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Evolution of cooperation with respect to fixation probabilities in multi-player games with random payoffs

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ABSTRACT

We study the effect of variability in payoffs on the evolution of cooperation (C) against defection (D) in multi-player games in a finite well-mixed population. We show that an increase in the covariance between any two payoffs to D, or a decrease in the covariance between any two payoffs to C, increases the probability of ultimate fixation of C when represented once, and decreases the corresponding fixation probability for D. This is also the case with an increase in the covariance between any payoff to C and any payoff to D if and only if the sum of the numbers of C-players in the group associated with these payoffs is large enough compared to the group size. In classical social dilemmas with random cost and benefit for cooperation, the evolution of C is more likely to occur if the variances of the cost and benefit, as well as the group size, are small, while the covariance between cost and benefit is large.

1. Introduction

Evolutionary game dynamics is a mathematical framework to study frequency-dependent selection (Maynard Smith and Price, 1973; Maynard Smith, 1982; Hofbauer and Sigmund, 1988). The payoffs received by interacting individuals are assumed to determine their reproductive success.

Evolutionary game dynamics in finite populations have been studied through two major concepts: average abundance and fixation probability. Consider a population of fixed finite size $N \geq 2$, where each individual can either cooperate or defect. Let C and D, respectively, denote these strategies. In the presence of recurrent mutation, the frequency of C over time reaches a stationary state. A strategy is said to be favored in abundance if its average frequency in the stationary state is greater than the average frequency in the absence of selection (Antal et al., 2009; Kroumi and Lessard, 2015a,b for pairwise interactions and Gokhale and Traulsen, 2011 for interactions in groups of size $d \geq 2$). In the absence of mutation, the frequency of C reaches one of the two absorbing states, 0 if the population ends up with all defecting individuals and 1 if the population ends up with all cooperating individuals. Let F_C be the probability that a single individual of type C among $N-1$ individuals of type D generates a lineage forward in time that will take over the whole population. Selection is said to favor the evolution of C if F_C is greater than its value in the absence of selection (see Nowak et al., 2004 for pairwise interactions and Kurokawa and Ihara, 2019 for interactions in groups of size $d \geq 2$). If selection is weak and the population size is large enough, then a diffusion approximation can be used to study the fixation probability F_C or the stationary distribution for the frequency of C (see, e.g., chapter 4 in Ewens, 2004).

Random fluctuations in the environment can affect the fitness of traits in a population. Unknown risk of predation and variability in available resources, competition capabilities as well as birth and death rates (May, 1973; Kaplan et al., 1990; Lande et al., 2003) are among multiple factors that can introduce uncertainty in evolutionary models. Early studies on the effect of varying selection coefficients between generations or offspring numbers within generations in haploid as well as diploid population genetic models in the absence or presence of mutation include Kimura (1954), Gillespie (1973, 1974), Karlin and Levikson (1974), Karlin and Liberman (1974) and Frank and Slatkin (1990). Extensions can be found in Starrfelt and Kokko (2012), Schreiber (2015) or Rychtar and Taylor (2019). Moreover, the fixation probability for a given type in a population whose size fluctuates dynamically was addressed in Lambert (2006), Parsons and Quince (2007a,b)

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and Otto and Whitlock (1997), among others, while Uecker and Hermisson (2011) studied a population with temporal variation not only in its size but also in selection pressure. Competing populations distributed over habitat patches where environmental conditions fluctuate in time and space were considered too in Evans et al. (2015) and Schreiber (2012).

Evolutionary game dynamics can be extended to take into account stochastic changes in environmental conditions. A stochastic version of the continuous-time replicator equation with a random noise added to the growth rate of every strategy was considered in Fudenberg and Harris (1992). Recently, the effect of stochastic changes in payoffs in discrete time was studied with particular attention to stochastic local stability of fixation states and constant polymorphic equilibria in an infinite population (Zheng et al., 2017, 2018), the fixation probability in a large population that reproduces according to a Wright–Fisher model (Li and Lessard, 2020) and the average abundance of strategies in a finite population that reproduces according to a Moran model (Kroumi and Lessard, 2021a,b).

More recently, Kroumi et al. (2021) studied the effect of random payoffs in two-player games in a finite well-mixed population. The payoffs to C and D against C and D in random pairwise interactions fluctuate in a way such that their means, variances and covariances are proportional to some small positive constant δ that measures the magnitude of selection. Higher moments of the different payoffs are assumed to be insignificant compared to δ. It was shown that increasing uncertainty in the payoffs to D or decreasing uncertainty in the payoffs to C increases the fixation probability F_C and decreases the corresponding fixation probability F_D. More importantly, it is possible for selection to favor the evolution of cooperation in a Prisoner's dilemma when the payoffs are subject to random fluctuations contrary to what happens when the payoffs are constant.

This paper extends the analysis to multi-player games in a well-mixed population of fixed size $N \geq 2$. We assume that interactions occur in random groups of fixed size $d \geq 2$ in which the payoffs to C and D are random variables. We deduce the probability of ultimate fixation of C given an initial frequency $1/N$, represented by F_C, and the corresponding fixation probability F_D for D. This allows us to study the effect of uncertainty in the different payoffs on the evolution of C in classical social dilemmas for any group size d.

The rest of this paper is organized as follows. In Section 2, we present the model. In Section 3, we derive the fixation probabilities F_C and F_D under weak selection for any population size $N \geq 2$ and any group size $d \geq 2$. In Section 4, we analyze the effects of the scaled variances and covariances of the payoffs on the evolution of C. In the next sections, we will pay attention to classical social dilemmas, public goods game in Section 5, synergistic benefits in Section 6, the stag hunt game in Section 7, and the snowdrift game in Section 8. We conclude with a discussion of the results in Section 9.

2. Multi-player game with random payoffs

We consider a multi-player game in a well-mixed population of finite size $N \geq 2$. There are two possible strategies for the individuals, cooperation and defection denoted by C and D, respectively. Time is discrete and, at each time step, interactions occur within groups of d individuals chosen at random without replacement, where $2 \leq d \leq N$. The payoff received by an individual interacting with k cooperators and $d-1-k$ defectors at time step t is denoted by $P_k(t)$ if the individual cooperates and $Q_k(t)$ if the individual defects. We make the assumptions that

$$E\left[P_k(t)\right] = \delta\mu_{C,k} + o(\delta), \tag{1a}$$

$$E\left[Q_k(t)\right] = \delta\mu_{D,k} + o(\delta), \tag{1b}$$

$$E\left[P_k(t)P_l(t)\right] = \delta\sigma_{CC,kl} + o(\delta), \tag{1c}$$

$$E\left[Q_k(t)Q_l(t)\right] = \delta\sigma_{DD,kl} + o(\delta), \tag{1d}$$

$$E\left[P_k(t)Q_l(t)\right] = \delta\sigma_{CD,kl} + o(\delta), \tag{1e}$$

for $k, l = 0, \ldots, d-1$. The parameter $\delta \geq 0$ represents a magnitude of selection. The coefficients $\mu_{S_1,k}$ and $\sigma_{S_1S_2,kl}$ for $k, l = 0, 1, \ldots, d-1$ and $S_1, S_2 = C$ or D represent the scaled means and covariances of the payoffs, respectively. Moreover, all the higher-order moments of the payoffs are negligible compared to the first and second moments. More precisely, we assume that

$$E\left[\prod_{k=0}^{d-1} |P_k(t)|^{i_k} |Q_k(t)|^{j_k}\right] = o(\delta) \tag{2}$$

as long as $\sum_{k=0}^{d-1}(i_k + j_k) \geq 3$, where i_k and j_k are two nonnegative integers for $k = 0, 1, \ldots, d-1$. Finally, the payoffs at a given time step are supposed to be independent of the payoffs at all other time steps.

An example of payoffs satisfying the above conditions is given by the collection of independent random variables $\{(P_k, Q_k), 0 \leq k \leq d-1\}$, where $P_k = -\sqrt{\sigma_{CC,kk}\delta} + \mu_{C,k}\delta$ or $\sqrt{\sigma_{CC,kk}\delta} + \mu_{C,k}\delta$ with the same probability 1/2, and $Q_k = -\sqrt{\sigma_{DD,kk}\delta} + \mu_{D,k}\delta$ or $\sqrt{\sigma_{DD,kk}\delta} + \mu_{D,k}\delta$ with the same probability 1/2, for $k = 0, 1, \ldots, d-1$. Here, we assume $\sigma_{CC,kk}, \sigma_{DD,kk} > 0$. It is easy to check that

$$E\left(P_k\right) = \delta\mu_{C,k}, \tag{3a}$$

$$E\left(P_k^2\right) = \sigma_{CC,kk}\delta + o(\delta), \tag{3b}$$

$$E\left(|P_k|^l\right) = A_l\delta^{l/2} + o\left(\delta^{l/2}\right) = o(\delta), \tag{3c}$$

$$E\left(Q_k\right) = \delta\mu_{D,k}, \tag{3d}$$

$$E\left(Q_k^2\right) = \sigma_{DD,kk}\delta + o(\delta), \tag{3e}$$

$$E\left(|Q_k|^l\right) = B_l\delta^{l/2} + o\left(\delta^{l/2}\right) = o(\delta), \tag{3f}$$

for $l \geq 3$, where A_l (respectively, B_l) is a constant that depends on $\sigma_{CC,kk}$ and $\mu_{C,k}$ (respectively, $\sigma_{DD,kk}$ and $\mu_{D,k}$). In addition, these payoffs satisfy condition (2).

Another example is obtained if P_k and Q_k are uniformly distributed on

$$\left(-\sqrt{3\delta\sigma_{CC,kl}}, \sqrt{3\delta\sigma_{CC,kl}} + 2\delta\mu_{C,k}\right)$$

and

$$\left(-\sqrt{3\delta\sigma_{DD,kl}}, \sqrt{3\delta\sigma_{DD,kl}} + 2\delta\mu_{D,k}\right),$$

respectively, for $k = 0, 1, \ldots, d-1$, and are independent. Using the fact that the k-th moment of a random variable uniformly distributed on (a, b) is given by $\frac{1}{k+1}\sum_{l=0}^{k} a^l b^{k-l}$, it is easy to show that

$$E\left(P_k\right) = \delta\mu_{C,k}, \tag{4a}$$

$$E\left(P_k^2\right) = \delta\sigma_{CC,kk} + o(\delta), \tag{4b}$$

$$E\left(|P_k|^l\right) = o(\delta), \tag{4c}$$

and similarly for Q_k, for $l \geq 3$ and $k = 0, 1 \ldots, d-1$. Moreover, these payoffs satisfy condition (2).

Note that, in the limit of weak selection, the effect of any moment of order $o(\delta)$ will be negligible. As such, the model behaves differently from one where payoffs are constant.

Given a population of i cooperators and $N-i$ defectors at time step t, the probability that a defector interacts with k cooperators and $d-1-k$ other defectors is

$$C(i,k) = \frac{\binom{i}{k}\binom{N-1-i}{d-1-k}}{\binom{N-1}{d-1}} \tag{5}$$

for $k = 0, 1, \ldots, d-1$, according to a hypergeometric distribution. Then, the average payoff to a defector at time step t is

$$\Pi_D(i,t) = \sum_{k=0}^{d-1} C(i,k)Q_k(t). \tag{6}$$

Similarly, the average payoff to a cooperator at time step t is

$$\Pi_C(i,t) = \sum_{k=0}^{d-1} C(i-1,k)P_k(t). \tag{7}$$

These average payoffs are added to a baseline value 1 to determine the reproductive fitnesses to C and D given by

$$f_C(i,t) = 1 + \Pi_C(i,t) \text{ and } f_D(i,t) = 1 + \Pi_D(i,t), \tag{8a}$$

respectively. The update of the population from one time step to the next occurs according to a Moran model (Moran, 1962; Ewens, 2004): an individual is chosen with probability proportional to its reproductive fitness to give birth to an identical offspring and this offspring replaces an individual chosen at random to die, possibly the parent of the offspring but not the offspring itself.

3. Fixation probabilities

The number of individuals of type C increases from i to $i+1$ from time step t to time step $t+1$ if an individual of type C is selected to produce an offspring and an individual of type D is selected to die. This occurs with probability

$$\begin{aligned} T_i^+ &= E\left[\frac{if_C(i,t)}{if_C(i,t)+(N-i)f_D(i,t)}\frac{N-i}{N}\right] \\ &= \frac{i}{N}\left(1-\frac{i}{N}\right)E\left[\frac{1+\Pi_C(i,t)}{1+\bar{\Pi}(i,t)}\right], \end{aligned} \tag{9}$$

where

$$\bar{\Pi}(i,t) = \frac{i}{N}\Pi_C(i,t) + \left(1-\frac{i}{N}\right)\Pi_D(i,t) \tag{10}$$

is the average payoff in the population at time step t. Similarly, the number of individuals of type C decreases from i to $i-1$ from time step t to time step $t+1$ with probability

$$\begin{aligned} T_i^- &= E\left[\frac{(N-i)f_D(i,t)}{if_C(i,t)+(N-i)f_D(i,t)}\frac{i}{N}\right] \\ &= \frac{i}{N}\left(1-\frac{i}{N}\right)E\left[\frac{1+\Pi_D(i,t)}{1+\bar{\Pi}(i,t)}\right]. \end{aligned} \tag{11}$$

The number of individuals of type C over the successive time steps is a birth–death process on the state space $\{0, 1, \ldots, N\}$. The states $1, 2, \ldots, N-1$ are transient, while 0 and N are absorbing states. Given any initial state i different from 0 and N, the population takes a random number of time steps before being absorbed into either state 0 or state N and stays there forever.

Denote by F_C the fixation probability of C following its introduction as a single mutant, and by F_D the analogous fixation probability for D. It is known (see, e.g., Karlin and Taylor, 1975) that

$$F_C = \left(1 + \sum_{i=1}^{N-1}\prod_{j=1}^{i}\frac{T_j^-}{T_j^+}\right)^{-1}, \tag{12a}$$

$$F_D = \left(1 + \sum_{i=1}^{N-1}\prod_{j=1}^{i}\frac{T_{N-j}^+}{T_{N-j}^-}\right)^{-1}, \tag{12b}$$

$$\frac{F_C}{F_D} = \prod_{j=1}^{N-1}\frac{T_j^+}{T_j^-}. \tag{12c}$$

Under neutrality, which occurs when $\delta = 0$, the up/down ratio T_i^+/T_i^- is equal to 1. In this case, we have $F_C = F_D = 1/N$. Following Nowak et al. (2004), we say that *selection favors the evolution of C* if $F_C > 1/N$. Similarly, *selection disfavors the evolution of D* if $F_D < 1/N$. It is possible that selection favors the evolution of both C and D, or disfavors the evolution of both C and D. A second measure of the success of C is which strategy has the higher fixation probability. If $F_C > F_D$, then *selection favors the evolution of C more than the evolution of D*. Finally, we will say that *selection fully favors the evolution of C* if $F_C > 1/N > F_D$, and that *selection fully disfavors the evolution of C* if $F_C < 1/N < F_D$.

To derive the different expressions in (12), we have to find the up/down ratio T_i^+/T_i^-. First, as shown in Kroumi et al. (2021), we have

$$\begin{aligned} &E\left[\frac{1+\Pi_S(i,t)}{1+\bar{\Pi}(i,t)}\right] \\ &= E\Big[(1+\Pi_S(i,t))\left(1-\bar{\Pi}(i,t)+\bar{\Pi}^2(i,t)\right)\Big] + o(\delta) \\ &= 1 + E\Big[\Pi_S(i,t) - \bar{\Pi}(i,t) - \Pi_S(i,t)\bar{\Pi}(i,t) + \bar{\Pi}^2(i,t)\Big] + o(\delta) \\ &= 1 + E\Big[\Pi_S(i,t)\Big] - \frac{i}{N}E\Big[\Pi_S(i,t)\Pi_C(i,t)\Big] \\ &\quad - \frac{N-i}{N}E\Big[\Pi_S(i,t)\Pi_D(i,t)\Big] \\ &\quad + E\Big[\bar{\Pi}^2(i,t) - \bar{\Pi}(i,t)\Big] + o(\delta) \end{aligned} \tag{13}$$

for $S = C$ and D. Using the assumptions in (1), the first and second moments of the payoffs to C and D can be written as

$$E\Big[\Pi_C(i,t)\Big] = \delta\sum_{k=0}^{d-1} C(i-1,k)\mu_{C,k} + o(\delta), \tag{14a}$$

$$E\Big[\Pi_C^2(i,t)\Big] = \delta\sum_{k,l=0}^{d-1} C(i-1,k)C(i-1,l)\sigma_{CC,kl} + o(\delta), \tag{14b}$$

$$E\Big[\Pi_D(i,t)\Big] = \delta\sum_{k=0}^{d-1} C(i,k)\mu_{D,k} + o(\delta), \tag{14c}$$

$$E\Big[\Pi_D^2(i,t)\Big] = \delta\sum_{k,l=0}^{d-1} C(i,k)C(i,l)\sigma_{DD,kl} + o(\delta), \tag{14d}$$

$$E\Big[\Pi_C(i,t)\Pi_D(i,t)\Big] = \delta\sum_{k,l=0}^{d-1} C(i-1,k)C(i,l)\sigma_{CD,kl} + o(\delta). \tag{14e}$$

Inserting these expressions into (13), we obtain

$$E\left[\frac{1+\Pi_C(i,t)}{1+\bar{\Pi}(i,t)}\right] = 1 + \delta m_1(i) + o(\delta), \tag{15a}$$

$$E\left[\frac{1+\Pi_D(i,t)}{1+\bar{\Pi}(i,t)}\right] = 1 + \delta m_2(i) + o(\delta), \tag{15b}$$

where

$$\begin{aligned} m_1(i) &= \sum_{k=0}^{d-1} C(i-1,k)\mu_{C,k} - \frac{i}{N}\sum_{k,l=0}^{d-1} C(i-1,k)C(i-1,l)\sigma_{CC,kl} \\ &\quad - \left(1-\frac{i}{N}\right)\sum_{k,l=0}^{d-1} C(i-1,k)C(i,l)\sigma_{CD,kl} \\ &\quad + \frac{\partial}{\partial\delta}E\Big[\bar{\Pi}^2(i,t) - \bar{\Pi}(i,t)\Big]\Big|_{\delta=0}, \end{aligned} \tag{16a}$$

$$m_2(i) = \sum_{k=0}^{d-1} C(i,k)\mu_{D,k} - \frac{i}{N}\sum_{k,l=0}^{d-1} C(i-1,k)C(i,l)\sigma_{CD,kl} - \left(1-\frac{i}{N}\right)\sum_{k,l=0}^{d-1} C(i,k)C(i,l)\sigma_{DD,kl} + \frac{\partial}{\partial\delta}E\Big[\bar{\Pi}^2(i,t) - \bar{\Pi}(i,t)\Big]\Big|_{\delta=0}, \tag{16b}$$

Substituting (15) in (9) and (11), and thereafter dividing the results by one another, we have

$$\frac{T_i^+}{T_i^-} = 1 + \delta m(i) + o(\delta), \tag{17a}$$

$$\frac{T_i^-}{T_i^+} = 1 - \delta m(i) + o(\delta), \tag{17b}$$

where

$$\begin{aligned} m(i) &= m_1(i) - m_2(i) \\ &= \sum_{k=0}^{d-1}\big(C(i-1,k)\mu_{C,k} - C(i,k)\mu_{D,k}\big) \\ &\quad - \frac{i}{N}\sum_{k,l=0}^{d-1} C(i-1,k)C(i-1,l)\sigma_{CC,kl} \\ &\quad - \left(1-\frac{2i}{N}\right)\sum_{k,l=0}^{d-1} C(i-1,k)C(i,l)\sigma_{CD,kl} \\ &\quad + \left(1-\frac{i}{N}\right)\sum_{k,l=0}^{d-1} C(i,k)C(i,l)\sigma_{DD,kl}. \end{aligned} \tag{18}$$

Finally, using the approximations (17) in (12) and expanding the results up to the first order with respect to δ, we obtain

$$F_C = \frac{1}{1+\sum_{i=1}^{N-1}\prod_{j=1}^{i}[1-\delta m(j)] + o(\delta)} = \frac{1}{N} + \frac{\delta}{N^2}\sum_{i=1}^{N-1}(N-i)m(i) + o(\delta), \tag{19a}$$

$$F_D = \frac{1}{1+\sum_{i=1}^{N-1}\prod_{j=1}^{i}[1+\delta m(N-j)] + o(\delta)} = \frac{1}{N} - \frac{\delta}{N^2}\sum_{i=1}^{N-1} i m(i) + o(\delta), \tag{19b}$$

$$\frac{F_C}{F_D} = \prod_{i=1}^{N-1}[1+\delta m(i)] + o(\delta) = 1 + \delta\sum_{i=1}^{N-1} m(i) + o(\delta), \tag{19c}$$

for the fixation probabilities F_C and F_D.

4. Effects of variability in payoffs

In this section, we are interested in the effects of the scaled variances and covariances of the payoffs on F_C, F_D and F_C/F_D. From (18) and (19), we get

$$\frac{\partial F_C}{\partial \sigma_{CC,kl}} = -\frac{\delta}{N^3}\sum_{i=1}^{N-1}(N-i)iC(i-1,k)C(i-1,l) < 0, \tag{20a}$$

$$\frac{\partial F_C}{\partial \sigma_{DD,kl}} = \frac{\delta}{N^3}\sum_{i=1}^{N-1}(N-i)^2 C(i,k)C(i,l) > 0, \tag{20b}$$

since $C(i,k) > 0$ for $0 \le k \le i \le N-1$, and $C(i,k) = 0$ otherwise. This implies that any decrease in the scaled covariance between two payoffs to C, or any increase in the scaled covariance between two payoffs to D, increases the fixation probability F_C. The effect of the scaled covariance between a payoff to C and a payoff to D is less obvious since

$$\frac{\partial F_C}{\partial \sigma_{CD,kl}} = \frac{\delta}{N^3}\sum_{i=1}^{N-1}(N-2i)(N-i)C(i-1,k)C(i,l) \tag{21}$$

changes sign depending on the value of the parameters. This is a consequence of the facts that $N-2i < 0$ if $i > N/2$ and $N-i > 0$ if $i < N/2$. At least for $d \le N \le 100$, numerical computations have shown that the sign of the partial derivative is negative if $l+k \ge d$, and positive if $l+k \le d-1$.

Similarly, it can be shown that any decrease in the scaled covariance between two payoffs to C, or any increase in the scaled covariance between two payoffs to D, decreases the fixation probability F_D, while

$$\frac{\partial F_D}{\partial \sigma_{CD,kl}} = -\frac{\delta}{N^3}\sum_{i=1}^{N-1}(N-2i)iC(i-1,k)C(i,l). \tag{22}$$

For $d \le N \le 100$, numerical computations have shown that this partial derivative is negative if $l+k \le d-2$, and positive otherwise. To see whether these conditions hold for larger values of N, we will resort to further approximations.

In the case of a large population size, it can be shown by approximating Riemann sums with integrals (see Appendix A for details) that

$$F_C \approx \frac{1}{N} + \delta\Bigg[\sum_{k=0}^{d-1}\alpha_k\left(\mu_{C,k}-\mu_{D,k}\right) - \sum_{k,l=0}^{d-1}\alpha_{CC,kl}\left(\sigma_{CC,kl}-\sigma_{CD,kl}\right) + \sum_{k,l=0}^{d-1}\alpha_{DD,kl}\left(\sigma_{DD,kl}-\sigma_{CD,kl}\right)\Bigg], \tag{23a}$$

$$F_D \approx \frac{1}{N} - \delta\Bigg[\sum_{k=0}^{d-1}\beta_k(\mu_{C,k}-\mu_{D,k}) - \sum_{k,l=0}^{d-1}\beta_{CC,kl}(\sigma_{CC,kl}-\sigma_{CD,kl}) + \sum_{k,l=0}^{d-1}\beta_{DD,kl}(\sigma_{DD,kl}-\sigma_{CD,kl})\Bigg], \tag{23b}$$

$$\frac{F_C}{F_D} \approx 1 + N\delta\Bigg[\sum_{k=0}^{d-1}\gamma_k\left(\mu_{C,k}-\mu_{C,k}\right) - \sum_{k,l=0}^{d-1}\gamma_{CC,kl}\left(\sigma_{CC,kl}-\sigma_{CD,kl}\right) + \sum_{k,l=0}^{d-1}\gamma_{DD,kl}\left(\sigma_{DD,kl}-\sigma_{CD,kl}\right)\Bigg], \tag{23c}$$

where

$$\alpha_k = \binom{d-1}{k}B(k+1, d-k+1), \tag{24a}$$

$$\alpha_{CC,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+2, 2d-k-l), \tag{24b}$$

$$\alpha_{DD,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+1, 2d+1-k-l), \tag{24c}$$

$$\beta_k = \binom{d-1}{k}B(k+2, d-k), \tag{24d}$$

$$\beta_{DD,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+2, 2d-k-l), \tag{24e}$$

$$\beta_{CC,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+3, 2d-k-l-1), \tag{24f}$$

$$\gamma_k = \binom{d-1}{k}B(k+1, d-k), \tag{24g}$$

$$\gamma_{CC,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+2, d-k-l-1), \tag{24h}$$

$$\gamma_{DD,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+1, 2d-k-l), \tag{24i}$$

with

$$B(a,b) = \frac{(a-1)!(b-1)!}{(a+b-1)!} = \int_0^1 x^{a-1}(1-x)^{b-1}dx \approx \frac{1}{N}\sum_{i=1}^{N-1}\left(\frac{i}{N}\right)^{a-1}\left(1-\frac{i}{N}\right)^{b-1} \tag{25}$$

denoting the beta function for any positive integers a and b (see, e.g., Askey and Roy, 2010).

From (23), we confirm that a decrease in the scaled covariance between any two payoffs to C, or an increase in the scaled covariance between any two payoffs to D, increases the fixation probability F_C and decreases the fixation probability F_D. This makes it easier for weak selection to favor the evolution of C in any sense.

As for the coefficient of $\sigma_{CD,kl}$ in the first-order approximation of F_C, it is given by

$$\alpha_{CC,kl} - \alpha_{DD,kl} = \frac{\binom{d-1}{k}\binom{d-1}{l}}{2d+1}\left[\frac{1}{\binom{2d}{k+l+1}} - \frac{1}{\binom{2d}{k+l}}\right] = \frac{2k+2l+1-2d}{2d(2d+1)}\frac{\binom{d-1}{k}\binom{d-1}{l}}{\binom{2d-1}{k+l}}, \tag{26}$$

which is positive if $k+l \geq d$, and negative if $k+l \leq d-1$. This implies that increasing the scaled covariance between the payoffs P_k and Q_l will increase the fixation probability F_C if $k+l \geq d$, and decrease it if $k+l \leq d-1$.

Similarly, the coefficient of $\sigma_{CD,kl}$ in the first-order approximation of F_D is

$$\gamma_{CC,kl} - \gamma_{DD,kl} = \frac{\binom{d-1}{k}\binom{d-1}{l}}{2d+1}\left[\frac{1}{\binom{2d}{k+l+2}} - \frac{1}{\binom{2d}{k+l+1}}\right] = \frac{2k+2l+3-2d}{2d(2d+1)}\frac{\binom{d-1}{k}\binom{d-1}{l}}{\binom{2d-1}{k+l+1}}, \tag{27}$$

which is positive if $k+l \geq d-1$, and negative if $k+l \leq d-2$. Therefore, increasing the scaled covariance between the payoffs P_k and Q_l will decrease the fixation probability F_D if $k+l \geq d-1$, and increase it if $k+l \leq d-2$.

Finally, the coefficient of $\sigma_{CD,kl}$ in the first-order approximation of F_C/F_D is

$$\beta_{CC,kl} - \beta_{DD,kl} = \frac{\binom{d-1}{k}\binom{d-1}{l}}{2d}\left[\frac{1}{\binom{2d-1}{k+l+1}} - \frac{1}{\binom{2d-1}{k+l}}\right] = \frac{k+l+1-d}{d(2d-1)}\frac{\binom{d-1}{k}\binom{d-1}{l}}{\binom{2d-2}{k+l}}, \tag{28}$$

which is null if $k+l = d-1$. In this case, an increase in the scaled covariance between the payoffs P_k and Q_l will decrease the fixation probabilities F_C and F_D at the same rate so that this scaled covariance does not come into play in the condition for $F_C > F_D$.

5. Public goods game

In this section and Sections 6–8, we are interested in classical social dilemmas within groups of fixed size d where cooperation by an individual incurs a random cost c to the individual but provides a random benefit b to members belonging to the same group. The cost and benefit should actually be indexed by the time step but this is ignored to simplify the notation. As for their moments, we assume that

$$E[b] = \delta\mu_b + o(\delta), \tag{29a}$$

$$E[c] = \delta\mu_c + o(\delta), \tag{29b}$$

$$E[b^2] = \delta\sigma_b^2 + o(\delta), \tag{29c}$$

$$E[c^2] = \delta\sigma_c^2 + o(\delta), \tag{29d}$$

$$E[bc] = \delta\sigma_{bc} + o(\delta), \tag{29e}$$

while

$$E\left[b^i c^j\right] = o(\delta), \tag{30}$$

for any nonnegative integers i and j such that $i+j \geq 3$. Moreover, the scaled means satisfy $\mu_b > \mu_c > 0$, although the inequalities $b > c > 0$ may not necessarily hold almost surely.

We consider first a linear public goods game in which each cooperator incurs a cost c in order to contribute to the provision of a public good. A defector does not provide any public benefit and pays no cost. All effects of cooperation are additive and the public good provided by a cooperating individual is distributed equally among the $d-1$ other individuals in the same group (see, e.g., Hamburger, 1973; Fox and Guyer, 1978). In this case, the payoffs to C and D in interaction with k cooperators and $d-k-1$ defectors are

$$P_k = \frac{k}{d-1}b - c, \tag{31a}$$

$$Q_k = \frac{k}{d-1}b, \tag{31b}$$

whose scaled means are given by

$$\mu_{C,k} = \frac{k}{d-1}\mu_b - \mu_c, \tag{32a}$$

$$\mu_{D,k} = \frac{k}{d-1}\mu_b, \tag{32b}$$

and scaled variances and covariances by

$$\sigma_{CC,kl} = \frac{kl}{(d-1)^2}\sigma_b^2 + \sigma_c^2 - \frac{k+l}{d-1}\sigma_{bc}, \tag{33a}$$

$$\sigma_{CD,kl} = \frac{kl}{(d-1)^2}\sigma_b^2 - \frac{k}{d-1}\sigma_{bc}, \tag{33b}$$

$$\sigma_{DD,kl} = \frac{kl}{(d-1)^2}\sigma_b^2, \tag{33c}$$

for $k, l = 0, 1, \ldots, d-1$.

For a population of finite size N, we have the approximations

$$F_C \approx \frac{1}{N} + \delta\left[-\frac{\mu_b}{2N} - \frac{N-1}{2N}\mu_c + \frac{N+1}{6N^2}\sigma_b^2 - \frac{N^2-1}{6N^2}\sigma_c^2 + \frac{N-2}{6N}\sigma_{bc}\right], \tag{34a}$$

$$F_D \approx \frac{1}{N} + \delta\frac{N-1}{2N}\left[\frac{\mu_b}{N-1} + \mu_c - \frac{2N-1}{3N(N-1)}\sigma_b^2 + \frac{2N-1}{3N}\sigma_c^2 - \frac{2(N-2)}{3(N-1)}\sigma_{bc}\right], \tag{34b}$$

$$\frac{F_C}{F_D} \approx 1 + \delta\left[-\mu_b - (N-1)\mu_c + \frac{\sigma_b^2}{2} - \frac{N-1}{2}\sigma_c^2 + \frac{N-2}{2}\sigma_{bc}\right]. \tag{34c}$$

See Appendix B for the calculations. Note that d has no effect on the approximations of F_C and F_D up to the first-order with respect to δ. In addition, decreasing the scaled variance of the cost c, σ_c^2, or increasing the scaled covariance between the benefit b and the cost c, σ_{bc}, will increase the fixation probability F_C and decrease the fixation probability F_D. This is true for any finite population size $N \geq d \geq 2$.

Under weak selection, the conditions for $F_C > 1/N$, $F_D < 1/N$ and $F_C > F_D$ become

$$-\frac{\mu_b}{2N} - \frac{N-1}{2N}\mu_c + \frac{N+1}{6N^2}\sigma_b^2 - \frac{N^2-1}{6N^2}\sigma_c^2 + \frac{N-2}{6N}\sigma_{bc} > 0, \tag{35a}$$

$$\frac{\mu_b}{N-1} + \mu_c - \frac{2N-1}{3N(N-1)}\sigma_b^2 + \frac{2N-1}{3N}\sigma_c^2 - \frac{2(N-2)}{3(N-1)}\sigma_{bc} > 0, \tag{35b}$$

$$-\mu_b - (N-1)\mu_c + \frac{\sigma_b^2}{2} - \frac{N-1}{2}\sigma_c^2 + \frac{N-2}{2}\sigma_{bc} > 0, \tag{35c}$$

respectively, which reduce to

$$\sigma_{bc} - \sigma_c^2 > 3\mu_c, \quad \sigma_{bc} - \sigma_c^2 > \frac{3}{2}\mu_c, \quad \sigma_{bc} - \sigma_c^2 > 2\mu_c, \tag{36}$$

respectively, when the population size N is large. Note that neither σ_b^2 nor μ_b comes into play in these conditions. This is simply because the scaled mean μ_b has the same weight in $\mu_{C,k}$ as in $\mu_{D,k}$ for $k = 0, 1, \ldots, d-1$ (see Eq. (32)) and the weight of the scaled variance σ_b^2 is the same in all the scaled covariances $\sigma_{CC,kl}$, $\sigma_{CD,kl}$ and $\sigma_{DD,kl}$ for $k, l = 0, 1, \ldots, d-1$ (see Eq. (33)). This is not the case of σ_c^2 and σ_{bc}. An increase in σ_c^2 will increase only the scaled covariances $\sigma_{CC,kl}$ for $k, l = 0, 1, \ldots, d-1$, which plays against the evolution of C. Conversely, an increase in σ_{bc} will decrease the scaled covariances $\sigma_{CC,kl}$ more than the scaled covariances $\sigma_{CD,kl}$, while $\sigma_{DD,kl}$ will remain the same. This will play in favor of the evolution of C in any sense. Moreover, since $3\mu_c > 2\mu_c > (3/2)\mu_c > 0$, this will be the case only if the scaled covariance σ_{bc} is larger enough than the scaled variance σ_c^2 with the condition for $F_C > 1/N$ being the more stringent one. If b and c are not correlated, then all inequalities in (36) are reversed and the evolution of C is fully disfavored.

6. Synergistic benefits

In this section, we consider the public goods game with synergistically enhanced or discounted benefits (Hauert et al., 2006). In a group of size d, a benefit b is provided by a first cooperator, a benefit $b\omega$ by a second cooperator, and so on up to a benefit $b\omega^{d-1}$ provided by a d-th cooperator, where $\omega > 0$ represent a synergistic parameter. The public goods accumulated in a group are distributed equally among all members of the group. Then, the payoffs to C and D in interaction with k cooperators and $d-1-k$ defectors in a group of size d are given by

$$P_k = \frac{1}{d}\left(b + b\omega + \cdots + b\omega^k\right) - c = \frac{b}{d}\frac{1-\omega^{k+1}}{1-\omega} - c, \tag{37a}$$

$$Q_k = \frac{1}{d}\left(b + b\omega + \cdots + b\omega^{k-1}\right) = \frac{b}{d}\frac{1-\omega^k}{1-\omega}, \tag{37b}$$

respectively, for $k = 0, 1, \ldots, d-1$. The neutral case $\omega = 1$ leads to a linear benefit function, that is $(b + b\omega + \cdots + b\omega^{i-1}) = ib$, which corresponds to a public goods game with the cumulated benefit of cooperation in a group equally shared by all members of the group. In the case $\omega > 1$, the benefit function increases faster with respect to the number of cooperators than in the linear case, which means synergistically enhanced benefits for cooperation. In the case $\omega < 1$, it is the opposite with benefits for cooperation that are synergistically discounted.

The scaled means of the above payoffs are given by

$$\mu_{C,k} = \frac{1-\omega^{k+1}}{1-\omega}\frac{\mu_b}{d} - \mu_c, \tag{38a}$$

$$\mu_{D,k} = \frac{1-\omega^k}{1-\omega}\frac{\mu_b}{d}, \tag{38b}$$

and the scaled variances and covariances by

$$\sigma_{CC,kl} = \frac{(1-\omega^{k+1})(1-\omega^{l+1})}{(1-\omega)^2}\frac{\sigma_b^2}{d^2} + \sigma_c^2 - \frac{2-\omega^{k+1}-\omega^{l+1}}{1-\omega}\frac{\sigma_{bc}}{d}, \tag{39a}$$

$$\sigma_{CD,kl} = \frac{(1-\omega^{k+1})(1-\omega^l)}{(1-\omega)^2}\frac{\sigma_b^2}{d^2} - \frac{1-\omega^l}{1-\omega}\frac{\sigma_{bc}}{d}, \tag{39b}$$

$$\sigma_{DD,kl} = \frac{(1-\omega^k)(1-\omega^l)}{(1-\omega)^2}\frac{\sigma_b^2}{d^2}, \tag{39c}$$

for $k, l = 0, 1, \ldots, d-1$.

Assuming a large population size and using the above scaled moments, the approximations given in (23) of Section 4 become

$$F_C \approx \frac{1}{N} + \delta\left[\psi_b\mu_b - \frac{\mu_c}{2} - \frac{\sigma_c^2}{6} - \psi_{b^2}\sigma_b^2 + \psi_{bc}\sigma_{bc}\right], \tag{40a}$$

$$F_D \approx \frac{1}{N} - \delta\left[\phi_b\mu_b - \frac{\mu_c}{2} - \frac{\sigma_c^2}{3} - \phi_{b^2}\sigma_b^2 + \phi_{bc}\sigma_{bc}\right], \tag{40b}$$

$$\frac{F_C}{F_D} \approx 1 + N\delta\left[(\phi_b + \psi_b)\,\mu_b - \mu_c - \frac{\sigma_c^2}{2} - \left(\phi_{b^2} + \psi_{b^2}\right)\sigma_{b^2} + (\phi_{bc} + \psi_{bc})\,\sigma_{bc}\right], \tag{40c}$$

where

$$\psi_b = \frac{1}{d^2(d+1)}\sum_{k=0}^{d-1}(d-k)\omega^k, \tag{41a}$$

$$\psi_{b^2} = \sum_{k=0}^{d-2}\frac{(k+1)(4d^2-3kd-k)}{4d^3(d+1)(2d+1)}\omega^k + \sum_{k=d-1}^{2d-2}\frac{(2d-k-1)(2d-k)}{4d^3(d+1)(2d+1)}\omega^k, \tag{41b}$$

$$\psi_{bc} = \sum_{k=0}^{d-1}\frac{(d-k)\left(d^2+d-kd+2k+2\right)}{2d^2(d+1)(d+2)}\omega^k, \tag{41c}$$

$$\phi_b = \frac{1}{d^2(d+1)}\sum_{k=0}^{d-1}(k+1)\omega^k, \tag{41d}$$

$$\phi_{b^2} = \sum_{k=0}^{d-2}\frac{(k+1)\,(k+2)\,(3d+1)}{4d^3\,(d+1)\,(2d+1)}\omega^k + \sum_{k=d-1}^{2d-2}\frac{(2d-k-1)(2d+k+2)}{4d^3(2d+1)}\omega^k, \tag{41e}$$

$$\phi_{bc} = \sum_{k=0}^{d-1}\frac{(d-k)\left(d^2+(k+3)d+2k+2\right)}{2d^2(d+1)(d+2)}\omega^k. \tag{41f}$$

See Appendix C for the calculations.

In the approximation of F_C up to the first-order with respect to δ, the coefficient of σ_{bc} is positive while the coefficients of σ_b^2 and σ_c^2 are negative. Note also that the coefficients of σ_b^2 and σ_c^2 in the approximation of F_D are positive while the coefficient of σ_{bc} is negative. Therefore, decreasing the scaled variance of the benefit b or cost c, or increasing their scaled covariance, will increase the fixation probability F_C and decrease the fixation probability F_D.

Using the above approximations, the conditions for $F_C > 1/N$, $F_D < 1/N$ and $F_C > F_D$ in a large population under weak selection reduce to

$$\psi_b\mu_b - \frac{\mu_c}{2} - \frac{\sigma_c^2}{6} - \psi_{b^2}\sigma_b^2 + \psi_{bc}\sigma_{bc} > 0, \tag{42a}$$

$$\phi_b\mu_b - \frac{\mu_c}{2} - \frac{\sigma_c^2}{3} - \phi_{b^2}\sigma_b^2 + \phi_{bc}\sigma_{bc} > 0, \quad (42b)$$

$$(\phi_b + \psi_b)\,\mu_b - \mu_c - \frac{\sigma_c^2}{2} - \left(\phi_{b^2} + \psi_{b^2}\right)\sigma_{b^2} + (\phi_{bc} + \psi_{bc})\,\sigma_{bc} > 0, \quad (42c)$$

respectively.

A first point of interest is the effect of the parameter ω on the fixation probabilities F_C and F_D when d is fixed. Note that $\psi_b, \phi_b, \psi_{b^2}, \phi_{b^2}, \psi_{bc}, \phi_{bc}$ are polynomial functions of ω with only positive coefficients. Then, increasing the parameter ω will increase the weights of μ_b, σ_b^2 and σ_{bc} in F_C and F_D, while this has no effect on the weights of μ_c and σ_c^2. For ω large enough, ψ_b and ψ_{bc} are negligible compared to $\psi_{b^2} \approx \frac{\omega^{2d-2}}{2d^3(d+1)(2d+1)}$, from which we have the approximation

$$F_C \approx \frac{1}{N} - \delta\frac{\omega^{2d-2}\sigma_b^2}{2d^3(d+1)(2d+1)}, \quad (43)$$

which is always less than $1/N$. Similarly, ϕ_b and ϕ_{bc} are negligible compared to $\phi_{b^2} \approx \frac{\omega^{2d-2}}{d^2(2d+1)}$ when ω is large enough. This leads to the approximation

$$F_D \approx \frac{1}{N} + \frac{\delta\omega^{2d-2}}{d^2(2d+1)}\sigma_b^2, \quad (44)$$

which is always greater than $1/N$. Note that only σ_b^2 matters in the approximations of F_C and F_D. This is simply because the effects of σ_c^2 and σ_{bc} in the scaled variances and covariances in Eq. (39) are insignificant compared to the effect of σ_b^2. We conclude that, if ω is large enough, then weak selection fully disfavors the evolution of C, that is, $F_C < 1/N < F_D$, for any group size $d \geq 2$ in a large population.

Note that this is not the case in the absence of variability in b are c, since then

$$F_C \approx \frac{1}{N} + \delta\frac{\omega^{d-1}\mu_b}{d^2(d+1)} > \frac{1}{N} > \frac{1}{N} - \delta\frac{\omega^{d-1}\mu_b}{d(d+1)} \approx F_D, \quad (45)$$

which implies that weak selection fully favors the evolution of C.

Conversely, decreasing the value of ω will decrease the weights of μ_b, σ_{bc} and σ_b^2, but not enough for them to vanish. If ω is small enough such that

$$\psi_b \approx \frac{1}{d(d+1)}, \quad (46a)$$

$$\psi_{b^2} \approx \frac{1}{d(d+1)(2d+1)}, \quad (46b)$$

$$\psi_{bc} \approx \frac{d^2+d+2}{2d(d+1)(d+2)}, \quad (46c)$$

$$\phi_b \approx \frac{1}{d^2(d+1)}, \quad (46d)$$

$$\phi_{b^2} \approx \frac{3d+1}{2d^3(d+1)(2d+1)}, \quad (46e)$$

$$\phi_{bc} \approx \frac{1}{2d}, \quad (46f)$$

then the conditions for $F_C > 1/N$, $F_D < 1/N$ and $F_C > F_D$ in a large population under weak selection become

$$\frac{\mu_b}{d(d+1)} + \frac{(d^2+d+2)\sigma_{bc}}{2d(d+1)(d+1)} > \frac{\mu_c}{2} + \frac{\sigma_c^2}{6} + \frac{\sigma_b^2}{d(d+1)(2d+1)}, \quad (47a)$$

$$\frac{\mu_b}{d^2(d+1)} + \frac{\sigma_{bc}}{2d} > \frac{\mu_c}{2} + \frac{\sigma_c^2}{3} + \frac{(3d+1)\sigma_b^2}{2d^3(d+1)(2d+1)}, \quad (47b)$$

$$\frac{\mu_b}{d^2} + \frac{(d^2+2d+2)\sigma_{bc}}{d(d+1)(d+2)} > \mu_c + \frac{\sigma_c^2}{2} + \frac{\sigma_b^2}{2d^3}, \quad (47c)$$

respectively.

Figs. 1–3 illustrate the effect of the scaled variances and covariance of the benefit and cost on the fixation probability F_C for a given set of parameter values, showcasing its relationship with the value of the synergistic parameter ω. In these figures, F_C increases as either σ_b^2 or σ_c^2 decreases, or as σ_{bc} increases for $\omega < 1$ as well as $\omega > 1$. Moreover, as shown in Fig. 4, F_C tends to take larger values when ω is close to 1 and d is small, while it is the opposite for F_D.

We turn now our attention to the case of a large group size d for a fixed synergistic parameter ω. See Appendix C for the calculations.

6.1. Synergistically discounted benefits

In the case where $\omega < 1$ and d is large, all the expressions in (41) are negligible compared to μ_c and σ_c^2, in which case (40) leads to

$$F_C \approx \frac{1}{N} - \frac{\delta}{6}\left(3\mu_c + \sigma_c^2\right), \quad (48a)$$

$$F_D \approx \frac{1}{N} + \frac{\delta}{6}\left(3\mu_c + 2\sigma_c^2\right). \quad (48b)$$

Then, we have $F_C < 1/N < F_D$ so that the evolution of C is fully disfavored by weak selection if d is large enough. Note that this is also the case when $\sigma_c^2 = 0$ in the absence of variability in cost and benefit.

6.2. Synergistically enhanced benefits

In the case where $\omega > 1$ and d is large, the fixation probabilities in (40) can be approximated as

$$F_C \approx \frac{1}{N} - \frac{\delta\omega^{2d+1}}{4d^5(\omega-1)^3}\sigma_b^2, \quad (49a)$$

$$F_D \approx \frac{1}{N} + \frac{\delta\omega^{2d+1}}{4d^5(\omega-1)^3}\sigma_b^2. \quad (49b)$$

In this case, we have $F_C < 1/N < F_D$, which means that weak selection fully disfavors the evolution of C when d is large enough. Note that this is not the case in the absence of variability in b and c, since then

$$F_C \approx \frac{1}{N} + \delta\frac{\omega^{d+1}\mu_b}{d^3(\omega-1)^2} > \frac{1}{N} > \frac{1}{N} - \delta\frac{\omega^{d}\mu_b}{d^2(\omega-1)} \approx F_D, \quad (50)$$

which fully favors the evolution of C.

6.3. Synergistically neutral benefits

Finally, in the case where $\omega = 1$ and d is large, we obtain the approximations

$$F_C \approx \frac{1}{N} + \frac{\delta}{6}\left[\sigma_{bc} - \sigma_c^2 - 3\mu_c\right], \quad (51a)$$

$$F_D \approx \frac{1}{N} - \frac{\delta}{3}\left[\sigma_{bc} - \sigma_c^2 - \frac{3\mu_c}{2}\right], \quad (51b)$$

$$\frac{F_C}{F_D} \approx 1 + \frac{N\delta}{2}\left[\sigma_{bc} - \sigma_c^2 - 2\mu_c\right]. \quad (51c)$$

We conclude that, in the case of synergistically neutral benefits in a large population under weak selection, we have $F_C > 1/N$, $F_D < 1/N$ and $F_C > F_D$ as long as

$$\sigma_{bc} - \sigma_c^2 > 3\mu_c, \quad \sigma_{bc} - \sigma_c^2 > \frac{3}{2}\mu_c, \quad \sigma_{bc} - \sigma_c^2 > 2\mu_c, \quad (52)$$

respectively. These results are in agreement with the conclusion of the previous section for a public goods game.

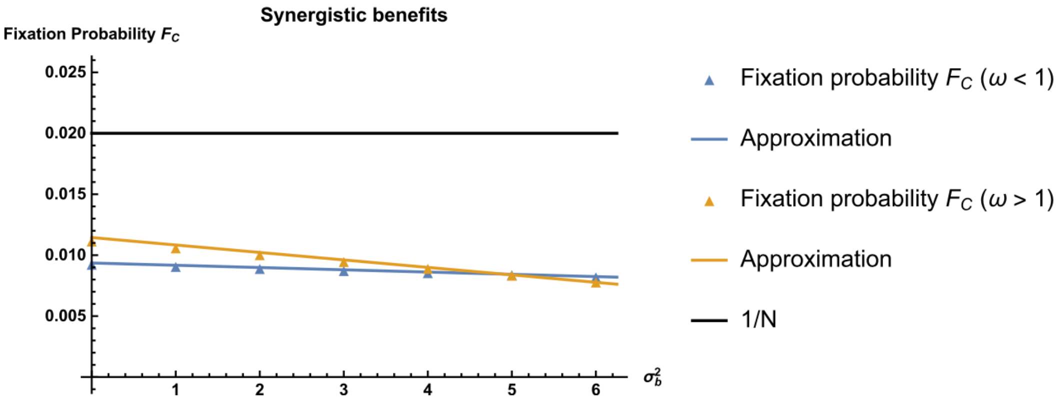

Fig. 1. Effect of σ_b^2 on F_C for $d = 5$, $N = 50$, $\delta = 1/100$, $\mu_b = 3$, $\mu_c = 2$, $\sigma_c^2 = 9/4$ and $\sigma_{bc} = 1/2$, with $\omega = 1.2$ and $\omega = 0.8$ as values of the synergistic parameter. The curves of the approximations are obtained from (40).

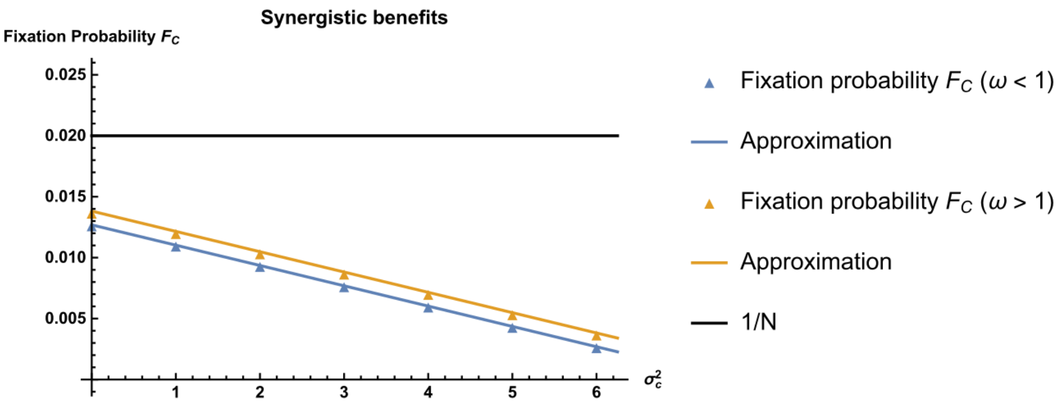

Fig. 2. Effect of σ_c^2 on F_C for $d = 5$, $N = 50$, $\delta = 1/100$, $\mu_b = 3$, $\mu_c = 2$, $\sigma_b^2 = 9/4$ and $\sigma_{bc} = 1/2$, with $\omega = 1.2$ and $\omega = 0.8$ as values of the synergistic parameter. The curves of the approximations are obtained from (40).

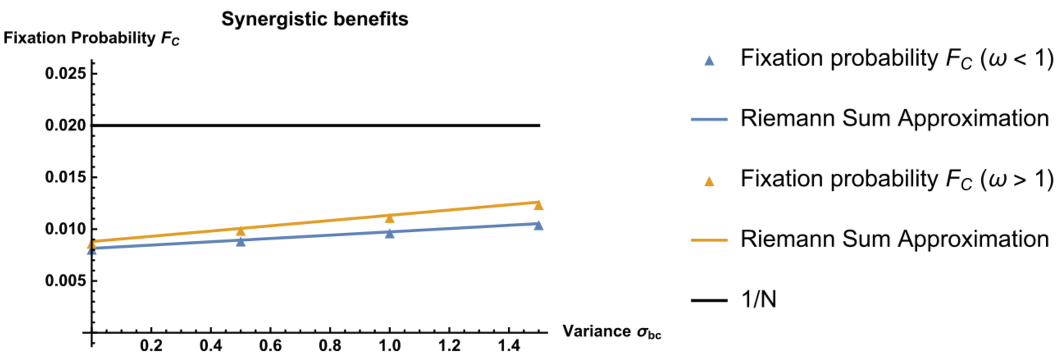

Fig. 3. Effect of σ_{bc} on F_C for $d = 5$, $N = 50$, $\delta = 1/100$, $\mu_b = 3$, $\mu_c = 2$, $\sigma_b^2 = 9/4$ and $\sigma_c^2 = 9/4$, with $\omega = 1.2$ and $\omega = 0.8$ as values of the synergistic parameter. The curves of the approximations are obtained from (40).

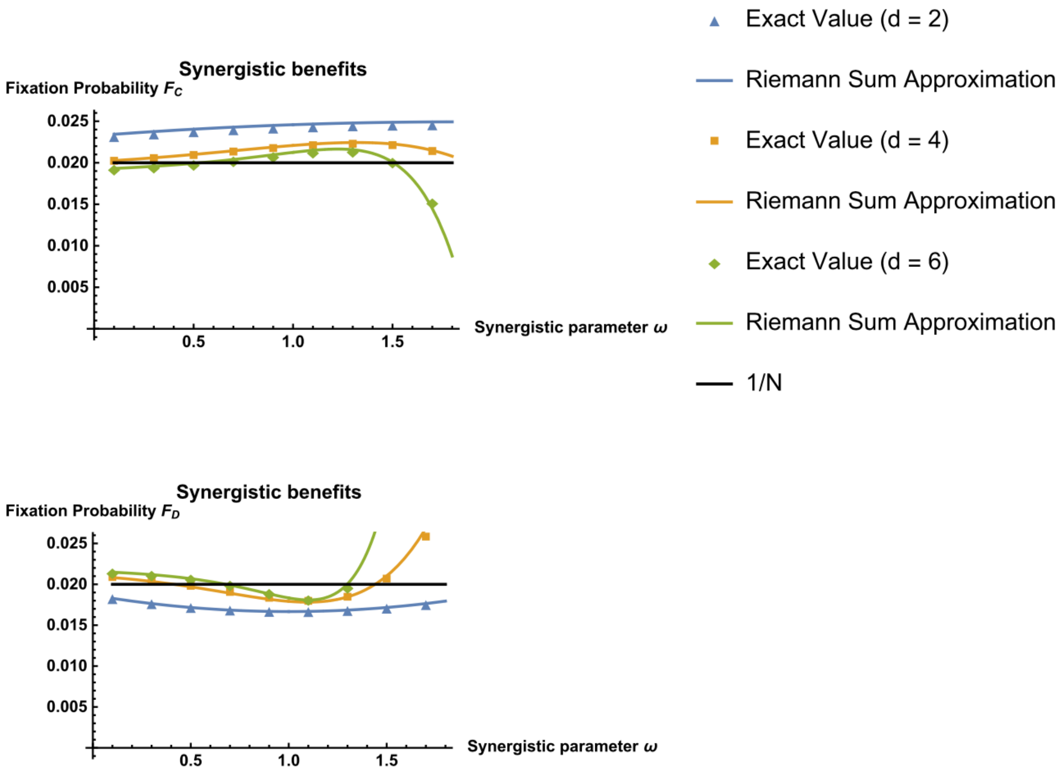

Fig. 4. Effect of synergistic parameter ω on F_C and F_D for $d = 2, 4, 6$ when $N = 50$, $\delta = 1/100$, $\mu_b = 3$, $\mu_c = 1/3$, $\sigma_b = 2$, $\sigma_c = 1/2$ and $\sigma_{bc} = 1$. The curves of the approximations are obtained from (40).

7. Stag hunt game

We consider next a stag hunt game where each cooperator pays a cost c, and receives in return a benefit b but only if everyone else in the same group cooperates, while a defector does not pay anything and receives nothing (Skyrms, 2004; Pacheco et al., 2009). Then, the payoff to C in interaction with k cooperators and $d-1-k$ defectors in a group of size d is $P_k = -c$ if $k = 0, 1, \ldots, d-2$ and $b - c$ if $k = d-1$, while the payoff to D in interaction with l cooperators and $d-1-l$ defectors is $Q_l = 0$ for $l = 0, 1, \ldots, d-1$. In this case, the scaled means, variances and covariances of these payoffs are given by

$$\mu_{C,k} = \mu_b \mathbf{1}_{\{k=d-1\}} - \mu_c, \tag{53a}$$

$$\mu_{D,l} = 0, \tag{53b}$$

$$\sigma_{CC,kl} = \sigma_b^2 \mathbf{1}_{\{k=l=d-1\}} + \sigma_c^2 - \sigma_{bc}\left(\mathbf{1}_{\{k=d-1\}} + \mathbf{1}_{\{l=d-1\}}\right), \tag{53c}$$

$$\sigma_{CD,kl} = \sigma_{DD,kl} = 0, \tag{53d}$$

for $k, l = 0, 1, \ldots, d-1$. Here, $\mathbf{1}_A$ is the indicator of an event A defined by

$$\mathbf{1}_A = \begin{cases} 1 & \text{if the event } A \text{ is true,} \\ 0 & \text{if the event } A \text{ is false.} \end{cases} \tag{54}$$

Inserting the above scaled moments in Eq. (18) and using the identity

$$\sum_{k=0}^{d-1} C(i,k) = 1 \tag{55}$$

yield

$$m(i) = \frac{\binom{i-1}{d-1}}{\binom{N-1}{d-1}}\mu_b - \mu_c - \frac{i}{N}\frac{\binom{i-1}{d-1}^2}{\binom{N-1}{d-1}^2}\sigma_b^2 - \frac{i}{N}\sigma_c^2 + \frac{2i}{N}\frac{\binom{i-1}{d-1}}{\binom{N-1}{d-1}}\sigma_{bc}, \tag{56}$$

from which (19) leads to the approximations

$$F_C \approx \frac{1}{N} + \delta\left[\frac{N-d}{Nd(d+1)}\mu_b - \frac{N-1}{2N}\mu_c - \frac{N^2-1}{6N^2}\sigma_c^2 - \frac{A_1}{N^2}\sigma_b^2 + \frac{2(N+1)(N-d)}{N^2(d+1)(d+2)}\sigma_{bc}\right], \tag{57a}$$

$$F_D \approx \frac{1}{N} - \delta\left[\frac{N-d}{N(d+1)}\mu_b - \frac{N-1}{2N}\mu_c - \frac{(N-1)(2N-1)}{6N^2}\sigma_c^2 - \frac{A_2}{N^2}\sigma_b^2 + \frac{2(N(d+1)-1)(N-d)}{N^2(d+1)(d+2)}\sigma_{bc}\right], \tag{57b}$$

$$\frac{F_C}{F_D} \approx 1 + N\delta\left[\frac{N-d}{Nd}\mu_b - \frac{N-1}{N}\mu_c - \frac{N-1}{2N}\sigma_c^2 - \frac{A_3}{N}\sigma_b^2 + \frac{2(N-d)}{N(d+1)}\sigma_{bc}\right], \tag{57c}$$

where

$$A_1 = \sum_{i=1}^{N-1}(N-i)\frac{i}{N}\frac{\binom{i-1}{d-1}^2}{\binom{N-1}{d-1}^2}, \tag{58a}$$

$$A_2 = \sum_{i=1}^{N-1}\frac{i^2}{N}\frac{\binom{i-1}{d-1}^2}{\binom{N-1}{d-1}^2}, \tag{58b}$$

$$A_3 = \sum_{i=1}^{N-1} \frac{i}{N} \frac{\binom{i-1}{d-1}^2}{\binom{N-1}{d-1}^2}. \tag{58c}$$

In the first-order approximations of F_C and F_D, the coefficients of σ_b^2 and σ_c^2 are negative, while the coefficient of σ_{bc} is positive. Therefore, a decrease in the scaled variance of the cost c or benefit b, or an increase in their scaled covariance, will increase the fixation probability F_C and decrease the fixation probability F_D. This is true for any finite population size $N \geq d \geq 2$. These conclusions are in agreement with the observation that an increase in σ_{bc} or a decrease in σ_b^2 or σ_c^2 will decrease the scaled covariance $\sigma_{CC,kl}$, while the scaled covariances $\sigma_{CD,kl}$ and $\sigma_{DD,kl}$ will remain the same, for $k, l = 0, 1, \ldots, d-1$. This will favor the evolution of C in any sense.

In the case of a large population size, using

$$\frac{\binom{i-1}{d-1}}{\binom{N-1}{d-1}} = \left(\frac{i}{N}\right)^{d-1} + O(N^{-1}) \tag{59}$$

uniformly for $1 \leq i \leq N$, it can be shown (as in Appendix A) that

$$\frac{A_1}{N^2} = \frac{1}{N}\sum_{i=1}^{N-1}\left(1-\frac{i}{N}\right)\left(\frac{i}{N}\right)^{2d-1} + O(N^{-1}) \approx \int_0^1 (1-x)x^{2d-1}dx = \frac{1}{2d(2d+1)}, \tag{60a}$$

$$\frac{A_2}{N^2} = \frac{1}{N}\sum_{i=1}^{N-1}\left(\frac{i}{N}\right)^{2d} + O(N^{-1}) \approx \int_0^1 x^{2d}dx = \frac{1}{2d+1}, \tag{60b}$$

$$\frac{A_3}{N} = \frac{1}{N}\sum_{i=1}^{N-1}\left(\frac{i}{N}\right)^{2d-1} + O(N^{-1}) \approx \int_0^1 x^{2d-1}dx = \frac{1}{2d}. \tag{60c}$$

Inserting these approximations in (57), we obtain

$$F_C \approx \frac{1}{N} + \delta\left[\frac{\mu_b}{d(d+1)} - \frac{\mu_c}{2} - \frac{\sigma_b^2}{2d(2d+1)} - \frac{\sigma_c^2}{6} + \frac{2\sigma_{bc}}{(d+1)(d+2)}\right], \tag{61a}$$

$$F_D \approx \frac{1}{N} - \delta\left[\frac{\mu_b}{d+1} - \frac{\mu_c}{2} - \frac{\sigma_b^2}{2d+1} - \frac{\sigma_c^2}{3} + \frac{2\sigma_{bc}}{d+2}\right], \tag{61b}$$

$$\frac{F_C}{F_D} \approx 1 + N\delta\left[\frac{\mu_b}{d} - \mu_c - \frac{\sigma_b^2}{2d} - \frac{\sigma_c^2}{2} + \frac{2\sigma_{bc}}{d+1}\right]. \tag{61c}$$

In this case, the conditions for $F_C > 1/N$, $F_D < 1/N$ and $F_C > F_D$ in a large population under weak selection become

$$\frac{\mu_b}{d(d+1)} - \frac{\mu_c}{2} - \frac{\sigma_b^2}{2d(2d+1)} - \frac{\sigma_c^2}{6} + \frac{2\sigma_{bc}}{(d+1)(d+2)} > 0, \tag{62a}$$

$$\frac{\mu_b}{d+1} - \frac{\mu_c}{2} - \frac{\sigma_b^2}{2d+1} - \frac{\sigma_c^2}{3} + \frac{2\sigma_{bc}}{d+2} > 0, \tag{62b}$$

$$\frac{\mu_b}{d} - \mu_c - \frac{\sigma_b^2}{2d} - \frac{\sigma_c^2}{2} + \frac{2\sigma_{bc}}{d+1} > 0, \tag{62c}$$

respectively. Increasing d will decrease the weights of μ_b, σ_b^2 and σ_{bc} in the first-order approximations of the fixation probabilities F_C and F_D, while the weights of μ_C and σ_c^2 remain the same. This makes it more difficult for weak selection to favor the evolution of C in any sense. In particular, for d large, the above conditions can be written as

$$-3\mu_c - \sigma_c^2 > 0, \quad -3\mu_c - 2\sigma_c^2 > 0, \quad -2\mu_c - \sigma_c^2 > 0, \tag{63}$$

respectively. This is never the case when $\mu_c > 0$. Then, we have $F_C < 1/N < F_D$, which means that weak selection will fully disfavor the evolution of C. This is a consequence of the fact that a cooperator will receive the benefit if all its partners cooperate, which will occur rarely if d is large. On average, the weight of σ_c^2 in $\sigma_{CC,kl}$ will be larger compared to the weights of σ_{bc} and σ_b^2.

The above properties on the effects of the scaled variances and covariance of the cost and benefit on the fixation probabilities F_C and F_D are illustrated in Figs. 5–7 for a particular set of parameter values. As for the effect of the group size d, it is illustrated in 8.

8. Snowdrift game

Another classical social dilemma is the snowdrift game (Zheng et al., 2007). In this game, the cost c for cooperation is shared equally by all cooperators in the same group, while the benefit b for cooperation is received by every individual in a group with at least one cooperator. In a group of k cooperators and $d-1-k$ defectors, the payoffs to C and D are given by

$$P_k = b - \frac{c}{k+1}, \tag{64a}$$

$$Q_k = b\mathbf{1}_{k\neq 0}, \tag{64b}$$

respectively, for $k = 0, 1, \ldots, d-1$. In this case, the payoff to C is a non-linear decreasing function with respect to the number of cooperators in the group rather than a constant as in the previous games. Moreover, the scaled means, variances and covariances of the payoffs to C and D according to the numbers of cooperating partners in the same group are given by

$$\mu_{C,k} = \mu_b - \frac{\mu_c}{k+1}, \tag{65a}$$

$$\mu_{D,k} = \mu_b\mathbf{1}_{\{k\neq 0\}}, \tag{65b}$$

$$\sigma_{CC,kl} = \sigma_b^2 - \left(\frac{1}{k+1} + \frac{1}{l+1}\right)\sigma_{bc} + \frac{\sigma_c^2}{(k+1)(l+1)}, \tag{65c}$$

$$\sigma_{DD,kl} = \sigma_b^2\mathbf{1}_{\{k\neq 0, l\neq 0\}}, \tag{65d}$$

$$\sigma_{CD,kl} = \left(\sigma_b^2 - \frac{\sigma_{bc}}{k+1}\right)\mathbf{1}_{\{l\neq 0\}}, \tag{65e}$$

for $k, l = 0, 1, \ldots, d-1$. Inserting these scaled moments in (18) yields the expression

$$m(i) = C(i,0)\mu_b - \left(\frac{N}{d} - \frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right)\frac{\mu_c}{i} - \left[1 - \left(1-\frac{i}{N}\right)C(i,0)\right]C(i,0)\sigma_b^2 - \frac{1}{Ni}\left(\frac{N}{d} - \frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right)^2\sigma_c^2 + \left[1 - \left(1-\frac{2i}{N}\right)C(i,0)\right]\left(\frac{N}{d} - \frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right)\frac{\sigma_{bc}}{i}. \tag{66}$$

See Appendix D for the calculations. Note that the coefficients of σ_c^2 and σ_b^2 in the above expression are negative, while the coefficient of σ_{bc} is positive. Therefore, a decrease in the scaled variance of the cost c or benefit b, or an increase in their scaled covariance, will increase the fixation probability F_C and decrease the fixation probability F_D.

Assuming a large population size, the above expression of $m(i)$ leads to the approximations

$$F_C \approx \frac{1}{N} + \delta\left[\frac{\mu_b}{d+1} - \frac{H_{d+1}-1}{d}\mu_c - \frac{d\sigma_b^2}{(d+1)(2d+1)} - \frac{2H_{d+1} - H_{2d+1} - 1}{d^2}\sigma_c^2 + \left(\frac{1}{(d+1)(2d+1)} + \frac{2H_{d+1} - H_{2d+1} - 1}{d}\right)\sigma_{bc}\right], \tag{67a}$$

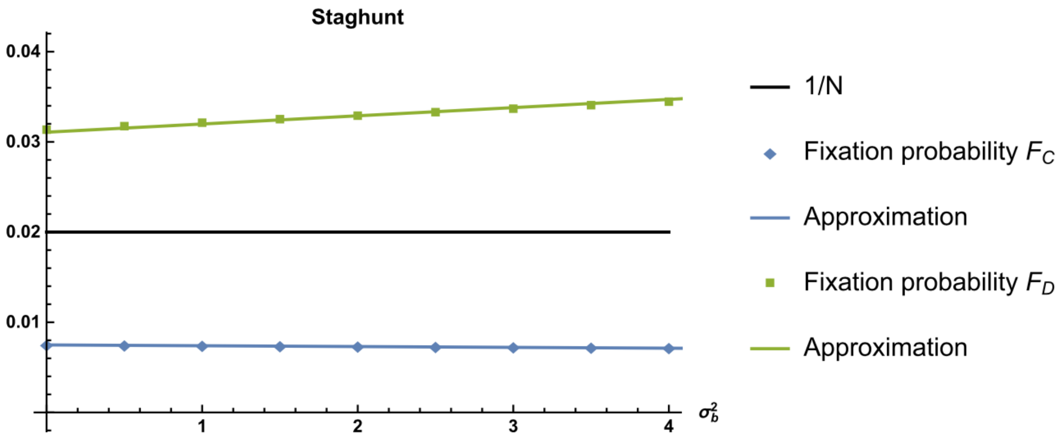

Fig. 5. Effect of σ_b^2 on F_C and F_D when $N = 50$, $\delta = 1/100$, $\mu_b = 3$, $\mu_c = 2$, $\sigma_c^2 = 9/4$ and $\sigma_{bc} = 1/2$ in the stag hunt game. The curves of the approximations are obtained from (61).

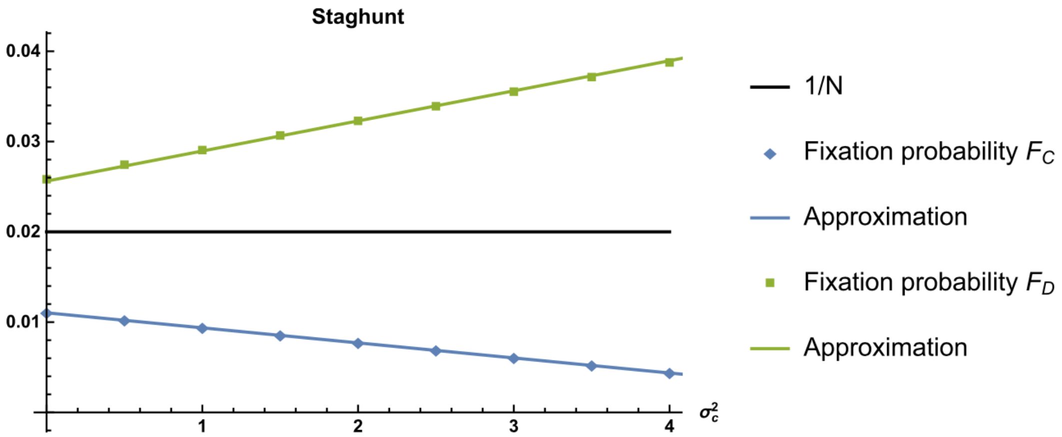

Fig. 6. Effect of σ_c^2 on F_C and F_D when $N = 50$, $\delta = 1/100$, $\mu_b = 3$, $\mu_c = 2$, $\sigma_b^2 = 9/4$ and $\sigma_{bc} = 1/2$ in the stag hunt game. The curves of the approximations are obtained from (61).

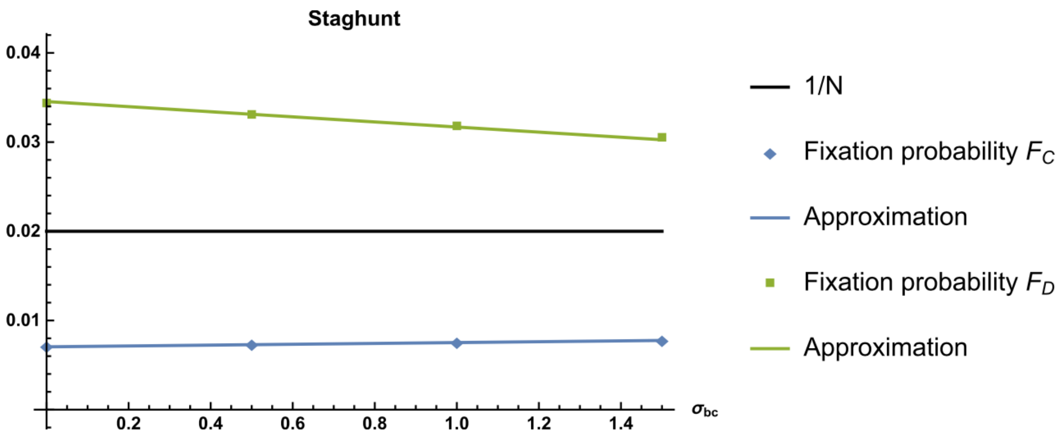

Fig. 7. Effect of σ_{bc} on F_C and F_D when $N = 50$, $\delta = 1/100$, $\mu_b = 3$, $\mu_c = 2$, $\sigma_b^2 = 9/4$ and $\sigma_c^2 = 9/4$ in the stag hunt game. The curves of the approximations are obtained from (61).

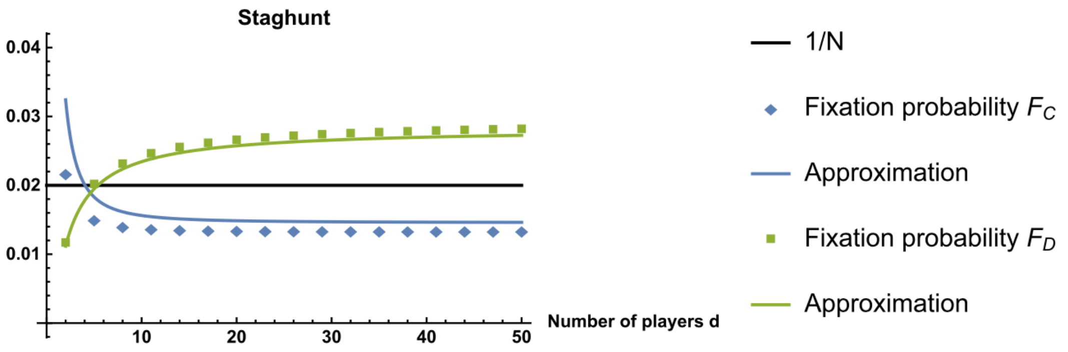

Fig. 8. Effect of group size d on F_C and F_D when $N = 50, \delta = 1/100, \mu_b = 5, \mu_c = 1, \sigma_b = 1, \sigma_c = 1$ and $\sigma_{bc} = 1/2$ in the stag hunt game. The curves of the approximations are obtained from (61).

$$F_D \approx \frac{1}{N} - \frac{\delta}{d+1}\left[\frac{\mu_b}{d} - \mu_c - \frac{3d+1}{2d(2d+1)}\sigma_b^2 - \frac{2\sigma_c^2}{2d+1} + \frac{4d^3+3d+1}{2d^2(2d+1)}\sigma_{bc}\right], \tag{67b}$$

$$\frac{F_C}{F_D} \approx 1 + N\delta\left[\frac{\mu_b}{d} - \frac{H_d}{d}\mu_c - \frac{\sigma_b^2}{2d} - \frac{2H_d - H_{2d}}{d^2}\sigma_c^2 + \left(\frac{1}{2d^2} + \frac{2H_d - H_{2d}}{d}\right)\sigma_{bc}\right], \tag{67c}$$

where

$$H_k = \sum_{n=1}^{k}\frac{1}{k} \tag{68}$$

for $k \geq 1$ and $H_0 = 0$, as shown in Appendix D. Finally, assuming d large and using the approximation $H_k \approx \ln(k)$ for k large enough, we get

$$F_C \approx \frac{1}{N} + \frac{\delta\ln(d)}{d}(\sigma_{bc} - \mu_c), \tag{69a}$$

$$F_D \approx \frac{1}{N} - \frac{\delta}{d}(\sigma_{bc} - \mu_c), \tag{69b}$$

$$\frac{F_C}{F_D} \approx 1 + \frac{N\delta\ln(d)}{d}(\sigma_{bc} - \mu_c). \tag{69c}$$

This implies that weak selection will fully favor the evolution of C, that is, $F_C > 1/N > F_D$, as long as $\sigma_{bc} > \mu_c$. If this inequality is reversed, then the evolution of C will be fully disfavored by weak selection.

Note that the benefit b comes into the payoffs to C and D with the same weight except in the case where an individual interacts with $d-1$ defectors, which will rarely occur if d is large enough. The weight of μ_b in the mean of the payoff to C in interaction with k cooperators and $d-1-k$ defectors is the same as in the mean of the payoff to D in interaction with k cooperators and $d-1-k$ defectors for $k = 1, \ldots, d-1$ (see Eq. (65)). Also, the weight of σ_b^2 is the same on $\sigma_{CC,kl}$, $\sigma_{CD,kl}$ and $\sigma_{DD,kl}$ for $k, l \neq 0$. Note that the weight of σ_{bc} in $\sigma_{CC,kl}$ is higher than its weight in $\sigma_{DD,kl}$, for $k, l \neq 0$. An increase in σ_{bc} will decrease $\sigma_{CC,kl}$ more than $\sigma_{DD,kl}$ which is more favorable for the evolution of C. Finally, the weight of σ_c^2 in the scaled covariances in Eq. (65) is lower than the weight of σ_{bc}. This explains why σ_c^2 does not come into play in the approximations (69).

The fixation probabilities F_C and F_D as functions of σ_{bc} and d are represented in Figs. 9 and 10 for particular sets of parameter values. The general patterns are similar to those observed in the previous social dilemmas.

9. Discussion

In this paper, we have examined the effect of variability in payoffs on the evolution of cooperation (C) against defection (D) in multi-player games in a finite population. Consider a well-mixed population of size $N \geq 2$ where interactions occur in random groups of size $d \geq 2$. Denote by P_k and Q_k the payoffs to a C-player and a D-player, respectively, in interaction with k cooperators and $d-1-k$ defectors for $k = 0, 1, \ldots, d-1$. We have shown that an increase in $\sigma_{DD,kl}$, or a decrease in $\sigma_{CC,kl}$, will increase the probability of ultimate fixation of C from an initial frequency $1/N$, represented by F_C, and decrease the corresponding fixation probability for D, represented by F_D. Here, $\sigma_{CC,kl}$ (respectively, $\sigma_{DD,kl}$) is the scaled covariance between P_k and P_l (respectively, Q_k and Q_l) with respect to the order of all the first and second moments, which is assumed to be small to model weak selection. In addition, an increase in the scaled covariance between P_k and Q_l will increase F_C and decrease F_D if $k+l > d-1$, decrease F_C and increase F_D if $k+l < d-1$, and decrease both F_C and F_D at the same rate if $k+l = d-1$. These conclusions are valid for any group size $d \geq 2$ and extend previous results obtained for the case $d = 2$ by Kroumi et al. (2021).

In particular, we have studied the evolution of cooperation in some classical social dilemmas characterized by a random cost c and a random benefit b. In the case of a public goods game, we have shown that weak selection can favor the evolution of C ($F_C > 1/N$), disfavor the evolution of D ($F_D < 1/N$), and favor the evolution of C more than the evolution of D ($F_C > F_D$), contrary to what can happen in the case of constant cost and benefit, where selection fully favors the evolution of D, that is $F_C < 1/N < F_D$ (see van Veelen and Nowak, 2012).

Moreover, the conditions for these evolutionary properties to hold do not depend on the group size d. Therefore, they correspond to the conditions obtained by Kroumi et al. (2021) in the case of a two-player Prisoner's Dilemma. An increase in σ_c^2, the scaled variance of c, will increase $\sigma_{CC,kl}$ (see Eq. (33)) without any effect on the other scaled covariances. This will play in disfavor of the evolution of cooperation in any sense since it decreases F_C and increases F_D. This is not the case if σ_{bc}, the scaled covariance between b and c, is increased since this will decrease the scaled covariance between any two payoffs to C without any effect on the scaled covariance between any two payoffs to D (see Eq. (33)). Then, an increase in σ_{bc} will increase F_C and decrease F_D, which will play in favor of the evolution of C in any sense. In the case of a large population size, the conditions for $F_C > 1/N$, $F_D < 1/N$ and $F_C > F_D$, respectively, are given in Eq. (36). Note that the

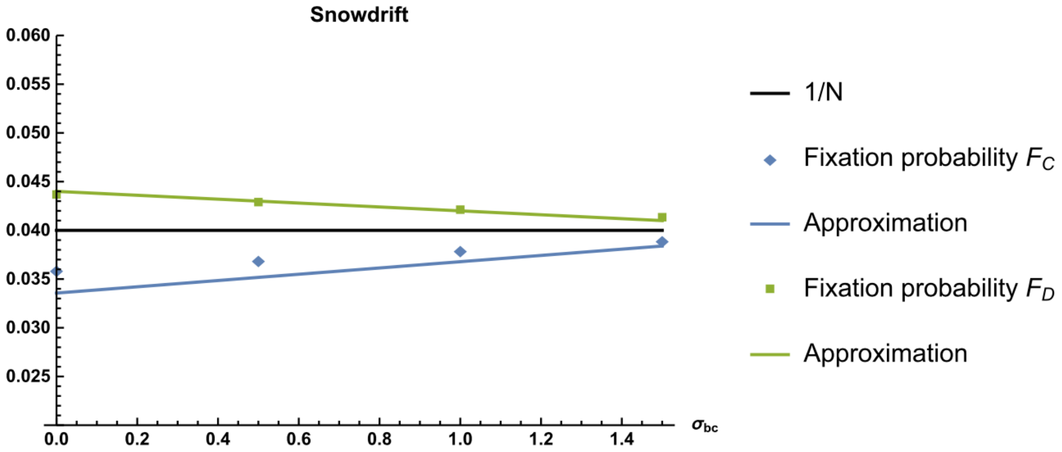

Fig. 9. Effect of σ_{bc} on F_C and F_D when $N = 50, \delta = 1/100\mu_b = 3, \mu_c = 2, \sigma_b = 3/2$ and $\sigma_c = 3/2$ in the snowdrift game. The curves of the approximations are obtained from (69).

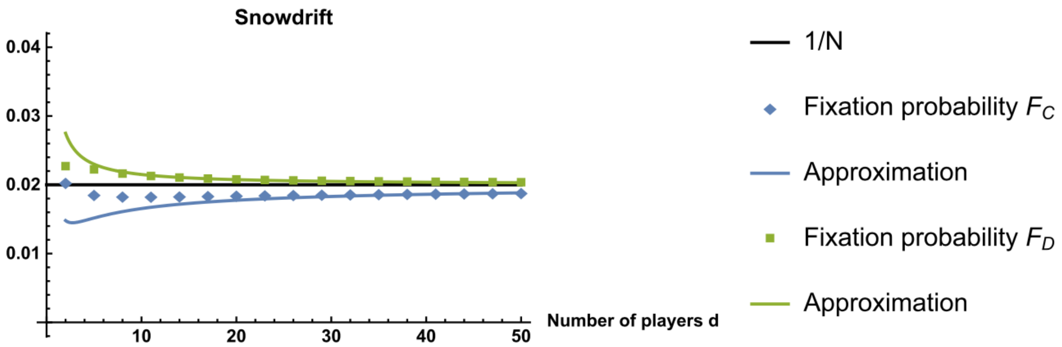

Fig. 10. Effect of group size d on F_C and F_D when $N = 50, \delta = 1/100, \mu_b = 3, \mu_c = 2, \sigma_b = 1, \sigma_c = 1$ and $\sigma_{bc} = 1/2$ in the snowdrift game. The curves of the approximations are obtained from (69).

condition for $F_C > F_D$ is the same as the one obtained by Kroumi and Lessard (2021a) for weak selection to favor the abundance of C more than the abundance of D in a multi-player public goods game in the presence of recurrent symmetric mutation.

The second dilemma studied is the public goods game with synergistically enhanced or discounted benefits. A benefit b is provided by a first cooperator, a benefit $b\omega$ by a second co-operator, and so on up to a benefit $b\omega^{d-1}$ provided by a dth cooperator, where $\omega > 0$ represents a synergistic parameter. The public goods accumulated in a group are distributed equally among all members of the group. In this case, we have shown that not only a decrease in σ_c^2 or an increase in σ_{bc} will increase F_C and decrease F_D, but also a decrease in σ_b^2, the scaled variance of b, even in a large population. In addition, increasing ω will increase the weight of σ_b^2 more than the weights of the scaled means and other scaled covariances of the payoffs to C and D in F_C and F_D. This makes it more difficult for weak selection to favor the evolution of C in any sense. If ω is large enough, then weak selection will fully disfavor the evolution of C since then $F_C < 1/N < F_D$ (see Eqs. (43) and (44)) for any group size $d \geq 2$. Note that it is the opposite in the absence of variability in b and c (see Eq. (45)). It is also the opposite if interactions occur in groups of large enough size d for any synergistically enhanced benefits ($\omega > 1$, see Eq. (49)) as well as any synergistically discounted benefits ($\omega < 1$, see Eq. (48)) .

Another social dilemma of interest is the stag hunt game where a cooperator receives a benefit b only if everyone else in the same group cooperates. In this case, increasing σ_{bc}, or decreasing σ_b^2 or σ_c^2, will increase F_C and decrease F_D for any group size $d \geq 2$. On the other hand, increasing the group size d will reduce the weight of σ_{bc} in F_C and F_D compared to the weights of σ_b^2 and σ_c^2, and this plays against the evolution of C. For a group size d large enough, weak selection will fully disfavor the evolution of C. This is a consequence of the fact that a cooperator will receive a benefit very rarely if d is large. Note that the same conclusion holds in the absence of variability in b and c.

The last social dilemma considered is the snowdrift game where the cooperation cost is distributed equally among all co-operators in the same group. The conclusions in the previous case are still valid except the one in the case of a large group size d. In this case, we have shown that the conditions for $F_C >$

$1/N$, $F_D < 1/N$ and $F_C > F_D$ are all equivalent to $\sigma_{bc} > \mu_c$, which can occur only with random cost and benefit. Note that the same condition has been obtained by Kroumi and Lessard (2021a) for weak selection to favor the abundance of C in the case of interactions in large groups in the presence of recurrent symmetric mutation.

In general, variability in cost and benefit in social dilemmas introduces variances and covariances in payoffs for cooperation and defection. We have seen that the probability for cooperation to ultimately fix after being introduced as a single mutant is increased, and the corresponding probability for defection is decreased, when the variances of the cost and benefit are decreased, while their covariance is increased. Moreover, the effects are more important when the number of interacting players is small. These are the conditions that can best play in favor of the evolution of cooperation.

CRediT authorship contribution statement

Dhaker Kroumi: Completed the analysis, Wrote the first draft of the paper. **Éloi Martin:** Obtained the first results on fixation probabilities, Designed the figures. **Sabin Lessard:** Initiated the project, Revised the paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Fixation probabilities in a large population

Let us start with a preliminary result on the limit of a Riemann sum to an integral.

Lemma 1. *Let*

$$a(i,N) = f\left(\frac{i}{N}\right) + O(N^{-1}) \tag{70}$$

for $1 \le i \le N$, where f is a continuous function defined on $[0,1]$ and $O(N^{-1}) \to 0$ uniformly for $0 \le i \le N$ as $N \to \infty$. Then, we have

$$\lim_{N\to\infty} \frac{1}{N}\sum_{i=1}^{N} a(i,N) = \int_0^1 f(x)dx. \tag{71}$$

Proof. It suffices to note that the assumptions imply the identity

$$\frac{1}{N}\sum_{i=1}^{N} a(i,N) = \frac{1}{N}\sum_{i=1}^{N} f\left(\frac{i}{N}\right) + O(N^{-1}), \tag{72}$$

from which

$$\lim_{N\to\infty} \frac{1}{N}\sum_{i=1}^{N} a(i,N) = \lim_{N\to\infty} \frac{1}{N}\sum_{i=1}^{N} f\left(\frac{i}{N}\right) = \int_0^1 f(x)dx \tag{73}$$

owing to the properties of the Riemann integral. □

In order to apply this result to fixation probabilities in multiplayer games, note first that

$$C(i,k) = \frac{\binom{i}{k}\binom{N-i-1}{d-1-k}}{\binom{N-1}{n}} = \binom{d-1}{k}\left(\frac{i}{N}\right)^k\left(1-\frac{i}{N}\right)^{d-1-k} + O(N^{-1}). \tag{74}$$

Then, we have

$$\begin{aligned}
&\frac{1}{N^2}\sum_{i=1}^{N-1}(N-i)C(i-1,k)\\
&= \binom{d-1}{k}\frac{1}{N}\sum_{i=1}^{N-1}\left(\frac{i}{N}\right)^k\left(1-\frac{i}{N}\right)^{d-k} + O(N^{-1})\\
&\approx \binom{d-1}{k}\int_0^1 x^k(1-x)^{d-k}dx = \alpha_k,
\end{aligned} \tag{75}$$

where

$$\alpha_k = \binom{d-1}{k}B(k+1, d-k+1) = \frac{d-k}{(d+1)d}, \tag{76}$$

with B being the beta function (see e.g. Askey and Roy, 2010) defined as

$$B(a,b) = \int_0^1 x^{a-1}(1-x)^{b-1}dx. \tag{77}$$

Analogously, we have

$$\frac{1}{N^2}\sum_{i=1}^{N-1}(N-i)C(i,k) \approx \alpha_k. \tag{78}$$

By a similar reasoning, we find

$$\begin{aligned}
&\frac{1}{N^2}\sum_{i=1}^{N-1}(N-i)\frac{i}{N}C(i-1,k)C(i-1,l)\\
&= \frac{1}{N}\sum_{i=1}^{N-1}\binom{d-1}{k}\binom{d-1}{l}\left(\frac{i}{N}\right)^{k+l+1}\left(1-\frac{i}{N}\right)^{2d-k-l-1}\\
&\quad + O(N^{-1})\\
&\approx \binom{d-1}{k}\binom{d-1}{l}\int_0^1 x^{k+l+1}(1-x)^{2d-k-l-1}dx = \alpha_{CC,kl},
\end{aligned} \tag{79}$$

$$\begin{aligned}
&\frac{1}{N^2}\sum_{i=1}^{N-1}(N-i)\left(1-\frac{i}{N}\right)C(i,k)C(i,l)\\
&= \frac{1}{N}\sum_{i=1}^{N-1}\binom{d-1}{k}\binom{d-1}{l}\left(\frac{i}{N}\right)^{k+l}\left(1-\frac{i}{N}\right)^{2d-k-l} + O(N^{-1})\\
&\approx \binom{d-1}{k}\binom{d-1}{l}\int_0^1 x^{k+l}(1-x)^{2d-k-l}dx = \alpha_{DD,kl}
\end{aligned} \tag{80}$$

and

$$\begin{aligned}
&\frac{1}{N^2}\sum_{i=1}^{N-1}(N-i)\left(1-\frac{2i}{N}\right)C(i-1,k)C(i,l)\\
&= \frac{1}{N}\sum_{i=1}^{N-1}\binom{d-1}{k}\binom{d-1}{l}\left(\frac{i}{N}\right)^{k+l}\\
&\quad\times\left(1-\frac{i}{N}\right)^{2d-k-l-1}\left(1-\frac{2i}{N}\right) + O(N^{-1})
\end{aligned}$$

$$\approx \binom{d-1}{k}\binom{d-1}{l}\int_0^1 x^{k+l}(1-x)^{2d-k-l-1}(1-2x)dx$$

$$= \alpha_{DD,kl} - \alpha_{CC,kl}, \tag{81}$$

where

$$\alpha_{CC,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+2, 2d-k-l), \tag{82a}$$

$$\alpha_{DD,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+1, 2d+1-k-l). \tag{82b}$$

Using these approximations in (18) and (19) for the fixation probability F_C, we get

$$F_C \approx \frac{1}{N} + \delta\Bigg[\sum_{k=0}^{d-1}\alpha_k\left(\mu_{C,k}-\mu_{D,k}\right) - \sum_{k,l=0}^{d-1}\alpha_{CC,kl}\left(\sigma_{CC,kl}-\sigma_{CD,kl}\right) + \sum_{k,l=0}^{d-1}\alpha_{DD,kl}\left(\sigma_{DD,kl}-\sigma_{CD,kl}\right)\Bigg]. \tag{83}$$

By symmetry, the fixation probability F_D can be approximated as

$$F_D \approx \frac{1}{N} - \delta\Bigg[\sum_{k=0}^{d-1}\beta_k(\mu_{C,k}-\mu_{D,k}) + \sum_{k,l=0}^{d-1}\beta_{DD,kl}(\sigma_{DD,kl}-\sigma_{CD,kl}) - \sum_{k,l=0}^{d-1}\beta_{CC,kl}(\sigma_{CC,kl}-\sigma_{CD,kl})\Bigg], \tag{84}$$

where

$$\beta_k = \binom{d-1}{k}B(k+2, d-k), \tag{85a}$$

$$\beta_{DD,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+2, 2d-k-l), \tag{85b}$$

$$\beta_{CC,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+3, 2d-k-l-1). \tag{85c}$$

As for the ratio of these fixation probabilities, we can deduce the approximation

$$\frac{F_C}{F_D} \approx 1 + N\delta\Bigg[\sum_{k=0}^{d-1}\gamma_k\left(\mu_{C,k}-\mu_{C,k}\right) - \sum_{k,l=0}^{d-1}\gamma_{CC,kl}\left(\sigma_{CC,kl}-\sigma_{CD,kl}\right) + \sum_{k,l=0}^{d-1}\gamma_{DD,kl}\left(\sigma_{DD,kl}-\sigma_{CD,kl}\right)\Bigg], \tag{86}$$

where

$$\gamma_k = \binom{d-1}{k}B(k+1, d-k), \tag{87a}$$

$$\gamma_{CC,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+2, d-k-l-1), \tag{87b}$$

$$\gamma_{DD,kl} = \binom{d-1}{k}\binom{d-1}{l}B(k+l+1, 2d-k-l). \tag{87c}$$

Appendix B. Public goods game

Note that the hypergeometric distribution probabilities defined in (5) satisfy the combinatorial identities

$$\sum_{k=0}^{d-1} C(i,k) = 1 \tag{88}$$

and

$$\sum_{k=0}^{d-1} kC(i,k) = \sum_{k=0}^{d-1}\frac{k\binom{i}{k}\binom{N-1-i}{d-1-k}}{\binom{N-1}{d-1}} = \frac{i}{\binom{N-1}{d-1}}\sum_{k=0}^{d-2}\binom{i-1}{k}\binom{N-i-1}{d-2-k}$$

$$= i\frac{d-1}{N-1}, \tag{89}$$

owing to Vandermonde's identity

$$\sum_{k=0}^{r}\binom{m}{k}\binom{n}{r-k} = \binom{m+n}{r}. \tag{90}$$

Therefore, we have

$$\sum_{k=0}^{d-1}\left(C(i-1,k)\mu_{C,k} - C(i,k)\mu_{D,k}\right)$$

$$= \frac{1}{d-1}\sum_{k=0}^{d-1}kC(i-1,k)\mu_b - \sum_{k=0}^{d-1}C(i-1,k)\mu_c - \frac{1}{d-1}\sum_{k=0}^{d-1}kC(i,k)\mu_b$$

$$= -\frac{1}{N-1}\mu_b - \mu_c, \tag{91}$$

while

$$\sum_{k,l=0}^{d-1}\Bigg[\left(1-\frac{i}{N}\right)C(i,k)C(i,l)\sigma_{DD,kl} - \frac{i}{N}C(i-1,k)C(i-1,l)\sigma_{CC,kl} - \left(1-\frac{2i}{N}\right)C(i-1,k)C(i,l)\sigma_{CD,kl}\Bigg]$$

$$= \left(1-\frac{i}{N}\right)\sum_{k,l=0}^{d-1}C(i,k)C(i,l)\frac{kl}{(d-1)^2}\sigma_b^2 - \frac{i}{N}\sum_{k,l=0}^{d-1}C(i-1,k)C(i-1,l)\left[\frac{kl}{(d-1)^2}\sigma_b^2 + \sigma_c^2 - \frac{k+l}{d-1}\sigma_{bc}\right] - \left(1-\frac{2i}{N}\right)\sum_{k,l=0}^{d-1}C(i-1,k)C(i,l)\left[\frac{kl}{(d-1)^2}\sigma_b^2 - \frac{k}{d-1}\sigma_{bc}\right]$$

$$= \left(1-\frac{i}{N}\right)\frac{i^2}{(N-1)^2}\sigma_b^2 - \frac{i}{N}\left[\left(\frac{i-1}{N-1}\right)^2\sigma_b^2 + \sigma_c^2 - \frac{2(i-1)}{N-1}\sigma_{bc}\right] - \left(1-\frac{2i}{N}\right)\left[\frac{i(i-1)}{(N-1)^2}\sigma_b^2 - \frac{i-1}{N-1}\sigma_{bc}\right]$$

$$= \frac{i}{N(N-1)}\sigma_b^2 - \frac{i}{N}\sigma_c^2 + \frac{i-1}{N-1}\sigma_{bc}. \tag{92}$$

Inserting (91) and (92) in (18), the function $m(i)$ can be written as

$$m(i) = -\frac{1}{N-1}\mu_b - \mu_c + \frac{i}{N(N-1)}\sigma_b^2 - \frac{i}{N}\sigma_c^2 + \frac{i-1}{N-1}\sigma_{bc}. \tag{93}$$

Substituting $m(i)$ in (19) and summing over all i from 1 to $N-1$, we obtain the approximations given in (34) for the fixation probabilities F_C and F_D.

Appendix C. Synergistic benefits

In this appendix, we show the approximations of the fixation probabilities F_C and F_D in the case of synergistically enhanced or discounted benefits in a large population. Beforehand, note the identity

$$\sum_{k=0}^{d-1}\binom{d-1}{k}B(k+i,d-1-k+j)$$
$$=\sum_{k=0}^{d-1}\binom{d-1}{k}\int_0^1 x^{k+i-1}(1-x)^{d-2-k+j}dx$$
$$=\int_0^1 x^{i-1}(1-x)^{j-1}\sum_{k=0}^{d-1}\binom{d-1}{k}x^k(1-x)^{d-1-k}dx$$
$$=\int_0^1 x^{i-1}(1-x)^{j-1}dx=B(i,j) \tag{94}$$

for any two integers $i,j\geq 1$.

C.1. Fixation probability F_C

Using the identity in (94) and the expressions in (76), (82) and (85), we have

$$\sum_{k=0}^{d-1}\alpha_k=\sum_{k=0}^{d-1}\binom{d-1}{k}B(k+1,d-k+1)$$
$$=B(1,2)=\frac{1}{2}, \tag{95a}$$

$$\sum_{k,l=0}^{d-1}\alpha_{CC,kl}=\sum_{k=0}^{d-1}\binom{d-1}{k}\sum_{l=0}^{d-1}\binom{d-1}{l}B(k+l+2,2d-k-l)$$
$$=\sum_{k=0}^{d-1}\binom{d-1}{k}B(k+2,d+1-k)$$
$$=B(2,2)=\frac{1}{6}, \tag{95b}$$

$$\sum_{k,l=0}^{d-1}\alpha_{DD,kl}=\sum_{k=0}^{d-1}\binom{d-1}{k}\sum_{l=0}^{d-1}\binom{d-1}{l}$$
$$\times B(k+l+1,2d+1-k-l)$$
$$=\sum_{k=0}^{d-1}\binom{d-1}{k}B(k+1,d+2-k)$$
$$=B(1,3)=\frac{1}{3}, \tag{95c}$$

$$\sum_{k=0}^{d-1}\alpha_k\omega^k=\sum_{k=0}^{d-1}\binom{d-1}{k}B(k+1,d-k+1)\omega^k$$
$$=\sum_{k=0}^{d-1}\frac{d-k}{d(d+1)}\omega^k, \tag{95d}$$

$$\sum_{k,l=0}^{d-1}\alpha_{CC,kl}\omega^k=\sum_{k=0}^{d-1}\binom{d-1}{k}\omega^k\sum_{k=0}^{d-1}\binom{d-1}{l}$$
$$\times B(k+l+2,2d-k-l)$$
$$=\sum_{k=0}^{d-1}\binom{d-1}{k}B(k+2,d-k+1)\omega^k$$
$$=\sum_{k=0}^{d-1}\frac{(k+1)(d-k)}{d(d+1)(d+2)}\omega^k, \tag{95e}$$

$$\sum_{k,l=0}^{d-1}\alpha_{DD,kl}\omega^k=\sum_{k=0}^{d-1}\binom{d-1}{k}\omega^k\sum_{l=0}^{d-1}\binom{d-1}{l}$$
$$\times B(k+l+1,2d+1-k-l)$$
$$=\sum_{k=0}^{d-1}\binom{d-1}{k}B(k+1,d-k+2)\omega^k$$
$$=\sum_{k=0}^{d-1}\frac{(d-k+1)(d-k)}{d(d+1)(d+2)}\omega^k. \tag{95f}$$

In addition, we have

$$\sum_{k,l=0}^{d-1}\alpha_{CC,kl}\omega^{k+l}=\sum_{k,l=0}^{d-1}\binom{d-1}{k}\binom{d-1}{l}$$
$$\times B(k+l+2,2d-k-l)\omega^{k+l}$$
$$=\sum_{n=0}^{2d-2}B(n+2,2d-n)\omega^n\sum_{k=\max\{0,n+1-d\}}^{\min\{n,d-1\}}\binom{d-1}{k}$$
$$\times\binom{d-1}{n-k}$$
$$=\sum_{n=0}^{2d-2}B(n+2,2d-n)\omega^n\binom{2d-2}{n}$$
$$=\sum_{n=0}^{2d-2}\frac{(2d-n-1)(n+1)}{2d(2d+1)(2d-1)}\omega^n, \tag{96a}$$

$$\sum_{k,l=0}^{d-1}\alpha_{DD,kl}\omega^{k+l}=\sum_{k,l=0}^{d-1}\binom{d-1}{k}\binom{d-1}{l}$$
$$\times B(k+l+1,2d+1-k-l)\omega^{k+l}$$
$$=\sum_{n=0}^{2d-2}B(n+1,2d+1-n)\omega^n$$
$$\times\sum_{k=\max\{0,n+1-d\}}^{\min\{n,d-1\}}\binom{d-1}{k}\binom{d-1}{n-k}$$
$$=\sum_{n=0}^{2d-2}B(n+1,2d+1-n)\omega^n\binom{2d-2}{n}$$
$$=\sum_{n=0}^{2d-2}\frac{(2d-n-1)(2d-n)}{2d(2d+1)(2d-1)}\omega^n, \tag{96b}$$

where we use the identity

$$\sum_{k=\max\{0,n+1-d\}}^{\min\{n,d-1\}}\binom{d-1}{k}\binom{d-1}{n-k}=\binom{2d-2}{n} \tag{97}$$

for $n=0,1,\ldots,2d-2$. Inserting the expressions above and the scaled moments given in (38) and (39) in the approximation (83) for the fixation probability F_C, we obtain

$$F_C\approx\frac{1}{N}+\delta\left[\psi_b\mu_b-\frac{\mu_c}{2}-\frac{\sigma_c^2}{6}-\psi_{b^2}\sigma_b^2+\psi_{bc}\sigma_{bc}\right], \tag{98}$$

where

$$\psi_b=\frac{1}{d}\sum_{k=0}^{d-1}\alpha_k\omega^k=\frac{1}{d^2(d+1)}\sum_{k=0}^{d-1}(d-k)\omega^k, \tag{99a}$$

$$\psi_{b^2} = -\frac{1}{d^2(1-\omega)}\left[\omega\sum_{k,l=0}^{d-1}\alpha_{CC,kl}\omega^{k+l} + \sum_{k,l=0}^{d-1}\alpha_{DD,kl}\omega^{k+l} - \sum_{k,l=0}^{d-1}\alpha_{CC,kl}\omega^{l} - \sum_{k,l=0}^{d-1}\alpha_{DD,kl}\omega^{k}\right]$$
$$= -\frac{1}{d^2(1-\omega)}\left[\frac{1}{2d(2d+1)}\sum_{k=0}^{2d-1}(2d-k)\omega^k - \frac{1}{d(d+1)}\sum_{k=0}^{d-1}(d-k)\omega^k\right]$$
$$= -\frac{1}{d^2(1-\omega)}\left[-\frac{1}{2d(2d+1)}\sum_{k=0}^{2d-1}(2d-k)(1-\omega^k) + \frac{1}{d(d+1)}\sum_{k=0}^{d-1}(d-k)(1-\omega^k)\right]$$
$$= \sum_{k=0}^{2d-2}\frac{(2d-k)(2d-k-1)}{4d^3(2d+1)}\omega^k - \sum_{k=0}^{d-2}\frac{(d-k)(d-k-1)}{2d^3(d+1)}\omega^k$$
$$= \sum_{k=0}^{d-2}\frac{(k+1)(4d^2-3kd-k)}{4d^3(d+1)(2d+1)}\omega^k + \sum_{k=d-1}^{2d-2}\frac{(2d-k-1)(2d-k)}{4d^3(d+1)(2d+1)}\omega^k, \tag{99b}$$

$$\psi_{bc} = \frac{1}{d(1-\omega)}\left[\sum_{k,l=0}^{d-1}\left(\alpha_{CC,kl}+\alpha_{DD,kl}\right) + (1-\omega)\sum_{k,l=0}^{d-1}\alpha_{CC,kl}\omega^l - \sum_{k,l=0}^{d-1}\alpha_{CC,kl}\omega^{k+1} - \sum_{k,l=0}^{d-1}\alpha_{DD,kl}\omega^l\right]$$
$$= \frac{1}{d(1-\omega)}\left[\frac{1}{2} + \frac{1-\omega}{d(d+1)(d+2)}\sum_{k=0}^{d-1}(k+1)(d-k)\omega^k - \sum_{k=0}^{d}\frac{d-k+1}{(d+1)(d+2)}\omega^k\right]$$
$$= \sum_{k=0}^{d-1}\frac{(k+1)(d-k)}{d^2(d+1)(d+2)}\omega^k + \sum_{k=0}^{d}\frac{d-k+1}{d(d+1)(d+2)}\frac{1-\omega^k}{1-\omega}$$
$$= \sum_{k=0}^{d-1}\frac{(k+1)(d-k)}{d^2(d+1)(d+2)}\omega^k + \sum_{k=0}^{d}\frac{(d-k)(d-k+1)}{2d(d+1)(d+2)}\omega^k$$
$$= \sum_{k=0}^{d-1}\frac{(d-k)\left(d^2+d-kd+2k+2\right)}{2d^2(d+1)(d+2)}\omega^k. \tag{99c}$$

Note that, in the development of ψ_{b^2} and ψ_{bc}, we have used the identities

$$\frac{1}{2d(2d+1)}\sum_{k=0}^{2d-1}(2d-k) = \frac{1}{d(d+1)}\sum_{k=0}^{d-1}(d-k) \tag{100a}$$

and

$$\frac{1}{2} = \sum_{k=0}^{d}\frac{d-k+1}{(d+1)(d+2)}, \tag{101a}$$

respectively.

C.2. Fixation probability F_D

Similarly to the previous analysis, we have

$$\sum_{k=0}^{d-1}\beta_k = \frac{1}{2}, \tag{102a}$$
$$\sum_{k,l=0}^{d-1}\beta_{CC,kl} = \frac{1}{3}, \tag{102b}$$
$$\sum_{k,l=0}^{d-1}\beta_{DD,kl} = \frac{1}{6}, \tag{102c}$$
$$\sum_{k=0}^{d-1}\beta_k\omega^k = \sum_{k=0}^{d-1}\frac{k+1}{d(d+1)}\omega^k, \tag{102d}$$
$$\sum_{k,l=0}^{d-1}\beta_{CC,kl}\omega^k = \sum_{k=0}^{d-1}\frac{(k+1)(k+2)}{d(d+1)(d+2)}\omega^k, \tag{102e}$$
$$\sum_{k,l=0}^{d-1}\beta_{DD,kl}\omega^k = \sum_{k=0}^{d-1}\frac{(k+1)(d-k)}{d(d+1)(d+2)}\omega^k, \tag{102f}$$
$$\sum_{k,l=0}^{d-1}\beta_{CC,kl}\omega^{k+l} = \sum_{k=0}^{2d-2}\frac{(k+1)(k+2)}{2d(2d+1)(2d-1)}\omega^k, \tag{102g}$$
$$\sum_{k,l=0}^{d-1}\beta_{DD,kl}\omega^{k+l} = \sum_{k=0}^{2d-2}\frac{(k+1)(2d-k-1)}{2d(2d+1)(2d-1)}\omega^k, \tag{102h}$$

from which the fixation probability F_D can be approximated as

$$F_D \approx \frac{1}{N} - \delta\left[\phi_b\mu_b - \frac{\mu_c}{2} - \frac{\sigma_c^2}{3} - \phi_{b^2}\sigma_b^2 + \phi_{bc}\sigma_{bc}\right], \tag{103}$$

where

$$\phi_b = \frac{1}{d}\sum_{k=0}^{d-1}\beta_k\omega^k = \frac{1}{d^2(d+1)}\sum_{k=0}^{d-1}(k+1)\omega^k, \tag{104a}$$

$$\phi_{b^2} = -\frac{1}{d^2(1-\omega)}\left[\omega\sum_{k,l=0}^{d-1}\beta_{CC,kl}\omega^{k+l} + \sum_{k,l=0}^{d-1}\beta_{DD,kl}\omega^{k+l} - \sum_{k,l=0}^{d-1}\beta_{CC,kl}\omega^{l} - \sum_{k,l=0}^{d-1}\beta_{DD,kl}\omega^{k}\right]$$
$$= -\frac{1}{d^2(1-\omega)}\left[\frac{1}{2d(2d+1)}\sum_{k=0}^{2d-1}(k+1)\omega^k + \frac{1}{d(d+1)}\sum_{k=0}^{d-1}(k+1)\omega^k\right]$$
$$= -\frac{1}{d^2(1-\omega)}\left[-\frac{1}{2d(2d+1)}\sum_{k=0}^{2d-1}(k+1)(1-\omega^k) + \frac{1}{d(d+1)}\sum_{k=0}^{d-1}(k+1)(1-\omega^k)\right]$$
$$= \sum_{k=0}^{2d-2}\frac{(2d-k-1)(2d+k+2)}{4d^3(2d+1)}\omega^k - \sum_{k=0}^{d-2}\frac{(d-k-1)(d+k+2)}{2d^3(d+1)}\omega^k$$
$$= \sum_{k=0}^{d-2}\frac{(k+1)\,(k+2)\,(3d+1)}{4d^3\,(d+1)\,(2d+1)}\omega^k$$

$$\psi_b = \frac{\omega^{d+1} + d - \omega - d\omega}{d^2(d+1)(\omega-1)^2}, \tag{106a}$$

$$\phi_b = \frac{d\omega^{d+1} + 1 - (d+1)\omega^d}{d^2(d+1)(\omega-1)^2}, \tag{106b}$$

$$\psi_{b^2} = \frac{d^3(\omega-1)^2\omega^{d-1} + 2d^2(\omega-1)(2\omega^d - \omega^{d-1} + 2) + d(\omega^{d-1} + 6\omega - 4\omega^d - 3\omega^{d+1})}{4d^3(d+1)(2d+1)(\omega-1)^3} + \frac{\omega^{d-1}\left[2\omega^2(\omega^d-1) - d(3\omega-1)(\omega-1) - d^2(\omega-1)^2\right] - 2\omega(\omega^d-1)}{4d^3(d+1)(2d+1)(\omega-1)^3}, \tag{106c}$$

$$\phi_{b^2} = \frac{d(d-1)\omega^{d+1} + d(d+1)\omega^{d-1} - 2(d^2-1)\omega^d - 2 + \omega^{d-1}\left[2\omega^2(\omega^d-1) - d(3\omega-1)(\omega-1) - 3d^2(\omega-1)^2\right]}{4d^3(d+1)(2d+1)(\omega-1)^3}, \tag{106d}$$

$$\psi_{bc} = \frac{2d(2\omega^{d+2} + \omega - \omega^{d+1} - \omega^2 - 1) - d^3(\omega-1)^2 - d^2(3\omega-1)(\omega-1) - 4\omega(\omega^d-1)}{2d^2(d+1)(d+2)(\omega-1)^2}, \tag{106e}$$

$$\phi_{bc} = \frac{d(\omega-1)(2\omega^{d+1} + 1 - \omega) - d^2(\omega-1)^2 - 2\omega(\omega^d-1)}{2d^2(d+1)(d+2)(\omega-1)^2}. \tag{106f}$$

Box I.

$$+ \sum_{k=d-1}^{2d-2} \frac{(2d-k-1)(2d+k+2)}{4d^3(2d+1)}\omega^k, \tag{104b}$$

$$\begin{aligned}
\phi_{bc} &= \frac{1}{d(1-\omega)}\left[\sum_{k,l=0}^{d-1}\left(\beta_{CC,kl} + \beta_{DD,kl}\right) + (1-\omega)\sum_{k,l=0}^{d-1}\beta_{CC,kl}\omega^l - \sum_{k,l=0}^{d-1}\beta_{CC,kl}\omega^{k+1} - \sum_{k,l=0}^{d-1}\beta_{DD,kl}\omega^l\right] \\
&= \frac{1}{d(1-\omega)}\left[\frac{1}{2} + \frac{1-\omega}{d(d+1)(d+2)}\sum_{k=0}^{d-1}(k+1)(k+2)\omega^k - \sum_{k=0}^{d}\frac{k+1}{(d+1)(d+2)}\omega^k\right] \\
&= \sum_{k=0}^{d-1}\frac{(k+1)(k+2)}{d^2(d+1)(d+2)}\omega^k + \sum_{k=0}^{d}\frac{k+1}{d(d+1)(d+2)}\frac{1-\omega^k}{1-\omega} \\
&= \sum_{k=0}^{d-1}\frac{(k+1)(d-k)}{d^2(d+1)(d+2)}\omega^k + \sum_{k=0}^{d-1}\frac{(d-k)(d+k+3)}{2d(d+1)(d+2)}\omega^k \\
&= \sum_{k=0}^{d-1}\frac{(d-k)\left(d^2+(k+3)d+2k+2\right)}{2d^2(d+1)(d+2)}\omega^k.
\end{aligned} \tag{104c}$$

C.3. Large group size

Using the elementary identities

$$\sum_{k=0}^{n} x^k = \frac{x^{n+1}-1}{x-1}, \tag{105a}$$

$$\sum_{k=0}^{n} kx^k = \frac{nx^{n+2} - (n+1)x^{n+1} + x}{(x-1)^2}, \tag{105b}$$

$$\sum_{k=0}^{n} k^2x^k = \frac{n^2(x-1)^2x^{n+1} - 2n(x-1)x^{n+1} + (x^{n+1}-x)(x+1)}{(x-1)^3}, \tag{105c}$$

the expressions given in (41) can be written as Eqs. (106a)–(106f) as given in Box I. To go further, we have to consider the value of the synergistic parameter ω compared to the value 1.

C.3.1. Synergistic discounted benefits

If $\omega < 1$, then all the expressions in (106) tend to 0 as the group size d increases to infinity. Therefore, for d large enough, they can be neglected in (40), which yields the approximations in (48) for the fixation probabilities F_C and F_D.

C.3.2. Synergistic enhanced benefits

In the case where $\omega > 1$ and d is large, the expressions in (106) can be approximated as

$$\psi_b \approx \frac{\omega^{d+1}}{d^3(\omega-1)^2}, \tag{107a}$$

$$\psi_{b^2} \approx \frac{\omega^{2d+1}}{4d^5(\omega-1)^3}, \tag{107b}$$

$$\psi_{bc} \approx \frac{(2\omega-1)\omega^{d+1}}{d^3(\omega-1)^2}, \tag{107c}$$

$$\phi_b \approx \frac{\omega^d}{d^2(\omega-1)}, \tag{107d}$$

$$\phi_{b^2} \approx \frac{\omega^{2d+1}}{4d^5(\omega-1)^3}, \tag{107e}$$

$$\phi_{bc} \approx \frac{\omega^{d+1}}{d^3(\omega-1)}. \tag{107f}$$

Then, ψ_b, ψ_{bc} ϕ_b and ϕ_{bc} are negligible compared to ψ_{b^2} and ϕ_{b^2}, from which (40) leads to the approximations given in (49) for F_C and F_D.

C.3.3. Synergistic neutral benefits

In the case where $\omega = 1$, using the elementary summations

$$\sum_{k=n}^{m} k = \frac{(m+1-n)(m+n)}{2}, \tag{108a}$$

$$\sum_{k=n}^{m} k^2 = \frac{(m+1-n)(m+2m^2+2mn+n(2n-1))}{6}, \tag{108b}$$

the expressions in (41) become

$$\psi_b = \frac{1}{2d}, \tag{109a}$$

$$\psi_{b^2} = \frac{1}{4(2d+1)}, \tag{109b}$$

$$\psi_{bc} = \frac{1}{6} + \frac{1}{6d}, \tag{109c}$$

$$\phi_b = \frac{1}{2d}, \tag{109d}$$

$$\phi_{b^2} = \frac{1}{3d}, \tag{109e}$$

$$\phi_{bc} = \frac{1}{3} + \frac{1}{6d}. \tag{109f}$$

Inserting these expressions in (40) and assuming that d is large, we obtain the approximations for F_C and F_D as given in (51).

Appendix D. Snowdrift game

D.1. Expression of $m(i)$

Using Vandermonde's identity (90) yields

$$\begin{aligned}\sum_{k=0}^{d-1}\frac{C(i,k)}{k+1} &= \sum_{k=0}^{d-1}\frac{\binom{i}{k}\binom{N-i-1}{d-k-1}}{(k+1)\binom{N-1}{d-1}} \\ &= \sum_{l=1}^{d}\frac{\binom{i+1}{l}\binom{N-i-1}{d-l}}{(i+1)\binom{N-1}{d-1}} \\ &= \frac{1}{(i+1)\binom{N-1}{d-1}} \\ &\quad\times\left[\sum_{l=0}^{d}\binom{i+1}{l}\binom{N-i-1}{d-l}-\binom{N-i-1}{d}\right] \\ &= \frac{1}{(i+1)\binom{N-1}{d-1}}\left[\binom{N}{d}-\binom{N-i-1}{d}\right] \\ &= \frac{1}{i+1}\left(\frac{N}{d}-\frac{\binom{N-i-1}{d}}{\binom{N-1}{d-1}}\right),\end{aligned} \tag{110}$$

for $i = 0, 1, \ldots, N-1$. Then, using the identity in (88) and the scaled moments in (65), the first summation in (18) can be written as

$$\begin{aligned}&\sum_{k=0}^{d-1}\left(C(i-1,k)\mu_{C,k}-C(i,k)\mu_{D,k}\right) \\ &= \mu_b\sum_{k=0}^{d-1}C(i-1,k)-\mu_c\sum_{k=0}^{d-1}\frac{C(i,k)}{k+1}-\mu_b\sum_{k=1}^{d-1}C(i,k) \\ &= -\frac{\mu_c}{i}\left(\frac{N}{d}-\frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right)+C(i,0)\mu_b.\end{aligned} \tag{111}$$

On the other hand, we have

$$\begin{aligned}&\sum_{k,l=0}^{d-1}C(i-1,k)C(i-1,l)\sigma_{CC,kl} \\ &\quad= \sigma_b^2-2\sum_{k=0}^{d-1}\frac{C(i-1,k)}{k+1}\sigma_{bc} \\ &\quad\quad+\left(\sum_{k=0}^{d-1}\frac{C(i-1,k)}{k+1}\right)^2\sigma_c^2 \\ &\quad= \sigma_b^2-\frac{2}{i}\left(\frac{N}{d}-\frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right)\sigma_{bc} \\ &\quad\quad+\frac{1}{i^2}\left(\frac{N}{d}-\frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right)^2\sigma_c^2,\end{aligned} \tag{112a}$$

$$\begin{aligned}&\sum_{k,l=0}^{d-1}C(i-1,k)C(i,l)\sigma_{CD,kl} \\ &\quad= (1-C(i,0))\,\sigma_b^2-(1-C(i,0)) \\ &\quad\quad\times\left(\frac{N}{d}-\frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right)\frac{\sigma_{bc}}{i} \\ &\quad= (1-C(i,0))\,\sigma_b^2-(1-C(i,0)) \\ &\quad\quad\times\left(\frac{N}{d}-\frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right)\frac{\sigma_{bc}}{i},\end{aligned} \tag{112b}$$

$$\begin{aligned}&\sum_{k,l=0}^{d-1}C(i,k)C(i,l)\sigma_{DD,kl} \\ &\quad= \left(\sum_{k,l=0}^{d-1}C(i,k)C(i,l)\right. \\ &\quad\quad\left.-2C(i,0)\sum_{k,l=0}^{d-1}C(i,k)+C(i,0)^2\right)\sigma_b^2 \\ &\quad= (1-C(i,0))^2\,\sigma_b^2.\end{aligned} \tag{112c}$$

Inserting these expressions in (18), we obtain the expression of $m(i)$ given in (66).

D.2. Fixation probabilities

In the case of a large population size, using

$$C(i,0) = \frac{\binom{N-i-1}{d-1}}{\binom{N-1}{d-1}} = \left(1-\frac{i}{N}\right)^{d-1}+O(N^{-1}), \tag{113a}$$

$$\frac{1}{i}\left(\frac{N}{d}-\frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right) = \frac{1}{d}\sum_{n=0}^{d-1}\left(1-\frac{i}{N}\right)^n+O(N^{-1}), \tag{113b}$$

$$\frac{1}{N}\left(\frac{N}{d}-\frac{\binom{N-i}{d}}{\binom{N-1}{d-1}}\right) = \frac{1}{d}\left[1-\left(1-\frac{i}{N}\right)^d\right]+O(N^{-1}), \tag{113c}$$

uniformly for $1 \le i \le N$, we have

$$m(i) = g\left(\frac{i}{N}\right)+O(N^{-1}), \tag{114}$$

where

$$\begin{aligned}g(x) &= \mu_b(1-x)^{d-1}-\frac{\mu_c}{d}\sum_{n=0}^{d-1}(1-x)^n \\ &\quad-\sigma_b^2\left[1-(1-x)^d\right](1-x)^{d-1} \\ &\quad-\frac{\sigma_c^2}{d^2}\sum_{n=0}^{d-1}(1-x)^n\left[1-(1-x)^d\right] \\ &\quad+\frac{\sigma_{bc}}{d}\sum_{n=0}^{d-1}(1-x)^n\left[1-(1-2x)(1-x)^{d-1}\right].\end{aligned} \tag{115}$$

This leads to the approximations (as in Appendix A)

$$F_C \approx \frac{1}{N}+\frac{\delta}{N^2}\sum_{i=1}^{N-1}(N-i)m(i)$$

$$\approx \frac{1}{N} + \delta \int_0^1 (1-x)g(x)dx,$$

$$\approx \frac{1}{N} + \delta \left(\frac{\mu_b}{d+1} - \frac{\mu_c}{d} \sum_{n=0}^{d-1} \frac{1}{n+2} - \frac{d\sigma_b^2}{(d+1)(2d+1)} - \frac{\sigma_c^2}{d} \sum_{n=0}^{d-1} \frac{1}{(n+2)(n+2+d)} + \left[\frac{1}{(d+1)(2d+1)} + \sum_{n=0}^{d-1} \frac{1}{(n+2)(n+2+d)} \right] \sigma_{bc} \right), \tag{116a}$$

$$F_D \approx \frac{1}{N} - \frac{\delta}{N^2} \sum_{i=1}^{N-1} im(i)$$

$$\approx \frac{1}{N} - \delta \int_0^1 xg(x)dx$$

$$\approx \frac{1}{N} - \delta \left(\frac{\mu_b}{d(d+1)} - \frac{\mu_c}{d+1} - \frac{3d+1}{2d(d+1)(2d+1)} \sigma_b^2 - \frac{2\sigma_c^2}{(d+1)(2d+1)} + \frac{4d^3+3d+1}{2d^2(d+1)(2d+1)} \sigma_{bc} \right), \tag{116b}$$

$$\frac{F_C}{F_D} \approx 1 + \delta \sum_{i=1}^{N-1} m(i)$$

$$\approx 1 + N\delta \int_0^1 g(x)dx$$

$$\approx 1 + N\delta \left(\frac{\mu_b}{d} - \frac{\mu_c}{d} \sum_{n=0}^{d-1} \frac{1}{n+1} - \frac{\sigma_b^2}{2d} - \frac{\sigma_c^2}{d} \sum_{n=0}^{d-1} \frac{1}{(n+1)(n+1+d)} + \left[\frac{1}{2d^2} + \sum_{n=0}^{d-1} \frac{1}{(n+1)(n+1+d)} \right] \sigma_{bc} \right). \tag{116c}$$

Note that we have the identity

$$\sum_{n=0}^{d-1} \frac{1}{(n+k)(n+k+d)} = \frac{H_{k-1} - 2H_{d+k-1} + H_{2d+k-1}}{d}, \tag{117}$$

where

$$H_k = \sum_{n=1}^{k} \frac{1}{k} \tag{118}$$

for $k \geq 1$ and $H_0 = 0$. Owing to this identity, the above approximations lead to the expressions for the fixation probabilities F_C and F_D given in (67).

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