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The effect of variability in payoffs on average abundance in two-player linear games under symmetric mutation

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ABSTRACT

Classical studies in evolutionary game theory assume constant payoffs. Randomly fluctuating environments in real populations make this assumption idealistic. In this paper, we study randomized two-player linear games in a finite population in a succession of birth-death events according to a Moran process and in the presence of symmetric mutation. Introducing identity measures under neutrality that depend on the mutation rate and calculating these in the limit of a large population size by using the coalescent process, we study the first-order effect of the means, variances and covariances of the payoffs on average abundance in the stationary state under mutation and selection. This shows how the average abundance of a strategy is driven not only by its mean payoffs but also by the variances and covariances of its payoffs. In Prisoner's Dilemmas with additive cost and benefit for cooperation, where constant payoffs always favor the abundance of defection, stochastic fluctuations in the payoffs can change the strategy that is more abundant on average in the stationary state. The average abundance of cooperation is increased if the variance of any payoff to cooperation against cooperation or defection, or their covariance, is decreased, or if the variance of any payoff to defection against cooperation or defection, or their covariance, is increased. This is also the case for a Prisoner's Dilemma with independent payoffs that is repeated a random number of times. As for the mutation rate, it comes into play in the coefficients of the variances and covariances that determine average abundance. Increasing the mutation rate can enhance or lessen the condition for a strategy to be more abundant on average than another.

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1. Introduction

Evolutionary game theory was an extension of classical game theory by adding two concepts: a population of players and the idea that a payoff is interpreted as biological fitness or reproductive rate (Maynard Smith and Price, 1973; Maynard Smith, 1982; Hofbauer and Sigmund, 1988; Nowak, 2006). The standard model, called the replicator equation, was formulated in an infinitely large well-mixed population where any two individuals have the same probability to interact (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman et al., 1980). Evolutionary concepts such as evolutionary stability (Maynard Smith and Price, 1973), continuous stability (Eshel, 1983) or convergence stability (Christiansen, 1991) were first studied in this framework (see, e.g., Taylor, 1989; Hofbauer and Sigmund, 1988).

Deterministic dynamics ignore the fact that real populations are finite. To take this into account, we may resort to stochastic processes such as continuous or discrete time Markov chains on finite state spaces. In the absence of mutation, such a Markov chain has fixation states that are absorbing. In a context of two-player linear games with possible strategies C and D such as a Prisoner's Dilemma (PD) with C for cooperation and D for defection, selection has been said to favor more the evolution of C than the evolution of D if the fixation probability of C introduced as a single mutant is greater than the fixation probability of D introduced as a single mutant (Nowak et al., 2004; Imhof and Nowak, 2006). In the presence of symmetric mutation, the Markov chain is irreducible and, as a result, it possesses a stationary state. In this case, selection has been said to favor the abundance of C if the average frequency of C in the stationary state is greater than the average frequency of D (Antal et al., 2009). Note that the favored strategy in models without selection is the same as the one in models with mutation if the mutation rate is small enough (Rousset and Billiard, 2000; Rousset, 2003; Fudenberg and Imhof, 2006).

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Environmental conditions can change from one time to another or from one place to another, and this can affect payoffs that individuals receive. Early studies on the effects of varying selection coefficients between generations and varying offspring numbers within generations in population genetics models for haploid as well as diploid populations, large or small, include Gillespie (1973), Gillespie (1974), Karlin and Levikson (1974), Karlin and Liberman (1974), Frank and Slatkin (1990). In general, fixation probabilities and/or stationary distributions depend not only on the means of the fitness parameters, but also on their variances that tend to diminish the effective fitness. More recent treatments and extensions can be found in Starrfelt and Kokko (2012), Schreiber (2015) or Rychtar and Taylor (2020).

Fudenberg and Harris (1992) considered a stochastic version of the classical replicator equation for strategy frequencies obtained by adding a random noise to the growth rate of every strategy. This stochastic differential equation was investigated by Fudenberg and Harris (1992) in the presence of an evolutionarily stable strategy. See also Evans et al. (2015) and Schreiber (2012) for studies of competing populations distributed over habitat patches where environmental conditions fluctuate in time and space.

Recently, Li and Lessard (2020) considered Prisoner's Dilemmas with random payoffs to study the effect of temporal fluctuations on evolutionary game dynamics. Assuming a finite population in discrete time updated according to a Wright-Fisher process and ascertaining a diffusion approximation in the limit of a large population with the intensity of selection proportional to the inverse of the population size taken as unit of time, conditions on the means, variances and covariances of the payoffs for selection to favor the evolution of C with respect to fixation probabilities were deduced. The main conclusion reached in that paper by focusing on a PD game with independent payoffs and its repeated version with tit-for-tat starting with C and always-defect as possible strategies was that the conditions that favor the evolution of C (or tit-for-tat in a repeated game) are lessened with an increase in the variances of the payoffs for D (or always-defect in a repeated game) or a decrease in the variances of the payoffs for C (or tit-for-tat in a repeated game).

In this paper, we study the effect of stochastic fluctuations in two-player linear games in the presence of mutation. Payoffs are assumed to fluctuate over time in a random manner to account for environmental and ecological changes. The population is finite and updated at each time step following a birth-death event according to a Moran process, which keeps the population size constant. The two strategies are represented by C and D , which stand for cooperation and defection, respectively, in the special case of a Prisoner's Dilemma. We consider the average abundance of C in the stationary state under symmetric mutation and deduce conditions for weak selection to favor the abundance of C . The conditions are examined in detail with regard to the mutation rate in different scenarios and games.

The remainder of this paper is arranged as follows. In Section 2, we state the assumptions and present the model. In Section 3, we derive the average abundance of C in the stationary state under symmetric mutation and weak selection. In Section 4, the first-order effect of selection on average abundance is expressed in terms of scaled means, variances and covariances of the payoffs and identity measures under neutrality that depend on the mutation rate in the limit of a large population. Thereafter, in Sections 5 and 6, we study in more detail the effects of selection and mutation on average abundance of cooperation in a Prisoner's Dilemma with cost and benefit for cooperation that are additive in mean and pointwise additive, respectively. In Section 7, we examine the case of a Prisoner's Dilemma with independent payoffs that is repeated a random number of times. Our results are summarized and their interpretations discussed in Section 8. The more technical calculations are relegated to appendices, Appendix A for the conditional expected change in frequency of C and Appendices B-G for the identity measures based on the coalescent process for up to five lineages in the limit of a large population.

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2. Model

Consider a finite well-mixed population composed of N individuals. Any individual can interact with any other individual. Here, for simplicity, self-interaction is allowed. Each individual can adopt one strategy among $\{C, D\}$: C for cooperation and D for defection in the special case of a Prisoner's Dilemma. Interactions occur in pairs and the payoffs to the two strategies at any given time step are given by the entries of the matrix

$$\begin{matrix} & \begin{matrix} C & D \end{matrix} \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} \eta_{11} & \eta_{12} \\ \eta_{23} & \eta_{24} \end{pmatrix} \end{matrix} \quad (1)$$

Here, we suppose that the payoffs are random variables whose first and second moments are given in the form

$$E[\eta_{ij}] = \mu_i \delta + o(\delta), \quad (2a)$$

$$E[\eta_{ij}^2] = \sigma_i^2 \delta + o(\delta), \quad (2b)$$

$$E[\eta_{ij} \eta_{kl}] = \sigma_{ij} \delta + o(\delta), \quad (2c)$$

for $i, j = 1, 2, 3, 4$ with $i \neq j$. We assume that there exists a constant M in $(0, 1)$ such that $|\eta_{ij}| \leq M$ almost surely for $i = 1, 2, 3, 4$. The parameter $\delta \geq 0$, which corresponds to an intensity of selection, measures the order of the first and second moments of the payoffs. Note that this implies that the standard deviations are of larger order. The parameters μ_i, σ_i^2 and $\sigma_{ij} = \sigma_{ji}$ for $i, j = 1, 2, 3, 4$ with $i \neq j$ correspond to scaled means, variances and covariances, respectively. In addition, all higher-order moments of the payoffs are assumed to be negligible compared to δ , that is,

$$E\left[\prod_{i=1}^4 |\eta_{ij}|^{k_i}\right] = o(\delta) \quad (3)$$

as soon as $k_1 + k_2 + k_3 + k_4 \geq 3$ for $k_1, k_2, k_3, k_4 \geq 0$. Moreover, the payoffs at a given time step are assumed to be independent of the payoffs at all other time steps.

Following random pairwise interactions in the population, each individual accumulates some payoff which is translated into reproductive fitness. This fitness is given by a sum of two terms, a constant value equal to 1 and an average payoff assuming a large number of interactions. If the population is made up of Nx cooperators and $N - Nx$ defectors, then the reproductive fitnesses of C and D are given by

$$f_C(x) = 1 + [x\eta_{11} + (1-x)\eta_{21}] = 1 + P_1(x), \quad (4a)$$

$$f_D(x) = 1 + [x\eta_{31} + (1-x)\eta_{41}] = 1 + P_2(x), \quad (4b)$$

where $P_1(x)$ and $P_2(x)$ represent average payoffs to C and D , respectively. As for the average reproductive fitness in the population, it can be expressed as

$$\begin{aligned} \bar{f}(x) &= x f_C(x) + (1-x) f_D(x) = 1 + [x P_1(x) + (1-x) P_2(x)] \\ &= 1 + \bar{P}(x), \end{aligned} \quad (5)$$

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

The updating of the population from one time step to the next follows a Moran model with symmetric mutation. At each time step, an individual is selected with a probability proportional to its reproductive fitness, and this individual gives birth to an off-

spring. This offspring is subject to mutation with probability u in $(0, 1)$. In the case of mutation, the offspring adopts a strategy chosen at random among C and D , that is, strategy C with probability $1/2$ or strategy D with probability $1/2$. In the case of no mutation, the offspring adopts the strategy of its parent. On the other hand, an individual is chosen at random in the population, that is, each one with probability $1/N$, and the individual chosen is replaced by the offspring.

Let X be the frequency of C in the population at a given time step. The state space of X is $S = \{0, 1/N, \dots, (N-1)/N, 1\}$. To describe the population state, we need only to know X , since then the frequency of D is $1 - X$. In the presence of mutation, the frequency of C over all time steps is an aperiodic irreducible Markov chain on a finite state space. Owing to the ergodic theorem, the chain tends to an equilibrium state given by a unique stationary probability distribution $\{\Pi^0(x)\}_{x \in S}$ where $\Pi^0(x) = \mathbb{P}^0(X = x) > 0$ and $\sum_{x \in S} \Pi^0(x) = 1$. For a review of Markov chain theory, see, e.g., Karlin and Taylor (1975).

Denote by \mathbb{E}^δ the expectation with respect to the stationary probability distribution if the intensity of selection is $\delta \geq 0$. Define the average abundance of C as

$$\mathbb{E}^\delta[X] = \sum_{x \in S} x \Pi^\delta(x). \quad (6)$$

We say that weak selection favors the abundance of C if its average abundance under weak enough selection exceeds what it would be under neutrality, that is,

$$\mathbb{E}^\delta[X] > \mathbb{E}^0[X] \quad (7)$$

for $\delta > 0$ small enough. Here, $\mathbb{E}^0[X]$ represents the average abundance of C under neutrality when $\delta = 0$.

In the remainder, we are interested in conditions for weak selection to favor the abundance of C .

3. Average abundance under symmetric mutation and weak selection

Let $\Delta X = X' - X$ be the change in the frequency of C from one time step to the next. This change can take only the values $-1/N, 0, 1/N$, the first one when an individual C is replaced by an offspring D , the last one when it is the other way around, and 0 otherwise. Let $T^-(x)$ and $T^+(x)$ be the probabilities of the first two events when $X = x$, that is,

$$T^-(x) = \mathbb{P}_x^\delta \left[\Delta X = -\frac{1}{N} \right] = \mathbb{P}^\delta \left[\Delta X = -\frac{1}{N} \mid X = x \right], \quad (8a)$$

$$T^+(x) = \mathbb{P}_x^\delta \left[\Delta X = \frac{1}{N} \right] = \mathbb{P}^\delta \left[\Delta X = \frac{1}{N} \mid X = x \right]. \quad (8b)$$

In the case of mutation, the offspring becomes C with probability $1/2$ and D with probability $1/2$ whatever the strategy of the parent is. In the case of no mutation, the strategy of the offspring is the same as the one of the parent, which depends on the fitnesses of C and D given in (4b). To sum up, we have

$$T^-(x) = \left[(1-u)E \left[\frac{(1-x)f_D(x)}{xf_C(x) + (1-x)f_D(x)} \right] + \frac{u}{2} \right] x, \quad (9a)$$

$$T^+(x) = \left[(1-u)E \left[\frac{xf_C(x)}{xf_C(x) + (1-x)f_D(x)} \right] + \frac{u}{2} \right] (1-x), \quad (9b)$$

where E denotes an expectation with respect to the probability distribution of the payoffs. Accordingly, the conditional expected change in the frequency of C is given by

$$\begin{aligned} \mathbb{E}_x^\delta[\Delta X] &= \mathbb{E}^\delta[\Delta X \mid X = x] = \frac{1}{N} (T^+(x) - T^-(x)) \\ &= \frac{1}{N} \left((1-u)x(1-x)E \left[\frac{f_C(x) - f_D(x)}{xf_C(x) + (1-x)f_D(x)} \right] + \frac{u(1-2x)}{2} \right) \\ &= \frac{u(1-2x)}{2N} + \frac{\delta}{N} (1-u)x(1-x)m(x) + o(\delta), \end{aligned} \quad (10)$$

where

$$m(x) = Ax^3 + Bx^2 + Cx + D \quad (11)$$

with

$$A = 2\sigma_{12} + 2\sigma_{13} + 2\sigma_{24} + 2\sigma_{34} - \sigma_1^2 - \sigma_2^2 - \sigma_3^2 - \sigma_4^2 - 2\sigma_{14} - 2\sigma_{23}, \quad (12a)$$

$$B = 2\sigma_2^2 + \sigma_3^2 + 3\sigma_4^2 + 3\sigma_{14} + 3\sigma_{23} - 2\sigma_{12} - \sigma_{13} - 5\sigma_{24} - 4\sigma_{34}, \quad (12b)$$

$$C = 4\sigma_{24} + 2\sigma_{34} - \sigma_2^2 - 3\sigma_4^2 - \sigma_{14} - \sigma_{23} + \mu_1 - \mu_2 - \mu_3 + \mu_4, \quad (12c)$$

$$D = \sigma_2^2 - \sigma_{24} + \mu_2 - \mu_4. \quad (12d)$$

See appendix A for the calculations.

Multiplying both sides in (10) by $\Pi^\delta(x)$, and summing up over all states in S , we get

$$\mathbb{E}^\delta[\Delta X] = \frac{u}{2N} [1 - 2\mathbb{E}^\delta[X]] + \frac{\delta}{N} (1-u)\mathbb{E}^\delta[X(1-X)m(X)] + o(\delta). \quad (13)$$

In the stationary state, the frequency of C in the population keeps a constant expected value, that is,

$$\mathbb{E}^\delta[\Delta X] = 0. \quad (14)$$

Therefore, (13) yields

$$\mathbb{E}^\delta[X] = \frac{1}{2} + \frac{\delta(1-u)}{u} \mathbb{E}^\delta[X(1-X)m(X)] + o(\delta). \quad (15)$$

Then, using

$$\mathbb{E}^\delta[X(1-X)m(X)] = \mathbb{E}^0[X(1-X)m(X)] + O(\delta), \quad (16)$$

we obtain the first-order approximation

$$\mathbb{E}^\delta[X] = \frac{1}{2} + \frac{\delta(1-u)}{u} \mathbb{E}^0[X(1-X)m(X)] + o(\delta) \quad (17)$$

for the expected frequency of C in the stationary state under selection and mutation.

4. Effect of variances and covariances of payoffs on average abundance

When $\delta = 0$, selection has no effect on the evolutionary outcome. The stationary state will be established under the sole effects of mutation and random drift. Moreover, mutation is neutral since a mutant offspring has the same probability to adopt C or D . Then these strategies have the same frequencies in the stationary state, that is,

$$\mathbb{E}^0[X] = \frac{1}{2}. \quad (18)$$

This intuitive result for $\delta = 0$ is confirmed by (15).

Owing to (17) and (18), and according to the definition in (7), weak selection favors the abundance of C as long as

$$\mathbb{E}^0[X(1-X)m(X)] > 0. \quad (19)$$

In addition, increasing $\mathbb{E}^0[X(1-X)m(X)]$ increases the average abundance of C , and consequently decreases the average abundance of D . We get our first results by considering the partial derivatives of the expected value in (19) with $m(X)$ given by (11) with respect to the variances and some covariances of the payoffs.

Result 1. We have

$$\frac{\partial}{\partial \sigma_1^2} \mathbb{E}^0[X(1-X)m(X)] = -\mathbb{E}^0[X^4(1-X)] < 0, \quad (20a)$$

$$\frac{\partial}{\partial \sigma_2^2} \mathbb{E}^0[X(1-X)m(X)] = -\mathbb{E}^0[X^2(1-X)^3] < 0, \quad (20b)$$

$$\frac{\partial}{\partial \sigma_{12}} \mathbb{E}^0[X(1-X)m(X)] = -\mathbb{E}^0[2X^3(1-X)^2] < 0. \quad (20c)$$

Therefore, increasing the variance of any payoff to C, σ_1^2 or σ_2^2 , or the covariance between the payoffs to C against C and D, σ_{12} , increases the average abundance of D and decreases the average abundance of C. More uncertainty in the payoffs to C makes it more difficult for selection to favor the abundance of C.

Result 2. Similarly, we have

$$\frac{\partial}{\partial \sigma_3^2} \mathbb{E}^0[X(1-X)m(X)] = \mathbb{E}^0[X^3(1-X)^2] > 0, \quad (21a)$$

$$\frac{\partial}{\partial \sigma_4^2} \mathbb{E}^0[X(1-X)m(X)] = \mathbb{E}^0[X(1-X)^4] > 0, \quad (21b)$$

$$\frac{\partial}{\partial \sigma_{34}} \mathbb{E}^0[X(1-X)m(X)] = \mathbb{E}^0[2X^2(1-X)^3] > 0. \quad (21c)$$

Then, increasing the variance of any payoff to D, σ_3^2 or σ_4^2 , or the covariance between the payoffs to D against C and D, σ_{34} , increases the average abundance of C and decreases the average abundance of D. More uncertainty in the payoffs to D makes it easier for selection to favor the abundance of C.

The effect of changes in the other covariances of the payoffs on average abundance cannot be decided so easily, since we have

$$\frac{\partial}{\partial \sigma_{13}} \mathbb{E}^0[X(1-X)m(X)] = \mathbb{E}^0\left[2X^3(1-X)\left(X - \frac{1}{2}\right)\right], \quad (22a)$$

$$\frac{\partial}{\partial \sigma_{24}} \mathbb{E}^0[X(1-X)m(X)] = \mathbb{E}^0\left[2X(1-X)^3\left(X - \frac{1}{2}\right)\right], \quad (22b)$$

$$\frac{\partial}{\partial \sigma_{14}} \mathbb{E}^0[X(1-X)m(X)] = \mathbb{E}^0\left[2X^2(1-X)^2\left(X - \frac{1}{2}\right)\right], \quad (22c)$$

$$\frac{\partial}{\partial \sigma_{23}} \mathbb{E}^0[X(1-X)m(X)] = \mathbb{E}^0\left[2X^2(1-X)^2\left(X - \frac{1}{2}\right)\right], \quad (22d)$$

which can be *a priori* negative or positive.

Now let us introduce the identity measures

$$\phi_n = \mathbb{P}^0\{S(I_1) = \dots = S(I_n)\} \quad (23)$$

for $n = 2, 3, 4, 5$. Here, I_1, \dots, I_n designate n distinct individuals chosen at random at the same time step in a neutral population at stationarity, and $S(I)$ stands for the strategy used by individual I . These identity measures come into play to derive an expression for the expected value in (19). As a matter of fact, we have

$$\begin{aligned} \mathbb{E}^0[X(1-X)m(X)] &= D\mathbb{E}^0[X] + (C-D)\mathbb{E}^0[X^2] + (B-C)\mathbb{E}^0[X^3] + (A-B)\mathbb{E}^0[X^4] - A\mathbb{E}^0[X^5] \\ &= \frac{9}{2} + (C-D)\left[\frac{\phi_2}{2} + \frac{1}{20}\right] + (B-C)\left[\frac{\phi_2}{2} + \frac{3N-2}{2N^2}\right] \\ &\quad + (A-B)\left[\frac{\phi_4}{2} + \frac{6N^2\phi_3 + 7N-6}{2N^4}\right] \\ &\quad - A\left[\frac{\phi_4}{2} + \frac{10N^3\phi_4 + 25N^2\phi_3 + 15N\phi_2 + 15N-14}{2N^4}\right] \\ &= \frac{1}{2}[D + (C-D)\phi_2 + (B-C)\phi_3 + (A-B)\phi_4 - A\phi_5] + O(N^{-1}). \end{aligned} \quad (24)$$

See Appendix B for a proof.

Then, condition (19) for weak selection to favor the abundance of C in a large population becomes

$$D + (C-D)\phi_2 + (B-C)\phi_3 + (A-B)\phi_4 - A\phi_5 > 0.$$

By using coalescent theory (see Appendices D-G for details), it can be shown that the identity measures in the limit of a large population can be expressed as

$$\phi_2 = \frac{1+\theta}{1+2\theta}, \quad (26a)$$

$$\phi_3 = \frac{2+\theta}{2(1+2\theta)}, \quad (26b)$$

$$\phi_4 = \frac{(\theta+2)(\theta+3)}{2(2\theta+3)(2\theta+1)}, \quad (26c)$$

$$\phi_5 = \frac{(\theta+3)(\theta+4)}{4(2\theta+3)(2\theta+1)}, \quad (26d)$$

where $\theta = \lim_{N \rightarrow \infty} uN/2$ represents a mutation rate with $N^2/2$ time steps as unit of time as $N \rightarrow \infty$. Then, condition (25) takes the form

$$\begin{aligned} \mu_1 + \mu_2 - \mu_3 - \mu_4 + \frac{1}{2(2\theta+3)} \times [2(\theta+1)(\sigma_{34} - \sigma_{12}) \\ + 2(\sigma_{13} - \sigma_{24} + (\theta+1)(\sigma_3^2 - \sigma_2^2) + (\theta+3)(\sigma_4^2 - \sigma_1^2))] > 0. \end{aligned} \quad (27)$$

We are now in a position to state our next result.

Result 3. At least in a large population, increasing the covariance between the payoffs to C and D against C, σ_{13} , or decreasing the covariance between the payoffs to C and D against D, σ_{24} , increases the average abundance of C and decreases the average abundance of D. The covariance between the payoff to C against C and the payoff to D against D, σ_{14} , as well as the covariance between the payoff to C against D and the payoff to D against C, σ_{23} , have no effect on average abundance.

Note that Results 1 and 2 are valid for any finite population size $N \geq 2$, while Result 3 is ascertained only for a large population size.

5. Simplified Prisoner's Dilemma

In this section, we assume that the payoffs have scaled means given by

$$\begin{pmatrix} \mu_1 & \mu_2 \\ \mu_3 & \mu_4 \end{pmatrix} = \begin{pmatrix} \bar{b} - \bar{c} & -\bar{c} \\ \bar{b} & 0 \end{pmatrix}, \quad (28)$$

where \bar{c} and \bar{b} represent expected cost and benefit for cooperation, respectively, in a Prisoner's Dilemma.

Note that in the absence of stochastic fluctuations, which holds with constant payoffs, condition (27) for weak selection to favor the abundance of C can never be satisfied. As a matter of fact, the average abundance of D always exceeds the average abundance of C. In the following subsections, we will study the effect of stochastic fluctuations of the payoffs on the average abundance of C in some extreme cases.

5.1. Case 1: $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = 0$ and $\sigma_4^2 = \sigma^2 > 0$

This is an extreme case where the variance of the payoff to D against D is larger than the variances of all the other payoffs. In this case, condition (27) for weak selection to favor the abundance of C is

$$\frac{\sigma^2}{\bar{c}} > \frac{4(2\theta+3)}{\theta+3}. \quad (29)$$

Note that the critical ratio on the right-hand side of the above inequality is increasing with respect to θ (see Fig. 1).

As $\theta \rightarrow 0$, the average abundance of C in the stationary state exceeds the average abundance of D if

$$\sigma^2 > 4\bar{c}. \quad (30)$$

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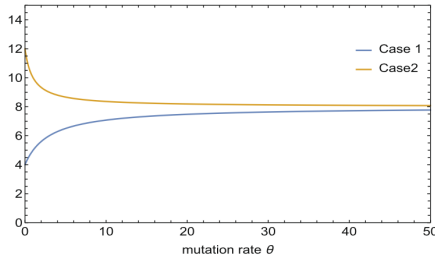


Fig. 1. Exact threshold value σ^2/\bar{c} that σ^2/\bar{c} must exceed in Cases 1 and 2 for weak selection to favor the abundance of C as a function of the mutation rate θ . Strategy C is most abundant in the $\theta \rightarrow 0$ limit in Case 1 and in the $\theta \rightarrow \infty$ limit in Case 2. For a high mutation rate, both Cases 1 and 2 share the same threshold value given by $\sigma^2 = 8\bar{c}$.

The same condition was obtained by Li and Lessard (2020) in Case 2 for a finite population that follows a Wright-Fisher model in the absence of mutation. By using a diffusion approximation in the limit of a large population size, it was shown that, if condition (30) is satisfied, then selection favors the evolution of C more than the evolution of D. This means that the probability of ultimate fixation of C introduced as a single mutant in an all D population is larger than the corresponding probability for a single mutant D introduced in an all C population. If this is the case, it is known that selection favors the abundance of C in the presence of mutation in the limit of a small mutation rate (Rousset and Billiard, 2000; Rousset, 2003; Fudenberg and Imhof, 2006). Note that Li and Lessard (2020) obtained condition (30) under the assumption that σ^2 and \bar{c} are small enough.

On the other hand, as $\theta \rightarrow \infty$, the average abundance of C exceeds the average abundance of D if

$$\sigma^2 > 8\bar{c}. \quad (31)$$

For an intermediate mutation rate, the variance σ^2 must exceed some value that increases from $4\bar{c}$ and $8\bar{c}$ as θ goes from 0 to ∞ .

Let us summarize these findings.

Result 4. In Case 1, increasing the mutation rate θ increases the critical value that the ratio σ^2/\bar{c} must exceed to favor the abundance of C. In other words, increasing the mutation rate strengthens the condition for weak selection to favor the abundance of C.

$$5.2. \text{ Case 2: } \sigma_1^2 = \sigma_2^2 = \sigma_4^2 = 0 \text{ and } \sigma_3^2 = \sigma^2 > 0$$

This is an extreme case where the variance of the payoff to D against C is larger than the variances of all the other payoffs. In this case, condition (27) for weak selection to favor the abundance of C is

$$\frac{\sigma^2}{\bar{c}} > \frac{4(2\theta + 3)}{\theta + 1}. \quad (32)$$

Here, the critical ratio on the right-hand side of the above inequality is decreasing with respect to θ (see Fig. 1).

As $\theta \rightarrow 0$, the average abundance of C exceeds the average abundance of D if

$$\sigma^2 > 12\bar{c}. \quad (33)$$

This is exactly the condition obtained by Li and Lessard (2020) in Case 2 for weak selection to favor the evolution of C more than the evolution of D in a large Wright-Fisher population in the absence of mutation and under the assumption that σ^2 is small enough.

On the other hand, as $\theta \rightarrow \infty$, the average abundance of C exceeds the average abundance of D if

$$\sigma^2 > 8\bar{c}. \quad (34)$$

For $0 < \theta < \infty$, the variance σ^2 must exceed some value that decreases from $12\bar{c}$ to $8\bar{c}$ as θ increases.

Result 5. In Case 2, increasing the mutation rate θ decreases the value that the ratio σ^2/\bar{c} must exceed to favor the abundance of C. In other words, increasing the mutation rate lessens the condition for weak selection to favor the abundance of C.

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

In this case, the variances of the payoffs to D against C and D, σ_3^2 and σ_4^2 , are significant and of the same order, while the other variances are negligible. Moreover, we suppose that the payoffs to D against C and D are related by a correlation coefficient $\rho_{34} = \rho$. Note that

$$\text{Cov}[\eta_3, \eta_4] = E[\eta_3\eta_4] - E[\eta_3]E[\eta_4] = \sigma_{34}\delta + o(\delta). \quad (35)$$

On the other hand, we have

$$\begin{aligned} \text{Cov}[\eta_3, \eta_4] &= \rho\sqrt{\text{Var}[\eta_3]\text{Var}[\eta_4]} = \rho\sqrt{(\sigma^2\delta + o(\delta))^2} \\ &= \rho\sigma^2\delta + o(\delta). \end{aligned} \quad (36)$$

As a result, we must have $\sigma_{34} = \rho\sigma^2$. Then, condition (27) for weak selection to favor the abundance of C can be written as

$$\sigma^2 > \sigma_c^2 = \frac{2(2\theta + 3)}{(\theta + 1)\rho + \theta + 2}\bar{c} \quad (37)$$

for any $-1 \leq \rho \leq 1$. This means that the abundance of C can be favored if the variance σ^2 is large enough. The threshold value σ_c^2 is a decreasing function of ρ and an increasing function of θ . It is more favorable for the abundance of C to increase the correlation between the payoffs to D against C and D and to decrease the mutation rate.

We turn now our attention to three extreme cases of particular interest (see Fig. 2). The first case is when the payoffs to D against C and D are uncorrelated, that is, $\rho = 0$. In this case, we have

$$\sigma_c^2 = \frac{2(2\theta + 3)}{\theta + 2}\bar{c}, \quad (38)$$

which is increasing with respect to θ . In the limit of a high mutation rate, that is, $\theta \rightarrow \infty$, we have $\sigma_c^2 \rightarrow 4\bar{c}$. On the other hand, in the limit of a low mutation rate, that is, $\theta \rightarrow 0$, we find $\sigma_c^2 \rightarrow 3\bar{c}$. The

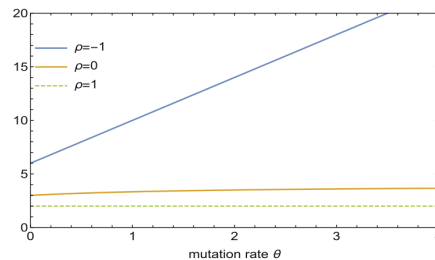


Fig. 2. Exact threshold value σ_c^2/\bar{c} that σ^2/\bar{c} must exceed in Case 3 for weak selection to favor the abundance of C as a function of the mutation rate θ for different values of the correlation coefficient ρ . The worst scenario for the abundance of C is when $\rho = -1$ and $\theta \rightarrow \infty$, where $\sigma_c^2 \rightarrow \infty$. The best scenario for the abundance of C is when $\rho = 1$ and any mutation rate, where $\sigma_c^2 = 2\bar{c}$.

condition $\sigma^2 > 3\bar{c}$ was obtained by Li and Lessard (2020) in Case 3 for the evolution of C to be more favored than the evolution of D in the absence of mutation under the assumption that σ^2 and \bar{c} are small enough.

The second extreme case is when the payoffs to D against C and D are in perfect direct correlation, that is, $\rho = 1$. Then we get

$$\sigma_c^2 = 2\bar{c}, \quad (39)$$

which does not depend on the mutation rate θ .

The last case is when the payoffs to D against C and D are in opposite direct correlation, that is, $\rho = -1$. In this case, we have

$$\sigma_c^2 = 2(2\theta + 3)\bar{c}, \quad (40)$$

which is an increasing function of the mutation rate θ . Note that σ_c^2 diverges as $\theta \rightarrow \infty$, which means that a mutation rate that is high enough opposes the abundance of C and favors the abundance of D . Therefore, a smaller mutation rate is more favorable for the abundance of C .

Let us summarize.

Result 6. In Case 3, decreasing the mutation rate θ or increasing the correlation coefficient ρ decreases the value that the ratio σ^2/\bar{c} must exceed to favor the abundance of C . In other words, a lower mutation rate or a higher positive correlation coefficient between the payoffs to D against C and D is more favorable for the abundance of C .

5.4. Case 4: $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = \sigma_4^2 = \sigma^2$ and $\sigma_{34} = \rho\sigma^2$

Here, we assume that the variances of all the payoffs are of the same order and far from being insignificant. Moreover, we suppose that all the payoffs are uncorrelated but the payoffs to D against C and D , which have a correlation coefficient given by $\rho_{34} = \rho$. As in Case 3, this implies that $\sigma_{34} = \rho\sigma^2$. Here, condition (27) for weak selection to favor the abundance of C can be written as

$$\frac{\sigma^2}{\bar{c}} > \sigma_c^2 = \frac{2(2\theta + 3)}{\rho(\theta + 1)}\bar{c} \quad (41)$$

for $\rho > 0$. If $\rho \leq 0$, then condition (27) can never be satisfied and the average abundance of C never exceeds the average abundance of D .

Note that σ_c^2 is a decreasing function of both θ and ρ . Moreover, we have $\sigma_c^2 \rightarrow \infty$ as $\rho \rightarrow 0$, which means that weak selection favors the abundance of D if ρ is close enough to 0. This is true for any mutation rate $\theta > 0$. On the other hand, if $\rho = 1$, then

$$\sigma_c^2 = \frac{2(2\theta + 3)}{\theta + 1}\bar{c} \quad (42)$$

with $\sigma_c^2 \rightarrow 6\bar{c}$ as $\theta \rightarrow 0$ and $\sigma_c^2 \rightarrow 4\bar{c}$ as $\theta \rightarrow \infty$.

In summary, the following conclusion can be drawn.

Result 7. In Case 4, increasing the mutation rate θ or increasing the correlation coefficient ρ decreases the value that the ratio σ^2/\bar{c} must exceed to favor the abundance of C . In other words, a higher mutation rate or a higher positive correlation coefficient is more favorable for the abundance of C .

6. Additive Prisoner's Dilemma

In this section, we assume that cooperation by an individual incurs a random cost $c > 0$ to the individual but provides a random benefit $b > c$ to the opponent. More precisely, the payoff matrix is given by

$$\begin{pmatrix} \eta_1 & \eta_2 \\ \eta_3 & \eta_4 \end{pmatrix} = \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix}. \quad (43)$$

Moreover, we make the following assumptions:

1. $E[b] = \mu_b\delta + o(\delta)$ and $E[c] = \mu_c\delta + o(\delta)$, so that the scaled means of the payoffs $\eta_1, \eta_2, \eta_3, \eta_4$ are given by

$$\mu_1 = \mu_b - \mu_c, \mu_2 = -\mu_c, \mu_3 = \mu_b, \mu_4 = 0. \quad (44)$$

2. $E[b^2] = \sigma_b^2\delta + o(\delta)$, $E[c^2] = \sigma_c^2\delta + o(\delta)$, $E[bc] = \sigma_{bc}\delta + o(\delta)$, so that the scaled variances and covariances of the payoffs $\eta_1, \eta_2, \eta_3, \eta_4$ are

$$\sigma_1^2 = \sigma_b^2 + \sigma_c^2 - 2\sigma_{bc}, \quad (45a)$$

$$\sigma_2^2 = \sigma_c^2, \quad (45b)$$

$$\sigma_3^2 = \sigma_b^2, \quad (45c)$$

$$\sigma_4^2 = \sigma_{14} = \sigma_{24} = \sigma_{34} = 0, \quad (45d)$$

$$\sigma_{12} = \sigma_c^2 - \sigma_{bc}, \quad (45e)$$

$$\sigma_{13} = \sigma_b^2 - \sigma_{bc}, \quad (45f)$$

$$\sigma_{23} = -\sigma_{bc}. \quad (45g)$$

Under these assumptions, condition (27) for weak selection to favor the abundance of C is

$$\sigma_{bc} - \sigma_c^2 > 2\mu_c. \quad (47)$$

Here, note that neither the mutation rate θ nor the scaled variance of the benefit σ_b^2 come into play in this condition. Only the scaled variance of the cost c and its scaled covariance with b do. Note also that condition (47) is the same as the one derived by Li and Lessard (2020) for selection to favor the evolution of C more than the evolution of D in a large Wright-Fisher population without mutation and under the assumption that μ_c , σ_c^2 and σ_{bc} are of the same small enough order. Let us summarize.

Result 8. In the case of an additive Prisoner's Dilemma, decreasing the level of uncertainty in the cost c or increasing its covariance with the benefit b increases the average abundance of C irrespective of the mutation rate.

7. Repeated Prisoner's Dilemma

We consider now the Prisoner's Dilemma with independent payoffs repeated a random number of times. The payoffs in a single round are given by the entries of the matrix

$$\begin{pmatrix} R & S \\ T & P \end{pmatrix}, \quad (48)$$

where $T > R > P > S$ and $2R > T + S$. If the interacting players cooperate, then each one of them receives some reward R , while P is the punishment payoff that each player receives if both defect. Moreover, if a cooperator interacts with a defector, then the former receives a sucker payoff S and the latter a temptation payoff T . We suppose that at each time step, any interaction between two players is composed of n rounds, where $n \geq 1$ is a random variable that is independent of R, S, T and P .

We assume two possible strategies: *TFT* for tit-for-tat and *AllD* for always-defect (Axelrod and Hamilton, 1981; Axelrod, 1984). A *TFT*-player cooperates in the first round and, in the next rounds, adopts the strategy used by its partner in the previous round. An *AllD*-player defects in all rounds. If they interact, two *TFT*-players will cooperate all the time and then each one of them will receive nR , while two *AllD*-players will defect all the time and then each one of them will receive nP . If the interacting players are of different types, the *TFT*-player will cooperate in the first round and thereafter it will defect, while the *AllD*-player will defect all the time. So, the *TFT*-player will receive $S + (n-1)P$, while the *AllD*-player will receive $T + (n-1)P$. The different payoffs are given by the entries of the 2×2 matrix

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$$\begin{pmatrix} \eta_1 & \eta_2 \\ \eta_3 & \eta_4 \end{pmatrix} = \begin{pmatrix} nR & S + (n-1)P \\ T + (n-1)P & nP \end{pmatrix}. \quad (49)$$

Then, the scaled means, variances and covariances of these payoffs are given by

$$\mu_1 = \mu_R E(n), \quad (49a)$$

$$\mu_2 = \mu_S + \mu_P E(n-1), \quad (49b)$$

$$\mu_3 = \mu_T + \mu_P E(n-1), \quad (49c)$$

$$\mu_4 = \mu_P E(n), \quad (49d)$$

and

$$\sigma_1^2 = \sigma_R^2 E(n^2), \quad (50a)$$

$$\sigma_2^2 = \sigma_S^2 + \sigma_P^2 E((n-1)^2), \quad (50b)$$

$$\sigma_3^2 = \sigma_T^2 + \sigma_P^2 E((n-1)^2), \quad (50c)$$

$$\sigma_4^2 = \sigma_P^2 E(n^2), \quad (50d)$$

$$\sigma_{12} = \sigma_{13} = \sigma_{14} = 0, \quad (50e)$$

$$\sigma_{23} = \sigma_P^2 E((n-1)^2), \quad (50f)$$

$$\sigma_{24} = \sigma_{34} = \sigma_P^2 E(n(n-1)). \quad (50g)$$

Here, μ_R, μ_S, μ_T and μ_P ($\sigma_R^2, \sigma_S^2, \sigma_T^2$ and σ_P^2 , respectively) are the scaled means (variances, respectively) of the payoffs R, S, T and P , respectively.

In this case, condition (27) for weak selection to favor the abundance of C can be written as

$$\begin{aligned} \mu_R + \mu_S - \mu_T - \mu_P + (\mu_R - \mu_P)E(n-1) - \frac{\theta+3}{2(2\theta+3)}E(n^2)\sigma_R^2 \\ - \frac{\theta+1}{2(2\theta+3)}\sigma_S^2 + \frac{\theta+1}{2(2\theta+3)}\sigma_T^2 + c_P\sigma_P^2 > 0, \end{aligned} \quad (51)$$

where

$$c_P = \frac{3(\theta+1)}{2(2\theta+3)}E((n-1)^2) + E(n-1) + \frac{\theta+3}{2(2\theta+3)} > 0. \quad (52)$$

In condition (51), the coefficients of σ_R^2 and σ_S^2 are negative, while the coefficients of σ_T^2 and σ_P^2 are positive. Therefore, decreasing the variance of the payoff to C against C or D , σ_R^2 or σ_S^2 , or increasing the variance of the payoff to D against C or D , σ_T^2 or σ_P^2 , increases the average abundance of TFT . Note that, in the limit of a low mutation rate, that is, $\theta \rightarrow 0$, condition (51) coincides with the condition obtained by Li and Lessard (2020) for weak selection to favor more the evolution of TFT than the evolution of $AllD$ in the absence of mutation.

7.1. Case $E(n) = 1$

If $E(n) = 1$, then $n = 1$ with probability one, which means only one round. Condition (51) for weak selection to favor the abundance of TFT becomes

$$\mu_R + \mu_S - \mu_T - \mu_P + \frac{\theta+3}{2(2\theta+3)}(\sigma_P^2 - \sigma_R^2) + \frac{\theta+1}{2(2\theta+3)}(\sigma_T^2 - \sigma_S^2) > 0, \quad (53)$$

which is condition (27) in the case of independent payoffs. Since the coefficient of $\sigma_P^2 - \sigma_R^2$ is decreasing and the coefficient of $\sigma_T^2 - \sigma_S^2$ increasing with respect to θ , increasing the mutation rate decreases the weight of the former difference and increases the weight of the latter in condition (53). Moreover, in the limit of a low mutation rate, that is, $\theta \rightarrow 0$, this condition becomes

$$\mu_R + \mu_S - \mu_T - \mu_P + \frac{1}{6}(-3\sigma_R^2 - \sigma_S^2 + \sigma_T^2 + 3\sigma_P^2) > 0, \quad (54)$$

while in the limit of a high mutation rate, that is, $\theta \rightarrow \infty$, it becomes

$$\mu_R + \mu_S - \mu_T - \mu_P + \frac{1}{4}(-\sigma_R^2 - \sigma_S^2 + \sigma_T^2 + \sigma_P^2) > 0. \quad (55)$$

Therefore, changing the mutation rate can change the strategy between TFT and $AllD$ that is more abundant on average.

Suppose, for instance, that the variances of all payoffs vanish, which is the case if the payoffs are constant. The condition for the average abundance of TFT to exceed the average abundance of $AllD$ reduces to simple risk dominance, that is,

$$\mu_R + \mu_S > \mu_T + \mu_P \quad (56)$$

irrespective of the mutation rate. This is the condition obtained by Antal et al. (2009) in well-mixed populations with any mutation rate. This is also the condition for weak selection to favor more the evolution of TFT than the evolution of $AllD$ in a large population in the absence of mutation (Nowak et al., 2004).

7.2. Case $E(n) \gg 1$

In the case of a large number of rounds with $E(n) \gg 1$, so that $E(n^2) \gg E(n)$, condition (51) for weak selection to favor the abundance of TFT reduces to

$$\sigma_P^2 > \frac{\theta+3}{3(\theta+1)}\sigma_R^2. \quad (57)$$

In this case, only the variances of the payoffs to C against C and to D against D come into play. In addition, increasing the mutation rate lessens the condition for weak selection to favor the abundance of TFT . For a low mutation rate, the condition becomes simply $\sigma_P^2 > \sigma_R^2$, while for a high mutation rate, it becomes $\sigma_P^2 > \sigma_R^2/3$. If $\sigma_R^2 = 0$, then weak selection favors the abundance of TFT as long as $\sigma_P^2 > 0$.

If the variances of all the payoffs vanish, then condition (51) can be written as

$$\mu_R > \mu_P, \quad (58)$$

which is always satisfied. Then, weak selection favors the abundance of TFT . This is the conclusion reached by Nowak (2006) in the case of a simplified Prisoner's Dilemma with constant payoffs that is repeated enough times.

8. Discussion

In this paper, we have studied a randomized two-player linear game in a finite well-mixed population in the presence of weak selection and symmetric recurrent mutation. The payoff matrix is no more constant like in classical evolutionary game theory but fluctuates in time due perhaps to random noise in the environment. We have shown that the average abundance of a strategy in the stationary state is driven not only by the means of the payoffs but also by their variances and covariances.

With strategies C and D in equal frequencies in a large population, the scaled mean payoff to C is $(\mu_1 + \mu_2)/2$, where μ_1 and μ_2 are the scaled means of the payoffs to C against C and D , respectively. Similarly, the scaled mean payoff to D is the average of its scaled mean payoffs which is given by $(\mu_3 + \mu_4)/2$. These are the scaled mean payoffs to C and D , respectively, if the opponent is C or D with the same probability $1/2$. In the case of constant payoffs, the strategy that has the higher scaled mean payoff has the higher average abundance in the stationary state (Antal et al., 2009). Note that the mutation rate does not come into play in this condition.

In the case of random payoffs, the scaled mean payoff is no more sufficient to determine the more abundant strategy on aver-

age and we have to resort to an extended scaled mean payoff. For C in a large population, it is defined as

$$\frac{\mu_1 + \mu_2}{2} - \frac{1}{4(2\theta + 3)} [(\theta + 3)\sigma_1^2 + (\theta + 1)\sigma_2^2 + 2(\theta + 1)\sigma_{12} + (\sigma_{24} - \sigma_{13})], \quad (59)$$

where σ_1^2 , σ_2^2 and σ_{12} are the scaled variances and covariance of the payoffs to C against C and D , respectively, while σ_{24} is the scaled covariance of the payoffs to C and D against D and σ_{13} is the scaled covariance of the payoffs to C and D against C . Similarly, the extended scaled mean payoff to D in a large population is

$$\frac{\mu_3 + \mu_4}{2} - \frac{1}{4(2\theta + 3)} [(\theta + 1)\sigma_3^2 + (\theta + 3)\sigma_4^2 + 2(\theta + 1)\sigma_{34} + (\sigma_{13} - \sigma_{24})]. \quad (60)$$

We have shown (see (27)) that the strategy that has the higher extended scaled mean payoff has the higher average abundance in the stationary state. This result shows the effect of any variance or covariance of payoffs on the difference between average abundances. Note that the scaled covariance of the payoffs to C against C and D against D , σ_{14} , as well as the scaled covariance of the payoffs to C against D and to D against C , σ_{23} , do not have any effect on this difference (Result 3). The intuitive reason is that, by symmetry, each of these covariances must have the same effect on the average abundances of C and D .

The above extended scaled mean payoffs to C and D show that an increase in the scaled variance of any payoff to D , σ_3^2 or σ_4^2 , or in their scaled covariance, σ_{34} , should increase the average abundance of C . We have shown that this should be true for any fixed population size (Result 2). This scenario makes it easier for selection to favor the abundance of C . Similarly, an increase in the scaled variance of any payoff to C , σ_1^2 or σ_2^2 , or in their scaled covariance, σ_{12} , should reduce the average abundance of C , and this scenario makes it more difficult for selection to favor the abundance of C . Again, this conclusion is valid for any finite population size $N \geq 2$ (Result 1).

These results agree with the fact that conditions for selection to favor the evolution of cooperation, favor more the evolution of cooperation than the evolution of defection, and disfavor the evolution of defection, all with respect to fixation probability in the absence of mutation, are lessened with an increase in the variances of the payoffs for defection and a decrease in the variances of the payoffs for cooperation (Li and Lessard, 2020). They agree also with the fact that the evolution of cooperation tends to be favored by selection in a large population with respect to the concepts of stochastic local stability (SLS) and stochastic evolutionary stability (SES) applied to Prisoner's Dilemmas with random payoffs (Zheng et al., 2017; Zheng et al., 2018) if the coefficients of variation of the payoffs are smaller for cooperation than for defection (Li et al., 2020). Moreover, all these conclusions are in agreement with the generally negative effect of the variance in fitness on the evolution of an allele in population genetics models in the absence of mutation (Gillespie, 1973; Gillespie, 1974; Karlin and Levikson, 1974; Karlin and Liberman, 1974; Frank and Slatkin, 1990; Starrfelt and Kokko, 2012; Schreiber, 2015; Rychtar and Taylor, 2020).

Returning to the extended scaled mean payoff of D in the presence of mutation, the weight of σ_3^2 given by $\theta + 3$ is higher than the weight of σ_4^2 given by $\theta + 1$, where θ is the mutation rate. As a consequence, an increase in the variance of the payoff to D against D (Case 1 in Section 5) is more favorable for the abundance of C than an increase in the variance of the payoff to D against C (Case 2 in Section 5). This difference vanishes in the limit of a high mutation

rate. Moreover, increasing the mutation rate increases the average abundance of C in Case 1 but decreases it in Case 2 as illustrated in Fig. 1. In the limit of a low mutation rate, the condition for weak selection to favor the abundance of C is $\sigma^2 > 4\bar{c}$ in Case 2 and $\sigma^2 > 12\bar{c}$ in Case 1. In the limit of a high mutation rate, the condition is the same in both cases, and given by $\sigma^2 > 8\bar{c}$.

In Case 3 of Section 5, we have shown that an increase in both the variances of the payoffs to D against C and to D against D , while the other payoffs are kept constant, is more favorable for the abundance of C than an increase in only one of them. Moreover, introducing a scaled correlation coefficient ρ between these payoffs, weak selection favors the abundance of C as long as $\sigma^2 > \sigma_c^2$, where σ_c^2 is increasing with respect to θ and decreasing with respect to ρ . The best scenario for the abundance of C is a correlation coefficient $\rho = 1$ and a mutation rate $\theta \rightarrow 0$, in which case $\sigma_c^2 = 2$, while the worst scenario is a correlation coefficient $\rho = -1$ and a mutation rate $\theta \rightarrow \infty$, in which case the average abundance of C can never exceed the average abundance of D as illustrated in Fig. 2.

In Case 4 of Section 5, where all the variances are equal, we have shown that increasing the scaled correlation coefficient ρ between the payoffs to D against C and to D against D can change the strategy that is more abundant on average. For nonpositive ρ , the abundance of C can never be favored by weak selection. However, for positive ρ , it is possible for weak selection to favor the abundance of C as long as $\sigma^2 > \sigma_c^2$, where the threshold value σ_c^2 is reduced by an increase in the mutation rate θ or in the correlation coefficient ρ , which plays in favor of the abundance of C .

More generally, an increase in the mutation rate θ plays in favor of the abundance of C if

$$\sigma_3^2 - 3\sigma_4^2 + 2\sigma_{34} + 4\sigma_{24} > \sigma_1^2 - 3\sigma_2^2 + 2\sigma_{12} + 4\sigma_{13}. \quad (61)$$

This is the condition for the difference between the extended scaled mean payoffs to C and D given in (59) and (60), respectively, to be strictly increasing with respect to θ . The left-hand side and the right-hand side of (61) are the coefficients that quantify the effect of increasing the mutation rate on the fitnesses of D and C , respectively. Increasing the mutation rate will increase the quantity of interactions between individuals of different types, C against D , and decrease the quantity of interactions between individuals of the same type, C against C and D against D . In a population of defectors, increasing θ will introduce type C . This will decrease the weight of the variance of the payoff to D against D , σ_4^2 , increase the weight of the variance of the payoff to D against C , σ_3^2 , and then increase the weight of their covariance, σ_{34} . Also, this increases the weight of the covariance between the payoffs to C and D against D , σ_{24} . In a population of cooperators, increasing θ will introduce type D . This will increase the weight of the variance of the payoff to C against C , σ_1^2 , decrease the weight of the variance of the payoff to C against D , σ_2^2 , and then increase the weight of their covariance, σ_{12} . Moreover, this increases the weight of the covariance between the payoffs to C and D against C , σ_{13} . The strategy that has the lower effect will have an increasing abundance with respect to the mutation rate.

In the case of a Prisoner's Dilemma with additive random cost c and benefit b for cooperation represented by C , weak selection favors the abundance of C if $\sigma_{bc} - \sigma_c^2 > 2\mu_c$ as shown in Section 6. Here, μ_c is the scaled expected cost, σ_c^2 is the scaled variance of the cost, and σ_{bc} is the scaled covariance between the benefit and the cost. The mutation rate has no effect on the abundance of C . However, an increase in σ_c^2 will increase the abundance of defection represented by D , since a large fluctuation in the cost will lessen the fitness of C . This disadvantage can be reduced and even counteracted by an increase in the covariance σ_{bc} . If the benefit and the cost are uncorrelated, weak selection favors the abundance of D .

In the case of a Prisoner's Dilemma with independent payoffs repeated a random number of times, players can choose to cooperate in the first round and then adopt direct reciprocity, *TFT*, or to defect all the time, *AllD*. We have confirmed that an increase in the variance of any payoff to *D* against *C* or *D* or a decrease in the variance of any payoff to *C* against *C* or *D* will enhance the average abundance of *TFT*, and therefore promote cooperation. Increasing the mutation rate will decrease the weight of $\sigma_P^2 - \sigma_R^2$ and increase the weight of $\sigma_C^2 - \sigma_D^2$ in the condition for weak selection to favor the abundance of *TFT*. If the game is played a very large number of rounds, then $\sigma_P^2 > \frac{\theta+3}{3(\theta+1)} \sigma_R^2$ guarantees that weak selection favors the abundance of *C*. Increasing the mutation rate will lessen this condition. Note that, in this case, the scaled means as well as the other scaled variances have an insignificant effect on the average abundance of *TFT*.

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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. Conditional expected frequency change

For the first two moments of $P_1(x)$, we have

$$E[P_1(x)] = E[x\eta_1 + (1-x)\eta_2] = [x\mu_1 + (1-x)\mu_2]\delta + o(\delta) \quad (62)$$

and

$$\begin{aligned} E[P_1^2(x)] &= E[(x\eta_1 + (1-x)\eta_2)^2] \\ &= E[x^2\eta_1^2 + 2x(1-x)\eta_1\eta_2 + (1-x)^2\eta_2^2] \\ &= [x^2\sigma_1^2 + 2x(1-x)\sigma_{12} + (1-x)^2\sigma_2^2]\delta + o(\delta). \end{aligned} \quad (63)$$

Similarly, the first two moments of $P_2(x)$ are given by

$$E[P_2(x)] = [x\mu_3 + (1-x)\mu_4]\delta + o(\delta), \quad (64a)$$

$$E[P_2^2(x)] = [x^2\sigma_3^2 + 2x(1-x)\sigma_{34} + (1-x)^2\sigma_4^2]\delta + o(\delta). \quad (64b)$$

Finally, we have

$$\begin{aligned} E[P_1(x)P_2(x)] &= E[(x\eta_1 + (1-x)\eta_2)(x\eta_3 + (1-x)\eta_4)] \\ &= x^2E[\eta_1\eta_3] + x(1-x)E[\eta_1\eta_4 + \eta_2\eta_3] \\ &\quad + (1-x)^2E[\eta_2\eta_4] \\ &= [x^2\sigma_{13} + x(1-x)(\sigma_{14} + \sigma_{23}) + (1-x)^2\sigma_{24}]\delta \\ &\quad + o(\delta). \end{aligned} \quad (65)$$

Since $|\eta_i| < M$ almost surely for $i = 1, 2, 3, 4$, we have

$$|\bar{P}(x)| = |xP_1(x) + (1-x)P_2(x)| \leq M < 1 \quad (66)$$

almost surely for all x in $[0, 1]$. Then, by using Taylor's theorem, we obtain

$$\frac{1}{1+\bar{P}(x)} = 1 - \bar{P}(x) + \frac{\bar{P}^2(x)}{(1+\xi)^2}, \quad (67)$$

where ξ is a random variable that depends on $\bar{P}(x)$ and is such that $0 \leq \xi \leq \bar{P}(x)$ or $\bar{P}(x) \leq \xi \leq 0$. Multiplying the above expression by $P_1(x) - P_2(x)$ and taking the expected value, we get

$$E\left[\frac{P_1(x) - P_2(x)}{1+\bar{P}(x)}\right] = E\left[(P_1(x) - P_2(x))\left(1 - \bar{P}(x) + \frac{\bar{P}^2(x)}{(1+\xi)^2}\right)\right]. \quad (68)$$

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

$$\left|\frac{1}{1+\xi}\right| \leq 1. \quad (69)$$

If $\bar{P}(x) \leq 0$, then $0 < 1 + \bar{P}(x) \leq 1 + \xi \leq 1$, from which

$$\left|\frac{1}{1+\xi}\right| \leq \left|\frac{1}{1+\bar{P}(x)}\right| \leq \frac{1}{1-|\bar{P}(x)|} \leq \frac{1}{1-M}, \quad (70)$$

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

$$\frac{1}{(1+\xi)^2} \leq \sup\left\{1, \frac{1}{(1-M)^2}\right\} = K, \quad (71)$$

where K is a finite constant. Then, we have

$$\begin{aligned} \left|E\left[\frac{(P_1(x) - P_2(x))\bar{P}^2(x)}{(1+\xi)^2}\right]\right| &\leq E\left[\frac{|P_1(x) - P_2(x)||\bar{P}^2(x)|}{(1+\xi)^2}\right] \\ &\leq KE|P_1(x) - P_2(x)||\bar{P}^2(x)|. \end{aligned} \quad (72)$$

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

$$E[|P_1(x) - P_2(x)||\bar{P}^2(x)|] = o(\delta). \quad (73)$$

We deduce that

$$E\left[\frac{(P_1(x) - P_2(x))\bar{P}^2(x)}{(1+\xi)^2}\right] = o(\delta). \quad (74)$$

Moreover, by using Eqs. 62,63,64b,65, we have

$$\begin{aligned} E[(P_1(x) - P_2(x))(1 - \bar{P}(x))] &= E[P_1(x)] - E[P_2(x)] \\ &\quad - xE[P_1^2(x)] \\ &\quad + (2x - 1)E[P_1(x)P_2(x)] \\ &\quad + (1 - x)E[P_2^2(x)] \\ &= m(x)\delta + o(\delta), \end{aligned} \quad (75)$$

where $m(x) = m_1(x) + m_2(x)$ with $m_1(x)$ being a sum of effects of the first moments given by

$$m_1(x) = x(\mu_1 - \mu_2 - \mu_3 + \mu_4) + \mu_2 - \mu_4, \quad (76)$$

and $m_2(x)$ a sum of effects of the second moments given by

$$\begin{aligned} m_2(x) = & x^2[2\sigma_{12} + 2\sigma_{13} + 2\sigma_{34} + 2\sigma_{34} - \sigma_1^2 - \sigma_2^2 - \sigma_3^2 - \sigma_4^2 - 2\sigma_{14} - 2\sigma_{23}] \\ & + x^2[2\sigma_{12}^2 + \sigma_1^2 + 3\sigma_{14}^2 + 3\sigma_{14} + 3\sigma_{23} - 2\sigma_{12} - \sigma_{13} - 5\sigma_{34} - 4\sigma_{34}] \\ & + x[4\sigma_{24} + 2\sigma_{34} - \sigma_2^2 - 3\sigma_{14}^2 - \sigma_{14} - \sigma_{23}] + \sigma_4^2 - \sigma_{24}. \end{aligned} \quad (77)$$

Finally, inserting (74) and (75) into (68), we have

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$$E\left[\frac{P_1(x) - P_2(x)}{1 + P(x)}\right] = m(x)\delta + o(\delta).$$

Appendix B. Identity measures

Let ϕ_n be the probability that n distinct individuals chosen at random in the population at stationarity under recurrent mutation in the absence of selection are either all C or all D . Then we have

$$\phi_n = E^0\left[X\left(X - \frac{1}{N}\right) \cdots \left(X - \frac{n-1}{N}\right)\right] + E^0\left[(1-X)\left(1 - X - \frac{1}{N}\right) \cdots \left(1 - X - \frac{n-1}{N}\right)\right], \quad (79)$$

where the first term on the right-hand side is for the case of all C individuals and the second term for the case of all D individuals. Since mutation is symmetric, we actually have

$$\phi_n = 2E^0\left[X\left(X - \frac{1}{N}\right) \cdots \left(X - \frac{n-1}{N}\right)\right]. \quad (80)$$

On the other hand, we find

$$E^0[X^2] = E^0[X(X - \frac{1}{N})] + \frac{1}{N}E^0[X] = \frac{1}{2}\phi_2 + \frac{1}{2N}, \quad (81)$$

$$E^0[X^3] = E^0[X(X - \frac{1}{N})(X - \frac{2}{N})] + \frac{3}{N}E^0[X^2] - \frac{2}{N^2}E^0[X] = \frac{1}{2}\phi_3 + \frac{3}{N}\left(\frac{1}{2}\phi_2 + \frac{1}{2N}\right) - \frac{2}{N^2} = \frac{1}{2}\phi_3 + \frac{3N\phi_2 + 3N - 2}{2N^2}, \quad (82)$$

$$E^0[X^4] = E^0[X(X - \frac{1}{N})(X - \frac{2}{N})(X - \frac{3}{N})] + \frac{6}{N}E^0[X^3] - \frac{11}{N^2}E^0[X^2] + \frac{5}{N^3}E^0[X] = \frac{1}{2}\phi_4 + \frac{6}{N}\left(\frac{1}{2}\phi_3 + \frac{3}{2N}\phi_2 + \frac{3N-2}{2N^2}\right) - \frac{11}{N^2}\left(\frac{1}{2}\phi_2 + \frac{1}{2N}\right) + \frac{5}{N^3} = \frac{1}{2}\phi_4 + \frac{6N^2\phi_3 + 7N\phi_2 + 7N - 6}{2N^3} \quad (83)$$

and

$$E^0[X^5] = E^0[X(X - \frac{1}{N})(X - \frac{2}{N})(X - \frac{3}{N})(X - \frac{4}{N})] + \frac{10}{N}E^0[X^4] - \frac{25}{N^2}E^0[X^3] + \frac{20}{N^3}E^0[X^2] - \frac{24}{N^4}E^0[X] = \frac{1}{2}\phi_5 + \frac{10}{N}\left(\frac{1}{2}\phi_4 + \frac{3}{2N}\phi_3 + \frac{7}{2N^2}\phi_2 + \frac{7N-6}{2N^2}\right) - \frac{25}{N^2}\left(\frac{1}{2}\phi_3 + \frac{3}{2N}\phi_2 + \frac{3N-2}{2N^2}\right) + \frac{20}{N^3}\left(\frac{1}{2}\phi_2 + \frac{1}{2N}\right) - \frac{24}{N^4} = \frac{1}{2}\phi_5 + \frac{10N^3\phi_4 + 25N^2\phi_3 + 15N\phi_2 + 15N - 14}{2N^4}. \quad (84)$$

Appendix C. Limiting coalescent process

Consider a sample of $n \geq 2$ individuals chosen at random at a given time step in a population of size N at stationarity under recurrent mutation in the absence of selection. Without loss of generality, assume that the N individuals occupy N sites, one per site. At each time step, one individual at random produces an offspring, and this offspring replaces the individual located at a site chosen at random. For n individuals sampled at a given time step, we have two possibilities for their ancestors one time step back: a sample of size $n-1$ if a coalescence event occurred or a sample of size n if it did not. A transition from a sample size n to a sample size $n-1$ occurs if one of the n sampled individuals happens to be the

offspring produced one time step back by one of the $n-1$ others. This has probability

$$p_{n,n-1} = \frac{n}{N} \times \frac{n-1}{N} = \frac{n(n-1)}{N^2}.$$

The complementary probability

$$p_{n,n} = 1 - p_{n,n-1} = 1 - \frac{n(n-1)}{N^2} \quad (86)$$

gives the probability to stay with a sample of size n .

Now, let $t_N^k(I_1, \dots, I_k)$ be the number of time steps back before the first coalescence of two lineages among the k lineages of individuals I_1, \dots, I_k , and $t_N^{k-1}(I_1, \dots, I_k)$ the supplementary number of time steps back before the first coalescence of two lineages among the $k-1$ remaining lineages, and so on up to $t_N^2(I_1, \dots, I_k)$ the supplementary number of time steps back before the coalescence of the last 2 remaining lineages. These times are independent random variables. Moreover, note that

$$\begin{aligned} \mathbb{P}^0\{t_N^l(I_1, \dots, I_k) > t\} &= \mathbb{P}^0\{\text{no coalescence event occurs before } t \\ &\quad + 1 \text{ time steps back}\} \\ &= (p_{ll})^t = \left(1 - \frac{l(l-1)}{N^2}\right)^t \end{aligned} \quad (87)$$

for $2 \leq l \leq k$ and any integer $t \geq 0$. Rescaling time by taking $N^2/2$ time steps as the unit of time, we have

$$\begin{aligned} \mathbb{P}^0\left\{\frac{t_N^l(I_1, \dots, I_k)}{N^2/2} > \tau\right\} &= \mathbb{P}^0\left\{\frac{t_N^l(I_1, \dots, I_k)}{N^2/2} > \frac{N^2\tau}{2}\right\} \\ &= \left(1 - \frac{l(l-1)}{N^2}\right)^{\lfloor \frac{N^2\tau}{2} \rfloor} \end{aligned} \quad (88)$$

for $\tau > 0$. Here, $\lfloor x \rfloor$ denotes the greatest integer less or equal to the real number x . Since

$$\lim_{N \rightarrow \infty} \left(1 - \frac{a}{N^2}\right)^{\lfloor \frac{N^2\tau}{2} \rfloor} = e^{-ab} \quad (89)$$

for any real number $b \geq 0$, we get

$$\lim_{N \rightarrow \infty} \mathbb{P}^0\left\{\frac{t_N^l(I_1, \dots, I_k)}{N^2/2} > \tau\right\} = \exp\left\{-\frac{l(l-1)}{2}\tau\right\} \quad (90)$$

for $\tau > 0$. Accordingly, as $N \rightarrow \infty$, the time $t_N^l(I_1, \dots, I_k)$ divided by $N^2/2$ converges in distribution to a continuous random variable whose density is given by

$$f_l(\tau) = \frac{l(l-1)}{2} \exp\left\{-\frac{l(l-1)}{2}\tau\right\} \quad (91)$$

for $\tau > 0$. This is exactly the density of the time before the first coalescence event from a sample of size l in Kingman's coalescent (Kingman, 1982). Moreover, defining $\theta = \lim_{N \rightarrow \infty} uN/2$ as mutation rate, the number of mutations on a branch of the coalescent tree whose length is τ as $N \rightarrow \infty$ follows a Poisson probability distribution of parameter $\theta\tau$ (see, e.g., Kroumi and Lessard, 2015, for a proof in an analogous situation for a Wright-Fisher model).

Appendix D. Identity measure ϕ_2

Let $y(\tau_2)$ be the probability that two individuals chosen at random, I_1 and I_2 , use the same strategy, C or D , given that their lineages coalesce at time back $\tau_2 > 0$. In the case of mutation on at least one of the branches of length τ_2 from I_1 and I_2 back to the most recent common ancestor M , the strategies used by I_1 and I_2 are the same with probability $1/2$, while in the case of no mutation, these strategies are necessarily the same. Therefore, we have

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$$y(\tau_2) = (1 - e^{-2\theta\tau_2}) \times \frac{1}{2} + e^{-2\theta\tau_2} = \frac{1 + e^{-2\theta\tau_2}}{2}. \quad (92)$$

Note that this probability depends on the total length of the branches connecting I_1 to I_2 given by $2\tau_2$. Moreover, this probability leads to

$$\begin{aligned} \phi_2 &= \int_0^\infty y(\tau_2) f_2(\tau_2) d\tau_2 = \frac{1}{2} \int_0^\infty (1 + e^{-2\theta\tau_2}) e^{-\tau_2} d\tau_2 \\ &= \frac{1 + \theta}{1 + 2\theta}. \end{aligned} \quad (93)$$

Appendix E. Identity measure ϕ_3

Let $y(\tau_3, \tau_2)$ be the probability that three individuals chosen at random, I_1, I_2 and I_3 , use the same strategy given that the lineages of two of them, say I_1 and I_2 without loss of generality, coalesce first at time back $\tau_3 > 0$, and the two remaining lineages coalesce after an additional time back $\tau_2 > 0$.

Let $S(I)$ denote the strategy, C or D, used by I and M_i be the most recent common ancestor (MRCA) of I_1 and I_2 . To compute $y(\tau_3, \tau_2)$ taking into account the mutation process, we consider two cases depending on the strategy used by M_1 compared to the strategy used by I_3 .

The first case corresponds to $S(I_1) = S(M_1), S(I_2) = S(M_1)$ and $S(I_3) = S(M_1)$. These are independent events and, owing to the previous subsection, their probabilities are $(1 + e^{-\theta\tau_3})/2, (1 + e^{-\theta\tau_3})/2$ and $(1 + e^{-\theta(2\tau_2+\tau_3)})/2$, respectively, since the branches connecting I_1, I_2 and I_3 to M_1 , represented by I_1M_1, I_2M_1 and I_3M_1 , respectively, do not overlap and have total lengths τ_3, τ_3 and $\tau_3 + 2\tau_2$, respectively. Therefore, we have

$$\mathbb{P}^0(\text{first case}) = \left(\frac{1 + e^{-\theta\tau_3}}{2}\right)^2 \times \frac{1 + e^{-\theta(2\tau_2+\tau_3)}}{2}. \quad (94)$$

As for the second case, it corresponds to $S(I_1) \neq S(M_1), S(I_2) \neq S(M_1)$ and $S(I_3) \neq S(M_1)$. These events are independent and their probabilities are given by $(1 - e^{-\theta\tau_3})/2, (1 - e^{-\theta\tau_3})/2$ and $(1 - e^{-\theta(2\tau_2+\tau_3)})/2$, respectively. The whole probability is

$$\mathbb{P}^0(\text{second case}) = \left(\frac{1 - e^{-\theta\tau_3}}{2}\right)^2 \times \frac{1 - e^{-\theta(2\tau_2+\tau_3)}}{2}. \quad (95)$$

Combining the above two equations, the probability that I_1, I_2 and I_3 use the same strategy is

$$\begin{aligned} y(\tau_3, \tau_2) &= \frac{1 + e^{-\theta(2\tau_2+\tau_3)}}{2} \left(\frac{1 + e^{-\theta\tau_3}}{2}\right)^2 + \frac{1 - e^{-\theta(2\tau_2+\tau_3)}}{2} \left(\frac{1 - e^{-\theta\tau_3}}{2}\right)^2 \\ &= \frac{1}{2} (1 + e^{-2\theta\tau_3} + 2e^{-2\theta(\tau_2+\tau_3)}). \end{aligned} \quad (96)$$

Multiplying this probability by the densities of the coalescence times and integrating over all possible values yield

$$\begin{aligned} \phi_3 &= \int_0^\infty \int_0^\infty y(\tau_3, \tau_2) f_2(\tau_2) f_3(\tau_3) d\tau_2 d\tau_3 \\ &= \frac{3}{4} \int_0^\infty \int_0^\infty (1 + e^{-2\theta\tau_3} + 2e^{-2\theta(\tau_2+\tau_3)}) e^{-(3\tau_3+\tau_2)} d\tau_2 d\tau_3 \\ &= \frac{3}{4} \left[\frac{2}{(2\theta+3)(2\theta+1)} + \frac{1}{2\theta+3} + \frac{1}{3} \right] \\ &= \frac{2+\theta}{2(1+2\theta)}. \end{aligned} \quad (97)$$

Appendix F. Identity measure ϕ_4

Let $y(\tau_4, \tau_3, \tau_2)$ be the probability of the event A_4 that four individuals chosen at random, I_1, I_2, I_3 and I_4 , use the same strategy given that the first two lineages to coalesce do it at time back τ_4 ,

the next two at time back $\tau_4 + \tau_3$, and the last two at time back $\tau_4 + \tau_3 + \tau_2$. We look at two possible scenarios for the coalescent process (see Fig. 3).

F.1. Scenario 1

In scenario 1, the lineages of I_1 and I_2 coalesce first, the lineages of I_3 and M_1 , the MRCA of I_1 and I_2 , coalesce second, and finally the lineages of I_4 and M_2 , the MRCA of I_3 and M_1 , coalesce last (see Fig. 3 (a)). Note that the branches $I_1M_1, I_2M_1, M_1M_2, I_3M_2$, and I_4M_2 do not overlap and have total lengths $\tau_4, \tau_4, \tau_4 + \tau_3$ and $\tau_4 + \tau_3 + 2\tau_2$, respectively. We consider four possible cases for A_4 to occur depending on the strategies used by M_1 and M_2 compared to the strategy used by I_4 .

The first case corresponds to $S(M_1) = S(M_2)$ and $S(M_2) = S(I_4)$ with $S(I_1) = S(M_1), S(I_2) = S(M_1)$ and $S(I_3) = S(M_2)$. This case occurs with probability

$$\frac{1 + e^{-\theta\tau_3}}{2} \times \frac{1 + e^{-\theta(\tau_4+\tau_3+2\tau_2)}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta(\tau_4+\tau_3)}}{2}. \quad (98)$$

In the second case, we have $S(M_1) = S(M_2)$ and $S(M_2) \neq S(I_4)$ with $S(I_1) \neq S(M_1), S(I_2) \neq S(M_1)$ and $S(I_3) \neq S(M_2)$. All these events simultaneously occur with probability

$$\frac{1 + e^{-\theta\tau_3}}{2} \times \frac{1 - e^{-\theta(\tau_4+\tau_3+2\tau_2)}}{2} \times \frac{1 - e^{-\theta\tau_4}}{2} \times \frac{1 - e^{-\theta\tau_4}}{2} \times \frac{1 - e^{-\theta(\tau_4+\tau_3)}}{2}. \quad (99)$$

As for the third case, we consider $S(M_1) \neq S(M_2)$ and $S(M_2) = S(I_4)$ with $S(I_1) = S(M_1), S(I_2) = S(M_1)$ and $S(I_3) = S(M_2)$, whose total probability is

$$\frac{1 - e^{-\theta\tau_3}}{2} \times \frac{1 - e^{-\theta(\tau_4+\tau_3+2\tau_2)}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 - e^{-\theta(\tau_4+\tau_3)}}{2}. \quad (100)$$

Finally, the last case corresponds to $S(M_1) \neq S(M_2)$ and $S(M_2) \neq S(I_4)$ with $S(I_1) \neq S(M_1), S(I_2) \neq S(M_1)$ and $S(I_3) = S(M_2)$, whose total probability is

$$\frac{1 - e^{-\theta\tau_3}}{2} \times \frac{1 + e^{-\theta(\tau_4+\tau_3+2\tau_2)}}{2} \times \frac{1 - e^{-\theta\tau_4}}{2} \times \frac{1 - e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta(\tau_4+\tau_3)}}{2}. \quad (101)$$

Summing the probabilities in the above equations, we find

$$\mathbb{P}^0(A_4|\text{scenario1}) = \frac{e^{-2\theta(\tau_4+\tau_3+\tau_2)} + 3e^{-2\theta(\tau_4+\tau_3+\tau_2)} + 2e^{-2\theta(\tau_4+\tau_3)} + e^{-2\theta\tau_4} + 1}{8}. \quad (102)$$

F.2. Scenario 2

In scenario 2, the lineages of I_1 and I_2 coalesce first, the lineages of I_3 and I_4 coalesce second, and finally the lineages of M_1 , the MRCA of I_1 and I_2 , and M_2 , the MRCA of I_3 and I_4 , coalesce last (see Fig. 3 (b)). In this scenario, the non-overlapping branches $I_1M_1, I_2M_1, M_1M_2, M_2I_3$, and M_2I_4 have total lengths given by $\tau_4, \tau_4, \tau_4 + 2\tau_2, \tau_4 + \tau_3$ and $\tau_4 + \tau_3$, respectively. This time, the four cases considered in scenario 1 have probabilities given by

$$\frac{1 + e^{-\theta(\tau_3+2\tau_2)}}{2} \times \frac{1 + e^{-\theta(\tau_4+\tau_3)}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta(\tau_4+\tau_3)}}{2}, \quad (103a)$$

$$\frac{1 + e^{-\theta(\tau_3+2\tau_2)}}{2} \times \frac{1 - e^{-\theta(\tau_4+\tau_3)}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 - e^{-\theta(\tau_4+\tau_3)}}{2}, \quad (103b)$$

$$\frac{1 - e^{-\theta(\tau_3+2\tau_2)}}{2} \times \frac{1 - e^{-\theta(\tau_4+\tau_3)}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 - e^{-\theta(\tau_4+\tau_3)}}{2}, \quad (103c)$$

$$\frac{1 - e^{-\theta(\tau_3+2\tau_2)}}{2} \times \frac{1 + e^{-\theta(\tau_4+\tau_3)}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta\tau_4}}{2} \times \frac{1 + e^{-\theta(\tau_4+\tau_3)}}{2}. \quad (103d)$$

Summing the above probabilities, we get

$$\mathbb{P}^0(A_4|\text{scenario2}) = \frac{4e^{-2\theta(\tau_4+\tau_3+\tau_2)} + e^{-2\theta(2\tau_4+\tau_3)} + e^{-2\theta(\tau_4+\tau_3)} + e^{-2\theta\tau_4} + 1}{8}. \quad (104)$$

F.3. Final calculation

Scenario 1 occurs with probability

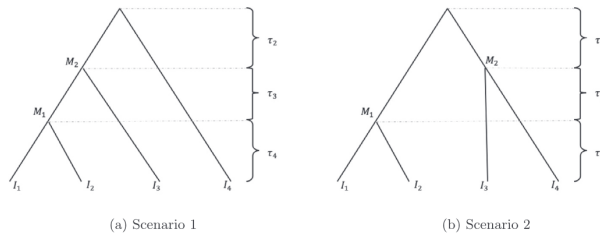


Fig. 3. Coalescence events of four lineages backward in time. We have two scenarios depending on the second coalescence event.

$$\frac{\binom{4}{2} \times \binom{2}{1}}{\binom{4}{2} \times \binom{3}{2}} = \frac{12}{18} = \frac{2}{3}, \quad (105)$$

while scenario 2 occurs with probability $1/3$. Therefore, we have

$$y(\tau_4, \tau_3, \tau_2) = \frac{2}{3} \times p^0(A_4 | \text{scenario1}) + \frac{1}{3} \times p^0(A_4 | \text{scenario2}), \quad (106)$$

from which we find

$$y(\tau_4, \tau_3, \tau_2) = \frac{1}{24} [2e^{-\theta(\tau_4+2\tau_3+2\tau_2)} + 10e^{-\theta(2\tau_4+2\tau_3+2\tau_2)} + 5e^{-\theta(2\tau_4+2\tau_3)} + e^{-\theta(4\tau_4+2\tau_3)} + 3e^{-2\theta\tau_4+3}], \quad (107)$$

Multiplying this probability by the densities of the coalescence times and integrating over all possible values give

$$\begin{aligned} \phi_4 &= \int_0^\infty \int_0^\infty \int_0^\infty y(\tau_4, \tau_3, \tau_2) f(\tau_4, \tau_3, \tau_2) d\tau_2 d\tau_3 d\tau_4 \\ &= \frac{3}{4} \int_0^\infty \int_0^\infty \int_0^\infty [2e^{-\theta(4\tau_4+2\tau_3+2\tau_2)} + 10e^{-\theta(2\tau_4+2\tau_3+2\tau_2)} \\ &\quad + 5e^{-\theta(2\tau_4+2\tau_3)} + e^{-\theta(4\tau_4+2\tau_3)} + 3e^{-2\theta\tau_4+3}] d\tau_2 d\tau_3 d\tau_4 \\ &= \frac{3}{4} \left[\frac{2}{(4\theta+6)(2\theta+3)(2\theta+1)} + \frac{10}{(2\theta+1)(2\theta+3)(2\theta+6)} + \frac{5}{(2\theta+6)(2\theta+3)} + \frac{1}{(4\theta+6)(2\theta+3)} + \frac{3}{3(2\theta+6)} + \frac{1}{6} \right] \\ &= \frac{(\theta+2)(\theta+3)}{2(2\theta+3)(2\theta+1)}. \end{aligned} \quad (108)$$

Appendix G. Identity measure ϕ_5

Let $y(\tau_5, \tau_4, \tau_3, \tau_2)$ be the probability of the event A_5 that five individuals chosen at random, I_1, I_2, I_3, I_4 and I_5 , use the same strategy given that their lineages coalesce two at a time at times back $\tau_5, \tau_4, \tau_3, \tau_2$ and $\tau_5 + \tau_4 + \tau_3 + \tau_2$. Let M_1, M_2 and M_3 be the most recent common ancestors associated to the first, second and third coalescence events, respectively, backward in time. For the coalescent process, we have five different scenarios to consider (see Fig. 4).

G.1. Scenario 1

In scenario 1, the lineages coalesce in the following order backward in time: I_1 and I_2, M_1 and I_3, M_2 and I_4, M_3 and I_5 (see Fig. 4 (a)). This scenario occurs with probability

$$\frac{\binom{5}{2} \binom{3}{1} \binom{2}{1}}{\binom{5}{2} \binom{4}{2} \binom{3}{2}} = \frac{1}{3}. \quad (109)$$

In this scenario, we have seven non-overlapping branches given by $I_1M_1, I_2M_1, M_1M_2, I_3M_2, M_2M_3, I_4M_3$ and I_5M_3 whose total lengths are $\tau_5, \tau_5, \tau_4, \tau_5 + \tau_4, \tau_3, \tau_5 + \tau_4 + \tau_3$ and $\tau_5 + \tau_4 + \tau_3 + 2\tau_2$, respectively. We have eight cases to consider for A_5 to occur depending on the strategies used by M_1, M_2 and M_3 compared to the strategy used by I_5 .

The first case corresponds to $S(M_1) = S(M_2), S(M_2) = S(M_3)$ and $S(I_5) = S(M_3)$ with $S(I_4) = S(M_3), S(I_3) = S(M_2), S(I_2) = S(M_1)$ and $S(I_1) = S(M_1)$. This occurs with probability

$$\frac{1 + e^{-\theta\tau_4}}{2} \frac{1 + e^{-\theta\tau_3}}{2} \frac{1 + e^{-\theta(\tau_5+\tau_4+\tau_3+2\tau_2)}}{2} \frac{1 + e^{-\theta(\tau_5+\tau_4+\tau_3)}}{2} \times \frac{1 + e^{-\theta(\tau_5+\tau_4)}}{2} \left(\frac{1 + e^{-\theta\tau_5}}{2} \right)^2.$$

Similarly, the case $S(M_1) = S(M_2), S(M_2) \neq S(M_3)$ and $S(I_5) \neq S(M_3)$ with $S(I_4) \neq S(M_3), S(I_3) = S(M_2), S(I_2) = S(M_1)$ and $S(I_1) = S(M_1)$ has probability

$$\frac{1 + e^{-\theta\tau_4}}{2} \frac{1 - e^{-\theta\tau_3}}{2} \frac{1 - e^{-\theta(\tau_5+\tau_4+\tau_3+2\tau_2)}}{2} \frac{1 - e^{-\theta(\tau_5+\tau_4+\tau_3)}}{2} \times \frac{1 + e^{-\theta(\tau_5+\tau_4)}}{2} \left(\frac{1 + e^{-\theta\tau_5}}{2} \right)^2,$$

the case $S(M_1) \neq S(M_2), S(M_2) \neq S(M_3)$ and $S(I_5) = S(M_3)$ with $S(I_4) = S(M_3), S(I_3) \neq S(M_2), S(I_2) = S(M_1)$ and $S(I_1) = S(M_1)$ probability

$$\frac{1 - e^{-\theta\tau_4}}{2} \frac{1 - e^{-\theta\tau_3}}{2} \frac{1 + e^{-\theta(\tau_5+\tau_4+\tau_3+2\tau_2)}}{2} \frac{1 + e^{-\theta(\tau_5+\tau_4+\tau_3)}}{2} \times \frac{1 - e^{-\theta(\tau_5+\tau_4)}}{2} \left(\frac{1 + e^{-\theta\tau_5}}{2} \right)^2,$$

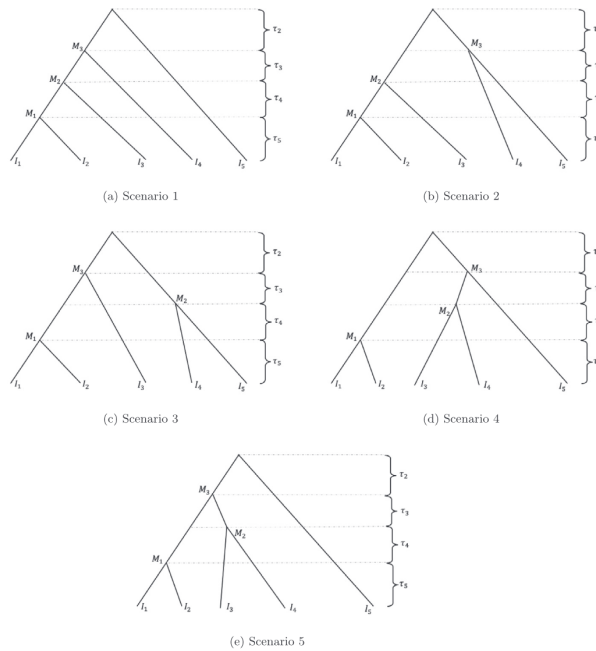


Fig. 4. Coalescence events of five lineages backward in time. We have five scenarios depending on the second and third coalescence events.

the case $S(M_1) \neq S(M_2), S(M_3) = S(M_3)$ and $S(I_5) = S(M_3)$ with $S(I_4) = S(M_3), S(I_3) = S(M_2), S(I_2) \neq S(M_1)$ and $S(I_1) \neq S(M_1)$ probability

$$\frac{1 - e^{-\theta\tau_4}}{2} \frac{1 + e^{-\theta\tau_3}}{2} \frac{1 + e^{-\theta(\tau_5 + \tau_4 + \tau_3 + 2\tau_2)}}{2} \frac{1 + e^{-\theta(\tau_5 + \tau_4 + \tau_3)}}{2} \times \frac{1 + e^{-\theta(\tau_5 + \tau_4)}}{2} \left(\frac{1 - e^{-\theta\tau_5}}{2} \right)^2,$$

the case $S(M_1) = S(M_2), S(M_3) \neq S(M_3)$ and $S(I_5) = S(M_3)$ with $S(I_4) = S(M_3), S(I_3) \neq S(M_2), S(I_2) \neq S(M_1)$ and $S(I_1) \neq S(M_1)$ probability

$$\frac{1 + e^{-\theta\tau_4}}{2} \frac{1 - e^{-\theta\tau_3}}{2} \frac{1 + e^{-\theta(\tau_5 + \tau_4 + \tau_3 + 2\tau_2)}}{2} \frac{1 + e^{-\theta(\tau_5 + \tau_4 + \tau_3)}}{2} \times \frac{1 - e^{-\theta(\tau_5 + \tau_4)}}{2} \left(\frac{1 - e^{-\theta\tau_5}}{2} \right)^2,$$

the case $S(M_1) \neq S(M_2), S(M_2) \neq S(M_3)$ and $S(I_5) \neq S(M_3)$ with $S(I_4) \neq S(M_3), S(I_3) = S(M_2), S(I_2) \neq S(M_1)$ and $S(I_1) \neq S(M_1)$ probability

$$\frac{1 - e^{-\theta\tau_4}}{2} \frac{1 - e^{-\theta\tau_3}}{2} \frac{1 - e^{-\theta(\tau_5 + \tau_4 + \tau_3 + 2\tau_2)}}{2} \frac{1 - e^{-\theta(\tau_5 + \tau_4 + \tau_3)}}{2} \times \frac{1 + e^{-\theta(\tau_5 + \tau_4)}}{2} \left(\frac{1 - e^{-\theta\tau_5}}{2} \right)^2,$$

the case $S(M_1) \neq S(M_2), S(M_2) = S(M_3)$ and $S(I_5) \neq S(M_3)$ with $S(I_4) \neq S(M_3), S(I_3) \neq S(M_2), S(I_2) = S(M_1)$ and $S(I_1) = S(M_1)$ probability

$$\frac{1 - e^{-\theta\tau_4}}{2} \frac{1 + e^{-\theta\tau_3}}{2} \frac{1 - e^{-\theta(\tau_5 + \tau_4 + \tau_3 + 2\tau_2)}}{2} \frac{1 - e^{-\theta(\tau_5 + \tau_4 + \tau_3)}}{2} \times \frac{1 - e^{-\theta(\tau_5 + \tau_4)}}{2} \left(\frac{1 + e^{-\theta\tau_5}}{2} \right)^2,$$

the case $S(M_1) = S(M_2), S(M_2) = S(M_3)$ and $S(I_5) \neq S(M_3)$ with $S(I_4) \neq S(M_3), S(I_3) \neq S(M_2), S(I_2) \neq S(M_1)$ and $S(I_1) \neq S(M_1)$ probability

$$\frac{1 + e^{-\theta\tau_4}}{2} \frac{1 + e^{-\theta\tau_3}}{2} \frac{1 - e^{-\theta(\tau_5 + \tau_4 + \tau_3 + 2\tau_2)}}{2} \frac{1 - e^{-\theta(\tau_5 + \tau_4 + \tau_3)}}{2} \times \frac{1 - e^{-\theta(\tau_5 + \tau_4)}}{2} \left(\frac{1 - e^{-\theta\tau_5}}{2} \right)^2.$$

Summing all these probabilities, the probability that five individuals chosen at random have the same strategy under the first scenario of the coalescent process is

$$p^0(A_5 | \text{scenario1}) = \frac{1}{16} [2e^{-2\theta(2\tau_5 + 2\tau_4 + \tau_3 + \tau_2)} + 2e^{-2\theta(2\tau_5 + \tau_4 + \tau_3 + \tau_2)} + 4e^{-2\theta(\tau_5 + \tau_4 + \tau_3 + \tau_2)} + e^{-2\theta(2\tau_5 + \tau_4 + \tau_3)} + 3e^{-2\theta(\tau_5 + \tau_4 + \tau_3)} + 2e^{-2\theta(\tau_5 + \tau_4)} + e^{-2\theta\tau_5} + 1]. \quad (110)$$

G.2. Scenario 2

In scenario 2, the lineages coalesce in the following order backward in time: I_1 and I_2 , M_1 and I_3 , I_4 and I_5 , M_2 and M_3 (see Fig. 4 (b)). This scenario occurs with probability

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$$\frac{\binom{5}{2}\binom{3}{2}\binom{2}{2}}{\binom{5}{2}\binom{4}{2}\binom{3}{2}} = \frac{1}{6}. \quad (111)$$

In this scenario, the seven non-overlapping branches $I_1M_1, I_2M_1, M_1M_2, I_3M_2, M_2M_3, I_4M_3$ and I_5M_3 have total lengths $\tau_5, \tau_5, \tau_4, \tau_5 + \tau_4, \tau_3 + 2\tau_2, \tau_5 + \tau_4 + \tau_3$ and $\tau_5 + \tau_4 + \tau_3$, respectively.

Considering all cases for the strategies used by M_1, M_2 and M_3 compared to the strategy used by I_5 and proceeding as in scenario 1, we find

$$\begin{aligned} \mathbb{P}^0(A_5 | \text{scenario2}) &= \frac{1}{16} [2e^{-2\theta(\tau_5 + \tau_4 + \tau_3 + \tau_2)} + 6e^{-2\theta(\tau_5 + \tau_4 + \tau_3 + \tau_2)} + 2e^{-2\theta(2\tau_5 + 2\tau_4 + \tau_3)} \\ &\quad + e^{-2\theta(2\tau_5 + \tau_4 + \tau_3)} + e^{-2\theta(\tau_5 + \tau_4 + \tau_3)} + 2e^{-2\theta(\tau_5 + \tau_4)} + e^{-2\theta\tau_5} + 1]. \end{aligned} \quad (112)$$

G.3. Scenario 3

In scenario 3, the lineages coalesce in the following order backward in time: I_1 and I_2, I_4 and I_5, M_1 and I_3, M_2 and M_3 (see Fig. 4 (c)). This scenario occurs with probability

$$\frac{\binom{5}{2}\binom{3}{2}\binom{2}{2}}{\binom{5}{2}\binom{4}{2}\binom{3}{2}} = \frac{1}{6}. \quad (113)$$

$$\begin{aligned} y(\tau_5, \tau_4, \tau_3, \tau_2) &= \frac{1}{6} \times \mathbb{P}^0(A_5 | \text{scenario1}) + \frac{1}{6} \times \mathbb{P}^0(A_5 | \text{scenario2}) + \frac{1}{6} \times \mathbb{P}^0(A_5 | \text{scenario3}) \\ &\quad + \frac{1}{6} \times \mathbb{P}^0(A_5 | \text{scenario4}) + \frac{1}{6} \times \mathbb{P}^0(A_5 | \text{scenario5}) \\ &= \frac{1}{96} [8e^{-2\theta(2\tau_5 + 2\tau_4 + \tau_3 + \tau_2)} + 10e^{-2\theta(2\tau_5 + \tau_4 + \tau_3 + \tau_2)} + 30e^{-2\theta(\tau_5 + \tau_4 + \tau_3 + \tau_2)} + 4e^{-2\theta(2\tau_5 + 2\tau_4 + \tau_3)} \\ &\quad + 5e^{-2\theta(2\tau_5 + \tau_4 + \tau_3)} + 15e^{-2\theta(\tau_5 + \tau_4 + \tau_3)} + 9e^{-2\theta(\tau_5 + \tau_4)} + 3e^{-2\theta(2\tau_5 + \tau_4)} + 6e^{-2\theta\tau_5} + 6]. \end{aligned} \quad (119)$$

In this scenario, the seven non-overlapping branches $I_1M_1, I_2M_1, M_1M_3, I_3M_3, M_2M_3, I_4M_2$ and I_5M_2 have total lengths $\tau_5, \tau_5, \tau_3 + \tau_4, \tau_5 + \tau_4 + \tau_3, \tau_3 + 2\tau_2, \tau_5 + \tau_4$ and $\tau_5 + \tau_4$, respectively.

Proceeding as in scenarios 1 and 2, we find

$$\begin{aligned} \mathbb{P}^0(A_5 | \text{scenario3}) &= \frac{1}{16} [2e^{-2\theta(2\tau_5 + \tau_3 + \tau_4 + \tau_2)} + 6e^{-2\theta(\tau_5 + \tau_3 + \tau_4 + \tau_2)} + 2e^{-2\theta(2\tau_5 + \tau_3 + 2\tau_4)} \\ &\quad + 2e^{-2\theta(\tau_5 + \tau_3 + \tau_4)} + e^{-2\theta(2\tau_5 + \tau_4)} + e^{-2\theta(\tau_5 + \tau_4)} + e^{-2\theta\tau_5} + 1]. \end{aligned} \quad (114)$$

G.4. Scenario 4

In scenario 4, the order of the coalescence events backward in time is: I_1 and I_2, I_3 and I_4, M_2 and I_5, M_1 and M_3 (see Fig. 4 (d)). This scenario has probability

$$\frac{\binom{5}{2}\binom{3}{2}\binom{2}{2}}{\binom{5}{2}\binom{4}{2}\binom{3}{2}} = \frac{1}{6}. \quad (115)$$

In this scenario, the lengths of the non-overlapping branches $I_1M_1, I_2M_1, M_1M_3, I_3M_2, I_4M_2, M_2M_3$ and I_5M_3 are $\tau_5, \tau_5, 2\tau_2 + \tau_3 + \tau_4, \tau_5 + \tau_4, \tau_5 + \tau_4, \tau_3$ and $\tau_5 + \tau_4 + \tau_3$, respectively.

Proceedings as previously, we find

$$\begin{aligned} \mathbb{P}^0(A_5 | \text{scenario4}) &= \frac{1}{16} [2e^{-2\theta(\tau_5 + \tau_2 + \tau_3 + 2\tau_4)} + 6e^{-2\theta(\tau_5 + \tau_2 + \tau_3 + \tau_4)} + 2e^{-2\theta(2\tau_5 + \tau_3 + \tau_4)} \\ &\quad + 2e^{-2\theta(\tau_5 + \tau_3 + \tau_4)} + e^{-2\theta(2\tau_5 + \tau_4)} + e^{-2\theta(\tau_5 + \tau_4)} + e^{-2\theta\tau_5} + 1]. \end{aligned} \quad (116)$$

G.5. Scenario 5

Finally, in scenario 5, the order of the coalescence events backward in time is: I_1 and I_2, I_3 and I_4, M_1 and M_2, I_5 and M_3 (see Fig. 4 (e)). This scenario has probability

$$\frac{\binom{5}{2}\binom{3}{2}\binom{2}{2}}{\binom{5}{2}\binom{4}{2}\binom{3}{2}} = \frac{1}{6}. \quad (117)$$

In this scenario, the lengths of the non-overlapping branches $I_1M_1, I_2M_1, M_1M_3, I_3M_2, I_4M_2, M_2M_3$ and I_5M_3 are $\tau_5, \tau_5, \tau_3 + \tau_4, \tau_5 + \tau_4, \tau_5 + \tau_4, \tau_3$ and $\tau_5 + \tau_4 + \tau_3 + 2\tau_2$, respectively.

Proceeding as previously, we find

$$\begin{aligned} \mathbb{P}^0(A_5 | \text{scenario5}) &= \frac{1}{16} [2e^{-2\theta(2\tau_5 + \tau_3 + 2\tau_4 + \tau_2)} + 4e^{-2\theta(\tau_5 + \tau_3 + \tau_4 + \tau_2)} + 2e^{-2\theta(2\tau_5 + \tau_3 + \tau_4 + \tau_2)} \\ &\quad + 4e^{-2\theta(\tau_5 + \tau_3 + \tau_4)} + e^{-2\theta(2\tau_5 + \tau_4)} + e^{-2\theta(\tau_5 + \tau_4)} + e^{-2\theta\tau_5} + 1]. \end{aligned} \quad (118)$$

G.6. Final calculation

Using the law of total probability, we have

Finally, multiplying by the joint densities of the coalescence times given by

$$f(\tau_5, \tau_4, \tau_3, \tau_2) = f_2(\tau_2)f_3(\tau_3)f_4(\tau_4)f_5(\tau_5) = 180e^{-(10\tau_5 + 6\tau_4 + 3\tau_3 + \tau_2)}$$

for $\tau_2, \tau_3, \tau_4, \tau_5 > 0$ and integrating over all possible values yield

$$\begin{aligned} \phi_5 &= \int_0^\infty \int_0^\infty \int_0^\infty \int_0^\infty y(\tau_5, \tau_4, \tau_3, \tau_2) f(\tau_5, \tau_4, \tau_3, \tau_2) d\tau_2 d\tau_3 d\tau_4 d\tau_5 \\ &= \frac{180}{96} \int_0^\infty \int_0^\infty \int_0^\infty \int_0^\infty [8e^{-2\theta(2\tau_5 + 2\tau_4 + \tau_3 + \tau_2)} + 10e^{-2\theta(2\tau_5 + \tau_4 + \tau_3 + \tau_2)} \\ &\quad + 30e^{-2\theta(\tau_5 + \tau_4 + \tau_3 + \tau_2)} + 4e^{-2\theta(2\tau_5 + 2\tau_4 + \tau_3)} + 5e^{-2\theta(2\tau_5 + \tau_4 + \tau_3)} \\ &\quad + 15e^{-2\theta(\tau_5 + \tau_4 + \tau_3)} + 9e^{-2\theta(\tau_5 + \tau_4)} + 3e^{-2\theta(2\tau_5 + \tau_4)} + 6e^{-2\theta\tau_5} + 6] \\ &\quad e^{-(10\tau_5 + 6\tau_4 + 3\tau_3 + \tau_2)} d\tau_2 d\tau_3 d\tau_4 d\tau_5 = \frac{180}{96} \left[\frac{8}{(4\theta + 10)(4\theta + 6)(2\theta + 3)(2\theta + 1)} \right. \\ &\quad + \frac{10}{(4\theta + 10)(2\theta + 6)(2\theta + 3)(2\theta + 1)} \\ &\quad + \frac{30}{(2\theta + 10)(2\theta + 6)(2\theta + 3)(2\theta + 1)} + \frac{4}{(4\theta + 10)(4\theta + 6)(2\theta + 3)} \\ &\quad + \frac{5}{(4\theta + 10)(2\theta + 6)(2\theta + 3)} + \frac{15}{(2\theta + 10)(2\theta + 6)(2\theta + 3)} \\ &\quad + \frac{9}{(2\theta + 10)(2\theta + 6)3} + \frac{3}{(4\theta + 10)(2\theta + 6)3} + \frac{6}{(2\theta + 10)6 \times 3} + \frac{6}{10 \times 6 \times 3} \left. \right] \\ &= \frac{(\theta + 3)(\theta + 4)}{4(2\theta + 3)(2\theta + 1)}. \end{aligned} \quad (121)$$

References

- Antal, T., Nowak, M.A., Traulsen, A., 2009. Strategy abundance in 2×2 games for arbitrary mutation rates. *J. Theor. Biol.* 257, 340–344.
- Axelrod, R.M., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390–1396.
- Axelrod, R.M., 1984. *The Evolution of Cooperation*. Basic Books, New York.
- Christiansen, F.B., 1991. On conditions for evolutionary stability for a continuous varying character. *Am. Natural.* 138, 37–50.
- Eshel, I., 1983. Evolutionary and continuous stability. *J. Theor. Biol.* 103, 99–111.
- Evans, S.N., Hening, A., Schreiber, S.J., 2015. Protected polymorphisms and evolutionary stability of patch-selection strategies in stochastic environments. *J. Math. Biol.* 71, 325–359.
- Frank, S.A., Slatkin, M., 1990. Evolution in a variable environment. *Am. Natural.* 136, 244–260.
- Fudenberg, D., Harris, C., 1992. Evolutionary dynamics with aggregate shocks. *J. Econ. Theory* 57, 420–441.
- Fudenberg, D., Imhof, L., 2006. Imitation processes with small mutations. *J. Econ. Theory* 131, 251–262.
- Gillespie, J.H., 1973. Natural selection with varying selection coefficients – a haploid model. *Genet. Res.* 21, 115–120.
- Gillespie, J.H., 1974. Natural selection for within-generation variance in offspring number. *Genetics* 76, 601–606.
- Hofbauer, J., Schuster, P., Sigmund, K., 1979. A note on evolutionary stable strategies and game dynamics. *J. Theor. Biol.* 81, 613–616.
- Hofbauer, J., Sigmund, K., 1988. *The Theory of Evolution and Dynamical Systems*. Cambridge University Press, Cambridge.
- Imhof, L., Nowak, M.A., 2006. Evolutionary game dynamics in a Wright-Fisher process. *J. Math. Biol.* 52, 667–681.
- Karlin, S., Levikson, B., 1974. Temporal fluctuations in selection intensities: case of small population size. *Theor. Popul. Biol.* 6, 383–412.
- Karlin, S., Liberman, U., 1974. Random temporal variation in selection intensities: case of large population size. *Theor. Popul. Biol.* 6, 35–382.
- Karlin, S., Taylor, H.M., 1975. *A First Course in Stochastic Processes*. Academic Press, New York.
- Kingman, J.F.C., 1982. *The coalescent*. *Stochastic Processes and their Applications* 13, 235–248.
- Kroumi, D., Lessard, S., 2015. Evolution of cooperation in a multidimensional phenotype space. *Theor. Popul. Biol.* 102, 60–75.
- Li, C., Lessard, S., 2020. Randomized matrix games in a finite population: effect of stochastic fluctuations in payoffs on the evolution of cooperation. *Theor. Popul. Biol.* 143, 77–91.
- Li, C., Ji, T., He, Q.Q., Zheng, X.D., Zhang, B.Y., Lessard, S., Tao, Y., 2020. Uncertainty in payoffs for defection could be conducive to the evolution of cooperative behavior. Preprint.
- Maynard Smith, J., 1982. *Evolution and the Theory of games*. Cambridge University Press, Cambridge.
- Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. *Nature* 246, 15–18.
- Nowak, M.A., 2006. Five rules for the evolution of cooperation. *Science* 314, 1560–1563.
- Nowak, M.A., Sasaki, A., Taylor, C., Fudenberg, D., 2004. Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428, 646–650.
- Rousset, F., Billiard, D., 2000. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. *J. Evol. Biol.* 13, 814–825.
- Rousset, F., 2003. A minimal derivation of convergence stability measures. *J. Theor. Biol.* 221, 665–668.
- Rychtar, J., Taylor, D.T., 2020. Moran process and Wright-Fisher process favor low variability. *Discrete and Continuous Dynamical Systems Series B, American Institute of Mathematical Sciences*. <https://doi.org/10.3934/dcdsb.2020242>.
- Schreiber, S.J., 2012. The evolution of patch selection in stochastic environments. *Am. Natural.* 180, 17–34.
- Schreiber, S.J., 2015. Unifying within- and between-generation bet-hedging theories: an ode to J.H. Gillespie. *Am. Natural.* 186, 792–796.
- Starrfelt, J., Kokko, H., 2012. Bet-hedging—a triple trade-off between means, variances and correlations. *Biol. Rev.* 87, 742–755.
- Taylor, P., Jonker, L., 1978. Evolutionary stable strategies and game dynamics. *Math. Biosci.* 40, 145–156.
- Taylor, P., 1989. Evolutionary stability in one-parameter models under weak selection. *Theor. Popul. Biol.* 36, 125–143.
- Zeeman, R.C., 1980. Populations dynamics from game theory. In: Nitecki, Z.H., Robinson, R.C. (Eds.), *Global Theory of Dynamical Systems*. Springer, New York.
- Zheng, X.D., Li, C., Lessard, S., Tao, Y., 2017. Evolutionary stability concepts in a stochastic environment. *Phys. Rev. E* 96, 032414.
- Zheng, X.D., Li, C., Lessard, S., Tao, Y., 2018. Environmental noise could promote stochastic local stability of behavioral diversity evolution. *Phys. Rev. Lett.* 120, 218101.