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Randomized matrix games in a finite population: Effect of stochastic fluctuations in the payoffs on the evolution of cooperation

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ABSTRACT

A diffusion approximation for a randomized 2 × 2-matrix game in a large finite population is ascertained in the case of random payoffs whose expected values, variances and covariances are of order given by the inverse of the population size N. Applying the approximation to a Randomized Prisoner's Dilemma (RPD) with independent payoffs for cooperation and defection in random pairwise interactions, conditions on the variances of the payoffs 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 are deduced. All these are obtained from probabilities of ultimate fixation of a single mutant. It is shown that the conditions are lessened with an increase in the variances of the payoffs for defection against cooperation and defection and a decrease in the variances of the payoffs for cooperation against cooperation and defection. A RPD game with independent payoffs whose expected values are additive is studied in detail to support the conclusions. Randomized matrix games with non-independent payoffs, namely the RPD game with additive payoffs for cooperation and defection based on random cost and benefit for cooperation and the repeated RPD game with Tit-for-Tat and Always-Defect as strategies in pairwise interactions with a random number of rounds, are studied under the assumption that the population-scaled expected values, variances and covariances of the payoffs are all of the same small enough order. In the first model, the conditions in favor of the evolution of cooperation hold only if the covariance between the cost and the benefit is large enough, while the analysis of the second model extends the results on the effects of the variances of the payoffs for cooperation and defection found for the one-round RPD game.

1. Introduction

Cooperative behavior is a phenomenon that is widely observed in nature. However, natural selection tends to enhance selfish behavior through fierce competition. In order to explain the rationality of cooperation and its evolution in natural populations, a two-player game known as the Prisoner's Dilemma (PD) has been widely studied as one of the most important theoretical frameworks (Axelrod and Hamilton, 1981; Maynard Smith, 1982; Axelrod, 1984; Poundstone, 1992; Nowak and Highfield, 2011). In an additive version of the PD game, cooperation takes the form of a donor who pays a cost c for a recipient to get a benefit b. Defection costs nothing and does not disqualify from receiving a benefit. Therefore, the payoff for cooperation never exceeds the payoff for defection (Nowak, 2006; Nowak and Sigmund, 2007). This is the case in more general versions of the PD game. Moreover, assuming random pairwise interactions in an infinite population and average payoffs as relative growth rates, the replicator equation (Taylor and Jonker, 1978) predicts global convergence to fixation of defection (Hofbauer and Sigmund, 1998).

In a finite population of constant size N undergoing discrete, non overlapping generations according to a Wright–Fisher model and more general models with exchangeable reproduction schemes (Fisher, 1930; Wright, 1931; Cannings, 1974; Ewens, 2004; Lessard, 2011), the fixation probability for a neutral mutant type represented only once initially is just the inverse of the population size, that is, N^{-1}. If this probability becomes larger than N^{-1} in the presence of selection, then the mutant type has been said to be favored by selection (Nowak et al., 2004). Several mechanisms have been considered to explain how cooperation could be favored by natural selection assuming additive effects of average payoffs on fitness (Nowak and Sigmund, 2007). This is the case, for instance, for cooperation taking the form of the "Tit-for-Tat" strategy (Trivers, 1971; Axelrod and Hamilton, 1981; Axelrod, 1984) starting with cooperation in a repeated PD game between randomly chosen partners if the number of rounds exceeds some threshold value (Nowak et al., 2004). This is also the case in group-structured or graph-structured populations

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for modeling some social or geographical networks with local interactions (Ohtsuki et al., 2006). However, with a one-round PD game and constant payoffs in a well-mixed population, the fitness of cooperation never exceeds the fitness of defection, and, as a result, cooperation cannot be favored by selection.

In nature, there are changes not only in the composition of a population but also in the surrounding environment in which the population finds itself. These can affect the payoffs that individuals receive as a result of interactions with others. Randomness in evolutionary games can take several forms such as probabilistic encounter rules or mixed strategies depending or not on the replies of others (Taylor and Jonker, 1978; Eshel and Cavalli-Sforza, 1982; Hofbauer and Sigmund, 1998). Of particular interest are stochastic games which allow the environment to change in response to the players' choices (Shapley, 1953; Fudenberg et al., 2012; Solan and Vieille, 2015; Hilbe et al., 2018). But also not to be forgotten are variations in payoffs caused by disturbances in the natural environment. These can be periodic, e.g., being seasonal or alternating day and night. But they can also be totally random as if occurring by accident (May, 1973; Kaplan et al., 1990; Lande et al., 2003). In the case of deterministically time-dependent payoffs in 2×2 matrix games, for instance, Broom (2005) compares the time average of the population state and the interior Nash equilibrium of the average payoff matrix and shows that they can be arbitrarily far apart. With periodic payoffs, even stable periodic orbits can be found from arbitrary starting points (Uyttendaele et al., 2012). On the other hand, it is shown in Stollmeier and Nagler (2018) that under the effects of random environmental noise, an evolutionary game involving two strategies with a strategy having a higher expected payoff at any frequency than the other can reach a stationary distribution with both strategies co-existing.

In a matrix game, unless stochastic fluctuations in the environment are small enough to be ignored, it is more accurate to use random payoffs than constant payoffs. In particular, the introduction of random payoffs extends the classical PD game to a randomized PD game. In order to reveal how environmental noise can generally affect the evolutionary game dynamics in an infinite population, the concepts of stochastic evolutionary stability (SES) and stochastic convergence stability (SCS) have been investigated (Zheng et al., 2017, 2018). Applying these concepts to a one-round randomized PD game in a well-mixed population, it can be shown that the evolution of cooperation tends to be more easily favored by natural selection if the coefficients of variation of the payoffs are smaller for cooperation than for defection (Li et al., 2019).

On the other hand, in a population genetics framework for a large finite population, Karlin and Levikson (1974) have shown that, when the mean and variance of frequency-independent genotypic fitnesses are of the same order given by the inverse of the population size, the effect of the variance matters. Actually, variability in selection, meaning fluctuating selection intensities, produces a "drift effect" away from the fixation states.

In order to study the effect of stochastic fluctuations in a context of an evolutionary game in a large finite population, we consider in this paper a matrix game with random payoffs for two players using one of two strategies. After ascertaining a diffusion approximation for this model, we focus on the Randomized Prisoner's Dilemma (RPD) with cooperation and defection as strategies, and we consider the probability of ultimate fixation of either strategy as a single mutant. Conditions that favor the evolution of cooperation are examined in detail in the case of independent payoffs such that the average effects of cooperation and defection are additive. A RPD game with random additive effects of cooperation and defection on the payoffs as well as a repeated RPD game are also studied.

2. The model

We consider a randomized matrix game with two strategies in a finite population of fixed finite size N. The two possible pure strategies used by the individuals in the population are denoted by S_1 and S_2. At time $t \geq 0$ corresponding to some generation, the frequencies of S_1 and S_2 are given by $x(t)$ and $1 - x(t)$, respectively, while their payoffs in pairwise interactions are given by the entries of the 2×2 random game matrix

$$\begin{pmatrix} \eta_1(t) & \eta_2(t) \\ \eta_3(t) & \eta_4(t) \end{pmatrix}. \tag{1}$$

Here, $\eta_1(t)$ and $\eta_2(t)$ are the payoffs to strategy S_1 against strategies S_1 and S_2, respectively, while $\eta_3(t)$ and $\eta_4(t)$ are the corresponding payoffs to strategy S_2 against the same two strategies. We assume that the value of these payoffs are random variables with values that are always larger than -1 and probability distributions that do not depend on time $t \geq 0$.

In addition, we assume that these payoffs have expected values, variances and covariances of order given by the inverse of the population size, which will be taken later on as the time interval between two successive generations (see below). More precisely, we assume

$$\eta_i(t) = \mu_i N^{-1} + \xi_i(t), \tag{2}$$

where $\mathbf{E}(\xi_i(t)) = 0$, $\mathbf{Var}(\xi_i(t)) = \sigma_i^2 N^{-1}$ and $\mathbf{Cov}(\xi_i(t), \xi_j(t)) = \sigma_{ij} N^{-1}$, for $i, j = 1, \ldots, 4$ with $i \neq j$. Therefore, we have

$$\mathbf{E}(\eta_i(t)) = \mu_i N^{-1}, \tag{3a}$$
$$\mathbf{E}(\eta_i(t)^2) = \sigma_i^2 N^{-1} + o(N^{-1}), \tag{3b}$$
$$\mathbf{E}(\eta_i(t)\eta_j(t)) = \sigma_{ij} N^{-1} + o(N^{-1}), \tag{3c}$$

so that μ_i, σ_i^2 and σ_{ij} represent population-scaled parameters for the expected value, variance and covariance of the payoffs, respectively, for $i, j = 1, \ldots, 4$ with $i \neq j$. Moreover, it is assumed that

$$\mathbf{E}(\xi_1(t)^k \xi_2(t)^l \xi_3(t)^m \xi_4(t)^n) = o(N^{-1}), \tag{4}$$

so that

$$\mathbf{E}(\eta_1(t)^k \eta_2(t)^l \eta_3(t)^m \eta_4(t)^n) = o(N^{-1}), \tag{5}$$

for non-negative integers k, l, m, n such that $k + l + m + n \geq 3$.

We suppose that the payoffs have additive effects on fitness understood as relative reproductive success with a baseline value equal to 1. Assuming random pairwise interactions, the mean fitness of strategy S_1 at time $t \geq 0$ can be expressed as

$$\mathbf{\Pi}_1(t) = 1 + x(t)\eta_1(t) + (1 - x(t))\eta_2(t), \tag{6}$$

and the corresponding mean fitness of strategy S_2 as

$$\mathbf{\Pi}_2(t) = 1 + x(t)\eta_3(t) + (1 - x(t))\eta_4(t). \tag{7}$$

Note that these quantities are always positive since we assume $\eta_i(t) > -1$ for $i = 1, \ldots, 4$.

Now, we consider discrete non-overlapping generations as in the Wright–Fisher model and we measure time in number of N generations. Then, $\Delta t = N^{-1}$ represents the time interval from one generation to the next. Given that the frequency of strategy S_1 is $x(t)$ at time $t \geq 0$ corresponding to some generation, the frequency of S_1 in the next generation, $x(t+\Delta t)$, is distributed as a binomial random variable divided by N. Actually, the conditional probability distribution is given by

$$x(t + \Delta t)|x(t) \sim \frac{1}{N}\mathrm{B}(N, x'(t)), \tag{8}$$

where $B(N, x'(t))$ denotes a binomial distribution of parameters N and $x'(t)$ with

$$x'(t) = \frac{x(t)\boldsymbol{\Pi}_1(t)}{x(t)\boldsymbol{\Pi}_1(t) + (1 - x(t))\boldsymbol{\Pi}_2(t)} \tag{9}$$

being the probability for an offspring to have been produced by an individual using strategy S_1 at time $t \geq 0$. Note that $x'(t)$ is a random variable even if the value of $x(t)$ is known, since $\boldsymbol{\Pi}_1(t)$ and $\boldsymbol{\Pi}_2(t)$ depend on the random payoffs $\eta_i(t)$ for $i = 1, \ldots, 4$.

3. Diffusion approximation

Let $\Delta x = x(t + \Delta t) - x(t)$ be the change in the frequency of individuals that use strategy S_1 from time t to time $t + \Delta t$. Given $x(t) = x$, the first, second and fourth moments of Δx can be calculated as (see Appendix A for details)

$$\mathbf{E}(\Delta x | x(t) = x) = m(x)\Delta t + o(\Delta t), \tag{10}$$

$$\mathbf{E}((\Delta x)^2 | x(t) = x) = v(x)\Delta t + o(\Delta t) \tag{11}$$

and

$$\mathbf{E}((\Delta x)^4 | x(t) = x) = o(\Delta t), \tag{12}$$

where

$$\begin{aligned} m(x) = x(1-x)\Big(&\mu_2 - \mu_4 + x\big(\mu_1 - \mu_2 - \mu_3 + \mu_4\big) \\ &+ x^3(\sigma_{13} - \sigma_1^2) + x(1-x)^2(2\sigma_{34} - \sigma_{14} - \sigma_{23} + \sigma_{24} - \sigma_2^2) \\ &+ x^2(1-x)(-2\sigma_{12} + \sigma_{14} + \sigma_{23} - \sigma_{13} + \sigma_3^2) \\ &+ (1-x)^3(\sigma_4^2 - \sigma_{24})\Big) \end{aligned} \tag{13}$$

and

$$\begin{aligned} v(x) = x(1-x)\Big(&1 + x^3(1-x)(\sigma_1^2 + \sigma_3^2 - 2\sigma_{13}) \\ &+ x(1-x)^3(\sigma_2^2 + \sigma_4^2 - 2\sigma_{24}) \\ &+ 2x^2(1-x)^2(\sigma_{12} + \sigma_{34} - \sigma_{14} - \sigma_{23})\Big). \end{aligned} \tag{14}$$

The above conditions ascertain a diffusion approximation with drift function $m(x)$ and diffusion function $v(x)$ in the limit of a large population with the population size N as unit of time (Kimura, 1964; Ewens, 2004).

In the diffusion approximation, the probability density function of S_1-frequency evaluated at x at time $t \geq 0$ given a value p at time 0, denoted by $f(x, p, t)$, satisfies the forward Kolmogorov (Fokker–Planck) equation

$$\frac{\partial f(x, p, t)}{\partial t} = -\frac{\partial}{\partial x}[m(x)f(x, p, t)] + \frac{\partial^2}{\partial x^2}\left[\frac{v(x)f(x, p, t)}{2}\right], \tag{15}$$

as well as the backward Kolmogorov equation

$$\frac{\partial f(x, p, t)}{\partial t} = m(p)\frac{\partial f(x, p, t)}{\partial p} + \frac{v(p)}{2}\frac{\partial^2 f(x, p, t)}{\partial p^2}. \tag{16}$$

Since no mutation is considered in the model at hand, the two boundaries $x = 0$ and $x = 1$ are absorbing states.

Let $u(p, t)$ denote the probability that strategy S_1 is fixed by time $t \geq 0$ so that $x(t) = 1$ given an initial frequency $x(0) = p$. This probability satisfies the backward Kolmogorov equation, that is,

$$\frac{\partial u(p, t)}{\partial t} = m(p)\frac{\partial u(p, t)}{\partial p} + \frac{v(p)}{2}\frac{\partial^2 u(p, t)}{\partial p^2} \tag{17}$$

with the boundary conditions $u(0, t) = 0$ and $u(1, t) = 1$. By letting $t \to \infty$, the limit

$$u(p) = \lim_{t \to \infty} u(p, t) \tag{18}$$

represents the probability of ultimate fixation of strategy S_1 given an initial frequency $x(0) = p$. As $t \to \infty$, the left-hand side in (17) tends to 0 so that we have

$$0 = m(p)\frac{du(p)}{dp} + \frac{v(p)}{2}\frac{d^2u(p)}{dp^2} \tag{19}$$

with the boundary conditions $u(0) = 0$ and $u(1) = 1$. The solution of this ordinary differential equation is known to be (Ewens, 2004; Risken, 1992)

$$u(p) = \frac{\int_0^p \psi(y)dy}{\int_0^1 \psi(y)dy}, \tag{20}$$

where

$$\psi(y) = \exp\left(-2\int_0^y \frac{m(x)}{v(x)}dx\right). \tag{21}$$

Note that the probability of ultimate fixation of strategy S_2 is given by

$$1 - u(p) = \frac{\int_p^1 \psi(y)dy}{\int_0^1 \psi(y)dy}, \tag{22}$$

since there is ultimate fixation of strategy S_1 or S_2 with probability 1.

4. Randomized Prisoner's Dilemma (RPD)

Consider a random game matrix (1) with independent payoffs whose expected values determine a classical Prisoner's Dilemma (PD). In this case, the population-scaled parameters in (3) verify $\sigma_{ij} = 0$ for $i, j = 1, \ldots, 4$ with $i \neq j$, since the payoffs are uncorrelated, and

$$\begin{pmatrix} \mu_1 & \mu_2 \\ \mu_3 & \mu_4 \end{pmatrix} = \begin{pmatrix} R & S \\ T & P \end{pmatrix} \tag{23}$$

with $T > R > P > S$ and $2R > T + S$, which defines a PD game. Then, we have a randomized Prisoner's Dilemma (RPD) with strategies S_1 and S_2 corresponding to cooperation (C) and defection (D), respectively.

Suppose that cooperation is introduced as a single mutant in an all defecting population so that the initial frequency of cooperation in the population of size N is $p = N^{-1}$. If the probability of ultimate fixation of cooperation, denoted by $F_C = u(N^{-1})$, exceeds the value N^{-1}, which is the fixation probability under neutrality, then we say that *the evolution of cooperation is favored by selection*. Analogously, $F_D = 1 - u(1 - N^{-1})$ represents the probability of ultimate fixation of a single defecting mutant in an all cooperating population, and we say that *the evolution of defection is disfavored (not favored) by selection* if F_D is less than N^{-1} (Nowak et al., 2004). Moreover, if $F_C > F_D$, then the invasion of a single cooperating mutant in an all defecting population is more likely than the reverse situation. In such a case, we say that *the evolution of cooperation is more favored by selection than the evolution of defection*. Finally, if all three conditions are satisfied, which occurs when $F_C > N^{-1} > F_D$, then we say that *the evolution of cooperation is fully favored by selection*.

Assuming the population size N large enough and using the diffusion approximation for the fixation probability, namely (20), the condition for the evolution of cooperation to be favored by selection becomes

$$F_C = \frac{\psi(0)}{N\int_0^1 \psi(y)dy} > \frac{1}{N}. \tag{24}$$

Since $\psi(0) = 1$, this condition is equivalent to

$$\int_0^1 \psi(y)dy < 1. \tag{25}$$

Moreover, owing to (13), (14) and (21), we have

$$\psi(y)=\exp\left(-2\int_0^y g(x)dx\right) \tag{26}$$

for $0 \le y \le 1$, where

$$g(x)=\frac{m(x)}{v(x)} \tag{27}$$

with drift function

$$m(x)=x(1-x)\Big(\mu_2-\mu_4+x\big(\mu_1-\mu_2-\mu_3+\mu_4\big) - \big(x^3\sigma_1^2+x(1-x)^2\sigma_2^2-x^2(1-x)\sigma_3^2-(1-x)^3\sigma_4^2\big)\Big) \tag{28}$$

and diffusion function

$$v(x)=x(1-x)\Big(1+x^3(1-x)(\sigma_1^2+\sigma_3^2)+x(1-x)^3(\sigma_2^2+\sigma_4^2)\Big). \tag{29}$$

Note that the function $g(x)$ actually depends on the population-scaled expected values and variances of the payoffs, μ_i and σ_i^2 for $i=1,\ldots,4$.

Similarly, the condition for the evolution of defection not to be favored by selection takes the form

$$F_D=\frac{\psi(1)}{N\int_0^1\psi(y)dy}=\frac{\phi(1)}{N\int_0^1\phi(y)dy}<\frac{1}{N}, \tag{30}$$

where

$$\phi(y)=\frac{\psi(y)}{\psi(1)}=\exp\left(2\int_y^1 g(x)dx\right). \tag{31}$$

Since $\phi(1)=1$, this condition is equivalent to

$$\int_0^1\phi(y)dy>1,\ \text{ that is, }\int_0^1\psi(y)dy>\psi(1). \tag{32}$$

Moreover, since $F_D=\psi(1)F_C$, the condition

$$\psi(1)=\phi(0)^{-1}<1 \tag{33}$$

ensures that $F_C > F_D$, in which case selection favors more the evolution of cooperation than the evolution of defection.

Let $h(x)=g(x)$ when $\sigma_i^2=0$ for $i=1,\ldots,4$. Then we have

$$h(x)=\mu_2-\mu_4+x(\mu_1-\mu_2-\mu_3+\mu_4). \tag{34}$$

Since $\mu_4>\mu_2$ and $\mu_3>\mu_1$ in the PD game (23), the function $h(x)$ is always negative for $0\le x\le 1$. Therefore, in the case where $\sigma_i^2=0$ for $i=1,\ldots,4$, we have $g(x)=h(x)<0$ in (26) so that $\psi(y)$ and $\phi(y)$ are both strictly increasing functions with respect to y with $\psi(0)=\phi(1)=1$. Therefore, we have $\psi(y)>1$ and $\phi(y)<1$ for $0<y<1$. In this case, conditions (25), (32) and (33) can never be satisfied. This means that the evolution of cooperation can never be favored by selection. This is in agreement with what is known for the classical PD game with deterministic payoffs (Maynard Smith, 1982; Nowak, 2006).

For the RPD game with independent payoffs, we consider the partial derivatives of $g(x)$ with respect to the variances of the payoffs. It can be shown (see Appendix B for details) that

$$\frac{\partial g(x)}{\partial\sigma_3^2}>0 \tag{35}$$

and

$$\frac{\partial g(x)}{\partial\sigma_4^2}>0 \tag{36}$$

for $0<x<1$. This implies that $g(x)$ for $0<x<1$ increases as σ_3^2 or σ_4^2 increases. Therefore, $\psi(y)$ in (26) for $0<y<1$, and its integral from 0 to 1 in (24) and (25), decrease as σ_3^2 or σ_4^2 increases. On the other hand, $\phi(y)$ in (31) for $0<y<1$, and its integral from 0 to 1 in (30) and (32), increase as σ_3^2 or σ_4^2 increases.

Let us summarize our findings.

Conclusion 1. *In a RPD game with independent payoffs, increasing the variance of at least one payoff for defection, that is, σ_3^2 or σ_4^2, increases the probability of ultimate fixation of cooperation introduced as a single mutant in an all defecting population, F_C, while it decreases the probability of ultimate fixation of defection introduced as a single mutant in an all cooperating population, F_D.*

5. RPD with independent payoffs

In this section, we focus on a RPD game with independent payoffs whose expected values are such that

$$\begin{pmatrix}\mu_1 & \mu_2\\ \mu_3 & \mu_4\end{pmatrix}=\begin{pmatrix}b-c & -c\\ b & 0\end{pmatrix}. \tag{37}$$

This payoff matrix determines an additive PD game in which cooperation (C) incurs a fixed cost $c>0$ to the individual adopting it, but provides a fixed benefit $b>0$ to the opponent, while defection (D) incurs no cost at all.

In this case, the function $h(x)$ in (34) is given by $h(x)=-c$. Moreover, if $c\le 1$, then it can be shown (see Appendix B for details) that the function $g(x)$ in (27) satisfies

$$\frac{\partial g(x)}{\partial\sigma_1^2}<0 \tag{38}$$

and

$$\frac{\partial g(x)}{\partial\sigma_2^2}<0 \tag{39}$$

for $0<x<1$.

This leads to the following complementary result.

Conclusion 2. *In a RPD game with independent payoffs whose population-scaled expected values determine an additive PD game in the form (37) with cost of cooperation $c\le 1$, diminishing the variance of at least one payoff for cooperation, that is, σ_1^2 or σ_2^2, increases the probability of ultimate fixation of cooperation introduced as a single mutant in an all defecting population, F_C, while it decreases the probability of ultimate fixation of defection introduced as a single mutant in an all cooperating population, F_D.*

In the rest of this section, we investigate some special cases of the RPD with additive expected payoffs to exhibit conditions under which the evolution of cooperation could be favored by selection.

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

This is a situation where the variance of the payoff for defection against defection is significantly larger than the variances of all the other payoffs.

With $h(x)=-c$, the function $g(x)$ in (27) takes the form

$$g_1(x):=g(x)=\frac{-c+(1-x)^3\sigma^2}{1+x(1-x)^3\sigma^2}. \tag{40}$$

This function satisfies $g(0)=\sigma^2-c$, $g(1)=-c$, $g'(0)=-\sigma^2(3+\sigma^2-c)$ and $g'(1)=0$ (see Appendix C for details).

If $\sigma^2<c$, then $g(x)<0$ for $0<x<1$. In this case, the function $\psi(y)$ in (26) satisfies $\psi(y)>1$ for $0<y\le 1$, which entails $\int_0^1\psi(y)dy>1$, that is, $F_C<1/N$.

On the other hand, if $\sigma^2>c$, then we have $g'(x)<0$ for $0<x<1$. In this case, $g(x)$ is a strictly decreasing function from

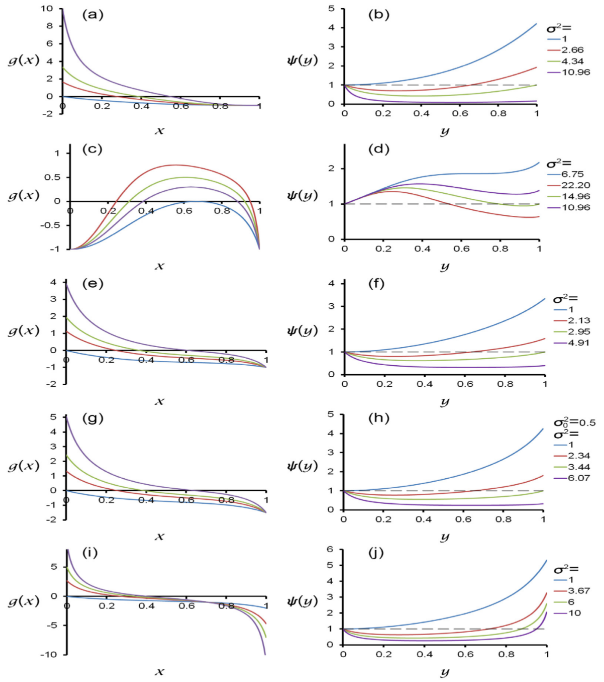

Fig. 1. Curves of $g(x)$ and $\psi(y)$ in cases 1 to 5. The population-scaled expected cost c for cooperation is set to 1. In each panel, the curve in Blue is for the threshold value of σ^2 such that $g(x) \leq 0$ for $0 \leq x \leq 1$, while the curves in Red, Green and Purple are for the threshold values σ_*^2, σ_{**}^2 and σ_{***}^2, respectively (except for case 5 where there are no σ_{**}^2 and σ_{***}^2). Panels (a) and (b) represent $g(x)$ and $\psi(y)$ in case 1, and so on up to case 5. In case 4, the value of σ_0^2 is set to 0.5. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$\sigma^2 - c > 0$ at $x = 0$ to $-c < 0$ at $x = 1$, while $\psi(y)$ is a strictly convex function for $0 \leq y \leq 1$. The unique point x^* between 0 and 1 where $g(x)$ crosses the x axis is the global minimum point of $\psi(y)$ for $0 \leq y \leq 1$ (see Fig. 1a,b). Since $\psi(0) = 1$ with $\psi'(0) = -2g(0) = -2(\sigma^2 - c) < 0$, the condition $\psi(1) < 1$, which implies $F_C > F_D$, guarantees also that $\int_0^1 \psi(y)dy < 1$, which implies $F_C > 1/N$.

Let σ_{**}^2 be the value of $\sigma^2 > c$ such that $\int_0^1 g(x)dx = 0$, that is, $\psi(1) = 1$. Recall that $g(x)$ is strictly increasing as a function of σ^2 owing to (36). Consequently, the condition $\sigma^2 > \sigma_{**}^2$ is necessary and sufficient to have $\int_0^1 g(x)dx > 0$, that is, $\psi(1) < 1$, which implies $F_C > F_D$.

Now, let σ_*^2 be the value of σ^2 strictly comprised between c and σ_{**}^2 such that $\int_0^1 \psi(y)dy = 1$. Then we have $\int_0^1 \psi(y)dy < 1$ for $\sigma_*^2 < \sigma^2 < \sigma_{**}^2$. We conclude that $F_C > 1/N$ as soon as $\sigma^2 > \sigma_*^2 > c$.

Finally, let σ_{***}^2 be the value of $\sigma^2 > \sigma_{**}^2$ such that $\int_0^1 \phi(y)dy = 1$. Then we have $\int_0^1 \phi(y)dy > 1$ for $\sigma^2 > \sigma_{***}^2$. This means that $F_D < 1/N$ if and only if $\sigma^2 > \sigma_{***}^2$ (see Appendix E for details).

If $\sigma^2/16$ is small, in which case $x(1-x)^3\sigma^2$ is small for $0 \leq x \leq 1$, we have the approximation

$$g(x) \approx -c + (1-x)^3\sigma^2 \tag{41}$$

for $0 \leq x \leq 1$. Moreover, using the approximation $e^z \approx 1 + z$ for z small enough, we get

$$\psi(y) = \exp\left(-2\int_0^y g(x)dx\right)$$
$$\approx 1 + 2cy - 2\sigma^2\left(y - \frac{3}{2}y^2 + y^3 - \frac{1}{4}y^4\right) \tag{42}$$

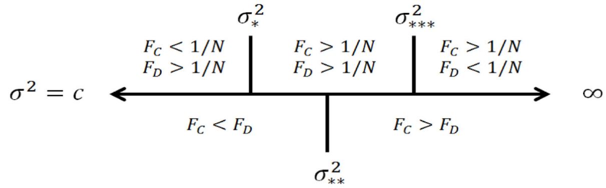

Fig. 2. Relationships between σ_*^2, σ_{**}^2, σ_{***}^2 and F_C, F_D in cases 1, 3 and 4. The regions where the fixation probabilities F_C and F_D are larger or smaller than N^{-1} and where F_C is larger or smaller than F_D are given according to the position of σ^2 with respect to the increasing threshold values σ_*^2, σ_{**}^2 and σ_{***}^2. In case 2, these threshold values are decreasing.

Table 1
Comparison between the numerical values and the approximate values of σ_*^2, σ_{**}^2, σ_{***}^2 in cases 1 to 5. The population-scaled expected cost c for cooperation is set to 1 or 0.5. The value of σ_0^2 in case 4 is set to 0.5. The approximate values are given first followed by the numerical values in brackets.

	c=1, σ_0^2=0.5			c=0.5, σ_0^2=0.5		
	σ_*^2	σ_{**}^2	σ_{***}^2	σ_*^2	σ_{**}^2	σ_{***}^2
Case 1	2.5 (2.66)	4 (4.34)	10 (10.92)	1.25 (1.29)	2 (2.08)	5 (5.21)
Case 2	15 (22.2)	12 (14.96)	10 (10.96)	7.5 (9.25)	6 (6.76)	5 (5.26)
Case 3	2.14 (2.13)	3 (2.95)	5 (4.91)	1.07 (1.07)	1.5 (1.49)	2.5 (2.47)
Case 4	2.36 (2.34)	3.5 (3.44)	6.17 (6.07)	1.29 (1.28)	2 (1.97)	3.66 (3.43)
Case 5	3.75 (3.67)			1.88 (1.86)		

and

$$\phi(y) = \exp\left(2\int_y^1 g(x)dx\right)$$
$$\approx 1 + 2c(y-1) - 2\sigma^2\left(y - \frac{3}{2}y^2 + y^3 - \frac{1}{4}y^4 - \frac{1}{4}\right) \quad (43)$$

for $0 \le y \le 1$. Then, $\psi(1) = 1$ when

$$\sigma^2 = \sigma_{**}^2 \approx 4c, \quad (44)$$

while $\int_0^1 \psi(y)dy = 1$ when

$$\sigma^2 = \sigma_*^2 \approx \frac{5c}{2} \quad (45)$$

and $\int_0^1 \phi(y)dy = 1$ when

$$\sigma^2 = \sigma_{***}^2 \approx 10c. \quad (46)$$

Here, we have $c < \sigma_*^2 < \sigma_{**}^2 < \sigma_{***}^2$ with $F_C > N^{-1}$, $F_C > F_D$ and $F_D < N^{-1}$ when $\sigma^2 > \sigma_*^2$, $\sigma^2 > \sigma_{**}^2$ and $\sigma^2 > \sigma_{***}^2$, respectively (see Fig. 2 for a schematic representation of the situation and Table 1 for some particular values).

Our result suggests that the evolution of cooperation tends to be fully favored by selection with an increase of the variance of the payoff for defection against defection.

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

Here, the variance of the payoff for defection against cooperation is significantly larger than the variances of all the other payoffs.

In this case, the function $g(x)$ in (27) becomes

$$g_2(x) := g(x) = \frac{-c + x^2(1-x)\sigma^2}{1 + x^3(1-x)\sigma^2}. \quad (47)$$

This function satisfies $g(0) = -c$, $g(1) = -c$, $g'(0) = 0$ and $g'(1) = -(c+1)\sigma^2$.

Note that $x^2(1-x) \le 4/27$ for $0 \le x \le 1$, so that $g(x) \le 0$ for $0 \le x \le 1$ if $\sigma^2 \le (27/4)c$. Proceeding as in the previous case, this entails $\int_0^1 \psi(y)dy > 1$, that is, $F_C < 1/N$. Actually, this inequality is reversed only when $\sigma^2 > \sigma_*^2 > (27/4)c$, where σ_*^2 is the value of σ^2 such that $\int_0^1 \psi(y)dy = 1$.

If $\sigma^2/16$ is small, then

$$g(x) \approx -c + x^2(1-x)\sigma^2 \quad (48)$$

for $0 \le x \le 1$, from which

$$\psi(y) \approx 1 + 2cy - 2\sigma^2\left(\frac{1}{3}y^3 - \frac{1}{4}y^4\right) \quad (49)$$

and

$$\phi(y) \approx 1 + 2c(y-1) - 2\sigma^2\left(\frac{1}{3}y^3 - \frac{1}{4}y^4 - \frac{1}{12}\right) \quad (50)$$

for $0 \le y \le 1$. Then, $\psi(1) = 1$ when

$$\sigma^2 = \sigma_{**}^2 \approx 12c, \quad (51)$$

while $\int_0^1 \psi(y)dy = 1$ when

$$\sigma^2 = \sigma_*^2 \approx 15c \quad (52)$$

and $\int_0^1 \phi(y)dy = 1$ when

$$\sigma^2 = \sigma_{***}^2 \approx 10c. \quad (53)$$

Note that σ_*^2 and σ_{**}^2 are larger in case 2 than in case 1 and satisfy the inequalities $\sigma_*^2 > \sigma_{**}^2 > \sigma_{***}^2 > c$ (see Fig. 1c,d and Table 1). The conditions for $F_C > 1/N$, $F_C > F_D$ and $F_D < 1/N$ remain the same as in the previous case, that is, $\sigma^2 > \sigma_*^2$, $\sigma^2 > \sigma_{**}^2$ and $\sigma^2 > \sigma_{***}^2$, respectively, but these conditions hold in a reverse order as the variance of the payoff for defection against cooperation increases.

We conclude that selection tends to fully favor the evolution of cooperation when the variance of the payoff for defection against cooperation increases.

5.3. Case 3: $\sigma_1^2 = \sigma_2^2 = 0$, $\sigma_3^2 = \sigma_4^2 = \sigma^2 > 0$

This is a situation where the payoffs for defection have a certain level of uncertainty while the payoffs for cooperation are much less variable.

In this case, the function $g(x)$ in (27) takes the form

$$g_3(x) := g(x) = \frac{-c + (1-x)\left(x^2 + (1-x)^2\right)\sigma^2}{1 + x(1-x)\left(x^2 + (1-x)^2\right)\sigma^2}. \tag{54}$$

This function satisfies $g(0) = \sigma^2 - c$, $g(1) = -c$, $g'(0) = -\sigma^2(3 + \sigma^2 - c)$ and $g'(1) = -(c+1)\sigma^2$.

Analogously to case 1, we have $g(x) < 0$ for $0 < x < 1$ when $\sigma^2 < c$. On the other hand, if $\sigma^2 > c$, then $g(x)$ is a decreasing function, while $\psi(y)$ and $\phi(y)$ are convex functions on [0, 1] (see Appendix C for details). Therefore, three threshold values of σ^2 satisfying the inequalities $c < \sigma_*^2 < \sigma_{**}^2 < \sigma_{***}^2$ can be found (see Appendix E for details). As in case 1, if σ_*^2, σ_{**}^2 and σ_{***}^2 are the values of σ^2 such that $\int_0^1 \psi(y)dy = 1$, $\psi(1) = 1$ and $\int_0^1 \phi(y)dy = 1$, respectively, then $F_C > 1/N$, $F_C > F_D$ and $F_D < 1/N$ when $\sigma^2 > \sigma_*^2$, $\sigma^2 > \sigma_{**}^2$ and $\sigma^2 > \sigma_{***}^2$, respectively, with $c < \sigma_*^2 < \sigma_{**}^2 < \sigma_{***}^2$ (see Appendix E and Figs. 1e,f and 2).

If $\sigma^2/16$ is small, we have the approximation

$$g(x) \approx -c + (1-x)\left(x^2 + (1-x)^2\right)\sigma^2 \tag{55}$$

for $0 \le x \le 1$, from which

$$\psi(y) \approx 1 + 2cy - 2\sigma^2\left(y - \frac{3}{2}y^2 + \frac{4}{3}y^3 - \frac{1}{2}y^4\right) \tag{56}$$

and

$$\phi(y) \approx 1 + 2c(y-1) - 2\sigma^2\left(y - \frac{3}{2}y^2 + \frac{4}{3}y^3 - \frac{1}{2}y^4 - \frac{1}{3}\right) \tag{57}$$

for $0 \le y \le 1$. Then, $\psi(1) = 1$ when

$$\sigma^2 = \sigma_{**}^2 \approx 3c, \tag{58}$$

while $\int_0^1 \psi(y)dy = 1$ when

$$\sigma^2 = \sigma_*^2 \approx \frac{15c}{7} \tag{59}$$

and $\int_0^1 \phi(y)dy = 1$ when

$$\sigma^2 = \sigma_{***}^2 \approx 5c. \tag{60}$$

Comparisons between numerical and approximate values are made in Table 1.

Note that

$$g_3(x) - g_1(x) = \frac{(1+cx)(1-x)x^2\sigma^2}{\left(1 + x(1-x)^3\sigma^2\right)\left(1 + x(1-x)\left(x^2 + (1-x)^2\right)\sigma^2\right)} > 0 \tag{61}$$

for $0 < x < 1$. Thus, we have

$$\psi_3(y) = \exp\left(-2\int_0^y g_3(x)dx\right) < \exp\left(-2\int_0^y g_1(x)dx\right) = \psi_1(y) \tag{62}$$

and

$$\phi_3(y) = \exp\left(2\int_y^1 g_3(x)dx\right) > \exp\left(2\int_y^1 g_1(x)dx\right) = \phi_1(y) \tag{63}$$

for $0 < y < 1$. This implies that the probability of ultimate fixation of cooperation (defection) introduced as a single mutant in case 3 is larger (smaller) than in case 1 for all values of $\sigma^2 > 0$. Moreover, the values σ_*^2, σ_{**}^2 and σ_{***}^2 are smaller in case 3 than in case 1.

In conclusion, increasing the variance in both σ_3^2 and σ_4^2 is always more favorable for the evolution of cooperation than increasing the variance in only one of them.

5.4. Case 4: $\sigma_1^2 = \sigma_2^2 = \sigma_0^2 > 0$, $\sigma_3^2 = \sigma_4^2 = \sigma^2 > 0$

Here, this is an example where the variances of the payoffs for cooperation are fixed while the variances of the payoffs for defection are changing.

With the given variances, the function $g(x)$ in (27) takes the form

$$g_4(x) := g(x) = \frac{-c + (1-x)\left(x^2 + (1-x)^2\right)\sigma^2 - x\left(x^2 + (1-x)^2\right)\sigma_0^2}{1 + x(1-x)\left(x^2 + (1-x)^2\right)(\sigma^2 + \sigma_0^2)}, \tag{64}$$

which satisfies $g(0) = \sigma^2 - c$, $g(1) = -c - \sigma_0^2$.

In this case, the functions $g(x)$, $\psi(y)$ (see Fig. 1g,h) and $\phi(y)$, and the threshold values of σ^2, namely σ_*^2, σ_{**}^2 and σ_{***}^2, have the same properties as in cases 1 and 3 (see Appendices C and E, and Fig. 2). Moreover, if $(\sigma^2 + \sigma_0^2)/16$ is small, then we have the approximation

$$g(x) \approx -c + (1-x)\left(x^2 + (1-x)^2\right)\sigma^2 - x\left(x^2 + (1-x)^2\right)\sigma_0^2 \tag{65}$$

for $0 \le x \le 1$, from which

$$\psi(y) \approx 1 + 2cy - 2\sigma^2\left(y - \frac{3}{2}y^2 + \frac{4}{3}y^3 - \frac{1}{2}y^4\right) + 2\sigma_0^2\left(\frac{1}{2}y^2 - \frac{2}{3}y^3 + \frac{1}{2}y^4\right) \tag{66}$$

and

$$\phi(y) \approx 1 + 2c(y-1) - 2\sigma^2\left(y - \frac{3}{2}y^2 + \frac{4}{3}y^3 - \frac{1}{2}y^4 - \frac{1}{3}\right) + 2\sigma_0^2\left(\frac{1}{2}y^2 - \frac{2}{3}y^3 + \frac{1}{2}y^4 - \frac{1}{3}\right) \tag{67}$$

for $0 \le y \le 1$. Then, $\psi(1) = 1$ when

$$\sigma^2 = \sigma_{**}^2 \approx 3c + \sigma_0^2, \tag{68}$$

while $\int_0^1 \psi(y)dy = 1$ when

$$\sigma^2 = \sigma_*^2 \approx \frac{15c + 3\sigma_0^2}{7} \tag{69}$$

and $\int_0^1 \phi(y)dy = 1$ when

$$\sigma^2 = \sigma_{***}^2 \approx \frac{15c + 7\sigma_0^2}{3}. \tag{70}$$

Some values are given in Table 1. Since the threshold values σ_*^2, σ_{**}^2 and σ_{***}^2 for σ^2 increase with σ_0^2, these results reveal that larger is the value of σ_0^2, larger must be the value of σ^2 for selection to favor the evolution of cooperation in any sense. Moreover, note that $\sigma_{***}^2 > \sigma_{**}^2 > \sigma_0^2$.

The main conclusion is that a higher level of uncertainty in the payoffs for defection than in the payoffs for cooperation is required for the evolution of cooperation to be fully favored by selection. This is somehow in agreement with results that can be found for the RPD in an infinite population (Li et al., 2019).

5.5. Case 5: $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = \sigma_4^2 = \sigma^2 > 0$

This is a situation where all the variances of the payoffs are of the same magnitude.

With all variances equal to σ^2, the function $g(x)$ in (27) takes the form

$$g_5(x) := g(x) = \frac{-c + (1-2x)\left(x^2 + (1-x)^2\right)\sigma^2}{1 + 2x(1-x)\left(x^2 + (1-x)^2\right)\sigma^2}, \tag{71}$$

which satisfies $g(0) = \sigma^2 - c$, $g(1) = -c - \sigma^2$.

In this case, results (35) and (36) can no longer determine the monotonicity of $g(x)$ with respect to σ^2. Actually, it may be an increasing function for x near 0, and a decreasing function for x near 1. Nevertheless, it can be shown that $\psi(y)$ is decreasing with respect to σ^2 for $y \in (0, 1]$, which guarantees the existence of σ_*^2, while σ_{**}^2 and σ_{***}^2 do not exist (see Appendices D and E, and Fig. 1i,j).

If $\sigma^2/16$ is small, then we have the approximation

$$g(x) \approx -c + (1-2x)\left(x^2 + (1-x)^2\right)\sigma^2 \tag{72}$$

for $0 \le x \le 1$, from which

$$\psi(y) \approx 1 + 2cy - 2\sigma^2\left(y - 2y^2 + 2y^3 - y^4\right) \tag{73}$$

for $0 \le y \le 1$. Then, $\int_0^1 \psi(y)dy = 1$ when

$$\sigma^2 = \sigma_*^2 \approx \frac{15c}{4}. \tag{74}$$

Note that σ_*^2 is the only threshold value of σ^2 in this case (see Table 1 for particular values).

Therefore, the evolution of cooperation can be favored by selection, that is, $F_C > N^{-1}$, but cannot be fully favored, which means that we cannot have $F_C > N^{-1} > F_D$. This is in agreement with the conclusion in case 4.

6. RPD with additive payoffs

In this section, we consider a RPD game with additive payoffs. At time $t \ge 0$, cooperation (C) incurs a random cost $c(t) > 0$ to the individual adopting it, but provides a random benefit $b(t) > 0$ to the opponent, while defection (D) incurs no cost at all, so that the random payoff matrix takes the form

$$\begin{pmatrix} \eta_1(t) & \eta_2(t) \\ \eta_3(t) & \eta_4(t) \end{pmatrix} = \begin{pmatrix} b(t) - c(t) & -c(t) \\ b(t) & 0 \end{pmatrix}. \tag{75}$$

The main difference with the model in the previous section is that the payoffs are not independent.

Here, $c(t)$ and $b(t)$ are assumed to be random variables with

$$\mathbf{E}(b(t)) = \mu_b N^{-1} > 0, \tag{76a}$$
$$\mathbf{E}(c(t)) = \mu_c N^{-1} > 0, \tag{76b}$$
$$\mathbf{Var}(b(t)) = \sigma_b^2 N^{-1}, \tag{76c}$$
$$\mathbf{Var}(c(t)) = \sigma_c^2 N^{-1}, \tag{76d}$$
$$\mathbf{Cov}(b, c) = \sigma_{bc} N^{-1}, \tag{76e}$$

so that the population-scaled parameters in (3) for the means, variances and covariances of the payoffs are given by

$$\mu_1 = \mu_b - \mu_c, \tag{77a}$$
$$\mu_2 = -\mu_c, \tag{77b}$$
$$\mu_3 = \mu_b, \tag{77c}$$
$$\mu_4 = 0, \tag{77d}$$

and

$$\sigma_1^2 = \sigma_b^2 + \sigma_c^2 - 2\sigma_{bc}, \tag{78a}$$
$$\sigma_2^2 = \sigma_c^2, \tag{78b}$$
$$\sigma_3^2 = \sigma_b^2, \tag{78c}$$
$$\sigma_{12} = \sigma_c^2 - \sigma_{bc}, \tag{78d}$$
$$\sigma_{13} = \sigma_b^2 - \sigma_{bc}, \tag{78e}$$
$$\sigma_{23} = -\sigma_{bc}, \tag{78f}$$
$$\sigma_{34} = \sigma_{24} = \sigma_{14} = \sigma_4^2 = 0. \tag{78g}$$

Substituting the above expressions into (13) and (14) yields

$$m(x) = x(1-x)\left(-\mu_c + x(\sigma_{bc} - \sigma_c^2)\right) \tag{79}$$

and

$$v(x) = x(1-x)\left(1 + x(1-x)\sigma_c^2\right) \tag{80}$$

as drift function and diffusion function, respectively. Note that σ_b^2 does not come into play in these functions.

If μ_c, σ_c^2 and σ_{bc} are of the same small enough order, then

$$\begin{aligned} \psi(y) &= \exp\left(-2\int_0^y \frac{m(x)}{v(x)}dx\right) \\ &\approx 1 - 2\int_0^y \left(-\mu_c + x(\sigma_{bc} - \sigma_c^2)\right)dx \\ &= 1 + 2\mu_c y - \left(\sigma_{bc} - \sigma_c^2\right)y^2 \end{aligned} \tag{81}$$

as in Lessard (2005). Therefore, the conditions

$$\int_0^1 \psi(y)dy < 1, \quad \psi(1) < 1, \quad \int_0^1 \psi(y)dy > \psi(1), \tag{82}$$

become

$$\sigma_{bc} - \sigma_c^2 > 3\mu_c, \quad \sigma_{bc} - \sigma_c^2 > 2\mu_c, \quad \sigma_{bc} - \sigma_c^2 > \frac{3}{2}\mu_c, \tag{83}$$

respectively. These are the conditions for selection to favor the evolution of C, favor more the evolution of C than the evolution of D, and disfavor the evolution of D, respectively. Since $\mu_c > 0$, these conditions can hold only if $\sigma_{bc} > \sigma_c^2$, in which case the first condition is the most stringent one and the third condition the least stringent one.

In the particular case $b(t) = rc(t)$ where $r > 0$ is a constant, the above conditions reduce to

$$r > 1 + 3\left(\frac{\mu_c}{\sigma_c^2}\right), \quad r > 1 + 2\left(\frac{\mu_c}{\sigma_c^2}\right), \quad r > 1 + \frac{3}{2}\left(\frac{\mu_c}{\sigma_c^2}\right), \tag{84}$$

respectively. These conditions can hold for $r > 1$ if σ_c^2 is large enough compared to μ_c. Moreover, it can be shown that at least the second condition does not depend on the assumption that σ_c^2 and σ_{bc} are small and of the same order (see Appendix F).

7. Repeated RPD

We turn now our attention to a RPD game that is repeated a random number of times. There are two pure actions, cooperation (C) and defection (D), and the payoffs in a single round of interaction between two players at time $t \ge 0$ are given by the random game matrix

$$\begin{pmatrix} R(t) & S(t) \\ T(t) & P(t) \end{pmatrix}. \tag{85}$$

Here, $R(t)$ and $S(t)$ are the payoffs to action C against C and D, respectively, while $T(t)$ and $P(t)$ are the corresponding payoffs to action D against the same two actions. These payoffs are assumed to be independent random variables whose distributions do not depend on time $t \ge 0$. Moreover, their expected values determine a classical PD game. Actually, we assume

$$\mathbf{E}(R(t)) = \mu_R N^{-1} > 0, \tag{86a}$$
$$\mathbf{E}(S(t)) = \mu_S N^{-1} > 0, \tag{86b}$$

$$\mathbf{E}(T(t)) = \mu_T N^{-1} > 0, \quad (86c)$$

$$\mathbf{E}(P(t)) = \mu_P N^{-1} > 0, \quad (86d)$$

with $\mu_T > \mu_R > \mu_P > \mu_S$ and $2\mu_R > \mu_T + \mu_S$. Finally, at each time $t \geq 0$, the number of rounds of interaction between the same two players is a random variable $n(t) \geq 1$ that is independent of $R(t)$, $S(t)$, $T(t)$ and $P(t)$.

In this repeated RPD game, we consider two strategies, Tit-for-Tat (*TFT*) and Always-Defect (*AllD*). In a pairwise interaction, a *TFT*-strategist uses action *C* in the first round and, in each of the next rounds, copies the action previously used by the opponent. On the other hand, an *AllD*-strategist uses action *D* in all the rounds. Thus, the payoffs to these two strategies at time $t \geq 0$ are given by

$$\begin{pmatrix} \eta_1(t) & \eta_2(t) \\ \eta_3(t) & \eta_4(t) \end{pmatrix} = \begin{pmatrix} n(t)R(t) & S(t) + (n(t)-1)P(t) \\ T(t) + (n(t)-1)P(t) & n(t)P(t) \end{pmatrix}. \quad (87)$$

Moreover, the population-scaled parameters (3) for the means, variances and covariances of the these payoffs take the form

$$\mu_1 = \mu_R \mathbf{E}(n(t)), \quad (88a)$$

$$\mu_2 = \mu_S + \mu_P \mathbf{E}(n(t) - 1), \quad (88b)$$

$$\mu_3 = \mu_T + \mu_P \mathbf{E}(n(t) - 1), \quad (88c)$$

$$\mu_4 = \mu_P \mathbf{E}(n(t)), \quad (88d)$$

and

$$\sigma_1^2 = \sigma_R^2 \mathbf{E}(n(t)^2), \quad (89a)$$

$$\sigma_2^2 = \sigma_S^2 + \sigma_P^2 \mathbf{E}((n(t)-1)^2), \quad (89b)$$

$$\sigma_3^2 = \sigma_T^2 + \sigma_P^2 \mathbf{E}((n(t)-1)^2), \quad (89c)$$

$$\sigma_4^2 = \sigma_P^2 \mathbf{E}(n(t)^2), \quad (89d)$$

$$\sigma_{23} = \sigma_P^2 \mathbf{E}((n(t)-1)^2), \quad (89e)$$

$$\sigma_{24} = \sigma_{34} = \sigma_P^2 \mathbf{E}(n(t)(n(t)-1)), \quad (89f)$$

$$\sigma_{12} = \sigma_{13} = \sigma_{14} = 0, \quad (89g)$$

where $\sigma_R^2 = N\mathbf{Var}(R(t))$, $\sigma_S^2 = N\mathbf{Var}(S(t))$, $\sigma_T^2 = N\mathbf{Var}(T(t))$ and $\sigma_P^2 = N\mathbf{Var}(P(t))$.

Substituting the above expressions into (13) and (14) yields

$$\begin{aligned} m(x) = x(1-x)\Big(&\mu_S - \mu_P + x(\mu_R - \mu_S - \mu_T + \mu_P) \\ &+ x(\mu_R - \mu_P)\mathbf{E}(n(t)-1) \\ &- x^3\sigma_R^2\mathbf{E}(n(t)^2) - x(1-x)^2\sigma_S^2 + x^2(1-x)\sigma_T^2 \\ &+ (1-x)\sigma_P^2 \\ &\times \mathbf{E}\big(((n(t)-1)x + 1 - x)((n(t)-1)(1+x) + 1 - x)\big)\Big) \end{aligned} \quad (90)$$

and

$$\begin{aligned} v(x) = x(1-x)\Big(&1 + x^3(1-x)\sigma_R^2\mathbf{E}(n(t)^2) + x(1-x)^3\sigma_S^2 \\ &+ x^3(1-x)\sigma_T^2 + x(1-x)\sigma_P^2\mathbf{E}\big(((n(t)-1)x + 1 - x)^2\big)\Big) \end{aligned} \quad (91)$$

as drift function and diffusion function, respectively. Assuming that μ_R, μ_S, μ_T and μ_P, as well as σ_R^2, σ_S^2, σ_T^2 and σ_P^2, are of the same small enough order, we have

$$\psi(y) = \exp\left(-2\int_0^y \frac{m(x)}{v(x)}dx\right) \approx 1 - 2\int_0^y \frac{m(x)}{x(1-x)}dx \quad (92)$$

as in Lessard (2005). Then, the condition for the evolution of *TFT* to be favored by selection when introduced as a single mutant, which is given by

$$\int_0^1 \psi(y)dy < 1, \quad (93)$$

becomes

$$2\int_0^1\int_0^y \frac{m(x)}{x(1-x)}dxdy > 0. \quad (94)$$

Using the expression of $m(x)$ given in (90), this condition can be written in the form

$$\begin{aligned} &\mu_S - \mu_P + \frac{1}{3}(\mu_R - \mu_S - \mu_T + \mu_P) + \frac{1}{3}(\mu_R - \mu_P)\mathbf{E}(n(t)-1) \\ &\quad - \frac{1}{10}\mathbf{E}(n(t)^2)\sigma_R^2 - \frac{1}{10}\sigma_S^2 + \frac{1}{15}\sigma_T^2 + c_P\sigma_P^2 > 0, \end{aligned} \quad (95)$$

where

$$\begin{aligned} c_P &= 2\mathbf{E}((n(t)-1)^2)\int_0^1\int_0^y (1-x)x(1+x)dxdy \\ &\quad + 2\mathbf{E}(n(t)-1)\int_0^1\int_0^y (1-x)^2(1+2x)dxdy \\ &\quad + 2\int_0^1\int_0^y (1-x)^3dxdy \\ &= \frac{7}{30}\mathbf{E}((n(t)-1)^2) + \frac{7}{10}\mathbf{E}(n(t)-1) + \frac{2}{5} > 0. \end{aligned} \quad (96)$$

If all the variances of the payoffs vanish, then the condition (95) corresponds to the one-third law of evolution (Nowak et al., 2004; Lessard, 2005), since it says then that the mean payoff to *TFT* exceeds the mean payoff to *AllD* when the frequency of *TFT* is equal to 1/3. Note that this condition holds if the expected number of rounds $\mathbf{E}(n(t))$ is large enough, since $\mu_R > \mu_P$. On the other hand, when the variances of the payoffs do not vanish, we see that an increase of σ_T^2 and σ_P^2, or a decrease of σ_R^2 and σ_S^2, makes it easier for the evolution of *TFT* to be favored by selection.

Similarly, from

$$\phi(y) = \exp\left(2\int_y^1 \frac{m(x)}{v(x)}dx\right) \approx 1 + 2\int_y^1 \frac{m(x)}{x(1-x)}dx, \quad (97)$$

the condition for the evolution of *AllD* not to be favored by selection when introduced as a single mutant, that is,

$$\int_0^1 \phi(y)dy > 1, \quad (98)$$

reduces to

$$2\int_0^1\int_y^1 \frac{m(x)}{x(1-x)}dxdy = 2\int_0^1\int_0^{1-y} \frac{m(1-x)}{x(1-x)}dxdy > 0, \quad (99)$$

which is equivalent to

$$\begin{aligned} &\mu_S - \mu_P + \frac{2}{3}(\mu_R - \mu_S - \mu_T + \mu_P) + \frac{2}{3}(\mu_R - \mu_P)\mathbf{E}(n(t)-1) \\ &\quad - \frac{2}{5}\mathbf{E}(n(t)^2)\sigma_R^2 - \frac{1}{15}\sigma_S^2 + \frac{1}{10}\sigma_T^2 + c_P\sigma_P^2 > 0, \end{aligned} \quad (100)$$

where

$$c_P = \frac{4}{15}\mathbf{E}((n(t)-1)^2) + \frac{3}{10}\mathbf{E}(n(t)-1) + \frac{1}{10} > 0. \quad (101)$$

Therefore, an increase of σ_T^2 and σ_P^2, or a decrease of σ_R^2 and σ_S^2, makes it also easier for the evolution of *AllD* not to be favored by selection.

Finally, we have

$$\psi(1) \approx 1 - 2\int_0^1 \frac{m(x)}{x(1-x)}dx < 1 \quad (102)$$

when

$$\int_0^1 \frac{m(x)}{x(1-x)}dx = \mu_S - \mu_P + \frac{1}{2}(\mu_R - \mu_S - \mu_T + \mu_P) + \frac{1}{2}(\mu_R - \mu_P)\mathbf{E}(n(t) - 1) - \frac{1}{4}\mathbf{E}(n(t)^2)\sigma_R^2 - \frac{1}{12}\sigma_S^2 + \frac{1}{12}\sigma_T^2 + c_P\sigma_P^2 > 0, \quad (103)$$

where

$$c_P = \frac{1}{4}\mathbf{E}((n(t) - 1)^2) + \frac{1}{2}\mathbf{E}(n(t) - 1) + \frac{1}{4} > 0. \quad (104)$$

This means that an increase of σ_T^2 and σ_P^2, or a decrease of σ_R^2 and σ_S^2, makes it easier for selection to favor more the evolution of *TFT* than the evolution of *AllD*.

8. Discussion

Environmental noise in the payoffs of a matrix game may have important effects on the evolutionary dynamics, and even change the outcome of evolution. As a matter of fact, the dynamics is driven not only by the expected values of the payoffs but also by their variances. Variability in payoffs can push the time average of a population state far from its interior Nash equilibrium (Broom, 2005) or even change the stability of a fixation state (Stollmeier and Nagler, 2018). In the case of a deterministic one-round Prisoner's Dilemma (PD), where all the payoffs are constant, cooperation can never be favored by natural selection. However, introducing uncertainty in the payoffs makes it possible for cooperation to be favored.

Assuming a Randomized Prisoner's Dilemma (RPD) with independent payoffs in a large finite population, we have shown that, if the means and variances of the payoffs are of the same order of magnitude given by the inverse of the population size N, increasing the variance in the payoffs for defection, tends to promote the evolution of cooperation (Conclusion 1). Moreover, if the payoffs have additive expected values, decreasing the variance in the payoffs for cooperation, at least for an expected cost for cooperation small enough, has the same effect (Conclusion 2). More precisely, increasing the variance of the payoff for defection against defection (case 1) increases the probability of ultimate fixation of cooperation introduced as a single mutant, F_C, while increasing the variance of the payoff for defection against cooperation (case 2) decreases the probability of ultimate fixation of defection introduced as a single mutant, F_D. Increasing both variances simultaneously (cases 3 and 4) enhances the effect.

In particular, we have shown that the evolution of cooperation is fully favored by selection, in the sense that $F_C > N^{-1} > F_D$, where N^{-1} is the probability of ultimate fixation of a single mutant under neutrality, if the population-scaled variance of the payoffs for defection against cooperation and defection, σ^2, exceeds $(15c + 7\sigma_0^2)/3$, where σ_0^2 is the population-scaled variance of the payoffs for cooperation against cooperation and defection (case 4 and case 3 for $\sigma_0^2 = 0$). Moreover, as σ^2 is increased, the conditions for $F_C > N^{-1}$, $F_C > F_D$, and $F_D < N^{-1}$ are satisfied when $\sigma^2 > \sigma_*^2$, $\sigma^2 > \sigma_{**}^2$, and $\sigma^2 > \sigma_{***}^2$, respectively, where σ_*^2, σ_{**}^2 and σ_{***}^2 represent three increasing threshold values (Fig. 2). These are the 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, respectively. We have analogous conditions with increasing threshold values when only the population-scaled variance of the payoff for defection against defection is increased (case 1), and with decreasing threshold values when only the population-scaled variance of the payoff for defection against cooperation is increased (case 2).

Our results are in agreement with the fact that, in the case of a RPD in an infinite population, a larger variance of the payoffs for defection is required for C-fixation to be stochastically locally stable and D-fixation stochastically locally unstable (Li et al., 2019). On the other hand, they are significantly different from results obtained with constant payoffs in finite populations. For instance, in the case of a PD game in a graph-structured population and the case of a repeated PD game in a well-mixed population (Nowak et al., 2004; Nowak, 2006), the condition $F_C > N^{-1}$ is sufficient for $F_C > N^{-1} > F_D$.

Note that more uncertainty in the payoffs for defection than for cooperation makes sense. Among the reasons, defectors are more isolated than cooperators and may not share with others increments or decrements of surrounding resources caused by variations in the environment. They may also suffer from punishment or lack of reward from others. Even if the expected payoffs may still be higher for defection than for cooperation, their variances may also be higher.

On the other hand, when increasing the variance of all the payoffs (case 5), we have shown that selection can favor the evolution of both cooperation and defection in the sense that $F_C > N^{-1}$ and $F_D > N^{-1}$. Note that, since genotypic fitnesses in a random mating diploid population can be viewed as payoffs in random pairwise interactions of haploid individuals (in which case the payoff matrix is symmetric), our results extend previous results stated without proofs for population genetics models (Karlin and Levikson, 1974). Increasing the variance of the payoffs for defection (cooperation, respectively) pushes the system away from fixation of defection (cooperation, respectively), and at the same time promotes fixation of cooperation (defection, respectively). When the variance of all the payoffs increases, the system state is more likely to stay away from fixation. The conclusion might be of general validity in agreement with the claim found in Karlin and Levikson (1974) that "variance in selection intensities compensate for the unfavorable initial frequency of an allele".

Of further interest is the effect of the variances of the cost and benefit in a RPD with additive payoffs which are not independent. At least when the population-scaled means and variances of the cost and benefit, as well as their population-scaled covariance, are of the same small enough order, the conditions for $F_C > N^{-1}$, $F_C > F_D$ and $F_D < N^{-1}$ take the form $\sigma_{bc} - \sigma_c^2 > 3\mu_c$, $\sigma_{bc} - \sigma_c^2 > 2\mu_c$ and $\sigma_{bc} - \sigma_c^2 > 3\mu_c/2$, respectively, where μ_c is the population-scaled expected cost, σ_{bc} the population-scaled covariance between the cost and benefit, and σ_c^2 the population-scaled variance of the cost. The first condition is the most stringent one and the last condition the least stringent one, but they all require that $\sigma_{bc} > \sigma_c^2$ since $\mu_c > 0$. Of course, this does not occur if the cost and benefit are constants or independent random variables.

In the case of a repeated RPD game, the payoffs to *TFT* and *AllD* in pairwise interactions with a random number of rounds between the same players are generally not independent even if the payoffs to cooperation and defection are independent in each round. Assuming that the population-scaled means and variances of these payoffs are of the same small enough order, we have shown that an increase in the variances of the payoffs for defection, or a decrease in the variances of the payoffs for cooperation, makes it easier for $F_{TFT} > N^{-1}$, $F_{TFT} > F_{AllD}$ and $F_{AllD} < N^{-1}$ to hold. Since fixation of *TFT* means fixation of cooperation, the conclusion is that these conditions tend to promote the evolution of cooperation in agreement with our results for a one-round RPD game.

As a final remark, our results are based on a diffusion approximation that has been ascertained for a randomized matrix game with payoffs that have expected values, variances and covariances of order given by the inverse of a large population size N. This approximation can be used to study not only fixation probabilities, but any dynamical properties.

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Appendix A. Conditional moments of Δx

First fourth moments of a binomial distribution

Let $\tilde{x}$ be a random variable such that $N\tilde{x}$ follows a binomial distribution of parameters N and x, denoted by $\mathrm{B}(N, x)$. The first moment of $\tilde{x}$ is $\mathbf{E}(\tilde{x}) = x$. As for the second moment, we have

$$\begin{aligned}\mathbf{E}(\tilde{x}^2) &= \sum_{i=0}^{N}\left(\frac{i}{N}\right)^2\binom{N}{i}x^i(1-x)^{N-i}\\ &= \frac{1}{N^2}\left[\sum_{i=0}^{N} i(i-1)\binom{N}{i}x^i(1-x)^{N-i}\right.\\ &\quad\left.+\sum_{i=0}^{N} i\binom{N}{i}x^i(1-x)^{N-i}\right]\\ &= \frac{1}{N^2}\left[N(N-1)x^2\sum_{i=2}^{N}\binom{N-2}{i-2}x^{i-2}(1-x)^{N-i}\right]+\frac{x}{N}\\ &= \frac{N-1}{N}x^2+\frac{x}{N}\\ &= x^2+\frac{x(1-x)}{N}. \end{aligned} \tag{105}$$

Analogously, using the above expression for $\mathbf{E}(\tilde{x}^2)$, the third moment is given by

$$\begin{aligned}\mathbf{E}(\tilde{x}^3) &= \sum_{i=0}^{N}\left(\frac{i}{N}\right)^3\binom{N}{i}x^i(1-x)^{N-i}\\ &= \frac{x(N-1)^2}{N^2}\left[\sum_{i=1}^{N}\frac{(i-1)^2+2(i-1)+1}{(N-1)^2}\right.\\ &\quad\left.\times\binom{N-1}{i-1}x^{i-1}(1-x)^{(N-1)-(i-1)}\right]\\ &= \frac{x(N-1)^2}{N^2}\left[x^2+\frac{x(1-x)}{N}+\frac{2}{N-1}x+\frac{1}{(N-1)^2}\right]\\ &= x^3+\frac{3x^2(1-x)}{N}+o(N^{-1}). \end{aligned} \tag{106}$$

Finally, as for the fourth moment, we find

$$\begin{aligned}\mathbf{E}(\tilde{x}^4) &= \sum_{i=0}^{N}\left(\frac{i}{N}\right)^4\binom{N}{i}x^i(1-x)^{N-i}\\ &= \frac{x(N-1)^3}{N^3}\\ &\quad\times\left[\sum_{i=1}^{N}\frac{(i-1)^3+3(i-1)^2+3(i-1)+1}{(N-1)^3}\right.\\ &\quad\left.\times\binom{N-1}{i-1}x^{i-1}(1-x)^{(N-1)-(i-1)}\right]\\ &= \frac{x(N-1)^3}{N^3}\\ &\quad\times\left[x^3+\frac{3x^2(1-x)}{N}+\frac{3}{N-1}\left(x^2+\frac{x(1-x)}{N}\right)\right.\\ &\quad\left.+\frac{3}{(N-1)^2}x+\frac{1}{(N-1)^3}+o(N^{-1})\right]\\ &= x^4+\frac{6x^3(1-x)}{N}+o(N^{-1}). \end{aligned} \tag{107}$$

First conditional moments of Δx

Given that $x(t) = x$, the frequency change $\Delta x = x(t+\Delta t)-x(t)$ has the same probability distribution as $\tilde{x} - x$, where $N\tilde{x} \sim \mathrm{B}(N, x')$. Here, the parameter

$$x' = \frac{x\mathbf{\Pi}_1}{x\mathbf{\Pi}_1+(1-x)\mathbf{\Pi}_2} \tag{108}$$

is a random variable with

$$\mathbf{\Pi}_1 = 1+x\eta_1+(1-x)\eta_2 \tag{109}$$

and

$$\mathbf{\Pi}_2 = 1+x\eta_3+(1-x)\eta_4, \tag{110}$$

where η_i has mean $N^{-1}\mu_i$, variance $N^{-1}\sigma_i^2+o(N^{-1})$ and covariance $N^{-1}\sigma_{ij}+o(N^{-1})$ with η_j for $i, j = 1, \ldots, 4$ with $j \neq i$. Note that

$$x' = \frac{x(1+P_1)}{1+P_3}, \tag{111}$$

where

$$P_1 = x\eta_1+(1-x)\eta_2, \tag{112a}$$

$$P_2 = x\eta_3+(1-x)\eta_4, \tag{112b}$$

$$P_3 = xP_1+(1-x)P_2. \tag{112c}$$

The random variables P_j for $j = 1, 2$ are homogeneous linear functions of $\eta_1, \ldots, \eta_4$, while P_3 is a homogeneous linear function of P_1 and P_2. Thus, the moments of P_1 and P_2 satisfy

$$\mathbf{E}(P_1) = N^{-1}\left(x\mu_1+(1-x)\mu_2\right), \tag{113a}$$

$$\mathbf{E}(P_2) = N^{-1}\left(x\mu_3+(1-x)\mu_4\right), \tag{113b}$$

$$\mathbf{E}(P_1^2) = N^{-1}\left(x^2\sigma_1^2+(1-x)^2\sigma_2^2+2x(1-x)\sigma_{12}\right)+o(N^{-1}), \tag{113c}$$

$$\mathbf{E}(P_2^2) = N^{-1}\left(x^2\sigma_3^2+(1-x)^2\sigma_4^2+2x(1-x)\sigma_{34}\right)+o(N^{-1}), \tag{113d}$$

$$\begin{aligned}\mathbf{E}(P_1P_2) &= N^{-1}\left(x^2\sigma_{13}+x(1-x)(\sigma_{14}+\sigma_{23})+(1-x)^2\sigma_{24}\right)\\ &\quad+o(N^{-1}),\end{aligned} \tag{113e}$$

and

$$\mathbf{E}(P_1^kP_2^l) = o(N^{-1}) \tag{114}$$

as soon as k, l are non-negative integers such that $k + l \geq 3$. Therefore, we have

$$\begin{aligned}\mathbf{E}(x') &= \mathbf{E}\left(x(1+P_1)(1-P_3+P_3^2)\right)+o(N^{-1})\\ &= \mathbf{E}\,\big(\,x+x(1-x)(P_1-P_2)+x(1-x)(P_2-P_1)\end{aligned}$$

$$\begin{aligned}&\times\ (xP_1+(1-x)P_2)\big)+o(N^{-1})\\&=x+x(1-x)\big(\mathbf{E}(P_1)-\mathbf{E}(P_2)\big)\\&\quad+x(1-x)\big(-x\mathbf{E}(P_1^2)+(1-x)\mathbf{E}(P_2^2)+(2x-1)\mathbf{E}(P_1P_2)\big)\\&\quad+o(N^{-1})\\&=x+\frac{x(1-x)}{N}\big(\mu_2-\mu_4+x(\mu_1-\mu_2-\mu_3+\mu_4)\big)\\&\quad+\frac{x(1-x)}{N}\Big(-x^3\sigma_1^2-x(1-x)^2\sigma_2^2-2x^2(1-x)\sigma_{12}\\&\quad+x^2(1-x)\sigma_3^2+(1-x)^3\sigma_4^2+2x(1-x)^2\sigma_{34}\\&\quad+(2x-1)\left(x^2\sigma_{13}+x(1-x)(\sigma_{14}+\sigma_{23})+(1-x)^2\sigma_{24}\right)\Big)\\&\quad+o(N^{-1}).\end{aligned}\tag{115}$$

Since

$$\mathbf{E}(\Delta x|x(t)=x)=\mathbf{E}(\tilde{x}-x)=\mathbf{E}(\tilde{x})-x=\mathbf{E}(x')-x,\tag{116}$$

the first conditional moment of Δx is given by

$$\begin{aligned}\mathbf{E}(\Delta x|x(t)=x)=\frac{x(1-x)}{N}\Big(&\mu_2-\mu_4\\&+x\big(\mu_1-\mu_2-\mu_3+\mu_4\big)\\&+x^3(\sigma_{13}-\sigma_1^2)+x(1-x)^2(2\sigma_{34}-\sigma_{14}-\sigma_{23}\\&+\sigma_{24}-\sigma_2^2)\\&+x^2(1-x)(-2\sigma_{12}+\sigma_{14}+\sigma_{23}-\sigma_{13}+\sigma_3^2)\\&+(1-x)^3(\sigma_4^2-\sigma_{24})\Big)\\&+o(N^{-1}),\end{aligned}\tag{117}$$

while its second conditional moment can be expressed as

$$\begin{aligned}\mathbf{E}((\Delta x)^2|x(t)=x)&=\mathbf{E}\big((\tilde{x}-x)^2\big)\\&=\mathbf{E}\big(\tilde{x}^2-2x\tilde{x}+x^2\big)\\&=\mathbf{E}\left(x'^2+\frac{x'(1-x')}{N}\right)-2x\mathbf{E}(x')+x^2\\&=\mathbf{E}\left((x'-x)^2\right)+\mathbf{E}\left(\frac{x'(1-x')}{N}\right)\\&=\mathbf{E}\left((x'-x)^2\right)+\frac{x(1-x)}{N}+o(N^{-1}).\end{aligned}\tag{118}$$

Moreover, we have

$$\begin{aligned}\mathbf{E}\left((x'-x)^2\right)&=\mathbf{E}\Big(\big(x(1-x)(P_2-P_1)(P_3-1)\big)^2\Big)+o(N^{-1})\\&=\mathbf{E}\big(x^2(1-x)^2(P_2-P_1)^2\big)+o(N^{-1})\\&=\frac{x^2(1-x)^2}{N}\Big(x^2(\sigma_1^2+\sigma_3^2)+(1-x)^2(\sigma_2^2+\sigma_4^2)\\&\quad+2x(1-x)(\sigma_{12}+\sigma_{34})\\&\quad-2x^2\sigma_{13}-2x(1-x)(\sigma_{14}+\sigma_{23})-2(1-x)^2\sigma_{24}\Big)\\&\quad+o(N^{-1}).\end{aligned}\tag{119}$$

Therefore, we get

$$\begin{aligned}&\mathbf{E}((\Delta x)^2|x(t)=x)\\&=\frac{x(1-x)}{N}\big(1+x^3(1-x)(\sigma_1^2+\sigma_3^2-2\sigma_{13})\\&\quad+x(1-x)^3(\sigma_2^2+\sigma_4^2-2\sigma_{24})\\&\quad+2x^2(1-x)^2(\sigma_{12}+\sigma_{34}-\sigma_{14}-\sigma_{23})\big)+o(N^{-1}).\end{aligned}\tag{120}$$

Finally, the fourth conditional moment of Δx can be expressed as

$$\begin{aligned}\mathbf{E}((\Delta x)^4|x(t)=x)&=\mathbf{E}\big((\tilde{x}-x)^4\big)\\&=\mathbf{E}\big(\tilde{x}^4-4x\tilde{x}^3+6x^2\tilde{x}^2-4x^3\tilde{x}+x^4\big)\\&=\mathbf{E}\left(x'^4+\frac{6x'^3(1-x')}{N}\right)\\&\quad-4x\mathbf{E}\left(x'^3+\frac{3x'^2(1-x')}{N}\right)\\&\quad+6x^2\mathbf{E}\left(x'^2+\frac{x'(1-x')}{N}\right)\\&\quad-4x^3\mathbf{E}(x')+x^4+o(N^{-1})\\&=\mathbf{E}\left((x'-x)^4\right)+\frac{6}{N}\mathbf{E}\left(x'(1-x')(x'-x)^2\right)\\&\quad+o(N^{-1}).\end{aligned}\tag{121}$$

Note that

$$\mathbf{E}\left((x'-x)^4\right)=\mathbf{E}\big(x^4(1-x)^4(P_2-P_1)^4\big)+o(N^{-1})=o(N^{-1})\tag{122}$$

and

$$\begin{aligned}&\mathbf{E}\left(x'(1-x')(x'-x)^2\right)\\&\quad=\mathbf{E}\big(x'(1-x')x^2(1-x)^2(P_2-P_1)^2\big)+o(N^{-1})=O(N^{-1}),\end{aligned}\tag{123}$$

from which we conclude that $\mathbf{E}((\Delta x)^4|x(t)=x)=o(N^{-1})$.

Appendix B. Partial derivatives of $g(x)$ with respect to σ_i^2

The function $g(x)$ is defined as the drift function in (13) divided by the diffusion function in (14), that is,

$$\begin{aligned}g(x)&=\frac{m(x)}{v(x)}\\&=\frac{h(x)-\left(x^3\sigma_1^2+x(1-x)^2\sigma_2^2-x^2(1-x)\sigma_3^2-(1-x)^3\sigma_4^2\right)}{1+x^3(1-x)(\sigma_1^2+\sigma_3^2)+x(1-x)^3(\sigma_2^2+\sigma_4^2)},\end{aligned}\tag{124}$$

where

$$h(x)=\mu_2-\mu_4+x(\mu_1-\mu_2-\mu_3+\mu_4).\tag{125}$$

Then the partial derivatives with respect to $\sigma_i^2>0$ for $i=1,\ldots,4$ are given by

$$\frac{\partial g(x)}{\partial\sigma_1^2}=-\frac{x^3\left(1+(1-x)h(x)+x^2(1-x)\sigma_3^2+(1-x)^3\sigma_4^2\right)}{\left(1+x^3(1-x)(\sigma_1^2+\sigma_3^2)+x(1-x)^3(\sigma_2^2+\sigma_4^2)\right)^2},\tag{126a}$$

$$\frac{\partial g(x)}{\partial\sigma_2^2}=-\frac{x(1-x)^2\left(1+(1-x)h(x)+x^2(1-x)\sigma_3^2+(1-x)^3\sigma_4^2\right)}{\left(1+x^3(1-x)(\sigma_1^2+\sigma_3^2)+x(1-x)^3(\sigma_2^2+\sigma_4^2)\right)^2},\tag{126b}$$

$$\frac{\partial g(x)}{\partial\sigma_3^2}=\frac{x^2(1-x)\left(1-xh(x)+x^3\sigma_1^2+x(1-x)^2\sigma_2^2\right)}{\left(1+x^3(1-x)(\sigma_1^2+\sigma_3^2)+x(1-x)^3(\sigma_2^2+\sigma_4^2)\right)^2},\tag{126c}$$

$$\frac{\partial g(x)}{\partial\sigma_4^2}=\frac{(1-x)^3\left(1-xh(x)+x^3\sigma_1^2+x(1-x)^2\sigma_2^2\right)}{\left(1+x^3(1-x)(\sigma_1^2+\sigma_3^2)+x(1-x)^3(\sigma_2^2+\sigma_4^2)\right)^2}.\tag{126d}$$

Under the assumptions $\mu_4>\mu_2$ and $\mu_3>\mu_1$, we have $h(x)<0$ for $0<x<1$, in which case

$$\frac{\partial g(x)}{\partial\sigma_3^2}>0\tag{127}$$

and

$$\frac{\partial g(x)}{\partial\sigma_4^2}>0.\tag{128}$$

On the other hand, the conditions

$$\frac{\partial g(x)}{\partial\sigma_1^2}<0\tag{129}$$

and

$$\frac{\partial g(x)}{\partial\sigma_2^2}<0\tag{130}$$

hold if and only if

$$h(x) > -\frac{1 + x^2(1-x)\sigma_3^2 + (1-x)^3\sigma_4^2}{1-x}. \quad (131)$$

Since the right-hand member in (131) is less than −1 for $0 < x < 1$, a sufficient condition for (129) and (130) to hold is $h(x) \geq -1$ on (0, 1).

Appendix C. Monotonicity of $g(x)$ and convexity of $\psi(y)$, $\phi(y)$ in cases 1, 3, 4, 5

In case 1, with $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = 0$ and $\sigma_4^2 = \sigma^2 > 0$, the expression of $g(x)$ takes the form

$$g(x) = \frac{-c + (1-x)^3\sigma^2}{1 + x(1-x)^3\sigma^2}, \quad (132)$$

whose derivative is given by

$$g'(x) = \frac{\sigma^2(1-x)^2\left[(c-\sigma^2)(1-x)^4 - cx^2(2+(2-x)^2) - 3\right]}{\left(1 + x(1-x)^3\sigma^2\right)^2}. \quad (133)$$

If $\sigma^2 > c$, then $g'(x) < 0$ for $0 < x < 1$. Thus, $g(x)$ is a strictly decreasing function on [0, 1].

In case 3, with $\sigma_1^2 = \sigma_2^2 = 0$ and $\sigma_3^2 = \sigma_4^2 = \sigma^2 > 0$, we have

$$g(x) = \frac{-c + (1-x)a\sigma^2}{1 + x(1-x)a\sigma^2}, \quad (134)$$

where $a = x^2 + (1-x)^2$. Under the condition $\sigma^2 > c$, the derivative of $g(x)$ for $0 < x < 1$ is given by

$$g'(x) = \frac{2x - 3a + c\left(2x^2 + (1-4x)a\right) - \sigma^2 a^2(1-x)^2}{\left(1 + x(1-x)a\sigma^2\right)^2}, \quad (135)$$

where $2x - 3a = -6x^2 + 8x - 3 \leq -1/3 < 0$ and

$$\begin{aligned} &c\left(2x^2 + (1-4x)a\right) - \sigma^2 a^2(1-x)^2 \\ &< c\left(2x^2 + (1-4x)a\right) - ca^2(1-x)^2 \\ &= c\left(a(1 - 4x - (1-x)^4 - x^2(1-x)^2) + 2x^2\right) \\ &= cx^2\left(a(-7 + 6x - 2x^2) + 2\right) \\ &= cx^2\left(-4x^4 + 16x^3 - 28x^2 + 20x - 5\right) \\ &= -cx^2\left(4(x-1)^4 + (2x-1)^2\right) \\ &< 0. \end{aligned} \quad (136)$$

Therefore, $g'(x) < 0$ for $0 < x < 1$. Consequently, the function $g(x)$ is strictly decreasing on [0, 1].

In case 4, with $\sigma_1^2 = \sigma_2^2 = \sigma_0^2 > 0$, $\sigma_3^2 = \sigma_4^2 = \sigma^2 > 0$ and $a = x^2 + (1-x)^2$, we have

$$g(x) = \frac{-c + (1-x)a\sigma^2 - xa\sigma_0^2}{1 + x(1-x)a(\sigma^2 + \sigma_0^2)}. \quad (137)$$

Under the condition $\sigma^2 > c$, the derivative of $g(x)$ for $0 < x < 1$ is given by

$$\begin{aligned} g'(x) = &\frac{1}{\left(1 + x(1-x)a(\sigma^2 + \sigma_0^2)\right)^2} \\ &\times \Big[(-6x^2 + 8x - 3)\sigma^2 + (-6x^2 - 4x - 1)\sigma_0^2 \\ &+ (\sigma^2 + \sigma_0^2)\left(-c(2x-1)^3 - \sigma^2 a^2(1-x)^2 - \sigma_0^2 a^2 x^2\right)\Big], \end{aligned} \quad (138)$$

where $-6x^2 + 8x - 3 \leq -\frac{1}{3} < 0$, $-6x^2 - 4x - 1 < 0$ and

$$\begin{aligned} &-c(2x-1)^3 - \sigma^2 a^2(1-x)^2 - \sigma_0^2 a^2 x^2 \\ &< -c\left((2x-1)^3 + a^2(1-x)^2\right) - \sigma_0^2 a^2 x^2 \\ &= -cx^2\left(4(x-1)^4 + (2x-1)^2\right) - \sigma_0^2 a^2 x^2 \\ &< 0. \end{aligned} \quad (139)$$

Thus, $g'(x) < 0$ for $0 < x < 1$, from which the function $g(x)$ is strictly decreasing on [0, 1].

Finally, in case 5, with $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = \sigma_4^2 = \sigma^2 > c > 0$ and $a = x^2 + (1-x)^2$, the expression of $g(x)$ takes the form

$$g(x) = \frac{-c + (1-2x)a\sigma^2}{1 + 2x(1-x)a\sigma^2}, \quad (140)$$

whose derivative for $0 < x < 1$ is

$$g'(x) = \frac{(-12x^2 + 12x - 4)\sigma^2 + 2\sigma^2\left(c(1-2x)^3 - \sigma^2 a^3\right)}{\left(1 + 2x(1-x)a\sigma^2\right)^2}, \quad (141)$$

where $-12x^2 + 12x - 4 \leq -1 < 0$ and

$$\begin{aligned} c(1-2x)^3 - \sigma^2 a^3 &< -c\left((2x-1)^3 + a^3\right) \\ &= -2cx^2\left((2x-1)^2 + 2a(x-1)^2\right) \\ &< 0. \end{aligned} \quad (142)$$

We conclude that $g'(x) < 0$ for $0 < x < 1$, from which the function $g(x)$ is strictly decreasing on [0, 1].

In addition, with $\psi(y) = \exp\left(-2\int_0^y g(x)dx\right) > 0$, $\phi(y) = \exp\left(2\int_y^1 g(x)dx\right) > 0$ and $g'(y) < 0$ for $0 < y < 1$ in cases 1, 3, 4, 5, we have

$$\psi''(y) = 2\psi(y)\left(2g^2(y) - g'(y)\right) > 0 \quad (143)$$

and

$$\phi''(y) = 2\phi(y)\left(2g^2(y) - g'(y)\right) > 0 \quad (144)$$

on (0, 1), from which $\psi(y)$ and $\phi(y)$ are strictly convex functions on [0,1].

Appendix D. Monotonicity of $\psi(y)$ as function of σ^2 in case 5

In case 5, with $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = \sigma_4^2 = \sigma^2 > 0$, we have

$$g(x) = \frac{-c + (1-2x)a\sigma^2}{1 + 2x(1-x)a\sigma^2}, \quad (145)$$

where $a = x^2 + (1-x)^2$. We show that, with respect to $\sigma^2 > 0$ and for every $y \in (0, 1]$, the function

$$k(y) = -\frac{\ln\psi(y)}{2} = \int_0^y g(x)dx \quad (146)$$

is strictly increasing so that

$$\psi(y) = \exp\left(-2k(y)\right) \quad (147)$$

is strictly decreasing. For $y \in (0, 1)$, we find

$$\frac{\partial k(y)}{\partial\sigma^2} = \int_0^y \frac{\partial g(x)}{\partial\sigma^2}dx = \int_0^y \frac{a\left(2cx(1-x) - (2x-1)\right)}{\left(1 + 2ax(1-x)\sigma^2\right)^2}dx. \quad (148)$$

It is easy to check that the integrand in (148) is positive on $[0, x^*)$ and negative on $(x^*, 1]$ with

$$x^* = \frac{1}{2} + \frac{\sqrt{c^2+1} - 1}{2c}. \quad (149)$$

This implies that the derivative in (148) is strictly increasing on $[0, x^*)$ and strictly decreasing on $(x^*, 1]$. Moreover, $\partial k(0)/\partial\sigma^2 = 0$

and

$$\begin{aligned}\frac{\partial k(1)}{\partial\sigma^2} &= \int_0^1 \frac{a\left(2cx(1-x)-(2x-1)\right)}{\left(1+2ax(1-x)\sigma^2\right)^2}dx\\ &= \int_0^{\frac{1}{2}} \frac{a\left(2cx(1-x)-(2x-1)\right)}{\left(1+2ax(1-x)\sigma^2\right)^2}dx\\ &\quad+\int_{\frac{1}{2}}^1 \frac{a\left(2cx(1-x)-(2x-1)\right)}{\left(1+2ax(1-x)\sigma^2\right)^2}dx\\ &= \int_0^{\frac{1}{2}} \frac{a\left(2cx(1-x)-(2x-1)\right)}{\left(1+2ax(1-x)\sigma^2\right)^2}dx\\ &\quad+\int_0^{\frac{1}{2}} \frac{a\left(2cx(1-x)+(2x-1)\right)}{\left(1+2ax(1-x)\sigma^2\right)^2}dx\\ &= \int_0^{\frac{1}{2}} \frac{4acx(1-x)}{\left(1+2ax(1-x)\sigma^2\right)^2}dx > 0. \end{aligned} \tag{150}$$

We can conclude that $\partial k(y)/\partial\sigma^2 > 0$ for $y \in (0, 1]$.

Appendix E. Existence of σ_*^2, σ_{**}^2 and σ_{***}^2 in cases 1 to 5

In cases 1 to 4, it is easy to check that

$$\lim_{\sigma^2\to\infty} g(x) = x^{-1}. \tag{151}$$

From (35) and (36) shown in Appendix B, $g(x)$ for $0 < x < 1$ strictly increases with respect to $\sigma^2 > 0$ and, therefore, $\psi(1) = \exp\left(-2\int_0^1 g(x)dx\right)$ strictly decreases. Moreover, when $\sigma^2 = 0$, we have $g(x) < 0$ for every $x \in [0, 1]$. This implies that $\psi(1) > 1$ for $\sigma^2 > 0$. On the other hand, owing to Fatou's lemma, we have

$$\lim_{\sigma^2\to\infty}\int_0^1 g(x)dx = \liminf_{\sigma^2\to\infty}\int_0^1 g(x)dx \geq \int_0^1 \lim_{\sigma^2\to\infty} g(x)dx. \tag{152}$$

Therefore, we get

$$\begin{aligned}\lim_{\sigma^2\to\infty}\psi(1) &= \lim_{\sigma^2\to\infty}\exp\left(-2\int_0^1 g(x)dx\right)\\ &\leq \exp\left(-2\int_0^1 \lim_{\sigma^2\to\infty} g(x)dx\right)\\ &= \exp\left(-2\int_0^1 x^{-1}dx\right)\\ &= 0. \end{aligned} \tag{153}$$

We conclude that the equation $\psi(1) = 1$ has a unique solution with respect to $\sigma^2 > 0$, denoted by σ_{**}^2. Then, we have $F_C > F_D$ if and only if $\sigma^2 > \sigma_{**}^2$.

In cases 1, 3 and 4, where $\psi(y)$ is a strictly convex function, the conditions $\psi(0) = 1$ and $\psi(1) = 1$ when $\sigma^2 = \sigma_{**}^2$ entail $\int_0^1 \psi(y)dy < 1$ when $\sigma^2 = \sigma_{**}^2$. Since this integral strictly decreases with respect to σ^2 and $\int_0^1 \psi(y)dy > 1$ when $\sigma^2 = 0$, the equation $\int_0^1 \psi(y)dy = 1$ has a unique solution with respect to σ^2 between 0 and σ_{**}^2, denoted by σ_*^2. Then, we have $F_C > N^{-1}$ if and only if $\sigma^2 > \sigma_*^2$.

Moreover, we know that $F_D = F_C > N^{-1}$ when $\sigma^2 = \sigma_{**}^2$. Using Fatou's lemma and the inequalities $e^x \geq 1 + x > x$ for $x > 0$, we get

$$\begin{aligned}\lim_{\sigma^2\to\infty} F_D &= \lim_{\sigma^2\to\infty}\frac{1}{N\int_0^1\phi(y)dy}\\ &= \left(N\lim_{\sigma^2\to\infty}\int_0^1\exp\left(2\int_y^1 g(x)dx\right)dy\right)^{-1}\\ &\leq \left(N\int_0^1\exp\left(2\int_y^1 \lim_{\sigma^2\to\infty} g(x)dx\right)dy\right)^{-1}\\ &= \left(N\int_0^1\exp\left(2(y^{-2}-1)\right)dy\right)^{-1}\\ &\leq \left(2N\int_0^1 (y^{-2}-1)dy\right)^{-1}\\ &= 0. \end{aligned} \tag{154}$$

Owing to (35) and (36) proved in Appendix B, we know that $\phi(y) = \exp\left(2\int_y^1 g(x)dx\right)$ is strictly increasing with respect to $\sigma^2 > 0$ for $y \in [0, 1)$. Therefore, F_D is a strictly decreasing function of σ^2. Thus, there must exist a threshold value of $\sigma^2 > \sigma_{**}^2$, denoted by σ_{***}^2, which is the unique solution of the equation $\int_0^1\phi(y)dy = 1$. If $\sigma^2 > \sigma_{***}^2$, then $F_D < N^{-1}$.

In case 2, it is still possible to ascertain the existence of σ_*^2, since $\int_0^1\psi(y)dy > 1$ when $\sigma^2 = 0$ and

$$\lim_{\sigma^2\to\infty}\int_0^1\psi(y)dy \leq \int_0^1\exp\left(-2\int_0^y x^{-1}dx\right)dy = 0. \tag{155}$$

However, $c < \sigma_*^2 < \sigma_{**}^2$ can no longer be guaranteed.

In case 5, we have

$$g(x) = \frac{-c + (1-2x)a\sigma^2}{1 + 2x(1-x)a\sigma^2} \tag{156}$$

with $a = x^2 + (1-x)^2$. Moreover, we find

$$\begin{aligned}\int_0^1 g(x)dx &= \int_0^{\frac{1}{2}} g(x)dx + \int_{\frac{1}{2}}^1 g(x)dx\\ &= \int_0^{\frac{1}{2}} g(x)dx + \int_0^{\frac{1}{2}} g(1-x)dx\\ &= \int_0^{\frac{1}{2}} \frac{-c+(1-2x)a\sigma^2}{1+2x(1-x)a\sigma^2}dx\\ &\quad+\int_0^{\frac{1}{2}} \frac{-c+(2x-1)a\sigma^2}{1+2x(1-x)a\sigma^2}dx\\ &= -2c\int_0^{\frac{1}{2}}\frac{1}{1+2x(1-x)a\sigma^2}dx. \end{aligned} \tag{157}$$

Since the integrand in (157) is bounded by 1 and uniformly converges to 0 as $\sigma^2 \to \infty$ on $[\varepsilon, 1/2]$ for $\varepsilon > 0$, we have

$$\begin{aligned}\lim_{\sigma^2\to\infty}\psi(1,\sigma^2) &= \lim_{\sigma^2\to\infty}\exp\left(-2\int_0^1 g(x)dx\right)\\ &= \exp\left(-2\lim_{\sigma^2\to\infty}\int_0^1 g(x)dx\right)\\ &= \exp\left(4c\lim_{\sigma^2\to\infty}\int_0^{\frac{1}{2}}\frac{1}{1+2x(1-x)a\sigma^2}dx\right)\\ &= 1. \end{aligned} \tag{158}$$

From Appendix C, we already know that $\psi(1)$ is strictly decreasing with respect to σ^2 for $y \in (0, 1]$. Thus, we have $\psi(1) > 1$ for $\sigma^2 > 0$, which implies that Eq. (33) can never be satisfied. As a matter of fact, we always have $F_C < F_D$ and σ_{**}^2 does not exist. Moreover, since $\phi(y)$ is a strictly convex function on [0, 1] with $\phi(0) = \psi(1)^{-1} < 1$ and $\phi(1) = 1$, we have $\phi(y) < 1$ for $y \in [0, 1)$. This tells us that condition (32) can never be satisfied. We always have $F_D > N^{-1}$ and σ_{***}^2 does not exist. The only threshold value of σ^2 in this case is σ_*^2, since $\psi(y)$ is a strictly convex function on [0, 1] and a strictly decreasing function with respect to σ^2 for $y \in (0, 1]$ (see Appendix D). Its boundary value

$\psi(0) = 1$ with $\psi'(0) = 2c - 2\sigma^2 < 0$ for σ^2 large enough, along with Eq. (158), guarantees the existence of σ_*^2 which is the unique value of $\sigma^2 > 0$ such that $\int_0^1 \psi(y)dy = 1$.

Appendix F. Condition for $\psi(1) < 1$ in the additive RPD with $b(t) = rc(t)$

We consider an additive RPD game where the benefit $b(t)$ is linear with respect to the cost $c(t)$, that is, $b(t) = rc(t)$. Here, r is a constant that represents the "benefit to cost ratio". Then we have $\sigma_{bc} = r\sigma_c^2$, from which

$$g(x) = \frac{-\mu_c + x(r-1)\sigma_c^2}{1 + x(1-x)\sigma_c^2}. \tag{159}$$

Moreover, the denominator can be expressed as

$$\begin{aligned} 1 + x(1-x)\sigma_c^2 &= 1 + \frac{\sigma_c^2}{4} - \left(-\frac{\sigma_c^2}{4} + x\sigma_c^2 - x^2\sigma_c^2\right) \\ &= \left(\frac{A}{2}\right)^2 - \left(\left(\frac{1}{2} - x\right)\sigma_c\right)^2 \\ &= \left(\frac{A}{2} + \left(\frac{1}{2} - x\right)\sigma_c\right)\left(\frac{A}{2} - \left(\frac{1}{2} - x\right)\sigma_c\right), \end{aligned} \tag{160}$$

where $A = \sqrt{4 + \sigma_c^2}$. Assuming $g(x)$ in the form

$$g(x) = \frac{S_1}{\frac{A}{2} + \left(\frac{1}{2} - x\right)\sigma_c} - \frac{S_2}{\frac{A}{2} - \left(\frac{1}{2} - x\right)\sigma_c}, \tag{161}$$

we have the equations

$$S_1\left(\frac{A}{2} - \frac{\sigma_c}{2}\right) - S_2\left(\frac{A}{2} + \frac{\sigma_c}{2}\right) = -\mu_c, \tag{162}$$

$$(S_1 + S_2)\sigma_c = (r-1)\sigma_c^2, \tag{163}$$

which are equivalent to

$$S_1 - S_2 = \frac{-2\mu_c + (r-1)\sigma_c^2}{A}, \tag{164}$$

$$S_1 + S_2 = (r-1)\sigma_c. \tag{165}$$

Thus, we get

$$\begin{aligned} \psi(y) &= \exp\left(-2\int_0^y g(x)dx\right) \\ &= \exp\Big(-2\Big(-\frac{S_1}{\sigma_c}\ln\left(\frac{A}{2} + \left(\frac{1}{2} - y\right)\sigma_c\right) \\ &\quad -\frac{S_2}{\sigma_c}\ln\left(\frac{A}{2} - \left(\frac{1}{2} - y\right)\sigma_c\right) \\ &\quad +\frac{S_1}{\sigma_c}\ln\left(\frac{A}{2} + \frac{\sigma_c}{2}\right) + \frac{S_2}{\sigma_c}\ln\left(\frac{A}{2} - \frac{\sigma_c}{2}\right)\Big)\Big) \\ &= \left(\frac{A + \sigma_c - 2\sigma_c y}{A + \sigma_c}\right)^{\frac{S_1}{\sigma_c}}\left(\frac{A - \sigma_c + 2\sigma_c y}{A - \sigma_c}\right)^{\frac{S_2}{\sigma_c}}, \end{aligned} \tag{166}$$

from which

$$\psi(1) = \left(\frac{A - \sigma_c}{A + \sigma_c}\right)^{\frac{S_1 - S_2}{\sigma_c}}. \tag{167}$$

Since $A + \sigma_c \geq A - \sigma_c > 0$, the condition $\psi(1) < 1$ is satisfied if and only if $S_1 - S_2 > 0$, which means

$$r - 1 > \frac{2\mu_c}{\sigma_c^2}. \tag{168}$$

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