



# Effect of Variability in Payoffs on Conditions for the Evolution of Cooperation in a Small Population

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## Abstract

In this paper, we study the effect of stochastic fluctuations in payoffs for two strategies, cooperation and defection, used in random pairwise interactions in a population of fixed finite size with an update according to a Moran model. We assume that the means, variances and covariances of the payoffs are of the same small order while all higher-order moments are negligible. We show that more variability in the payoffs to defection and less variability in the payoffs to cooperation contribute to the evolutionary success of cooperation over defection as measured by fixation probabilities under weak selection. This conclusion is drawn by comparing the probabilities of ultimate fixation of cooperation and defection as single mutants to each other and to what they would be under neutrality. These comparisons are examined in detail with respect to the population size and the second moments of the payoffs in five cases of additive Prisoner's Dilemmas. The analysis is extended to a Prisoner's Dilemma repeated a random number of times with Tit-for-Tat starting with cooperation and Always-Defect as strategies. Moreover, simulations with an update according to a Wright–Fisher model suggest that the conclusions are robust.

**Keywords** Fixation probability · Evolutionary game theory · Moran model · Prisoner's Dilemma · Random payoff

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## 1 Introduction

Evolutionary game theory was originally formulated in the framework of an infinite population in continuous time where payoffs of strategies are interpreted as growth rates and changes in strategy frequencies are described by a deterministic replicator equation [6,27,31]. However, deterministic dynamics fail to capture the fact that real populations are finite. To take this fact into account, we have to resort to stochastic processes such as Markov chains. In the situation of two strategies  $A$  and  $B$  in a population of fixed finite size  $N$  with updating at discrete time steps, the frequency of  $A$  is a Markov chain in discrete time. In the absence of recurrent mutation, this Markov chain possesses two absorbing states corresponding to  $A$  fixation and  $B$  fixation, and then the chain converges to these states with probability one (see, e.g., Karlin and Taylor [9]). Then, the success of  $A$  can be measured by comparing its fixation probability under selection to what it would be without selection. In a neutral model, the probability of ultimate fixation of  $A$  from any initial frequency is equal to this initial frequency. Therefore, in the absence of selection, the probability of ultimate fixation of a single  $A$  introduced in an all  $B$  population of fixed total size  $N$  is given by  $N^{-1}$ . In the presence of selection, selection is said to favor the evolution of  $A$  if the fixation probability of  $A$  from an initial frequency  $N^{-1}$  is larger than  $N^{-1}$  [13,14,19]. Note that this condition is neither sufficient nor necessary for the probability of ultimate fixation of a single  $A$  to exceed the probability of ultimate fixation of a single  $B$ . In such a case, selection is said to favor the evolution of  $A$  more than the evolution of  $B$  [19].

In the above situation but in the presence of recurrent mutation, the frequency of  $A$  over successive time steps is an irreducible Markov chain on a finite state space, and then the chain converges in law to a stationary distribution (see, e.g., Karlin and Taylor [9]). In the absence of selection, the average abundance of  $A$  with respect to the stationary distribution is  $1/2$ . If the average abundance of  $A$  becomes larger than  $1/2$  in the presence of selection, then selection is said to favor the abundance of  $A$  more than the abundance of  $B$  [1]. Note that the condition for selection to favor the evolution of  $A$  more than the evolution of  $B$  in the absence of mutation, and the condition for selection to favor the abundance of  $A$  more than the abundance of  $B$  in the presence of mutation, are the same in the limit of a low mutation rate [4,23,24].

The key assumption in all the above models is that the payoff matrix is constant. This supposes that the surrounding environment remains exactly the same over time, which is unrealistic. Environmental conditions are subject to fluctuations that happen at random, and so are competition capabilities as well as birth and/or death rates [7,11,17]. Such fluctuations can cause changes in the population size over time and many authors have explored the effects of such changes. These include Lambert [12], Parsons and Quince [21,22] and Otto and Whitlock [20] who studied the fixation probability for a mutant type in a well-mixed population whose size fluctuates dynamically according to a variety of demographic scenarios of growth or decline. Uecker and Hermisson [28] addressed the case of a single beneficial allele in a population that experiences temporal variation in its size and selection pressure.

Also, stochastic fluctuations will generally affect the payoffs of strategies used by interacting individuals that determine their reproductive successes, and consequently the underlying evolutionary game dynamics. Broom [2] has considered matrix games where the payoffs are functions of time. He showed that the evolution of a strategy is more complex than under constant payoffs, where increasing the variability of the payoffs pushes the time average of a population state far from its interior Nash equilibrium. Stollmeier and Naglar [25] showed that variability of the payoffs affects the stability of a fixation state. Zheng et al. [32,33]

have investigated stochastic stability in a two-strategy evolutionary game for an infinite well-mixed population under stochastic perturbations of the payoffs. Kroumi and Lessard [10] have studied the abundance of cooperation in a finite well-mixed population with random payoffs. They showed that increasing the variance coefficient of any payoff to defection against cooperation or defection, or their covariance, will increase the abundance of cooperation. In the case of an infinite well-mixed population and in the absence of mutation, Li et al. [16] have shown that natural selection tends to favor the evolution of cooperation if the variance coefficients of the payoffs to defection are larger than the variance coefficients of the payoffs to cooperation.

The effect of random noise in payoffs in two-player two-strategy linear games in a finite population, mainly Prisoner's Dilemmas with cooperation and defection as possible strategies, was studied recently by Li and Lessard [15]. Assuming an update of the population according to a Wright–Fisher model and using a diffusion approximation in the limit of a large population size with appropriately scaled first and second moments of the payoffs as in [8] for population genetics models, conditions for selection to favor the evolution of cooperation, disfavor the evolution of defection, and favor more the evolution of cooperation than the evolution of defection were deduced. These conditions are valid only in a large enough population and most of them are given only in the special case of independent payoffs.

In this paper, we study the effect of stochastic fluctuations in payoffs for two strategies, cooperation ( $C$ ) and defection ( $D$ ), used in random pairwise interactions in a population of finite size  $N \geq 2$ . The update of the population from one time step to the next is done through a birth–death event according to a Moran model that keeps the population size constant. Assuming that the first and second moments of the payoffs are of the same small order corresponding to the magnitude of selection and that all higher-order moments are negligible, we deduce the first-order effect of selection on the fixation probability of each strategy given an initial frequency  $N^{-1}$ . This allows us to study the effects of the population size, besides those of the second moments of the payoffs including their covariances, on conditions that could be favorable to the evolution of cooperation. This study is completed by simulations under both a Moran model and a Wright–Fisher model.

The remainder of this paper is organized as follows. In Sects. 2 and 3, we present the model and derive the probabilities of ultimate fixation of a single  $C$  and a single  $D$  under weak selection. In Sect. 4, we deduce the effects of increasing or decreasing the variances or covariances of the payoffs on these probabilities. Conditions for weak selection to favor the evolution of cooperation, disfavor the evolution of defection, and favor more the evolution of cooperation than the evolution of defection are studied in detail in the case of five particular Prisoner's Dilemmas with additive cost and benefit for cooperation in Section 5, and in the case of a repeated Prisoner's Dilemma in Section 6. Simulation results are presented in Section 7. The concluding Section 8 summarizes our findings and discusses their interpretations.

## 2 Two-Player Game with Random Payoffs

We consider a two-player game in discrete time in a well-mixed population composed of  $N$  individuals. Each individual can adopt one of two strategies,  $C$  for cooperation or  $D$  for defection. The payoffs to  $C$  and  $D$  against  $C$  and  $D$ , respectively, in a pairwise interaction are given by the entries of the matrix

$$\begin{matrix} & C & D \\ C & \left( \begin{matrix} \eta_1 & \eta_2 \\ \eta_3 & \eta_4 \end{matrix} \right) \\ D & & \end{matrix} \tag{1}$$

A cooperator interacting with another cooperator receives  $\eta_1$ , while a defector interacting with another defector obtains  $\eta_4$ . If a cooperator interacts with a defector, it receives  $\eta_2$ , whereas the defector obtains  $\eta_3$  in this situation. We suppose that  $\eta_i$  is a random variable whose probability distribution does not depend on time and such that  $|\eta_i| \leq M$  for some constant  $M$  in  $(0, 1)$  for  $i = 1, 2, 3, 4$ .

In addition, we assume that

$$E[\eta_i] = \mu_i \delta + o(\delta), \tag{2a}$$

$$E[\eta_i^2] = \sigma_i^2 \delta + o(\delta), \tag{2b}$$

$$E[\eta_i \eta_j] = \sigma_{ij} \delta + o(\delta), \tag{2c}$$

for  $i, j = 1, 2, 3, 4$  with  $i \neq j$ . The parameter  $\delta \geq 0$  represents a magnitude of selection. It measures the order of the first and second moments of the payoffs so that  $\mu_i, \sigma_i^2$  and  $\sigma_{ij}$  for  $i, j = 1, 2, 3, 4$  with  $i \neq j$  represent their scaled means, variances and covariances, respectively. Note that this is different from the assumption that the payoffs are in the form  $\delta$  times bounded random variables. As for the higher-order moments of the payoffs, they satisfy

$$E\left[\prod_{i=1}^4 |\eta_i|^{k_i}\right] = o(\delta), \tag{3}$$

for  $k_1 + k_2 + k_3 + k_4 \geq 3$  and  $k_1, k_2, k_3, k_4 \geq 0$ . It is assumed that  $\delta$  is small, so that  $o(\delta)$  terms can be neglected. Finally, the payoffs at a given time step are assumed to be independent of the payoffs at all other time steps. Such assumptions are current for selection parameters in random environments (see, e.g., Ewens [3, pp. 181–188] and references therein). Note that the inequalities  $\mu_3 > \mu_1 > \mu_4 > \mu_2$  and  $2\mu_1 > \mu_2 + \mu_3$  for the scaled means of the payoffs define a randomized Prisoner’s Dilemma (PD) game [15].

An example of payoffs satisfying the above conditions is given by  $\eta_2 = \eta_3 = \eta_4 = 0$  and  $\eta_1 = -\sigma_1 \sqrt{\delta} + \mu_1 \delta$  or  $\sigma_1 \sqrt{\delta} + \mu_1 \delta$  with the same probability  $1/2$ . Then, it is easy to check that  $E(\eta_1) = \delta \mu_1$  and  $E(\eta_1^2) = \sigma_1^2 \delta + o(\delta)$ , while

$$E(|\eta_1|^k) = C_k \times \delta^{k/2} + o(\delta^{k/2}) \tag{4}$$

for  $k \geq 3$ , where  $C_k$  is a constant that depends on  $\sigma_1$  and  $\mu_1$ .

Returning to the general model, pairwise interactions including self-interactions occur at random at each time step, and the payoff accumulated by an individual is translated into some reproductive fitness. More precisely, the reproductive fitness of an individual is given by a sum of a baseline term equal to 1 and the average payoff received by the individual. When the frequency of  $C$  in the whole population is  $x$ , the reproductive fitnesses of a cooperator and a defector, respectively, are

$$f_C(x) = 1 + P_C(x) = 1 + [x\eta_1 + (1 - x)\eta_2], \tag{5a}$$

$$f_D(x) = 1 + P_D(x) = 1 + [x\eta_3 + (1 - x)\eta_4]. \tag{5b}$$

Note that the reproductive fitnesses are positive random variables under the assumption of random payoffs that are less than 1 in absolute value. Moreover, the average reproductive

fitness is given by

$$\bar{f}(x) = x f_C(x) + (1 - x) f_D(x) = 1 + x P_C(x) + (1 - x) P_D(x) = 1 + \bar{P}(x), \quad (6)$$

where  $\bar{P}(x)$  is the average payoff in the whole population.

Finally, the update of the population from one time step to the next follows a Moran model. At each time step, an individual is selected with probability proportional to its reproductive fitness to give birth to an offspring. After reproduction, an individual is chosen at random to die, possibly the reproducing individual but not the new offspring.

### 3 Fixation Probabilities

Let  $X_n$  be the number of cooperators in the population at time step  $n \geq 0$ . From one time step to the next, there are three types of event that can happen:  $X_n$  increases by 1, decreases by 1, or remains the same. We denote by

$$T_i^+ = \mathbb{P}(X_{n+1} = i + 1 | X_n = i), \quad (7a)$$

$$T_i^- = \mathbb{P}(X_{n+1} = i - 1 | X_n = i), \quad (7b)$$

$$T_i^0 = \mathbb{P}(X_{n+1} = i | X_n = i), \quad (7c)$$

the different transition probabilities from time step  $n$  to time step  $n + 1$ , for  $i = 0, 1, \dots, N$ .

Note that  $X_n$  increases by 1 if a cooperator is selected to give birth to an offspring, which occurs with probability proportional to  $f_C(i/N)$ , and a defector is chosen to die, which occurs with probability  $1 - i/N$ . Therefore, we have

$$T_i^+ = \left(1 - \frac{i}{N}\right) E \left[ \frac{\frac{i}{N} f_C\left(\frac{i}{N}\right)}{\frac{i}{N} f_C\left(\frac{i}{N}\right) + \left(1 - \frac{i}{N}\right) f_D\left(\frac{i}{N}\right)} \right] = \frac{i}{N} \left(1 - \frac{i}{N}\right) E \left[ \frac{1 + P_C\left(\frac{i}{N}\right)}{1 + \bar{P}\left(\frac{i}{N}\right)} \right]. \quad (8)$$

Here,  $E$  denotes an expectation with respect to the probability distribution of the payoffs. Similarly,  $X_n$  decreases by 1 with probability

$$T_i^- = \frac{i}{N} E \left[ \frac{\left(1 - \frac{i}{N}\right) f_D\left(\frac{i}{N}\right)}{\frac{i}{N} f_C\left(\frac{i}{N}\right) + \left(1 - \frac{i}{N}\right) f_D\left(\frac{i}{N}\right)} \right] = \frac{i}{N} \left(1 - \frac{i}{N}\right) E \left[ \frac{1 + P_D\left(\frac{i}{N}\right)}{1 + \bar{P}\left(\frac{i}{N}\right)} \right]. \quad (9)$$

Finally,  $X_n$  does not change with probability  $T_i^0 = 1 - T_i^+ - T_i^-$ . The states 0 and  $N$  are absorbing since  $T_0^0 = T_N^0 = 1$ . The population spends some finite random time in the transient states  $1, \dots, N - 1$  before reaching one of the two absorbing states, 0 or  $N$ . (See, e.g., Karlin and Taylor [9] for properties of discrete-time birth–death Markov chains.)

Let

$$\tau = \min\{n \geq 0 : X_n = 0 \text{ or } N\} \quad (10)$$

be the absorbing time, so that  $X_\tau = 0$  or  $N$ , and

$$F_C = \mathbb{P}(X_\tau = N | X_0 = 1) \quad (11)$$

be the probability of ultimate fixation of  $C$  introduced as a single mutant in all  $D$  population. Analogously,

$$F_D = \mathbb{P}(X_\tau = 0 | X_0 = N - 1) \quad (12)$$

represents the probability of ultimate fixation of  $D$  introduced as a single mutant in an all  $C$  population.

It is known (see, e.g., Karlin and Taylor [9]) that

$$F_C = \frac{1}{1 + \sum_{j=1}^{N-1} \left( \prod_{i=1}^j \frac{T_i^-}{T_i^+} \right)}. \tag{13}$$

It is also known (see, e.g., Nowak et al. [19]) that

$$\frac{F_C}{F_D} = \prod_{i=1}^{N-1} \frac{T_i^+}{T_i^-}. \tag{14}$$

It remains to compute the products in these two expressions.

Using Eqs. (2) and (5), the first two moments of  $P_C(x)$  are found to be

$$E[P_C(x)] = [x\mu_1 + (1-x)\mu_2]\delta + o(\delta) \tag{15}$$

and

$$E[P_C^2(x)] = [x^2\sigma_1^2 + 2x(1-x)\sigma_{12} + (1-x)^2\sigma_2^2]\delta + o(\delta). \tag{16}$$

Analogously, the first two moments of  $P_D(x)$  are given by

$$E[P_D(x)] = [x\mu_3 + (1-x)\mu_4]\delta + o(\delta), \tag{17a}$$

$$E[P_D^2(x)] = [x^2\sigma_3^2 + 2x(1-x)\sigma_{34} + (1-x)^2\sigma_4^2]\delta + o(\delta). \tag{17b}$$

We have also

$$E[P_C(x)P_D(x)] = [x^2\sigma_{13} + x(1-x)(\sigma_{14} + \sigma_{23}) + (1-x)^2\sigma_{24}]\delta + o(\delta) \tag{18}$$

for the expected value of the product. Moreover, as shown in ‘‘Appendix A’’, we have

$$E\left[\frac{1 + P_C(x)}{1 + \bar{P}(x)}\right] = E\left[(1 + P_C(x))(1 - \bar{P}(x) + \bar{P}^2(x))\right] + o(\delta), \tag{19}$$

where  $\bar{P}(x) = xP_C(x) + (1-x)P_D(x)$ . Then, using Eqs. (15)–(18), we find

$$E\left[\frac{1 + P_C(x)}{1 + \bar{P}(x)}\right] = 1 + \delta m_1(x) + o(\delta), \tag{20}$$

where

$$\begin{aligned} m_1(x) = & x^4 [\sigma_1^2 + \sigma_2^2 + \sigma_3^2 + \sigma_4^2 + 2\sigma_{14} + 2\sigma_{23} - 2\sigma_{12} - 2\sigma_{13} - 2\sigma_{24} - 2\sigma_{34}] \\ & + x^3 [4\sigma_{12} + 3\sigma_{13} + 7\sigma_{24} + 6\sigma_{34} - \sigma_1^2 - 3\sigma_2^2 - 2\sigma_3^2 - 4\sigma_4^2 - 5\sigma_{14} - 5\sigma_{23}] \\ & + x^2 [3\sigma_2^2 + \sigma_3^2 + 6\sigma_4^2 + 4\sigma_{14} + 4\sigma_{23} - 2\sigma_{12} - \sigma_{13} - 9\sigma_{24} - 6\sigma_{34}] \\ & + x^2 [\mu_3 + \mu_2 - \mu_1 - \mu_4] \\ & + x [2\sigma_{34} + 5\sigma_{24} - \sigma_2^2 - 4\sigma_4^2 - \sigma_{14} - \sigma_{23} + \mu_1 - 2\mu_2 - \mu_3 + 2\mu_4] \\ & + \sigma_4^2 - \sigma_{24} + \mu_2 - \mu_4. \end{aligned} \tag{21}$$

Similarly, we find

$$E\left[\frac{1 + P_D(x)}{1 + \bar{P}(x)}\right] = 1 + \delta m_2(x) + o(\delta), \tag{22}$$

where

$$\begin{aligned}
 m_2(x) = & x^4 [\sigma_1^2 + \sigma_2^2 + \sigma_3^2 + \sigma_4^2 + 2\sigma_{14} + 2\sigma_{23} - 2\sigma_{12} - 2\sigma_{13} - 2\sigma_{24} - 2\sigma_{34}] \\
 & + x^3 [2\sigma_{12} + \sigma_{13} + 5\sigma_{24} + 4\sigma_{34} - 2\sigma_2^2 - \sigma_3^2 - 3\sigma_4^2 - 3\sigma_{14} - 3\sigma_{23}] \\
 & + x^2 [\sigma_2^2 + 3\sigma_4^2 + \sigma_{14} + \sigma_{23} - 2\sigma_{34} - 4\sigma_{24} + \mu_3 + \mu_2 - \mu_1 - \mu_4] \\
 & + x [\sigma_{24} - \sigma_4^2 + \mu_4 - \mu_2].
 \end{aligned} \tag{23}$$

Then, using these approximations in (8) and (9) leads to

$$\frac{T_i^+}{T_i^-} = \frac{1 + \delta m_1\left(\frac{i}{N}\right) + o(\delta)}{1 + \delta m_2\left(\frac{i}{N}\right) + o(\delta)} = 1 + \delta m\left(\frac{i}{N}\right) + o(\delta), \tag{24a}$$

$$\frac{T_i^-}{T_i^+} = \frac{1 + \delta m_2\left(\frac{i}{N}\right) + o(\delta)}{1 + \delta m_1\left(\frac{i}{N}\right) + o(\delta)} = 1 - \delta m\left(\frac{i}{N}\right) + o(\delta), \tag{24b}$$

where

$$m(x) = m_1(x) - m_2(x) = A_3x^3 + A_2x^2 + A_1x + A_0 \tag{25}$$

with

$$A_3 = 2\sigma_{12} + 2\sigma_{13} + 2\sigma_{24} + 2\sigma_{34} - \sigma_1^2 - \sigma_2^2 - \sigma_3^2 - \sigma_4^2 - 2\sigma_{14} - 2\sigma_{23}, \tag{26a}$$

$$A_2 = 2\sigma_2^2 + \sigma_3^2 + 3\sigma_4^2 + 3\sigma_{14} + 3\sigma_{23} - 2\sigma_{12} - \sigma_{13} - 5\sigma_{24} - 4\sigma_{34}, \tag{26b}$$

$$A_1 = 4\sigma_{24} + 2\sigma_{34} - \sigma_2^2 - 3\sigma_4^2 - \sigma_{14} - \sigma_{23} + \mu_1 - \mu_2 - \mu_3 + \mu_4, \tag{26c}$$

$$A_0 = \sigma_4^2 - \sigma_{24} + \mu_2 - \mu_4. \tag{26d}$$

Finally, using all this in (13) and (14) yields

$$F_C = \frac{1}{N} + \frac{\delta}{N^2} \sum_{i=1}^{N-1} (N-i)m\left(\frac{i}{N}\right) + o(\delta), \tag{27}$$

where (see ‘‘Appendix B’’)

$$\sum_{i=1}^{N-1} (N-i)m\left(\frac{i}{N}\right) = \frac{N^2 - 1}{2} \left[ \frac{3N^2 - 2}{30N^2} A_3 + \frac{A_2 + 2A_1}{6} + \frac{N}{N+1} A_0 \right], \tag{28}$$

and

$$\frac{F_C}{F_D} = 1 + \delta \sum_{i=1}^{N-1} m\left(\frac{i}{N}\right) + o(\delta), \tag{29}$$

where (see ‘‘Appendix B’’)

$$\sum_{i=1}^{N-1} m\left(\frac{i}{N}\right) = (N-1) \left[ \frac{N-1}{4N} A_3 + \frac{2N-1}{6N} A_2 + \frac{A_1}{2} + A_0 \right]. \tag{30}$$

These expressions give first-order approximations for  $F_C$  and  $F_C/F_D$  with respect to the magnitude of selection.

It is worth noting that  $m(x)$  can be written as

$$m(x) = \sum_{k=0}^3 (a_k - b_k) \binom{3}{k} x^k (1-x)^{3-k}, \tag{31}$$

where

$$a_0 = \mu_2 - \sigma_{24}, \tag{32a}$$

$$b_0 = \mu_4 - \sigma_4^2, \tag{32b}$$

$$a_1 = \frac{\mu_1 + 2\mu_2 - \sigma_{14} - \sigma_{23} - \sigma_2^2}{3}, \tag{32c}$$

$$b_1 = \frac{\mu_3 + 2\mu_4 - \sigma_{24} - 2\sigma_{34}}{3}, \tag{32d}$$

$$a_2 = \frac{2\mu_1 + \mu_2 - \sigma_{13} - 2\sigma_{12}}{3}, \tag{32e}$$

$$b_2 = \frac{2\mu_3 + \mu_4 - \sigma_{14} - \sigma_{23} - \sigma_3^2}{3}, \tag{32f}$$

$$a_3 = \mu_1 - \sigma_1^2, \tag{32g}$$

$$b_3 = \mu_3 - \sigma_{13}. \tag{32h}$$

Therefore, our two-player game with random payoffs is equivalent in the limit of weak selection to a four-player game with constant payoffs. In interaction with  $i$  cooperators and  $3 - i$  defectors, a cooperator in this four-player game receives a payoff  $a_i$  while a defector receives a payoff  $b_i$ . This game is summarized in the following table. Note the symmetries in the payoffs.

Opposing $C$ players	0	1	2	3
$C$	$\mu_2 - \sigma_{24}$	$\frac{\mu_1 + 2\mu_2 - \sigma_{14} - \sigma_{23} - \sigma_2^2}{3}$	$\frac{2\mu_1 + \mu_2 - \sigma_{13} - 2\sigma_{12}}{3}$	$\mu_1 - \sigma_1^2$
$D$	$\mu_4 - \sigma_4^2$	$\frac{\mu_3 + 2\mu_4 - \sigma_{24} - 2\sigma_{34}}{3}$	$\frac{2\mu_3 + \mu_4 - \sigma_{14} - \sigma_{23} - \sigma_3^2}{3}$	$\mu_3 - \sigma_{13}$

### 4 Conditions for the Evolution of Cooperation

In finite populations in the absence of recurrent mutation, three conditions have been proposed to characterize the effects of selection on the evolution of cooperation. The first two conditions are based on comparisons of fixation probabilities for  $C$  and  $D$  in the presence of selection to what they would be in the absence of selection. We say that *selection favors the evolution of cooperation* if  $F_C > N^{-1}$  [19]. Here,  $N^{-1}$  is the probability of ultimate fixation of  $C$  when represented only once in a population of size  $N$  under neutrality, while  $F_C$  is the corresponding probability under selection. Analogously, we say that *selection disfavors the evolution of defection* if  $F_D < N^{-1}$ . Selection may favor the evolution of cooperation and defection,  $F_C > N^{-1}$  and  $F_D > N^{-1}$ , or may disfavor the evolution of cooperation and defection,  $F_C < N^{-1}$  and  $F_D < N^{-1}$ . To have a complete view of the evolutionary success of cooperation, a third condition has been introduced [5,19]. We say that *selection favors the evolution of cooperation more than the evolution of defection* if  $F_C > F_D$ . In this case, the ultimate fixation of a single  $C$  is more likely than the ultimate fixation of a single  $D$ . Finally, if selection favors the evolution of cooperation and disfavors the evolution of defection, that is,  $F_C > N^{-1} > F_D$ , we say that *selection fully favors the evolution of cooperation* [15].



Owing to Eq. (27),  $F_C > N^{-1}$  and weak selection favors the evolution of cooperation if

$$\frac{3N^2 - 2}{30N^2}A_3 + \frac{A_2 + 2A_1}{6} + \frac{N}{N + 1}A_0 > 0. \tag{33}$$

In terms of the scaled means, variances and covariances of the payoffs, the above condition can be written as

$$\begin{aligned} & \frac{1}{3(N + 1)} \left[ (N + 1)\mu_1 + (2N - 1)\mu_2 - (N + 1)\mu_3 - (2N - 1)\mu_4 \right] \\ & - \frac{3N^2 - 2}{30N^2} (\sigma_1^2 + \sigma_2^2) - \frac{2(N^2 + 1)}{15N^2} \sigma_{12} + \frac{N^2 + 1}{15N^2} \sigma_3^2 + \frac{3N^2 - 2}{15N^2} \sigma_{34} \\ & + \frac{(2N - 1)(3N^2 - 3N - 1)}{15N^2(N + 1)} \sigma_4^2 + \frac{N^2 - 4}{30N^2} (\sigma_{13} - \sigma_{14} - \sigma_{23}) \\ & - \frac{(N - 2)(3N + 1)(3N - 2)}{30N^2(N + 1)} \sigma_{24} > 0. \end{aligned} \tag{34}$$

If the inequality is reversed, weak selection disfavors the evolution of cooperation, that is,  $F_C < N^{-1}$ . By symmetry,  $F_D < N^{-1}$  if the inequality is reversed and the indices 1 and 4 as well as 2 and 3 are permuted. This gives the condition

$$\begin{aligned} & \frac{1}{3(N + 1)} \left[ (N + 1)\mu_4 + (2N - 1)\mu_3 - (N + 1)\mu_2 - (2N - 1)\mu_1 \right] \\ & - \frac{3N^2 - 2}{30N^2} (\sigma_4^2 + \sigma_3^2) - \frac{2(N^2 + 1)}{15N^2} \sigma_{34} + \frac{(2N - 1)(3N^2 - 3N - 1)}{15N^2(N + 1)} \sigma_1^2 \\ & + \frac{N^2 + 1}{15N^2} \sigma_2^2 + \frac{3N^2 - 2}{15N^2} \sigma_{12} + \frac{N^2 - 4}{30N^2} (\sigma_{24} - \sigma_{14} - \sigma_{23}) \\ & - \frac{(N - 2)(3N + 1)(3N - 2)}{30N^2(N + 1)} \sigma_{13} < 0 \end{aligned} \tag{35}$$

for weak selection to disfavor the evolution of defection.

Note that the left-hand members in conditions (34) and (35) are the coefficients of  $\delta$  times  $(N^2 - 1)/(2N^2)$  in the approximations of  $F_C$  and  $F_D$ , respectively. The fixation probability of a strategy is not only driven positively by the means of the payoffs received by the individuals using this strategy as shown in classical studies with constant payoffs but also driven negatively by their variances and covariances in the case of random fluctuations in the payoffs. Less uncertainty in the payoffs to  $C$  or more uncertainty in the payoffs to  $D$  will increase the fixation probability of  $C$  as a single mutant and decrease the fixation probability of  $D$  as a single mutant, which plays in favor of the evolution of  $C$  in any sense. The best strategy has large average payoffs with low uncertainty, and the effect of lowering an average payoff can be compensated by lowering uncertainty as well.

Considering the signs of the coefficients of the different variances and covariances in these expressions, we can draw the following conclusions.

**Result 1** *An increase in the variance of any payoff to  $D$  against  $C$  or  $D$ ,  $\sigma_3^2$  or  $\sigma_4^2$ , their covariance,  $\sigma_{34}$ , or the covariance between the payoff to  $C$  against  $C$  and the payoff to  $D$  against  $C$ ,  $\sigma_{13}$ , will increase the probability of ultimate fixation of a single  $C$  and decrease the probability of ultimate fixation of a single  $D$  at least if selection is weak enough*

**Result 2** *An increase in the variance of any payoff to  $C$  against  $C$  or  $D$ ,  $\sigma_1^2$  or  $\sigma_2^2$ , their covariance,  $\sigma_{12}$ , or the covariance between the payoff to  $C$  against  $C$  and the payoff to  $D$*

against  $D$ ,  $\sigma_{24}$ , will decrease the probability of ultimate fixation of a single  $C$  and increase the probability of ultimate fixation of a single  $D$  at least if selection is weak enough

Another observation is that the coefficient of  $\sigma_{14}$  or  $\sigma_{23}$  in (34) is the same as the coefficient of  $\sigma_{14}$  or  $\sigma_{23}$  in (35). This leads to the following complementary conclusion.

**Result 3** *An increase in the covariance between the payoff to  $C$  against  $C$  and the payoff to  $D$  against  $D$ ,  $\sigma_{14}$ , or an increase in the covariance between the payoff to  $C$  against  $D$  and the payoff to  $D$  against  $C$ ,  $\sigma_{23}$ , will decrease both the probabilities of ultimate fixation of a single  $C$  and a single  $D$  at the same rate if selection is weak enough.*

Results 1 and 2 extend results obtained by Li and Lessard [15] for a Wright–Fisher model in the limit of a large population size to a Moran model with a fixed population size. They assumed that the fluctuations of the payoffs are of order proportional to the inverse of the population size. In that paper, using a diffusion approximation in the case of independent payoffs with  $\delta = N^{-1}$  in a Wright–Fisher population of large size  $N$ , it was shown that an increase in  $\sigma_3^2$  or  $\sigma_4^2$  or a decrease in  $\sigma_1^2$  or  $\sigma_2^2$  will increase the probability of ultimate fixation of a single  $C$  and decrease the probability of ultimate fixation of a single  $D$ . Results 1 and 2 show the same in the case of weak selection in a Moran population of any fixed size  $N$  and furthermore point out the effects of increasing or decreasing covariances of dependent payoffs.

Another point of interest is to know which strategy is more favored by weak selection. Owing to (29), weak selection favors the evolution of cooperation more than the evolution of defection, that is,  $F_C > F_D$ , if

$$\frac{N - 1}{4N} A_3 + \frac{2N - 1}{6N} A_2 + \frac{A_1}{2} + A_0 > 0. \tag{36}$$

In terms of the scaled means, variances and covariances of the payoffs, this condition can be written as

$$\begin{aligned} &\mu_1 + \mu_2 - \mu_3 - \mu_4 + \frac{N - 1}{2N} (\sigma_4^2 - \sigma_1^2) + \frac{N + 1}{6N} (\sigma_3^2 - \sigma_2^2) \\ &+ \frac{N + 1}{3N} (\sigma_{34} - \sigma_{12}) + \frac{N - 2}{3N} (\sigma_{13} - \sigma_{24}) > 0. \end{aligned} \tag{37}$$

If the inequality is reversed, weak selection favors the evolution of defection more than the evolution of cooperation, that is,  $F_C < F_D$ . It is clear that a decrease in any term among  $\{\sigma_1^2, \sigma_2^2, \sigma_{12}, \sigma_{24}\}$  or an increase in any term among  $\{\sigma_3^2, \sigma_4^2, \sigma_{13}, \sigma_{34}\}$  makes it easier for weak selection to favor more the evolution of cooperation than the evolution of defection. This is in agreement with Results 1 and 2. Moreover, it is clear that neither  $\sigma_{14}$  nor  $\sigma_{23}$  has an effect on the condition  $F_C > F_D$  since they do not come into play in (37). Note that this conclusion is in agreement with a result obtained by Kroumi and Lessard [10] in the case of a large well-mixed population in the presence of symmetric mutation, that is, neither  $\sigma_{14}$  nor  $\sigma_{23}$  comes into play in the condition for weak selection to favor the abundance of  $C$  more than the abundance of  $D$  for any mutation rate.

For a large population, conditions (34), (35) and (37), for  $F_C > N^{-1}$ ,  $F_D < N^{-1}$  and  $F_C > F_D$ , respectively, take the forms

$$\begin{aligned} &\frac{1}{3} \left[ \mu_1 + 2\mu_2 - \mu_3 - 2\mu_4 \right] - \frac{1}{10} \sigma_1^2 - \frac{1}{10} \sigma_2^2 - \frac{2}{15} \sigma_{12} + \frac{1}{15} \sigma_3^2 + \frac{2}{5} \sigma_4^2 \\ &+ \frac{1}{5} \sigma_{34} + \frac{1}{30} \sigma_{13} - \frac{1}{30} \sigma_{14} - \frac{1}{30} \sigma_{23} - \frac{3}{10} \sigma_{24} > 0, \end{aligned} \tag{38}$$

$$\begin{aligned} & \frac{1}{3} \left[ 2\mu_1 + \mu_2 - 2\mu_3 - \mu_4 \right] - \frac{2}{5}\sigma_1^2 - \frac{1}{15}\sigma_2^2 - \frac{1}{5}\sigma_{12} + \frac{1}{10}\sigma_3^2 + \frac{1}{10}\sigma_4^2 \\ & + \frac{2}{15}\sigma_{34} + \frac{1}{30}\sigma_{14} + \frac{1}{30}\sigma_{23} - \frac{1}{30}\sigma_{24} + \frac{3}{10}\sigma_{13} > 0 \end{aligned} \tag{39}$$

and

$$\begin{aligned} & \mu_1 + \mu_2 - \mu_3 - \mu_4 - \frac{1}{2}\sigma_1^2 - \frac{1}{6}\sigma_2^2 - \frac{1}{3}\sigma_{12} + \frac{1}{6}\sigma_3^2 + \frac{1}{2}\sigma_4^2 \\ & + \frac{1}{3}\sigma_{34} + \frac{1}{3}\sigma_{13} - \frac{1}{3}\sigma_{24} > 0, \end{aligned} \tag{40}$$

respectively. Note that (40) is also the condition for weak selection to favor the abundance of *C* more than the abundance of *D* in the mutation–selection equilibrium in a large well-mixed population for a low mutation rate [10].

### 5 Additive Prisoner’s Dilemma

In this section, we consider a two-player game with random payoffs  $\eta_1, \eta_2, \eta_3$  and  $\eta_4$  whose scaled means determine a Prisoner’s Dilemma in the additive form

$$\begin{pmatrix} \mu_1 & \mu_2 \\ \mu_3 & \mu_4 \end{pmatrix} = \begin{pmatrix} \mu_b - \mu_c & -\mu_c \\ \mu_b & 0 \end{pmatrix}, \tag{41}$$

where  $\mu_b > \mu_c > 0$ . Here,  $\mu_b$  and  $\mu_c$  are scaled mean benefit and cost for cooperation. We analyze below five special cases according to supplementary properties of the payoffs.

Note that, in the case of a deterministic Prisoner’s Dilemma (PD), where all the payoffs are constant, cooperation can never be favored by weak selection. This can be changed by introducing uncertainty in the payoffs. In the first two subsections, we compare the effect of uncertainty in the payoff to *D* against *C* (Case 1) to the effect of uncertainty in the payoff to *D* against *D* (Case 2). In the next subsection (Case 3), we study the effect of correlation with special attention to extreme cases ( $\rho = 0, -1, 1$ ). In the next subsection (Case 4), we introduce uncertainty in the payoffs to *C*. In the last subsection (Case 5), we consider a PD game with random benefit *b* and cost *c*.

#### 5.1 Case 1: $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = 0, \sigma_4^2 = \sigma^2$

This is a situation where only the payoff to *D* against *D* has a positive variance. In this case, condition (34) for weak selection to favor the evolution of cooperation,  $F_C > N^{-1}$ , can be written as

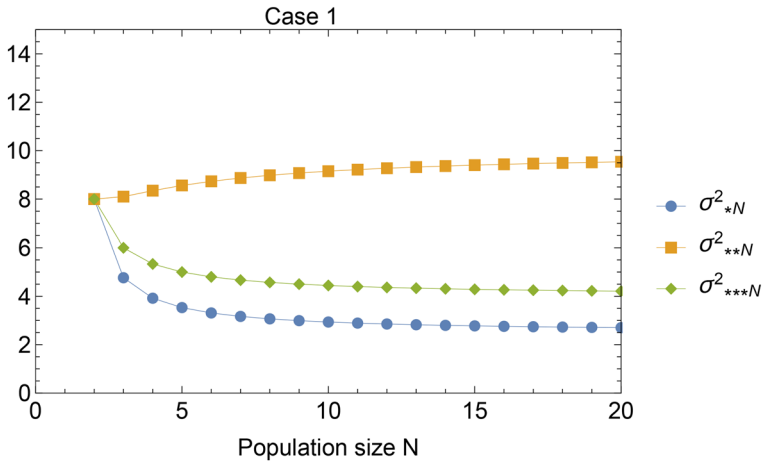
$$\sigma^2 > \sigma_{*N}^2 = \frac{15N^3}{(2N - 1)(3N^2 - 3N - 1)}\mu_c, \tag{42}$$

while condition (35) for weak selection to disfavor the evolution of defection,  $F_D < N^{-1}$ , becomes

$$\sigma^2 > \sigma_{**N}^2 = \frac{30N^3}{(N + 1)(3N^2 - 2)}\mu_c. \tag{43}$$

Finally, in accordance with (37), weak selection favors the evolution of cooperation more than the evolution of defection,  $F_C > F_D$ , as long as

$$\sigma^2 > \sigma_{***N}^2 = \frac{4N}{N - 1}\mu_c. \tag{44}$$



**Fig. 1** Exact values of the thresholds  $\sigma^2_{*N}$ ,  $\sigma^2_{**N}$  and  $\sigma^2_{***N}$  for the scaled variance  $\sigma^2$  in Case 1 as functions of the population size  $N$  when  $\mu_c = 1$ . Note that  $\sigma^2_{*N}$  and  $\sigma^2_{***N}$  are decreasing while  $\sigma^2_{**N}$  is increasing. Moreover, we have the inequalities  $\sigma^2_{***N} > \sigma^2_{**N} > \sigma^2_{*N}$  for  $N \geq 3$

Note that

$$\frac{d}{dx} \left( \frac{15x^3}{(2x - 1)(3x^2 - 3x - 1)} \right) = - \frac{5x^2 (9x - 1 - \sqrt{28})(9x - 1 + \sqrt{28})}{3(2x - 1)^2(3x^2 - 3x - 1)^2} < 0, \tag{45a}$$

$$\frac{d}{dx} \left( \frac{30x^3}{(x + 1)(3x^2 - 2)} \right) = \frac{10x^2 (3x - 2 - \sqrt{22})(3x - 2 + \sqrt{22})}{(x + 1)^2(3x^2 - 2)^2} > 0, \tag{45b}$$

$$\frac{d}{dx} \left( \frac{4x}{x - 1} \right) = - \frac{4}{(x - 1)^2} < 0, \tag{45c}$$

for  $x \geq 3$ . Therefore, increasing the population size  $N$  decreases the thresholds  $\sigma^2_{*N}$  and  $\sigma^2_{***N}$ , and increases the threshold  $\sigma^2_{**N}$ . Figure 1 illustrates this conclusion. This means that the conditions for  $F_C > N^{-1}$  and  $F_C > F_D$  become less stringent as  $N$  increases, while the condition for  $F_D < N^{-1}$  becomes more stringent.

Note also that

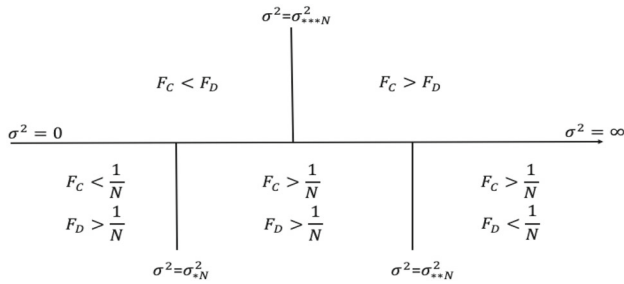
$$\sigma^2_{**N} - \sigma^2_{***N} = \frac{2N(N - 2)(3N + 1)(3N - 2)}{(N + 1)(N - 1)(3N^2 - 2)} \mu_c > 0, \tag{46a}$$

$$\sigma^2_{***N} - \sigma^2_{*N} = \frac{N(N - 2)(3N + 1)(3N - 2)}{(N - 1)(2N - 1)(3N^2 - 3N - 1)} \mu_c > 0, \tag{46b}$$

$$\sigma^2_{*N} - \mu_c = \frac{(N + 1)(3N + 1)(3N - 1)}{(2N - 1)(3N^2 - 3N - 1)} \mu_c > 0, \tag{46c}$$

for  $N \geq 3$ . In this case, we have the inequalities  $\sigma^2_{**N} > \sigma^2_{***N} > \sigma^2_{*N} > \mu_c$ . As a result, increasing the variance of the payoff to  $D$  against  $D$  will make it easier for weak selection to fully favor the evolution of cooperation,  $F_C > N^{-1} > F_D$ .

Let us summarize these findings.



**Fig. 2** Relationships between  $\sigma_{*N}^2$ ,  $\sigma_{**N}^2$ ,  $\sigma_{***N}^2$  and  $F_C$ ,  $F_D$  in Cases 1 and 3. The regions where  $F_C$  and  $F_D$  are larger or smaller than  $N^{-1}$ , and where  $F_C$  is larger or smaller than  $F_D$ , are given according to the position of  $\sigma^2$  with respect to the threshold values  $\sigma_{*N}^2$ ,  $\sigma_{**N}^2$  and  $\sigma_{***N}^2$

**Conclusion in Case 1**

- If  $\sigma^2 < \sigma_{*N}^2$ , then  $F_C < N^{-1} < F_D$ .
- If  $\sigma_{*N}^2 < \sigma^2 < \sigma_{**N}^2$ , then  $N^{-1} < F_C < F_D$ .
- If  $\sigma_{**N}^2 < \sigma^2 < \sigma_{***N}^2$ , then  $N^{-1} < F_D < F_C$ .
- If  $\sigma_{***N}^2 < \sigma^2$ , then  $F_D < N^{-1} < F_C$ .

This is valid for a population of any finite size  $N \geq 3$ . Note that it is impossible for weak selection to disfavor the evolution of both cooperation and defection, that is,  $F_C < N^{-1}$  and  $F_D < N^{-1}$  are not compatible.

This conclusion is illustrated in Fig. 2. In the limit of a large population size, we have

$$\sigma_*^2 = \lim_{N \rightarrow \infty} \sigma_{*N}^2 = \frac{5}{2} \mu_c, \tag{47a}$$

$$\sigma_{**}^2 = \lim_{N \rightarrow \infty} \sigma_{**N}^2 = 10 \mu_c, \tag{47b}$$

$$\sigma_{***}^2 = \lim_{N \rightarrow \infty} \sigma_{***N}^2 = 4 \mu_c. \tag{47c}$$

**5.2 Case 2:  $\sigma_1^2 = \sigma_2^2 = \sigma_4^2 = 0$ ,  $\sigma_3^2 = \sigma^2$**

This is a situation where only the payoff to  $D$  against  $C$  has a positive variance. In this case and in accordance with condition (34), (35) and (37), the conditions for  $F_C > N^{-1}$ ,  $F_D < N^{-1}$  and  $F_C > F_D$  can be written as

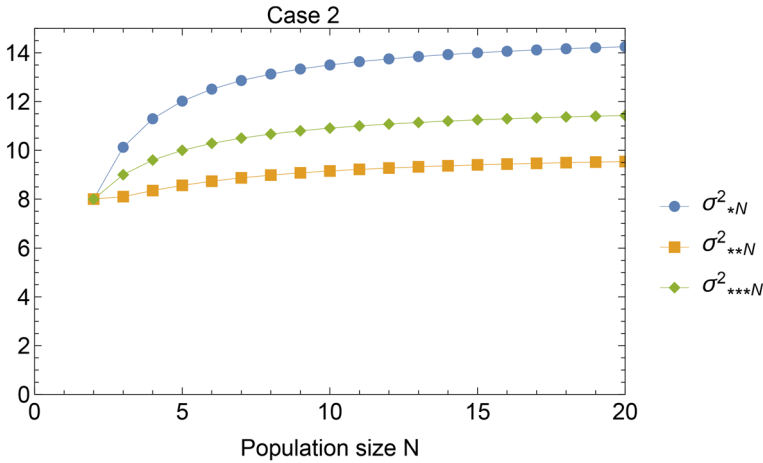
$$\sigma^2 > \sigma_{*N}^2, \sigma^2 > \sigma_{**N}^2, \sigma^2 > \sigma_{***N}^2, \tag{48}$$

respectively, where

$$\sigma_{*N}^2 = \frac{15N^3}{(N^2 + 1)(N + 1)} \mu_c, \tag{49a}$$

$$\sigma_{**N}^2 = \frac{30N^3}{(N + 1)(3N^2 - 2)} \mu_c, \tag{49b}$$

$$\sigma_{***N}^2 = \frac{12N}{N + 1} \mu_c. \tag{49c}$$



**Fig. 3** Exact values of the thresholds  $\sigma_{*N}^2, \sigma_{**N}^2$  and  $\sigma_{***N}^2$  for the scaled variance  $\sigma^2$  in Case 2 as functions of the population size  $N$  when  $\mu_c = 1$ . Note that  $\sigma_{*N}^2, \sigma_{**N}^2$  and  $\sigma_{***N}^2$  are increasing. Moreover, we have the inequalities  $\sigma_{*N}^2 > \sigma_{**N}^2 > \sigma_{***N}^2 > 1$  for  $N \geq 3$

Note that

$$\frac{d}{dx} \left( \frac{15x^3}{(x^2 + 1)(x + 1)} \right) = \frac{15x^2(x^2 + 2x + 3)}{(x^2 + 1)^2(x + 1)^2} > 0, \tag{50a}$$

$$\frac{d}{dx} \left( \frac{30x^3}{(x + 1)(3x^2 - 2)} \right) = \frac{10x^2(3x - 2 - \sqrt{22})(3x - 2 + \sqrt{22})}{(x + 1)^2(3x^2 - 2)^2} > 0, \tag{50b}$$

$$\frac{d}{dx} \left( \frac{12x}{x + 1} \right) = \frac{12}{(x + 1)^2} > 0, \tag{50c}$$

for  $x \geq 3$ . Therefore, increasing the population size  $N$  increases the thresholds  $\sigma_{*N}^2, \sigma_{**N}^2$  and  $\sigma_{***N}^2$ . Figure 3 illustrates this conclusion. This means that the conditions for weak selection to favor the evolution of cooperation, disfavor the evolution of defection, and favor the evolution of cooperation more than the evolution of defection become more stringent as  $N$  increases. The best scenario for the evolution of cooperation in any sense is a population of small size.

By a simple comparison, we find that

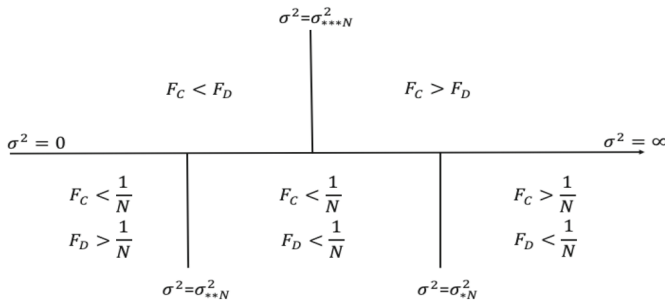
$$\sigma_{*N}^2 - \sigma_{***N}^2 = \frac{3N(N + 2)(N - 2)}{(N + 1)(N^2 + 1)} \mu_c > 0, \tag{51a}$$

$$\sigma_{***N}^2 - \sigma_{**N}^2 = \frac{6N(N + 2)(N - 2)}{(N + 1)(3N^2 - 2)} \mu_c > 0, \tag{51b}$$

$$\sigma_{**N}^2 - \mu_c = \frac{(3N + 1)(N(9N - 4) + 2)}{(N + 1)(3N^2 - 2)} \mu_c > 0, \tag{51c}$$

for  $N \geq 3$ . Therefore, we have  $\sigma_{*N}^2 > \sigma_{***N}^2 > \sigma_{**N}^2 > \mu_c$  for  $N \geq 3$ . As a result, we can draw the following conclusion as illustrated in Fig. 4.

**Conclusion in Case 2**



**Fig. 4** Relationships between  $\sigma_{*N}^2, \sigma_{**N}^2, \sigma_{***N}^2$  and  $F_C, F_D$  in Case 2. The regions where  $F_C$  and  $F_D$  are larger or smaller than  $N^{-1}$ , and where  $F_C$  is larger or smaller than  $F_D$ , are given according to the position of  $\sigma^2$  with respect to the threshold values  $\sigma_{**N}^2, \sigma_{***N}^2$  and  $\sigma_{*N}^2$

- If  $\sigma^2 < \sigma_{**N}^2$ , then  $F_C < N^{-1} < F_D$ .
- If  $\sigma_{**N}^2 < \sigma^2 < \sigma_{***N}^2$ , then  $F_C < F_D < N^{-1}$ .
- If  $\sigma_{***N}^2 < \sigma^2 < \sigma_{*N}^2$ , then  $F_D < F_C < N^{-1}$ .
- If  $\sigma_{*N}^2 < \sigma^2$ , then  $F_D < N^{-1} < F_C$ .

This is valid for any population size  $N \geq 3$ . Note that it is impossible for weak selection to favor the evolution of both cooperation and defection, that is,  $F_C > N^{-1}$  and  $F_D > N^{-1}$  are not compatible.

Comparing the probabilities of ultimate fixation of a single  $C$  and a single  $D$  in Cases 1 and 2 for a population size  $N$  yields

$$F_C^{\text{case1}} - F_C^{\text{case2}} = \delta \frac{(N - 1)(N - 2)}{6N^2} \sigma^2 + o(\delta), \tag{52a}$$

$$F_D^{\text{case1}} - F_D^{\text{case2}} = o(\delta). \tag{52b}$$

Therefore, it is more favorable for the evolution of cooperation to increase the variance of the payoff to  $D$  against  $D$ ,  $\sigma_4^2$ , than the variance of the payoff to  $D$  against  $C$ ,  $\sigma_3^2$ .

Finally, in the limit of a large population size, we have

$$\sigma_*^2 = \lim_{N \rightarrow \infty} \sigma_{*N}^2 = 15\mu_c, \tag{53a}$$

$$\sigma_{**}^2 = \lim_{N \rightarrow \infty} \sigma_{**N}^2 = 10\mu_c, \tag{53b}$$

$$\sigma_{***}^2 = \lim_{N \rightarrow \infty} \sigma_{***N}^2 = 12\mu_c. \tag{53c}$$

### 5.3 Case 3: $\sigma_1^2 = \sigma_2^2 = 0, \sigma_3^2 = \sigma_4^2 = \sigma^2 > 0, \sigma_{34} = \rho\sigma^2$

This is a situation where only the variances of the payoffs to  $D$  against  $C$  and  $D$  are positive and exhibit a correlation coefficient  $\rho$ . In accordance with (34), (35) and (37), the conditions

$$\sigma^2 > \sigma_{*N}^2, \sigma^2 > \sigma_{**N}^2, \sigma^2 > \sigma_{***N}^2, \tag{54}$$

entail  $F_C > N^{-1}, F_D < N^{-1}$  and  $F_C > F_D$ , respectively, under weak selection. Here, we have

$$\sigma_{*N}^2 = \frac{15N^3}{(N + 1)(3N^2 - 2)\rho + 7N^3 - 8N^2 + 2N + 2} \mu_c, \tag{55a}$$

$$\sigma_{**N}^2 = \frac{15N^3}{(N + 1)(2(N^2 + 1)\rho + 3N^2 - 2)}\mu_c, \tag{55b}$$

$$\sigma_{***N}^2 = \frac{6N}{(N + 1)\rho + 2N - 1}\mu_c. \tag{55c}$$

Note that increasing  $\rho$  decreases these thresholds for any fixed population size  $N \geq 2$ . This means that the conditions for  $F_C > N^{-1}$ ,  $F_D < N^{-1}$  and  $F_C > F_D$  become less stringent as  $\rho$  increases. This plays in favor of the evolution of cooperation and in disfavor of the evolution of defection.

In addition, we have

$$\sigma_{**N}^2(\rho) - \sigma_{***N}^2(\rho) \geq \sigma_{**N}^2(-1) - \sigma_{***N}^2(1) = \frac{N^2(13N - 2) + 8N + 8}{(N + 1)(N + 2)(N - 2)}\mu_c > 0, \tag{56a}$$

$$\sigma_{***N}^2(\rho) - \sigma_{*N}^2(\rho) \geq \sigma_{***N}^2(-1) - \sigma_{*N}^2(1) = \frac{9N^2}{(N - 2)(2N - 1)}\mu_c > 0, \tag{56b}$$

$$\sigma_{*N}^2(\rho) - \mu_c \geq \sigma_{*N}^2(-1) - \mu_c = \frac{(N + 1)(11N^2 - 4)}{(N - 2)(4N^2 - 3N - 2)}\mu_c > 0, \tag{56c}$$

for any  $N \geq 3$ . Here, we have used the fact the  $\sigma_{*N}$ ,  $\sigma_{**N}$  and  $\sigma_{***N}$  are decreasing as functions of  $\rho$ . This yields

$$\sigma_{**N}^2 > \sigma_{***N}^2 > \sigma_{*N}^2 > \mu_c, \tag{57}$$

for  $N \geq 3$  and  $\rho \in [-1, 1]$ . Therefore, the conclusion in Case 1 and Figs. 1 and 2 are still valid in Case 3, but with the new threshold values.

In the limit of a large population size, we have

$$\sigma_*^2 = \lim_{N \rightarrow \infty} \sigma_{*N}^2 = \frac{15}{3\rho + 7}\mu_c, \tag{58a}$$

$$\sigma_{**}^2 = \lim_{N \rightarrow \infty} \sigma_{**N}^2 = \frac{15}{2\rho + 3}\mu_c, \tag{58b}$$

$$\sigma_{***}^2 = \lim_{N \rightarrow \infty} \sigma_{***N}^2 = \frac{6}{\rho + 2}\mu_c. \tag{58c}$$

Comparing the probabilities of ultimate fixation of a single  $C$  and a single  $D$  in Cases 1 and 3 for a large population yields

$$F_C^{\text{case3}} - F_C^{\text{case1}} = \delta \frac{3\rho + 1}{30}\sigma^2 + o(\delta), \tag{59a}$$

$$F_D^{\text{case3}} - F_D^{\text{case1}} = -\delta \frac{4\rho + 3}{30}\sigma^2 + o(\delta). \tag{59b}$$

If the correlation coefficient between the payoff to  $D$  against  $C$  and the payoff to  $D$  against  $D$  satisfies the inequality  $\rho > -1/3$ , then the fixation probability of  $C$  in Case 3 exceeds the fixation probability of  $C$  in Case 1, that is,  $F_C^{\text{case3}} > F_C^{\text{case1}}$ , and the fixation probability of  $D$  in Case 1 exceeds the fixation probability of  $D$  in Case 3, that is,  $F_D^{\text{case3}} < F_D^{\text{case1}}$ . Combining these results with the facts that  $F_C^{\text{case1}} > F_C^{\text{case2}}$  and  $F_D^{\text{case1}} \approx F_D^{\text{case2}}$  (see Eq. (52)), it is more favorable for the evolution of cooperation in any sense to increase both variances  $\sigma_3^2$  and  $\sigma_4^2$  than only one of these. This is the case, for instance, when the payoffs to  $D$  against  $C$  and  $D$  are uncorrelated, that is,  $\rho = 0$ , or in perfect positive correlation, that is,  $\rho = 1$ .



Suppose now that the payoffs  $\eta_3$  and  $\eta_4$  are in perfect negative correlation, that is,  $\rho = -1$ . In this case, we have  $F_C^{\text{case1}} > F_C^{\text{case3}} > F_C^{\text{case2}}$  and  $F_D^{\text{case1}} \approx F_D^{\text{case2}} < F_D^{\text{case3}}$ . Then, Case 1 is the best scenario for the evolution of cooperation in any sense. The worst scenario for the evolution of cooperation is Case 2, while the best scenario for the evolution of defection is Case 3.

**5.4 Case 4:  $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = \sigma_4^2 = \sigma^2 > 0, \sigma_{34} = \rho\sigma^2$**

Here, we assume that the payoffs have the same positive variance  $\sigma^2$ . Moreover, they are all uncorrelated except  $\eta_3$  and  $\eta_4$  whose correlation coefficient is  $\rho$ . Then, in accordance with condition (34), weak selection favors the evolution of cooperation,  $F_C > N^{-1}$ , as long as

$$\sigma^2 > \sigma_{*N}^2 = \frac{15N^3}{(3N^2 - 2)(N + 1)\rho + (N - 2)(4N^2 - 3N - 2)}\mu_c. \tag{60}$$

Note that condition (35) for  $F_D < N^{-1}$  is violated for all  $\rho \in [-1, 1]$  as soon as  $N \geq 13$ , which means that weak selection can only favor the evolution of defection in this case. On the other hand, for  $N < 13$ , weak selection disfavors the evolution of defection if

$$\sigma^2 > \sigma_{**N}^2 = \frac{15N^3}{2(N^2 + 1)(N + 1)\rho - (N - 2)(4N^2 - 3N - 2)}\mu_c. \tag{61}$$

Finally, condition (37) for  $F_C > F_D$  takes the form

$$\sigma^2 > \sigma_{***N}^2 = \frac{6N}{(N + 1)\rho}\mu_c, \tag{62}$$

but only if  $\rho > 0$ . If  $\rho \leq 0$ , condition (37) can never be satisfied. In this case,  $\sigma_{***N}^2$  does not exist and the evolution of defection is always favored more than the evolution of cooperation. This is the case when the payoffs to  $D$  against  $C$  and  $D$  have a perfect negative correlation, that is,  $\rho = -1$ , or are uncorrelated, that is,  $\rho = 0$ .

Note that in the limit of a large population size, we have

$$\sigma_*^2 = \lim_{N \rightarrow \infty} \sigma_{*N}^2 = \frac{15}{3\rho + 4}\mu_c, \tag{63a}$$

$$\sigma_{***}^2 = \lim_{N \rightarrow \infty} \sigma_{***N}^2 = \frac{6}{\rho}\mu_c. \tag{63b}$$

**5.5 Case 5:  $\eta_1 = b - c, \eta_2 = -c, \eta_3 = b, \eta_4 = 0$**

This is a situation where a cooperator incurs a random cost  $c$  while its opponent receives a random benefit  $b$ . Here, we assume  $b > c > 0$  with  $E[b] = \mu_b\delta + o(\delta)$ ,  $E[c] = \mu_c\delta + o(\delta)$ ,  $E[b^2] = \sigma_b^2\delta + o(\delta)$ ,  $E[c^2] = \sigma_c^2\delta + o(\delta)$  and  $E[bc] = \sigma_{bc}\delta + o(\delta)$ , so that the scaled variances and covariances of the payoffs are given by

$$\sigma_1^2 = \sigma_b^2 + \sigma_c^2 - 2\sigma_{bc}, \tag{64a}$$

$$\sigma_2^2 = \sigma_c^2, \tag{64b}$$

$$\sigma_3^2 = \sigma_b^2, \tag{64c}$$

$$\sigma_4^2 = \sigma_{14} = \sigma_{24} = \sigma_{34} = 0, \tag{64d}$$

$$\sigma_{12} = \sigma_c^2 - \sigma_{bc}, \tag{64e}$$

$$\sigma_{13} = \sigma_b^2 - \sigma_{bc}, \tag{64f}$$

$$\sigma_{23} = -\sigma_{bc}. \tag{64g}$$

In this case, conditions (34), (35) and (37), for  $F_C > N^{-1}$ ,  $F_D < N^{-1}$  and  $F_C > F_D$ , respectively, become

$$\sigma_{bc} - \sigma_c^2 > \sigma_{*N}^2, \sigma_{bc} - \sigma_c^2 > \sigma_{**N}^2, \sigma_{bc} - \sigma_c^2 > \sigma_{***N}^2, \tag{65}$$

respectively, where

$$\sigma_{*N}^2 = \frac{3N}{N + 1} \mu_c, \tag{66a}$$

$$\sigma_{**N}^2 = \frac{3N}{2N - 1} \mu_c, \tag{66b}$$

$$\sigma_{***N}^2 = 2\mu_c. \tag{66c}$$

Note that  $\sigma_b^2$  does not come into play in the conditions given in (65).

Decreasing the variance of the cost  $c$  or increasing its covariance with the benefit  $b$  will increase the fixation probability of  $C$  and decrease the fixation probability of  $D$ , which makes it easier for weak selection to fully favor the evolution of cooperation. Comparing the above thresholds, we get  $\sigma_{*N}^2 > \sigma_{***N}^2 > \sigma_{**N}^2$  for  $N \geq 3$ .

These findings are summarized as follows.

**Conclusion in Case 5**

- If  $\sigma_{*N}^2 > \sigma_{bc} - \sigma_c^2$ , then  $F_C < N^{-1} < F_D$ .
- If  $\sigma_{**N}^2 > \sigma_{bc} - \sigma_c^2 > \sigma_{***N}^2$ , then  $F_C < F_D < N^{-1}$ .
- If  $\sigma_{*N}^2 > \sigma_{bc} - \sigma_c^2 > \sigma_{***N}^2$ , then  $F_D < F_C < N^{-1}$ .
- If  $\sigma_{bc} - \sigma_c^2 > \sigma_{*N}^2$ , then  $F_D < N^{-1} < F_C$ .

This is valid for any population size  $N \geq 3$ . It is impossible for weak selection to favor the evolution of both cooperation and defection, that is,  $F_C > N^{-1}$  and  $F_D > N^{-1}$ .

In the limit of a large population size, we have

$$\sigma_*^2 = \lim_{N \rightarrow \infty} \sigma_{*N}^2 = 3\mu_c, \tag{67a}$$

$$\sigma_{**}^2 = \lim_{N \rightarrow \infty} \sigma_{**N}^2 = \frac{3}{2}\mu_c, \tag{67b}$$

$$\sigma_{***}^2 = \lim_{N \rightarrow \infty} \sigma_{***N}^2 = 2\mu_c. \tag{67c}$$

**6 Repeated Prisoner’s Dilemma**

In this section, we consider a Prisoner’s Dilemma with random payoffs that is repeated a random number of rounds  $n \geq 1$ . The payoffs in each round of pairwise interactions are given by the entries of the game matrix

$$\begin{array}{cc}
 & C & D \\
 \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix}
 \end{array}
 \tag{68}$$

and these entries have scaled means satisfying the inequalities  $\mu_T > \mu_R > \mu_P > \mu_S$  and  $2\mu_R > \mu_T + \mu_S$ . We suppose that the number of rounds  $n$  is independent of the payoffs. An

individual can use a strategy among two possible strategies: *TFT* for Tit-for-Tat and *AllD* for Always-Defect. A *TFT*-player cooperates in the first round and thereafter it adopts the strategy of its opponent in the previous round. An *AllD*-player defects in all rounds. In such a case, two interacting *TFT*-players will cooperate all the time and then each one will receive  $nR$ . Similarly, two *AllD*-players will defect all the time and then each one will receive  $nP$ . Finally, if a *TFT*-player interacts with an *AllD*-player, the *TFT*-player will cooperate in the first round, and thereafter it will defect, while the *AllD*-player will defect all the time, so that the *TFT*-player will receive  $S + (n - 1)P$ , while the *AllD*-player will receive  $T + (n - 1)P$ . Therefore, the game matrix for this repeated Prisoner’s Dilemma with these two strategies is

$$\begin{pmatrix} \eta_1 & \eta_2 \\ \eta_3 & \eta_4 \end{pmatrix} = \begin{pmatrix} nR & S + (n - 1)P \\ T + (n - 1)P & nP \end{pmatrix}. \tag{69}$$

The scaled means, variances and covariances of these payoffs take the forms

$$\mu_1 = \mu_R E(n), \tag{70a}$$

$$\mu_2 = \mu_S + \mu_P E(n - 1), \tag{70b}$$

$$\mu_3 = \mu_T + \mu_P E(n - 1), \tag{70c}$$

$$\mu_4 = \mu_P E(n), \tag{70d}$$

and

$$\sigma_1^2 = \sigma_R^2 E(n^2), \tag{71a}$$

$$\sigma_2^2 = \sigma_S^2 + \sigma_P^2 E((n - 1)^2) + 2\sigma_{SP} E(n - 1), \tag{71b}$$

$$\sigma_3^2 = \sigma_T^2 + \sigma_P^2 E((n - 1)^2) + 2\sigma_{TP} E(n - 1), \tag{71c}$$

$$\sigma_4^2 = \sigma_P^2 E(n^2), \tag{71d}$$

$$\sigma_{12} = \sigma_{RS} E(n) + \sigma_{RP} E(n(n - 1)), \tag{71e}$$

$$\sigma_{13} = \sigma_{RT} E(n) + \sigma_{RP} E(n(n - 1)), \tag{71f}$$

$$\sigma_{14} = \sigma_{RP} E(n^2), \tag{71g}$$

$$\sigma_{23} = \sigma_P^2 E((n - 1)^2) + \sigma_{ST} + \sigma_{SP} E(n - 1) + \sigma_{TP} E(n - 1), \tag{71h}$$

$$\sigma_{24} = \sigma_P^2 E(n(n - 1)) + \sigma_{SP} E(n), \tag{71i}$$

$$\sigma_{34} = \sigma_P^2 E(n(n - 1)) + \sigma_{TP} E(n), \tag{71j}$$

where  $\sigma_R^2, \sigma_S^2, \sigma_T^2, \sigma_P^2$  stand for the scaled variances of  $R, S, T, P$ , and  $\sigma_{RS}, \sigma_{RT}, \sigma_{RP}, \sigma_{ST}, \sigma_{SP}, \sigma_{TP}$  for their scaled covariances.

Inserting the above expressions in conditions (38) and (39), we conclude that weak selection favors the evolution of *TFT* in a large population, that is,  $F_{TFT} > N^{-1}$ , if

$$\begin{aligned} & \frac{1}{3} [\mu_R + 2\mu_S - \mu_T - 2\mu_P] + \frac{1}{3} (\mu_R - \mu_P) E(n - 1) - \frac{1}{10} \sigma_R^2 E(n^2) \\ & - \frac{1}{10} \sigma_S^2 - \frac{2}{15} \sigma_{RS} E(n) + \frac{1}{15} \sigma_T^2 + \alpha_P \sigma_P^2 + \frac{1}{10} \sigma_{TP} E(3n - 1) + \frac{1}{30} \sigma_{RT} E(n) \\ & - \frac{1}{30} \sigma_{RP} E(n(4n - 3)) - \frac{1}{30} \sigma_{ST} - \frac{1}{30} \sigma_{SP} E(16n - 7) > 0, \end{aligned} \tag{72}$$

and disfavors the evolution of *AllD*, that is,  $F_{AllD} < N^{-1}$ , if

$$\frac{1}{3} [2\mu_R + \mu_S - 2\mu_T - \mu_P] + \frac{2}{3} (\mu_R - \mu_P) E(n - 1) - \frac{2}{5} \sigma_R^2 E(n^2) - \frac{1}{15} \sigma_S^2$$

$$\begin{aligned}
 & -\frac{1}{5}\sigma_{RS}E(n) + \frac{1}{10}\sigma_T^2 + \beta_P\sigma_P^2 + \frac{1}{30}\sigma_{TP}E(11n - 7) + \frac{1}{10}\sigma_{RT}E(n) \\
 & + \frac{1}{30}\sigma_{RP}E(n(4n - 3)) + \frac{1}{30}\sigma_{ST} - \frac{1}{30}\sigma_{SP}E(4n - 3) > 0,
 \end{aligned}
 \tag{73}$$

where

$$\alpha_P = \frac{7}{30}E((n - 1)^2) + \frac{7}{10}E(n - 1) + \frac{2}{5} > 0
 \tag{74}$$

and

$$\beta_P = \frac{4}{15}E((n - 1)^2) + \frac{3}{10}E(n - 1) + \frac{1}{10} > 0.
 \tag{75}$$

Note that, in conditions (72) and (73), the coefficients of  $\sigma_T^2$ ,  $\sigma_P^2$ ,  $\sigma_{RT}$  and  $\sigma_{TP}$  are positive. Therefore, an increase in the variance of any payoff to  $D$  against  $C$  or  $D$ ,  $\sigma_T^2$  or  $\sigma_P^2$ , their covariance  $\sigma_{TP}$ , or the covariance between the payoff to  $C$  against  $C$  and the payoff to  $D$  against  $C$ ,  $\sigma_{RT}$ , will increase the probability of ultimate fixation of a single  $TFT$  and decrease the probability of ultimate fixation of a single  $AllD$ , which promotes the evolution of cooperation in the population. In the same conditions (72) and (73), the coefficients of  $\sigma_R^2$ ,  $\sigma_S^2$ ,  $\sigma_{RS}$  and  $\sigma_{SP}$  are negative. Therefore, an increase in the variance of any payoff to  $C$  against  $C$  or  $D$ ,  $\sigma_R^2$  or  $\sigma_S^2$ , their covariance  $\sigma_{12}$ , or the covariance between the payoff to  $C$  against  $C$  and the payoff to  $D$  against  $D$ ,  $\sigma_{24}$ , will increase the fixation probability of  $AllD$  and decrease the fixation probability of  $TFT$ , which opposes the evolution of cooperation. These conclusions extend Results 1 and 2 of Section 4 for a one-round game to a game with a random number of rounds.

Moreover, substituting the above expressions in condition (40) leads to the conclusion that weak selection favors the evolution of  $TFT$  more than the evolution of  $AllD$  in a large population, that is,  $F_{TFT} > F_{AllD}$ , if

$$\begin{aligned}
 & \mu_R + \mu_S - \mu_T - \mu_P + (\mu_R - \mu_P)E(n - 1) - \frac{1}{2}\sigma_R^2E(n^2) \\
 & - \frac{1}{6}\sigma_S^2 - \frac{1}{3}\sigma_{RS}E(n) + \frac{1}{6}\sigma_T^2 + \frac{1}{2}\sigma_P^2E(n^2) + \frac{1}{3}\sigma_{TP}E(2n - 1) \\
 & + \frac{1}{3}\sigma_{RT}E(n) - \frac{1}{3}\sigma_{SP}E(2n - 1) > 0.
 \end{aligned}
 \tag{76}$$

A first observation is that an increase in any term among  $\{\sigma_T^2, \sigma_P^2, \sigma_{RT}, \sigma_{TP}\}$  or a decrease in any term among  $\{\sigma_R^2, \sigma_S^2, \sigma_{RS}, \sigma_{SP}\}$  will make it easier for weak selection to favor the evolution of  $TFT$  more than the evolution of  $AllD$ , which confirms the above conclusions. A second observation from (72) and (73) is that an increase in the covariance between the payoff to  $C$  against  $C$  and the payoff to  $D$  against  $D$ ,  $\sigma_{RP}$ , or an increase in the covariance between the payoff to  $C$  against  $D$  and the payoff to  $D$  against  $C$ ,  $\sigma_{ST}$ , decreases both the fixation probabilities of  $TFT$  and  $AllD$  with the same rate. However, neither  $\sigma_{RP}$  nor  $\sigma_{ST}$  has an effect on the condition for  $F_{TFT} > F_{AllD}$ , since they do not come into play in condition (76). This extends Result 3 for a one-round game to a game with a random number of rounds.

Note that, for independent payoffs  $R, S, T, P$ , conditions (72), (73) and (76) reduce to conditions obtained by Li and Lessard [15] in the case of a large Wright–Fisher population.

Suppose now a very large number of rounds so that  $E(n^2) \gg E(n)$ . Under this assumption, conditions (72), (73) and (76), for  $F_{TFT} > N^{-1}$ ,  $F_{AllD} < N^{-1}$  and  $F_{TFT} > F_{AllD}$ , respectively, reduce to

$$\frac{7}{30}\sigma_P^2 - \frac{1}{10}\sigma_R^2 - \frac{2}{15}\sigma_{RP} > 0,
 \tag{77a}$$

$$\frac{4}{15}\sigma_P^2 - \frac{2}{5}\sigma_R^2 + \frac{2}{15}\sigma_{RP} > 0, \tag{77b}$$

$$\sigma_P^2 - \sigma_R^2 > 0. \tag{77c}$$

Note that the first condition is the least stringent one while the third condition is the most stringent one. If  $\sigma_R^2 = 0$ , then weak selection favors the evolution of  $TFT$  in any sense as long as  $\sigma_P^2 > 0$ .

If all the variances vanish, then the conditions to have  $F_{TFT} > N^{-1}$ ,  $F_{AID} < N^{-1}$  and  $F_{TFT} > F_{AID}$  are the same, given by

$$\mu_R > \mu_P, \tag{78}$$

which is always satisfied by assumption. In this case, weak selection always favors the evolution of  $TFT$  in any sense. This extends a conclusion of Nowak [18] in the case of a large number of rounds.

### 7 Simulations and Robustness

In order to check our theoretical predictions, we ran simulations for Cases 1 and 2 of Section 5 with scaled mean benefit and cost  $\mu_b = 2$  and  $\mu_c = 1$ , respectively, and a magnitude of selection  $\delta = 0.02$ . In these cases, the fixation probabilities  $F_C$  and  $F_D$  are, to a first-order approximation with respect to the magnitude of selection, linear functions of the scaled variance  $\sigma^2$  and their values can be estimated by repeating the evolution of the population with an update according to a Moran model. Using  $10^6$  repetitions for each value of  $\sigma^2$  in a uniform probability distribution and least squares to find the best linear fits for  $F_C$  and  $F_D$  (see Figs. 9 and 10 in “Appendix C” for details), the threshold values  $\sigma_{*N}^2$ ,  $\sigma_{**N}^2$  and  $\sigma_{***N}^2$  that the scaled variance  $\sigma^2$  must exceed to have  $F_C > N^{-1}$ ,  $F_D < N^{-1}$  and  $F_C > F_D$ , respectively, for a population size  $N$  going from 2 to 20 have been obtained (see Figs. 5, 6). These results are in agreement with our theoretical predictions illustrated in Figs. 1 and 2.

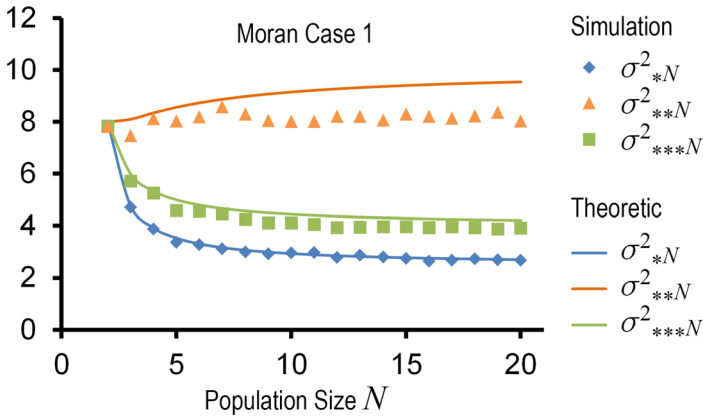
Moreover, we also ran simulations with an update according to a Wright–Fisher model to check the robustness of our results (see Figs. 7 and 8, and 11 and 12 in “Appendix C” for more details). These simulation results are similar to the previous ones.

As for a Fermi model in pairwise comparisons (see, e.g., Wu et al. [29] and references therein), let  $T_i^+$  be the probability that a defector is selected to update its strategy and that it imitates the strategy of a cooperator. Using Taylor’s theorem, this probability is given by

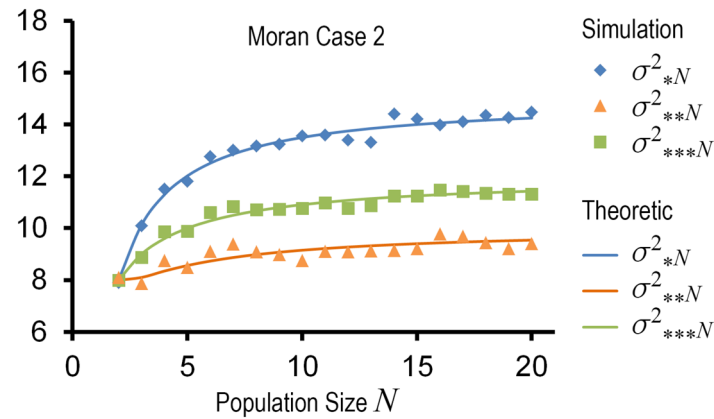
$$\begin{aligned} T_i^+ &= E \left[ \frac{i}{N} \left( 1 - \frac{i}{N} \right) \frac{1}{1 + e^{P_D(x) - P_C(x)}} \right] \\ &= \frac{i}{N} \left( 1 - \frac{i}{N} \right) \times E \left[ \frac{1}{2} + \frac{P_C(x) - P_D(x)}{4} - \frac{F^{(3)}(\xi)}{3!} (P_C(x) - P_D(x))^3 \right], \end{aligned} \tag{79}$$

where  $F(x) = 1/(1 + e^x)$  and  $\xi$  is a random variable that depends on  $P_C(x) - P_D(x)$  such that  $\xi \in (0, P_C(x) - P_D(x))$  if  $P_C(x) - P_D(x) > 0$  or  $\xi \in (P_C(x) - P_D(x), 0)$  if  $P_C(x) - P_D(x) < 0$ . Note that

$$\left| F^{(3)}(x) \right| = \left| -\frac{e^x (-4e^x + e^{2x} + 1)}{(1 + e^x)^4} \right| \leq \frac{4}{1 + e^x} \leq 4, \tag{80}$$



**Fig. 5** Simulation results under a Moran model in Case 1 with  $\delta = 0.02$ ,  $\mu_b = 2$  and  $\mu_c = 1$ . The dots represent the threshold values  $\sigma^2_{*N}$ ,  $\sigma^2_{**N}$  and  $\sigma^2_{***N}$  for the scaled variance  $\sigma^2$  obtained from the best linear fits of the fixation probabilities  $F_C$  and  $F_D$  (see Fig. 9 in “Appendix C” for more details). The curves represent the corresponding theoretical values as in Fig. 1



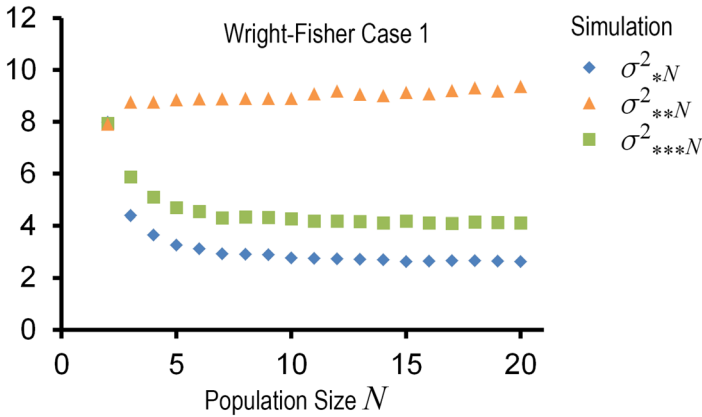
**Fig. 6** Simulation results under a Moran model in Case 2 with  $\delta = 0.02$ ,  $\mu_b = 2$  and  $\mu_c = 1$ . The dots represent the threshold values  $\sigma^2_{*N}$ ,  $\sigma^2_{**N}$  and  $\sigma^2_{***N}$  for the scaled variance  $\sigma^2$  obtained from the best linear fits of the fixation probabilities  $F_C$  and  $F_D$  (see Fig. 10 in “Appendix C” for more details). The curves represent the corresponding theoretical values as in Fig. 2

which leads to

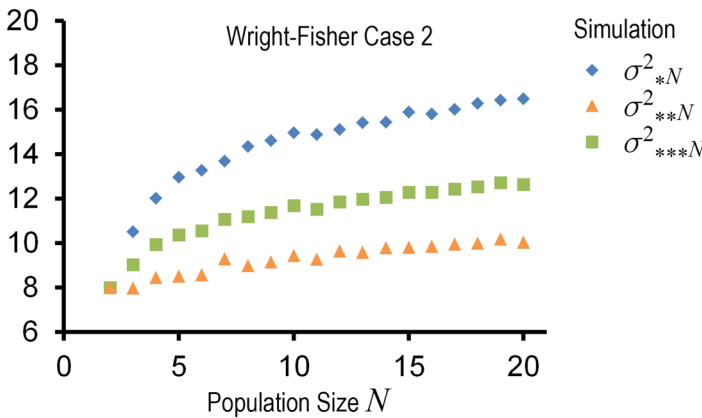
$$\begin{aligned} \left| E \left[ \frac{F^{(3)}(\xi)}{3!} (P_C(x) - P_D(x))^3 \right] \right| &\leq E \left[ \left| \frac{F^{(3)}(\xi)}{3!} (P_C(x) - P_D(x))^3 \right| \right] \\ &\leq \frac{4}{3!} E [ |P_C(x) - P_D(x)|^3 ] = o(\delta). \end{aligned} \tag{81}$$

Inserting (81) in (79), we get

$$T_i^+ = \frac{i}{2N} \left( 1 - \frac{i}{N} \right) \times \left[ 1 + \frac{E [P_C(x) - P_D(x)]}{2} \right] + o(\delta). \tag{82}$$



**Fig. 7** Simulation results under a Wright–Fisher model in Case 1 with  $\delta = 0.02$ ,  $\mu_b = 2$  and  $\mu_c = 1$ . The dots represent the threshold values  $\sigma_{*N}^2$ ,  $\sigma_{**N}^2$  and  $\sigma_{***N}^2$  for the scaled variance  $\sigma^2$  obtained from the best linear fits of the fixation probabilities  $F_C$  and  $F_D$  (see Fig. 11 in “Appendix C” for more details). The results are very similar to those obtained under a Moran model shown in Fig. 5



**Fig. 8** Simulation results under a Wright–Fisher model in Case 2 with  $\delta = 0.02$ ,  $\mu_b = 2$  and  $\mu_c = 1$ . The dots represent the threshold values  $\sigma_{*N}^2$ ,  $\sigma_{**N}^2$  and  $\sigma_{***N}^2$  for the scaled variance  $\sigma^2$  obtained from the best linear fits of the fixation probabilities  $F_C$  and  $F_D$  (see Fig. 12 in “Appendix C” for more details). The results are very similar to those obtained under a Moran model shown in Fig. 6

This means that the second moments do not come into play in the first-order approximation of  $T_i^+$ , and by symmetry the second moments do not come into play in the first-order approximation of  $T_i^-$  as well. Therefore, in this model, the first-order approximation of the fixation probability of  $C$  does not depend on the second moments of the different payoffs  $\eta_j$  for  $j = 1, 2, 3, 4$ .

### 8 Discussion

In this paper, we have extended the study of Li and Lessard [15] on the effect of random fluctuations in payoffs for two strategies in linear games in a finite population. We have

considered an update at each discrete time step according to a Moran model instead of a Wright–Fisher model, which has allowed us to calculate a first-order approximation for the probability of ultimate fixation of a single  $C$ ,  $F_C$ , or a single  $D$ ,  $F_D$ , with respect to the magnitude of selection for any population size  $N \geq 2$ . This has led to exact conditions for weak selection to favor the evolution of  $C$ ,  $F_C > N^{-1}$ , disfavor the evolution of  $D$ ,  $F_D < N^{-1}$ , and to favor the evolution of  $C$  more than the evolution of  $D$ ,  $F_C > F_D$ , in terms of the scaled means, variances and covariances of the payoffs.

We have shown that an increase in the scaled variance of any payoff to  $D$ ,  $\sigma_3^2$  or  $\sigma_4^2$ , their scaled covariance  $\sigma_{34}$ , or the scaled covariance between the payoff to  $C$  against  $C$  and the payoff to  $D$  against  $D$ ,  $\sigma_{13}$ , increases  $F_C$  and decreases  $F_D$  (Result 1), which makes it easier for weak selection to favor the evolution of  $C$  in all senses. Analogously, an increase in the scaled variance of any payoff to  $C$  against  $C$  or  $D$ ,  $\sigma_1^2$  and  $\sigma_2^2$ , their scaled covariance  $\sigma_{12}$ , or the scaled covariance between the payoff to  $C$  against  $D$  and the payoff to  $D$  against  $D$ ,  $\sigma_{24}$ , decreases  $F_C$  and increases  $F_D$  (Result 2). This scenario makes it more difficult for weak selection to favor the evolution of  $C$  in all senses. These conclusions have been supported by simulations not only for a Moran model but also for a Wright–Fisher model (Section 7), and this suggests that they are robust.

Note that the scaled covariances  $\sigma_{14}$  and  $\sigma_{23}$  are not present in the condition for  $F_C > F_D$ . The reason is that each term has an equal effect on  $F_C$  and  $F_D$  (Result 3). More precisely, an increase in the scaled covariance of the payoffs to  $C$  against  $C$  and to  $D$  against  $D$ ,  $\sigma_{14}$ , or the payoffs to  $C$  against  $D$  and to  $D$  against  $C$ ,  $\sigma_{23}$ , reduces both fixation probabilities at the same rate.

These conclusions are in agreement with the results obtained by Kroumi and Lessard [10] in the case of a large well-mixed population in the presence of symmetric mutation. In the stationary state and under weak selection, they have shown that a decrease in any term among  $\{\sigma_1^2, \sigma_2^2, \sigma_{12}, \sigma_{24}\}$  or an increase in any term among  $\{\sigma_3^2, \sigma_4^2, \sigma_{13}, \sigma_{34}\}$  will increase the average abundance of  $C$ . Moreover, neither  $\sigma_{14}$  nor  $\sigma_{23}$  comes into play in the condition for weak selection to favor the abundance of  $C$  more than the abundance of  $D$  for any mutation rate. Under a low mutation rate, the condition for weak selection to favor the abundance of  $C$  is exactly the condition to have  $F_C > F_D$  under weak selection in the absence of mutation. This condition can be written as

$$\sum_{i=0}^3 \Gamma_i a_i > \sum_{i=0}^3 \Gamma_i b_{3-i}, \tag{83}$$

where  $\Gamma_i = 1$ , for  $i = 0, 1, 2, 3$ , are the coefficients described in Tarnita et al. [26] in the case of pairwise interactions and in Wu et al. [30] in the case of interactions in groups of players, while  $a_i$  and  $b_i$  are the payoffs given in (32). Note that the coefficients  $\Gamma_i$  depend on the population structure and the update rule. They do not depend on the game matrix. They quantify the degree by which individuals of the same type are more likely to meet than individuals of different types. Note also that Li and Lessard [15] have reached a similar conclusion for a very large population that reproduces according to a Wright–Fisher model. However, their conclusion is limited to the case of independent payoffs in a very large population.

In the first-order approximation of  $F_C$ , the weight of  $\sigma_4^2$  is higher than the weight of  $\sigma_3^2$ , while they are the same in the first-order approximation of  $F_D$ . As a consequence, an increase in the scaled variance of the payoff to  $D$  against  $D$  (Case 1) increases  $F_C$  more than an increase in the scaled variance of the payoff to  $D$  against  $C$  (Case 2). The scaled variance has lower threshold values for  $F_C > N^{-1}$  and  $F_C > F_D$  in Case 1 than in Case 2, while



they are the same in both cases for  $F_D < N^{-1}$ . Note that in Case 1, it is impossible for weak selection to favor the evolution of  $C$  and  $D$ , while all the other scenarios are possible. In Case 2, it is impossible for weak selection to disfavor the evolution of  $C$  and  $D$ , while all the other scenarios are possible.

Finally, an increase in  $\sigma_4^2 = \sigma_3^2 = \sigma^2$  when  $\sigma_1^2 = \sigma_2^2 = 0$  (Case 3) increases  $F_C$  and decreases  $F_D$  more than an increase in only one of them for any population size  $N \geq 3$  and any correlation coefficient between the payoffs to  $D$  against  $C$  and  $D$  that satisfies  $\rho > -1/3$ . This holds in the particular cases of perfect positive correlation ( $\rho = 1$ ) and no correlation ( $\rho = 0$ ). Note that increasing the correlation coefficient  $\rho$  increases  $F_C$  and decreases  $F_D$ , which makes it easier for weak selection to fully favor the evolution of  $C$  in the sense that  $F_C > N^{-1} > F_D$ . When  $\sigma_1^2 = \sigma_2^2 = \sigma^2$  (Case 4), this is possible under more stringent conditions, that is,  $N < 13$  and  $\rho > 0$ .

For a Prisoner’s Dilemma with additive random cost  $c$  and random benefit  $b$  (Case 5), we have shown that the conditions for  $F_C > N^{-1}$ ,  $F_D < N^{-1}$  and  $F_C > F_D$  are  $\sigma_{bc} - \sigma_c^2 > \sigma_{*N}^2$ ,  $\sigma_{bc} - \sigma_c^2 > \sigma_{**N}^2$  and  $\sigma_{bc} - \sigma_c^2 > \sigma_{***N}^2$ , respectively. Note that the thresholds  $\sigma_{*N}^2$ ,  $\sigma_{**N}^2$  and  $\sigma_{***N}^2$  depend on the population size and  $\mu_C$ , the scaled mean cost. Increasing the scaled variance of the cost  $c$ ,  $\sigma_c^2$ , or its scaled covariance with the benefit  $b$ ,  $\sigma_{bc}$ , increases  $F_C$  and decreases  $F_D$ . In the case of no correlation between the cost and benefit, that is,  $\sigma_{bc} = 0$ , weak selection fully favors the evolution of  $D$  in the sense that  $F_C < N^{-1} < F_D$ .

We have extended our analysis to a general Prisoner’s Dilemma that is repeated a random number of rounds  $n$ . In this case, we have shown that an increase in the scaled variances of the payoffs to  $D$  against  $C$  and  $D$ ,  $\sigma_T^2$  and  $\sigma_P^2$ , their covariance  $\sigma_{TP}$  or the covariance between the payoffs to  $C$  and  $D$  against  $C$ ,  $\sigma_{RT}$ , makes it easier for weak selection to favor the evolution of  $TFT$  against  $AllD$  in all senses. Conversely, an increase in the variances of the payoffs to  $C$  against  $C$  and  $D$ ,  $\sigma_R^2$  and  $\sigma_S^2$ , their covariance  $\sigma_{RS}$  or the covariance between the payoffs to  $C$  and  $D$  against  $D$ ,  $\sigma_{SP}$ , makes it more difficult for weak selection to favor the evolution of  $TFT$  in all senses. In addition, an increase in  $\sigma_{RP}$  (respectively,  $\sigma_{ST}$ ) decreases  $F_{TFT}$  and  $F_{AllD}$  but does not play any role in the condition for  $F_{TFT} > F_{AllD}$ . If the mean number of rounds is large enough, only the variances of the payoff to  $C$  against  $C$  and the payoff to  $D$  against  $D$ , or their covariance, come into play in the conditions for  $F_{TFT} > N^{-1}$ ,  $F_{AllD} < N^{-1}$  and  $F_{TFT} > F_{AllD}$ . If  $\sigma_P^2$  is large enough or  $\sigma_P^2$  is small enough, then weak selection fully favors the evolution of  $TFT$ .

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### 9 Appendix A: A First-Order Approximation

Note that  $|\eta_i| < M$ , for  $i = 1, 2, 3, 4$ , which yields  $|\bar{P}(x)| \leq M < 1$  for any  $x$  in  $[0, 1]$ . Using Taylor’s theorem, we obtain

$$\frac{1}{1 + \bar{P}(x)} = 1 - \bar{P}(x) + \bar{P}^2(x) + \frac{\bar{P}^3(x)}{(1 + \xi)^3}, \tag{84}$$

where  $\xi$  is a random variable that depends on  $\bar{P}(x)$  such that  $\xi \in (0, \bar{P}(x))$  if  $\bar{P}(x) > 0$  or  $\xi \in (\bar{P}(x), 0)$  if  $\bar{P}(x) < 0$ . This leads to

$$\begin{aligned} E \left[ \frac{1 + P_C(x)}{1 + \bar{P}(x)} \right] &= E \left[ (1 + P_C(x)) \left( 1 - \bar{P}(x) + \bar{P}^2(x) + \frac{\bar{P}^3(x)}{(1 + \xi)^3} \right) \right] \\ &= E \left[ (1 + P_C(x)) (1 - \bar{P}(x) + \bar{P}^2(x)) \right] + E \left[ \frac{(1 + P_C(x))\bar{P}^3(x)}{(1 + \xi)^3} \right]. \end{aligned} \tag{85}$$

If  $\bar{P}(x) > 0$ , we have  $1 \leq 1 + \xi \leq 1 + \bar{P}(x)$ , which leads to

$$\left| \frac{1}{1 + \xi} \right| \leq 1. \tag{86}$$

If  $\bar{P}(x) < 0$ , we have  $0 < 1 + \bar{P}(x) \leq 1 + \xi \leq 1$ , which leads to

$$\left| \frac{1}{1 + \xi} \right| \leq \left| \frac{1}{1 + \bar{P}(x)} \right| \leq \frac{1}{1 - |\bar{P}(x)|} \leq \frac{1}{1 - M}, \tag{87}$$

since  $|\bar{P}(x)| \leq M < 1$ . Combining these inequalities, we get

$$\frac{1}{(1 + \xi)^3} \leq \sup \left\{ 1, \frac{1}{(1 - M)^3} \right\} = K, \tag{88}$$

where  $K$  is a finite constant. Then, we have

$$\begin{aligned} \left| E \left[ \frac{(1 + P_C(x))\bar{P}^3(x)}{(1 + \xi)^3} \right] \right| &\leq E \left[ \frac{|1 + P_C(x)||\bar{P}^3(x)|}{(1 + \xi)^3} \right] \\ &\leq KE [ |1 + P_C(x)||\bar{P}^3(x)| ]. \end{aligned} \tag{89}$$

On the other hand, by using condition (3), we have

$$E [ |1 + P_C(x)||\bar{P}^3(x)| ] = o(\delta). \tag{90}$$

We conclude that

$$E \left[ \frac{(1 + P_C(x))\bar{P}^3(x)}{(1 + \xi)^3} \right] = o(\delta). \tag{91}$$

### 10 Appendix B: Calculation of Summations

Using the elementary arithmetic identities

$$\sum_{i=1}^n i^4 = \frac{n(n + 1)(2n + 1)(3n^2 + 3n - 1)}{30}, \tag{92a}$$

$$\sum_{i=1}^n i^3 = \frac{n^2(n + 1)^2}{4}, \tag{92b}$$

$$\sum_{i=1}^n i^2 = \frac{n(n + 1)(2n + 1)}{6}, \tag{92c}$$

$$\sum_{i=1}^n i = \frac{n(n+1)}{2}, \tag{92d}$$

we get

$$\begin{aligned} & \sum_{i=1}^{N-1} (N-i)m\left(\frac{i}{N}\right) \\ &= A_3 \sum_{i=1}^{N-1} (N-i) \frac{i^3}{N^3} + A_2 \sum_{i=1}^{N-1} (N-i) \frac{i^2}{N^2} + A_1 \sum_{i=1}^{N-1} (N-i) \frac{i}{N} \\ & \quad + A_0 \sum_{i=1}^{N-1} (N-i) \\ &= A_3 \frac{(N^2-1)(3N^2-2)}{60N^2} + A_2 \frac{N^2-1}{12} + A_1 \frac{N^2-1}{6} + A_0 \frac{N(N-1)}{2} \\ &= \frac{N^2-1}{2} \left[ \frac{3N^2-2}{30N^2} A_3 + \frac{A_2+2A_1}{6} + \frac{N}{N+1} A_0 \right] \end{aligned} \tag{93}$$

and

$$\begin{aligned} & \sum_{i=1}^{N-1} m\left(\frac{i}{N}\right) \\ &= A_3 \sum_{i=1}^{N-1} \frac{i^3}{N^3} + A_2 \sum_{i=1}^{N-1} \frac{i^2}{N^2} + A_1 \sum_{i=1}^{N-1} \frac{i}{N} + A_0 \sum_{i=1}^{N-1} 1 \\ &= A_3 \frac{N^2(N-1)^2}{4N^3} + A_2 \frac{N(N-1)(2N-1)}{6N^2} + A_1 \frac{N(N-1)}{2N} + A_0(N-1) \\ &= (N-1) \left[ \frac{N-1}{4N} A_3 + \frac{2N-1}{6N} A_2 + \frac{A_1}{2} + A_0 \right]. \end{aligned} \tag{94}$$

### 11 Appendix C: Simulation Data

This appendix contains the simulation data in Cases 1 and 2 under a Moran model (Figs. 9, 10) and a Wright–Fisher model (Figs. 11, 12). For a population size going from 2 to 20 and parameter values  $\delta = 0.02$ ,  $\mu_b = 2$  and  $\mu_c = 1$ , the fixation probabilities  $F_C$  and  $F_D$  are calculated from  $10^6$  repeated runs for each value of the scaled variance  $\sigma^2$  in a uniform probability distribution.

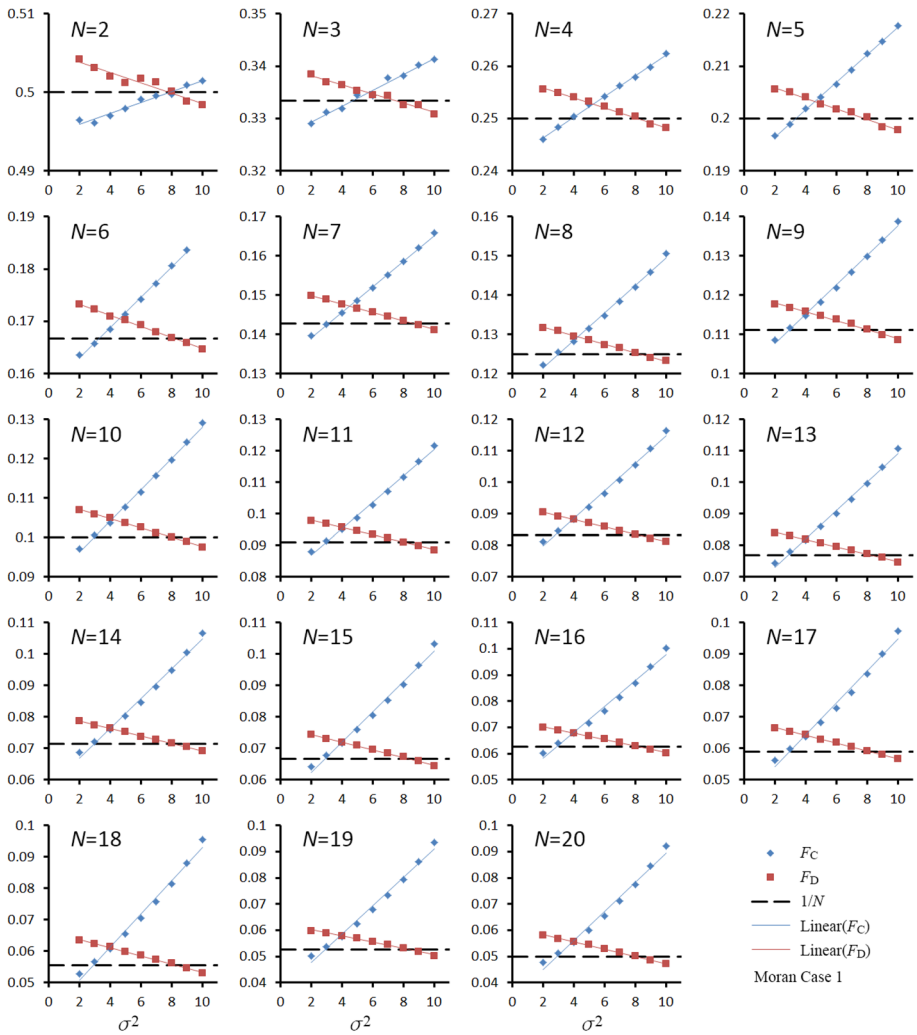


Fig. 9 Simulation data under a Moran model in Case 1

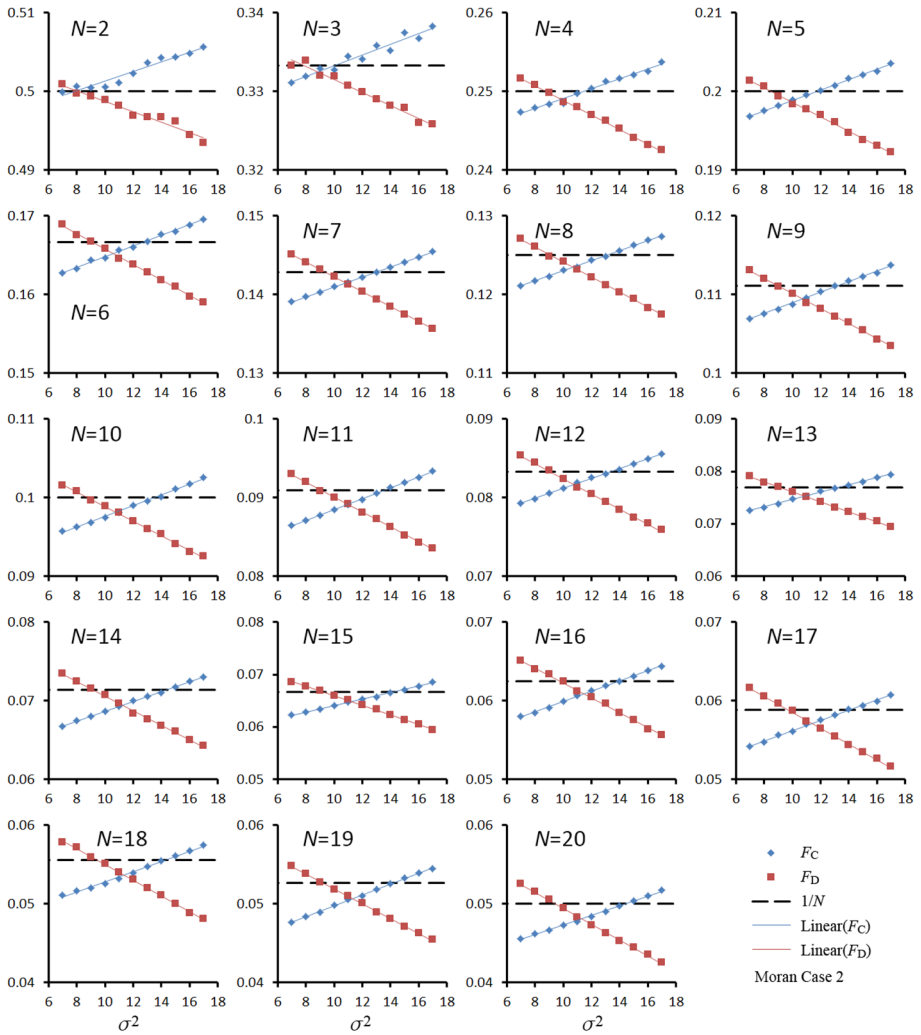


Fig. 10 Simulation data under a Moran model in Case 2

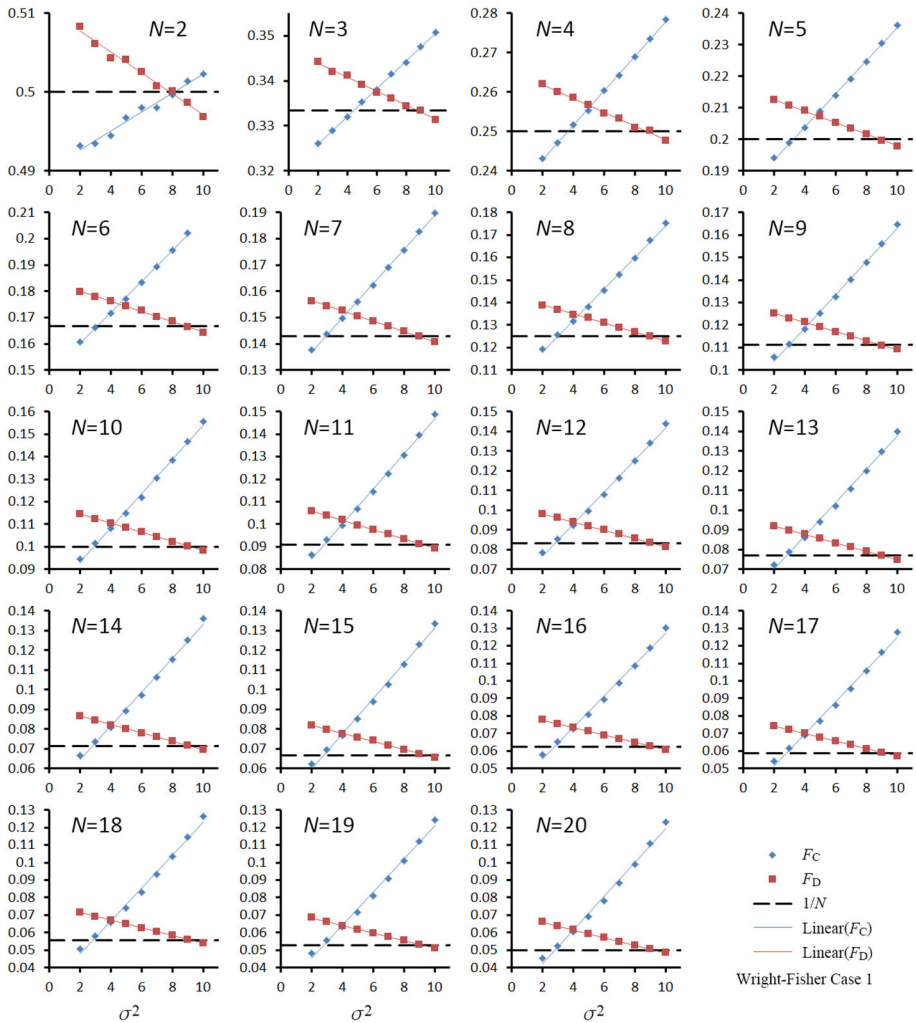


Fig. 11 Simulation data under a Wright–Fisher model in Case 1

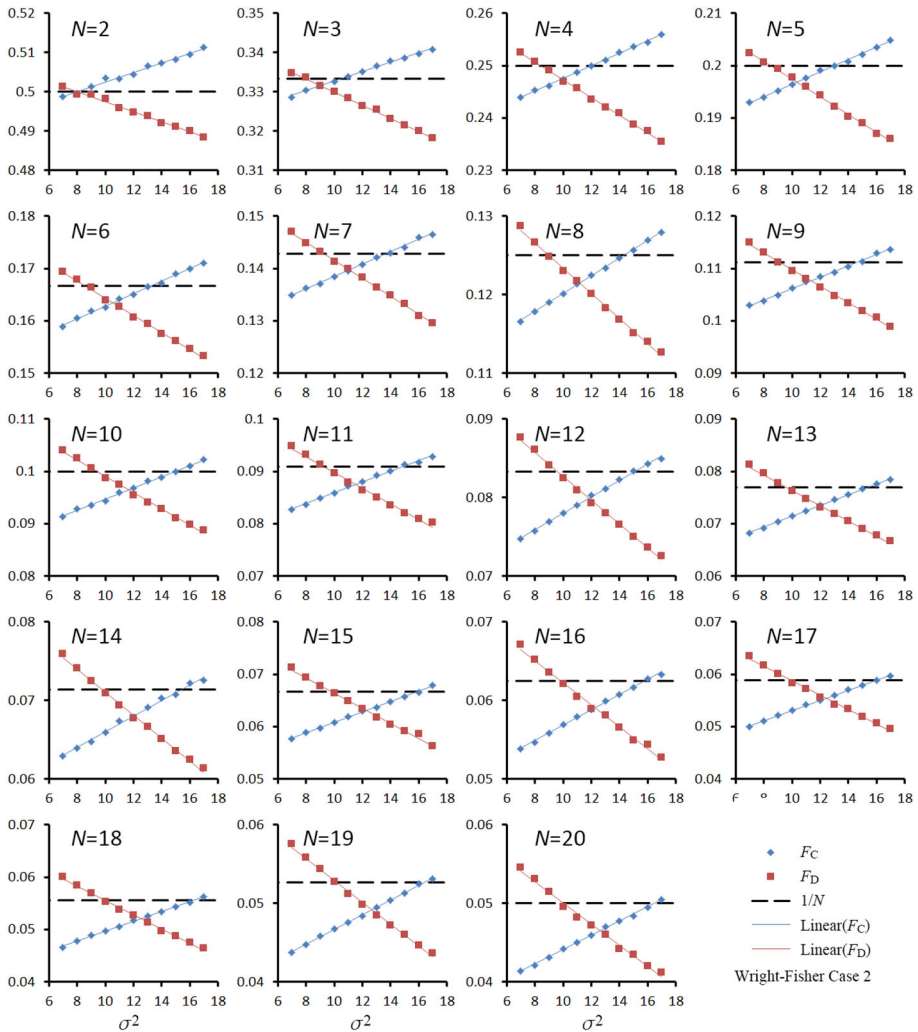


Fig. 12 Simulation data under a Wright–Fisher model in Case 2

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