i \neq j}}^3 \mathbb{E}_0[x_i(1-x_j)(m-x_l)] - \frac{(m-1)}{3}$$

$$\times \left\{ (1-v) \sum_{1 \leq l < i \leq 3} \mathbb{E}_0[x_i(1-x_i)(1-x_l)] + \frac{v}{2} \sum_{1 \leq l < i \leq 3} \sum_{\substack{j=1 \\ j \neq i}}^3 \mathbb{E}_0[x_i(1-x_j)(1-x_l)] \right\}.$$

Comparing with (15), (16), and (17), we note that $M'_1 = M_1$ and $M'_2 = M_2$. Moreover, using the symmetry of the model in the neutral case, we obtain that

$$\begin{aligned} M'_3 = M_3 &= (1-v)E_0[x_1(1-x_1)(m-x_2)] \\ &+ \frac{v}{2} \left\{ E_0[x_1(1-x_2)(m-x_1)] + E_0[x_1(1-x_2)(m-x_3)] \right\} \\ &- (1-v)(m-1)E_0[x_1(1-x_1)(1-x_2)] \\ &- \frac{v}{2} \left\{ E_0[x_1(1-x_2)^2] + E_0[x_1(1-x_2)(1-x_3)] \right\}. \end{aligned}$$

Therefore, the sufficient condition (21) for weak selection to favor TFT in the case of cyclic hierarchy is valid as well in the case of linear hierarchy.

References

1. Antal T, Nowak MA, Traulsen A (2009) Strategy abundance in 2×2 games for arbitrary mutation rates. *J Theor Biol* 257:340–344
2. Antal T, Traulsen A, Ohtsuki H, Tarnita CE, Nowak MA (2009) Mutation-selection equilibrium in games with multiple strategies. *J Theor Biol* 258:614–622
3. Antal T, Ohtsuki H, Wakeley J, Taylor PD, Nowak MA (2009) Evolutionary game dynamics in phenotype space. *Proc Natl Acad Sci USA* 106:8597–8600
4. Axelrod RM (1984) *The evolution of cooperation*. Basic Books, New York
5. Axelrod RM, Hamilton WD (1981) The evolution of cooperation. *Science* 211:1390–1396
6. Eshel I (1996) On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. *J Math Biol* 34:485–510
7. Fudenberg D, Imhof LA (2006) Imitation processes with small mutations. *J Econ Theory* 131:251–262
8. Fudenberg D, Nowak MA, Taylor C, Imhof LA (2006) Evolutionary game dynamics in finite populations with strong selection and weak mutation. *Theor Popul Biol* 70:352–363
9. Fudenberg D, Tirole J (1991) *Game theory*. MIT Press, Cambridge
10. Hamilton WD (1964) The genetical evolution of social behaviour. I and II. *J Theor Biol* 7:1–52
11. Hammerstein P (1981) The role of asymmetries in animal contests. *Anim Behav* 29:578–581
12. Hauert C, Doebeli M (2004) Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature* 428:643–646
13. Hilbe C (2011) Local replicator dynamics: a simple link between deterministic and stochastic models of evolutionary game theory. *Bull Math Biol* 73:2068–2087
14. Hofbauer J, Sigmund K (1988) *The theory of evolution and dynamical systems*. Cambridge University Press, Cambridge
15. Hofbauer J, Sigmund K (2003) Evolutionary game dynamics. *Bull Amer Math Soc* 40:479–519
16. Hofbauer J, Schuster P, Sigmund K (1979) A note on evolutionary stable strategies and games dynamics. *J Theor Biol* 81:609–612
17. Imhof LA, Nowak MA (2006) Evolutionary game dynamics in a Wright–Fisher process. *J Math Biol* 52:667–681
18. Ladret V, Lessard S (2007) Fixation probability for a beneficial allele and a mutant strategy in a linear game under weak selection in a finite island model. *Theor Popul Biol* 72:409–425
19. Ladret V, Lessard S (2008) Evolutionary game dynamics in a finite asymmetric two-deme population and emergence of cooperation. *J Theor Biol* 255:137–151
20. Lessard S (2005) Long-term stability from fixation probabilities in finite populations: new perspectives for ESS theory. *Theor Popul Biol* 68:19–27
21. Lessard S (2007) Cooperation is less likely to evolve in a finite population with a highly skewed distribution of family size. *Proc R Soc B* 274:1861–1865

22. Lessard S (2011a) Effective game matrix and inclusive payoff in group-structured populations. *Dyn Games Appl* 1:301–318
23. Lessard S (2011b) Evolutionary game dynamics. *Am Math Soc* 69:143–171
24. Lessard S, Ladret V (2007) The probability of fixation of a single mutant in an exchangeable selection model. *J Math Biol* 54:721–744
25. Lessard S, Lahaie P (2009) Fixation probability with multiple alleles and projected average allelic effect on selection. *Theor Popul Biol* 75:266–277
26. Maynard Smith J (1982) *Evolution and the theory of games*. Cambridge University Press, Cambridge
27. Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature* 246:15–18
28. Nash J (1951) Non-cooperative games and spatial chaos. *Ann Math* 54:286–295
29. Nowak MA (2006a) *Evolutionary dynamics*. Harvard University Press, Cambridge
30. Nowak MA (2006b) Five rules for the evolution of cooperation. *Science* 314:1560–1563
31. Nowak MA, May R (1992) Evolutionary games and spatial chaos. *Nature* 359:826–829
32. Nowak MA, Sasaki A, Taylor C, Fudenberg D (2004) Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428:646–650
33. Nowak MA, Sigmund K (2007) How populations cohere: five rules for cooperation. In *Theoretical Ecology, Third Edition*. Oxford Press, 7–16.
34. Nowak MA, Tarnita CE, Antal T (2010) Evolutionary dynamics in structured populations. *Phil Trans R Soc B* 365:19–30
35. Ohtsuki H, Nowak MA (2006a) Evolutionary games on cycles. *Proc R Soc B* 273:2249–2256
36. Ohtsuki H, Nowak MA (2006b) The replicator equation on graphs. *J Theor Biol* 243:86–97
37. Ohtsuki H, Hauert C, Lieberman E, Nowak MA (2006) A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441:502–505
38. Ohtsuki H, Pacheco J, Nowak MA (2007) Evolutionary graph theory: breaking the symmetry between interaction and replacement. *J Theor Biol* 246:681–694
39. Osborne MJ, Rubinstein A (1994) *A course in game theory*. MIT Press, Cambridge
40. Rousset F (2003) A minimal derivation of convergence stability measures. *J Theor Biol* 221:665–668
41. Rousset F (2006) Separation of time scales, fixation probabilities and convergence to evolutionarily stable states under isolation by distance. *Theor Popul Biol* 69:165–179
42. Rousset F, Billiard S (2000) A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. *J Evol Biol* 13:814–825
43. Tao Y, Xu JJ, Li C, Cressman R (2013) Dominance hierarchies induce a population's full cooperation. Submitted to *games*. [Preprint]
44. Tarnita CE, Antal T, Nowak MA (2009) Mutation-selection equilibrium in games with mixed strategies. *J Theor Biol* 261:50–57
45. Tarnita CE, Antal T, Ohtsuki H, Nowak MA (2009) Evolutionary dynamics in set structured populations. *Proc Natl Acad Sci USA* 106:8601–8604
46. Tarnita CE, Ohtsuki H, Antal T, Fu F, Nowak MA (2009) Strategy selection in structured populations. *J Theor Biol* 259:570–581
47. Tarnita CE, Wage N, Nowak MA (2011) Multiple strategies in structured populations. *Proc Natl Acad Sci USA* 108:2334–2337
48. Taylor C, Fudenberg D, Sasaki A, Nowak MA (2004) Evolutionary game dynamics in finite populations. *Bull Math Biol* 66:1621–1644
49. Taylor PD, Day T, Wild G (2007) Evolution of cooperation in a finite homogeneous graph. *Nature* 66:1621–1644
50. Taylor PD, Jonker L (1978) Evolutionarily stable strategies and game dynamics. *Math Biosci* 40:145–156
51. Von Neumann J, Morgenstern O (1944) *Theory of games and economic behavior*. Princeton University Press, Princeton
52. Zeeman EC (1980) Population dynamics from game theory. In: *Proceedings of International Conference on Global Theory of Dynamical Systems* (eds Nitecki ZH and Robinson RC) New York: Springer