

**Evolutionary stability concepts in a stochastic environment**Xiu-Deng Zheng,<sup>1</sup> Cong Li,<sup>2</sup> Sabin Lessard,<sup>2,\*</sup> and Yi Tao<sup>1,3,†</sup><sup>1</sup>Key Laboratory of Animal Ecology and Conservation Biology, Centre for Computational and Evolutionary Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China<sup>2</sup>Department of Mathematics and Statistics, University of Montreal, Montreal QC H3C 3J7, Canada<sup>3</sup>University of Chinese Academy of Sciences, Beijing 100101, China

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Over the past 30 years, evolutionary game theory and the concept of an evolutionarily stable strategy have been not only extensively developed and successfully applied to explain the evolution of animal behaviors, but also widely used in economics and social sciences. Nonetheless, the stochastic dynamical properties of evolutionary games in randomly fluctuating environments are still unclear. In this study, we investigate conditions for stochastic local stability of fixation states and constant interior equilibria in a two-phenotype model with random payoffs following pairwise interactions. Based on this model, we develop the concepts of stochastic evolutionary stability (SES) and stochastic convergence stability (SCS). We show that the condition for a pure strategy to be SES and SCS is more stringent than in a constant environment, while the condition for a constant mixed strategy to be SES is less stringent than the condition to be SCS, which is less stringent than the condition in a constant environment.

DOI: [10.1103/PhysRevE.96.032414](https://doi.org/10.1103/PhysRevE.96.032414)**I. INTRODUCTION**

It is clear that a range of problems in evolution theory can most appropriately be tackled by extending the theory of games which is a branch of mathematics. The problems are diverse and include not only the behavior of animals in contest situations but also some problems in the evolution of genetic mechanisms and in the evolution of ecosystems. Thirty-four years ago, Maynard Smith [1] monograph *Evolution and the Theory of Games* was published. A new fundamental theoretical framework to understand the evolution of animal behavior had reached maturity and was finally made available to a large readership. Since then evolutionary game theory has been very popular not only in biology but also in economics and social sciences.

Evolutionary game theory started with the concept of *evolutionarily stable strategy* (ESS) introduced by Maynard Smith and Price [2], which has become one of the principal tools for analyzing the dynamics of natural selection. Let us recall that an ESS is a strategy understood as a behavioral phenotype such that, if all the members of a population adopt it, then no mutant strategy could invade the population under the effect of natural selection [1,3]. In the context of symmetric pairwise interactions occurring at random in an infinite population, a strategy  $\mathbf{x}$  is an ESS if (1) the payoff to  $\mathbf{x}$  against itself is larger or equal to the payoff to any other strategy  $\mathbf{y}$  against  $\mathbf{x}$ , and (2) the payoff to  $\mathbf{x}$  against  $\mathbf{y}$  exceeds the payoff to  $\mathbf{y}$  against itself in the case of an equality in (1). With  $E(\mathbf{x}, \mathbf{y})$  representing the payoff received by an individual using strategy  $\mathbf{x}$  against an individual using strategy  $\mathbf{y}$ , this means that (1)  $E(\mathbf{x}, \mathbf{x}) \geq E(\mathbf{y}, \mathbf{x})$  for any strategy  $\mathbf{y} \neq \mathbf{x}$ , and (2)  $E(\mathbf{x}, \mathbf{y}) > E(\mathbf{y}, \mathbf{y})$  in the case of an equality in (1). These conditions are necessary and sufficient for the expected payoff to  $\mathbf{x}$  to exceed the expected payoff to  $\mathbf{y}$  in an infinite population of individuals using either  $\mathbf{x}$  or  $\mathbf{y}$  if the frequency of  $\mathbf{y}$  is small enough.

If the relative growth rate of a strategy is given by its expected payoff, which defines its fitness, then the dynamics of the strategy frequencies is described by the *replicator equation* [4,5]. For  $n$  pure strategies, we have  $\dot{x}_i = x_i((\mathbf{A}\mathbf{x})_i - \mathbf{x}\mathbf{A}\mathbf{x})$ , where  $\mathbf{x} = (x_1, \dots, x_n)$  is the strategy frequency vector, with  $x_i$  being the frequency of strategy  $i$  for  $i = 1, \dots, n$ , and  $\mathbf{A} = (a_{ij})$  is the payoff matrix, with  $a_{ij}$  being the payoff to strategy  $i$  against strategy  $j$  for  $i, j = 1, \dots, n$ . Here it is understood that  $\mathbf{x}\mathbf{A}\mathbf{x} = \sum_{i=1}^n x_i(\mathbf{A}\mathbf{x})_i = \sum_{i=1}^n \sum_{j=1}^n x_i x_j a_{ij}$  with  $(\mathbf{A}\mathbf{x})_i$  being the expected payoff to strategy  $i$  for  $i = 1, \dots, n$ . Moreover, if  $\mathbf{x}$  is an ESS with respect to the mixed strategies of the  $n$  pure strategies with the bilinear payoff function  $E(\mathbf{x}, \mathbf{y}) = \mathbf{x}\mathbf{A}\mathbf{y}$ , then it is an asymptotically stable rest point of the above replicator dynamics [5]. In the special case  $n = 2$ , the payoff matrix takes the form  $\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$ , and the replicator dynamics for the frequency of strategy 1, represented by  $x$ , reduces to  $\dot{x} = x(1-x)[(a_{11} - a_{12} - a_{21} + a_{22})x - (a_{22} - a_{21})]$ . Moreover, strategy 1 is an ESS if  $a_{11} > a_{21}$ , or  $a_{11} = a_{21}$  and  $a_{12} > a_{22}$ . These conditions are necessary and sufficient for the expected payoff to strategy 1 to exceed the expected payoff to strategy 2 in an infinite population when strategy 2 is rare enough. On the other hand, we have to point out that for the connection between evolutionary game dynamics and population dynamics in ecology, Hofbauer and Sigmund [5] show also that the classic Lotka-Volterra equation can be easily transformed into a replicator equation by introducing an auxiliary variable.

In a population of fixed finite size  $N$ , any fixation state can be reached from any initial state by random drift. In this framework, Nowak *et al.* [6] proposed to call strategy 1 an  $\text{ESS}_N$  if two conditions hold when the initial frequency of strategy 2 is  $N^{-1}$ : (1) strategy 2 has a lower expected payoff than strategy 1 as in Schaffer [7], in which case selection is said to oppose strategy 2 *invading* strategy 1; and (2) the probability of ultimate fixation of strategy 2 is less than  $N^{-1}$ , in which case selection is said to oppose strategy 2 *replacing* strategy 1. In general, these conditions depend on the population size  $N$  and the reproduction scheme [8]. Note that condition (2) is neither sufficient nor necessary for the probability of ultimate

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fixation of a single strategy 1 to exceed the probability of ultimate fixation of a single strategy 2. This condition ensures, however, that strategy 1 is more *abundant* on average than strategy 2 in the presence of recurrent mutation occurring at weak enough rate [9].

One key assumption in classical evolutionary game theory is that the payoff matrix is constant, and this supposes that the environmental conditions do not change over time. However, this assumption cannot be thought to be always true since environmental conditions in the real world are changing and uncertain. For the population dynamics in ecology, May [10] pointed out that since real environments are uncertain and stochastic, the birth rates, carrying capacities, competition coefficients, and other parameters which characterize natural biological systems all, to a greater or lesser degree, exhibit random fluctuations. One of May's studies reveals profoundly how the stochastic fluctuation of carrying capacity (i.e., environmental stochasticity) influences the dynamics of a single-species population. In fact, effects of environmental stochasticity on population and community ecology have been investigated by many authors [11–14]. Spagnolo *et al.* [13], for instance, investigated some phenomena in Lotka-Volterra systems induced by environmental noise, for examples, quasideterministic oscillations, stochastic resonance, noise-delayed extinction, and spatial patterns. All of these studies in ecology strongly imply that the effects of environmental stochasticity on evolutionary dynamics should be considered.

We here also have to point out that the previous work on stochastic evolutionary game theory in an infinite and classical population includes Foster and Young [15], who considered small perturbations of the deterministic replicator dynamics that arise through mutations as well as ordinary chance events that affect the reproductive success of strategies. Then the strategy frequencies obey the stochastic differential equation  $\dot{x}_i = x_i[(\mathbf{A}\mathbf{x})_i - \mathbf{x}\mathbf{A}\mathbf{x}] + \sigma[\Gamma(\mathbf{x})\mathbf{W}]_i$ . Here  $\mathbf{W}$  is a formal time derivative of a standard  $n$ -dimensional Brownian motion  $\mathbf{W}$ , called a white noise,  $\Gamma(\mathbf{x})$  is a variance-covariance matrix with all bounded entries and ones on the main diagonal such that  $\mathbf{x}\Gamma(\mathbf{x}) = \mathbf{0}$ , while  $\sigma > 0$  is a parameter that represents the strength of the perturbation. In this stochastic dynamical system, a set of states  $S$  is called a *stochastically stable set* (SSS) if, in the long run, it is nearly certain that the system lies within every open set containing  $S$  as  $\sigma$  tends to zero. The stochastically stable set is always nonempty and minimizes a suitably defined potential function. However, it is by no means equivalent to the set of evolutionary stable strategies even when the latter exist. It contains often only a subset of the evolutionarily stable strategies, and sometimes even none. So a natural and challenging question is what happens to evolutionary game concepts and dynamics under the effects of a stochastically varying environment.

Since environmental conditions in the real world are changing and uncertain, stochastic fluctuations in the surrounding environment of a population may cause changes in the occurrence of interactions between individuals and, more importantly, changes in the payoffs received by the interacting individuals. Therefore, unless stochastic fluctuations are so small that their effects can be neglected, there is no *a priori* reason to assume that the payoff matrix of an evolutionary game is constant if the environment is actually stochastic.

Now assuming that the payoff matrix is random, two questions arise: First, how should we define the concept of *stochastic evolutionary stability* (SES) so that it would be a natural extension of the evolutionary stability concept in a stochastic environment in the sense that, once fixed, it would still be probabilistically favored by selection? Second, what would be the exact evolutionary properties associated with a strategy that is SES? In particular, are there extra conditions that would make it *stochastically convergence stable* (SCS) in such a way that evolution toward it from other fixation states would be probabilistically favored by selection under random perturbations in an analogous way as a convergence stable strategy is favored in a deterministic environment [16–19]. Answers to these questions are important in order to understand and predict the evolution of animal behaviors in a randomly fluctuating environment.

In this study, we focus attention on the effect of a stochastic environment on a  $2 \times 2$  matrix game in an infinite population. Generations are discrete, nonoverlapping, and the payoff matrices over successive generations are independent identically distributed random matrices. The main mathematical tool in this study is the concept of *stochastic local stability*, which was developed in population genetics by Karlin and Liberman [20,21] (see also Ref. [22]).

## II. A TWO-PHENOTYPE MODEL

We consider an evolutionary game in an infinite population with discrete, nonoverlapping, generations. There are two phenotypes or pure strategies, 1 and 2, and the payoffs in pairwise interactions at time step  $t \geq 0$  are given by the game matrix

$$\mathbf{A}(t) = \begin{pmatrix} a_{11}(t) & a_{12}(t) \\ a_{21}(t) & a_{22}(t) \end{pmatrix} = \begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix}, \quad (1)$$

where  $a_{ij}(t)$  is the payoff to strategy  $i$  against strategy  $j$  for  $i, j = 1, 2$ . These payoffs are assumed to be positive random variables that are uniformly bounded below and above by some positive constants. Therefore, there exist real numbers  $A, B > 0$  such that  $A \leq a_{ij}(t) \leq B$  for  $i, j = 1, 2$  and all  $t \geq 0$ . Moreover, the probability distributions of  $a_{ij}(t)$  for  $i, j = 1, 2$  do not depend on  $t \geq 0$ . They have means, variances, and covariances given by

$$\begin{aligned} \mathbb{E}[a_{ij}(t)] &= \bar{a}_{ij}, \\ \mathbb{E}[\{a_{ij}(t) - \bar{a}_{ij}\}^2] &= \sigma_{ij}^2, \\ \mathbb{E}[\{a_{ij}(t) - \bar{a}_{ij}\}\{a_{kl}(t) - \bar{a}_{kl}\}] &= \sigma_{ij,kl}, \end{aligned} \quad (2)$$

respectively, for  $i, j, k, l = 1, 2$  with  $(i, j) \neq (k, l)$ , where  $\mathbb{E}$  denotes mathematical expectation. As for  $s \neq t$ , the payoffs  $a_{ij}(s)$  and  $a_{kl}(t)$  are assumed to be independent so that  $\mathbb{E}[\{a_{ij}(s) - \bar{a}_{ij}\}\{a_{kl}(t) - \bar{a}_{kl}\}] = 0$  for  $i, j, k, l = 1, 2$ .

Let  $x_t$  be the frequency of strategy 1 at time step  $t \geq 0$  and, similarly,  $1 - x_t$  the frequency of strategy 2. Then the mean payoffs to strategies 1 and 2 are given by

$$\begin{aligned} \pi_{1,t} &= x_t a_t + (1 - x_t) b_t, \\ \pi_{2,t} &= x_t c_t + (1 - x_t) d_t, \end{aligned} \quad (3)$$

respectively, and the mean payoff in the whole population by

$$\bar{\pi}_t = x_t \pi_{1,t} + (1 - x_t) \pi_{2,t}. \quad (4)$$

Assuming that payoff translates into reproductive success, referred to as fitness, so that the number of replicas of a strategy from one step to the next is proportional to its mean payoff, the frequency of strategy 1 at time step  $t + 1$  is given by the recurrence equation

$$x_{t+1} = \frac{x_t \pi_{1,t}}{\bar{\pi}_t} = \frac{x_t^2 a_t + x_t(1 - x_t) b_t}{x_t^2 a_t + x_t(1 - x_t)(b_t + c_t) + (1 - x_t)^2 d_t} \quad (5)$$

for  $t \geq 0$ . Defining

$$u_t = \frac{x_t}{1 - x_t}, \quad (6)$$

the recurrence equation takes the simple form

$$u_{t+1} = u_t \left[ \frac{u_t a_t + b_t}{u_t c_t + d_t} \right] \quad (7)$$

for  $t \geq 0$ .

### III. STOCHASTIC LOCAL STABILITY

We are interested in the asymptotic (or long-run) behavior of the process  $\{x_t\}$  for  $t \geq 0$ . Let  $\hat{x}$  represent a constant (non-random) equilibrium of this process, that is, an equilibrium of Eq. (5) that does not depend on the randomness of the payoff matrix. This is clearly the case for both  $\hat{x} = 0$  and  $\hat{x} = 1$ , called the *fixation states* or the *boundary equilibria*. This may also be the case for a constant equilibrium  $\hat{x}$  with  $0 < \hat{x} < 1$ , called a *constant interior equilibrium*.

Following Karlin and Liberman [20–22], a constant equilibrium  $\hat{x}$  is said to be *stochastically locally stable* (SLS) if for any  $\epsilon > 0$  there exists  $\delta_0 > 0$  such that

$$\mathbb{P}(x_t \rightarrow \hat{x}) \geq 1 - \epsilon \text{ as soon as } |x_0 - \hat{x}| < \delta_0. \quad (8)$$

This means that  $x_t$  tends to  $\hat{x}$  as  $t \rightarrow \infty$  with probability arbitrarily close to 1 (but different from 1) if the initial state  $x_0$  is sufficiently near  $\hat{x}$ . Notice, however, no matter how close  $x_0$  is to  $\hat{x}$  (but different from  $\hat{x}$ ), it is not ascertained that  $x_t$  will converge to  $\hat{x}$ . Statistical fluctuations could cause  $x_t$  to depart sharply from  $\hat{x}$ , but this will occur with small probability if  $x_0$  is close to  $\hat{x}$  and  $\hat{x}$  is stochastically locally stable.

On the other hand, a constant equilibrium  $\hat{x}$  can be said to be *stochastically locally unstable* (SLU) if

$$\mathbb{P}(x_t \rightarrow \hat{x}) = 0 \text{ as soon as } |x_0 - \hat{x}| > 0. \quad (9)$$

If this is the case, then  $\hat{x}$  cannot be reached with probability 1 from any initial state different from  $\hat{x}$ .

#### A. Stochastic local stability of fixation states

Consider first the fixation state  $\hat{x} = 0$  in Eq. (5), which corresponds to the equilibrium  $\hat{u} = \hat{x}/(1 - \hat{x}) = 0$  in Eq. (7). It can be shown that  $\hat{x} = 0$  is SLS if

$$\mathbb{E} \left[ \log \left( \frac{d_t}{b_t} \right) \right] = \mathbb{E}(\log d_t) - \mathbb{E}(\log b_t) > 0, \quad (10)$$

and SLU if the inequality is reversed (Result 1, proved in Appendix A 1).

Therefore, under generic conditions, the inequality Eq. (10) is necessary and sufficient for stochastic local stability of the fixation state  $\hat{x} = 0$ . This result in a population genetics framework, which corresponds to a symmetric game matrix [ $a_{12}(t) = a_{21}(t)$ , which can be assumed equal to one without loss of generality] was stated in Karlin and Liberman [20]. A proof in this framework which only slightly differs from the present more general game-theoretic framework is given in Karlin and Liberman [21]. It is based on the strong law of large numbers and Egorov's theorem.

Suppose random payoffs close enough to their means so that

$$\mathbb{E}(\log b_t) = \log \bar{b} - \frac{\sigma_b^2}{2\bar{b}^2} + o(\sigma^2), \quad (11)$$

$$\mathbb{E}(\log d_t) = \log \bar{d} - \frac{\sigma_d^2}{2\bar{d}^2} + o(\sigma^2),$$

where  $\bar{b}$  and  $\bar{d}$  are the means, and  $\sigma_b^2$  and  $\sigma_d^2$  the variances, of the random variables  $b_t$  and  $d_t$ , respectively. Here  $\sigma^2 = \max\{\sigma_a^2, \sigma_b^2, \sigma_c^2, \sigma_d^2\}$ . Thus, if  $\sigma^2$  is small enough, the condition in Eq. (10) for  $\hat{x} = 0$  to be SLS reduces to

$$\log \left( \frac{\bar{d}}{\bar{b}} \right) > \frac{1}{2} \left( \frac{\sigma_d^2}{\bar{d}^2} - \frac{\sigma_b^2}{\bar{b}^2} \right). \quad (12)$$

If the inequality is reversed, then  $\hat{x} = 0$  is SLU. Therefore, the condition for  $\hat{x} = 0$  to be SLS becomes less stringent as  $\sigma_b^2$  increases and more stringent as  $\sigma_d^2$  decreases. In the case where  $\sigma_b^2 = \sigma_d^2 = \sigma^2$ , the fixation state  $\hat{x} = 0$  is SLS if  $\bar{d} > \bar{b}$  and SLU if  $\bar{d} < \bar{b}$ . These are the conditions for  $\hat{x} = 0$  to be locally stable and locally unstable, respectively, with a constant payoff matrix which corresponds to the case  $\sigma^2 = 0$ .

By symmetry, Result 1 implies that the fixation state  $\hat{x} = 1$  in the recurrence equation [Eq. (5)] is stochastically locally stable if

$$\mathbb{E} \left[ \log \left( \frac{a_t}{c_t} \right) \right] > 0, \quad (13)$$

and stochastically locally unstable if the inequality is reversed. The above condition reduces to

$$\log \left( \frac{\bar{a}}{\bar{c}} \right) > \frac{1}{2} \left( \frac{\sigma_a^2}{\bar{a}^2} - \frac{\sigma_c^2}{\bar{c}^2} \right) \quad (14)$$

if  $a_t$  and  $c_t$  have means  $\bar{a}$  and  $\bar{c}$ , and variances  $\sigma_a^2$  and  $\sigma_c^2$  of order  $\sigma^2$  small enough.

As an example, consider successive rounds of the Prisoner's Dilemma, known as the iterated Prisoner's Dilemma (IPD), with two possible strategies in use, TFT for *tit-for-tat* starting with cooperation in the first round and the previous strategy of the opponent in the next rounds and AID for *always-defect* with defection in all rounds as strategies 1 and 2, respectively [23,24]. The payoff matrix at time step  $t \geq 0$  is given by

$$\begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix} = \begin{pmatrix} m_t R & S + (m_t - 1)P \\ T + (m_t - 1)P & m_t P \end{pmatrix},$$

where  $T > R > P > S$  are the payoffs in one round of the game with cooperation and defection as strategies, and  $m_t$  represents the number of rounds at time step  $t \geq 0$ . This

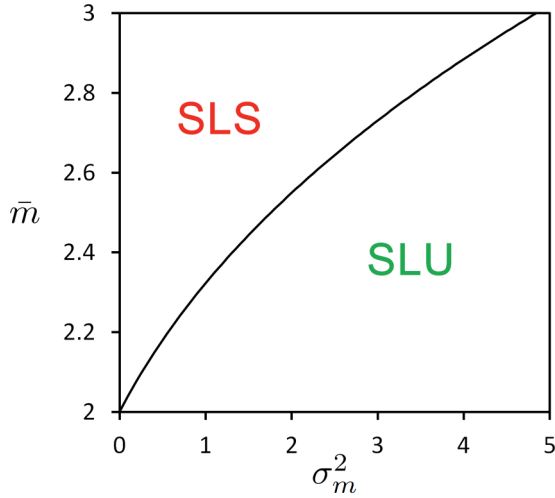


FIG. 1. Stochastic local stability of TFT fixation against ALLD with the random payoff matrix  $\begin{pmatrix} 3m_t & 2m_t - 1 \\ 2m_t & 2m_t - 1 \end{pmatrix}$ , where  $T = 4$ ,  $R = 3$ ,  $P = 2$ , and  $S = 1$ , while  $m_t$  is a random variable with mean  $\bar{m}$  and variance  $\sigma_m^2$  at every time step  $t \geq 0$ . The curve separates the regions for stochastic local stability and stochastic local instability: TFT fixation is SLS (or SLU) if the point  $(\sigma_m^2, \bar{m})$  is above (or below) the curve.

number is assumed to be a random variable of mean  $\bar{m}$  and small variance  $\sigma_m^2$  that is independent of  $m_s$  for all  $s \neq t$ . We are in the above context with

$$\begin{aligned} \bar{a} &= \bar{m}R, & \bar{b} &= S + (\bar{m} - 1)P, \\ \bar{c} &= T + (\bar{m} - 1)P, & \bar{d} &= \bar{m}P, \end{aligned}$$

while

$$\sigma_a^2 = R^2\sigma_m^2, \quad \sigma_b^2 = \sigma_c^2 = \sigma_d^2 = P^2\sigma_m^2.$$

Since  $\sigma_b^2 = \sigma_d^2$  and  $\bar{d} > \bar{b}$ , ALLD fixation is SLS. On the other hand, TFT fixation is SLS if

$$\log\left(\frac{\bar{a}}{\bar{c}}\right) > \frac{\sigma_m^2}{2\bar{c}^2\bar{a}^2}(\bar{c}^2R^2 - \bar{a}^2P^2)$$

with

$$-\bar{c}^2R^2 - \bar{a}^2P^2 = [\bar{m}RP + (T - R)R]^2 - (\bar{m}RP)^2 > 0.$$

This means a more stringent condition as  $\sigma_m^2$  increases compared to the condition  $\bar{a} > \bar{c}$  when  $\sigma_m^2 = 0$ , which is equivalent to  $\bar{m} > (T - P)/(R - P)$ . In a stochastic environment, the mean number of rounds must exceed a higher threshold value for TFT fixation to be SLS. For instance, let  $T = 4$ ,  $R = 3$ ,  $P = 2$ , and  $S = 1$ . Then, for the stochastic local stability of TFT fixation, the curve plotted on the  $(\sigma_m^2, \bar{m})$  plane (see Fig. 1) distinguishes the regions of SLS and SLU: TFT fixation is SLS (or SLU) if the point  $(\sigma_m^2, \bar{m})$  is above (or below) the curve. When  $\sigma_m^2 = 0$ , TFT fixation is SLS if  $\bar{m} > 2$ . When  $\sigma_m^2 > 0$ , however, this occurs if

$$\log\left[\frac{3\bar{m}}{2(\bar{m} + 1)}\right] > \frac{\sigma_m^2}{2\bar{m}^2(\bar{m} + 1)^2}(2\bar{m} + 1).$$

This inequality is satisfied if and only if  $\bar{m} > m(\sigma_m^2)$ , where the threshold value  $m(\sigma_m^2)$  is an increasing function of  $\sigma_m^2$ . This

clearly illustrates the fact that stochastic local stability of TFT fixation depends not only on the mean of the number of rounds  $\bar{m}$  but also on its variance  $\sigma_m^2$ , and that higher is the variance, higher must be the mean for TFT fixation to be SLS.

In the degenerate case where  $b_t = d_t$  for all  $t \geq 0$ , the stochastic local stability or instability of the fixation state  $\hat{x} = 0$  requires further analysis, and it can be shown that it is SLS if

$$\mathbb{E}\left(\frac{c_t}{d_t} - \frac{a_t}{d_t}\right) = \mathbb{E}\left(\frac{c_t}{d_t}\right) - \mathbb{E}\left(\frac{a_t}{d_t}\right) > 0, \quad (15)$$

and SLU if the inequality is reversed (Result 2, proved in Appendix A 2).

Developing the random variables around their means and using the approximations

$$\begin{aligned} \mathbb{E}\left(\frac{a_t}{d_t}\right) &= \frac{\bar{a}}{\bar{d}} + \frac{\bar{a}\sigma_d^2}{\bar{d}^3} - \frac{\sigma_{a,d}}{\bar{d}^2} + o(\sigma^2), \\ \mathbb{E}\left(\frac{c_t}{d_t}\right) &= \frac{\bar{c}}{\bar{d}} + \frac{\bar{c}\sigma_d^2}{\bar{d}^3} - \frac{\sigma_{c,d}}{\bar{d}^2} + o(\sigma^2), \end{aligned} \quad (16)$$

the condition in Result 2 for  $\hat{x} = 0$  to be SLS reduces to

$$\frac{\bar{c} - \bar{a}}{\bar{d}} > \frac{\sigma_{c,d} - \sigma_{a,d}}{\bar{d}^2 + \sigma_d^2} \quad (17)$$

if  $\sigma^2$  is small enough. If the inequality is reversed, then  $\hat{x} = 0$  is SLU. Therefore, the condition for  $\hat{x} = 0$  to be SLS becomes less stringent as  $\sigma_{a,d}$  increases and more stringent as  $\sigma_{c,d}$  decreases. In the case where  $\sigma_{a,d} = \sigma_{c,d}$ , the fixation state  $\hat{x} = 0$  is SLS if  $\bar{c} > \bar{a}$  and SLU if  $\bar{c} < \bar{a}$ . These are the conditions for  $\hat{x} = 0$  to be locally stable and locally unstable, respectively, with a constant payoff matrix.

## B. Stochastic local stability of a constant interior equilibrium

Now consider a constant equilibrium  $\hat{x}$  of Eq. (5) with  $0 < \hat{x} < 1$ . This corresponds to a constant equilibrium  $\hat{u} = \hat{x}/(1 - \hat{x}) > 0$  in Eq. (7). This is possible only if

$$\hat{u}(a_t - c_t) = d_t - b_t, \quad (18)$$

which implies a payoff matrix in the form

$$\begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix} = \begin{pmatrix} c_t + z_t & b_t \\ c_t & b_t + \hat{u}z_t \end{pmatrix} = \begin{pmatrix} a_t & d_t - \hat{u}z_t \\ a_t - z_t & d_t \end{pmatrix}, \quad (19)$$

where  $z_t = a_t - c_t$ . Moreover, taking expectation on both sides of Eq. (18) yields  $\hat{u} = (\bar{d} - \bar{b})/(\bar{a} - \bar{c})$  from which  $\hat{x} = (\bar{d} - \bar{b})/(\bar{a} - \bar{b} - \bar{c} + \bar{d})$ , where  $\bar{a}$ ,  $\bar{b}$ ,  $\bar{c}$ , and  $\bar{d}$  denote the expected values of  $a_t$ ,  $b_t$ ,  $c_t$ , and  $d_t$ , respectively.

It can be shown that the constant equilibrium  $\hat{x}$  with  $\hat{u} = \hat{x}/(1 - \hat{x}) > 0$  is SLS is

$$\mathbb{E}\left[\log\left(\frac{\hat{u}c_t + d_t}{\hat{u}a_t + d_t}\right)\right] = \mathbb{E}\left\{\log\left[1 - \frac{\hat{x}z_t}{\hat{x}a_t + (1 - \hat{x})d_t}\right]\right\} > 0, \quad (20)$$

and SLU if the inequality is reversed (Result 3, proved in Appendix A 3).



Assuming the approximation

$$\mathbb{E}[\log(\hat{u}a_t + d_t)] = \log(\hat{u}\bar{a} + \bar{d}) - \frac{\hat{u}^2\sigma_a^2 + \sigma_d^2 + 2\hat{u}\sigma_{a,d}}{2(\hat{u}\bar{a} + \bar{d})^2} + o(\sigma^2) \quad (21)$$

and the corresponding approximation for  $\mathbb{E}[\log(\hat{u}c_t + d_t)]$  lead to the condition

$$\log\left(\frac{\hat{u}\bar{c} + \bar{d}}{\hat{u}\bar{a} + \bar{d}}\right) > \frac{1}{2} \left[ \frac{\hat{u}^2\sigma_c^2 + 2\hat{u}\sigma_{c,d} + \sigma_d^2}{(\hat{u}\bar{c} + \bar{d})^2} - \frac{\hat{u}^2\sigma_a^2 + 2\hat{u}\sigma_{a,d} + \sigma_d^2}{(\hat{u}\bar{a} + \bar{d})^2} \right] \quad (22)$$

for the equilibrium  $\hat{x} = \hat{u}/(1 + \hat{u})$  to be SLS if  $\sigma^2$  is small enough. The reversed inequality guarantees that  $\hat{x}$  is SLU. If  $a_t, d_t$ , and  $z_t$  are independent random variables, then the above condition takes the form

$$\log\left[1 - \frac{\hat{x}\bar{z}}{\hat{x}\bar{a} + (1 - \hat{x})\bar{d}}\right] > \frac{1}{2} \left[ \frac{\hat{u}^2\sigma_a^2 + \hat{u}^2\sigma_z^2 + \sigma_d^2}{(\hat{u}\bar{a} - \hat{u}\bar{z} + \bar{d})^2} - \frac{\hat{u}^2\sigma_a^2 + \sigma_d^2}{(\hat{u}\bar{a} + \bar{d})^2} \right], \quad (23)$$

where  $\bar{z}$  and  $\sigma_z^2$  designate the mean and variance of  $z_t$ , respectively. When all variances vanish, the condition reduces to  $\bar{z} < 0$ , which means that  $\bar{a} < \bar{c}$  and  $\bar{d} < \bar{b}$ . Notice that this condition becomes more stringent as  $\sigma_z^2$  increases.

It is worth emphasizing that it is possible for a constant interior equilibrium and both fixation states to be simultaneously SLS. For instance, consider a payoff matrix in the form

$$\begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix} = \begin{pmatrix} 1 & 1 + \hat{u}\eta_t \\ 1 + \eta_t & 1 \end{pmatrix},$$

where  $\hat{u} > 0$  and  $\eta_t = -z_t$  is a random variable with mean  $\bar{\eta} = -\bar{z} > 0$  and variance  $\sigma_\eta^2 = \sigma_z^2$ . Then, it is easy to check that (1) the fixation state  $\hat{x} = 0$  is SLS if

$$\sigma_\eta^2 > 2 \left( \frac{1 + \hat{u}\bar{\eta}}{\hat{u}} \right)^2 \log(1 + \hat{u}\bar{\eta});$$

(2) the fixation state  $\hat{x} = 1$  is SLS if

$$\sigma_\eta^2 > 2(1 + \bar{\eta})^2 \log(1 + \bar{\eta});$$

and (3) the constant interior equilibrium  $\hat{x} = \hat{u}/(1 + \hat{u})$  is SLS if

$$\sigma_\eta^2 < 2 \left( \frac{1 + \hat{x}\bar{\eta}}{\hat{x}} \right)^2 \log(1 + \hat{x}\bar{\eta}).$$

On the other hand, the three equilibria are SLU if all the inequalities are reversed. In the special case where  $\hat{u} = 1$  (i.e.,  $\hat{x} = 1/2$ ), for instance, it can be shown that there exists a threshold value  $\eta_0 > 0$  such that  $(1 + \bar{\eta})^2 \log(1 + \bar{\eta}) < 2(1 + \bar{\eta})^2 \log(1 + \bar{\eta}/2)$  if and only if  $\bar{\eta} < \eta_0$ . Therefore, the constant interior equilibrium  $\hat{x} = 1/2$  and both fixation states,  $\hat{x} = 0$  and  $\hat{x} = 1$ , are simultaneously SLS when  $0 < \bar{\eta} < \eta_0$  and

$$2(1 + \bar{\eta})^2 \log(1 + \bar{\eta}) < \sigma_\eta^2 < 2(2 + \bar{\eta})^2 \log(1 + \bar{\eta}/2).$$

On the other hand, the three equilibria are simultaneously SLU when all the inequalities are reversed. To show this, the functions  $\sigma_\eta^2 = 2(1 + \bar{\eta})^2 \log(1 + \bar{\eta})$  (black curve) and

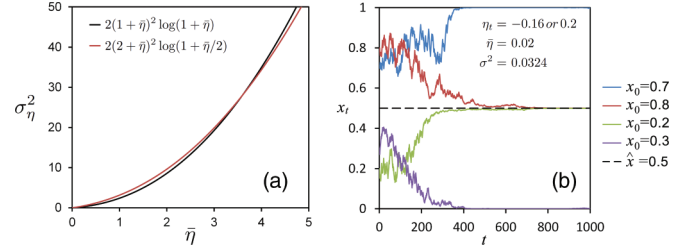


FIG. 2. Stochastic local stability or instability of a constant interior equilibrium and of both fixation states with the random payoff matrix  $\begin{pmatrix} 1 & 1 + \eta_t \\ 1 + \eta_t & 1 \end{pmatrix}$ . (a) The black curve represents the function  $\sigma_\eta^2 = 2(1 + \bar{\eta})^2 \log(1 + \bar{\eta})$  and the red curve the function  $\sigma_\eta^2 = 2(2 + \bar{\eta})^2 \log(1 + \bar{\eta}/2)$ . There is a critical value of  $\bar{\eta}$ , denoted by  $\eta_0$ , that corresponds to the intersection of the black and red curves. For  $\bar{\eta} < \eta_0$ , all of  $\hat{x} = 0$ ,  $\hat{x} = 1$ , and  $\hat{x} = 1/2$  are SLS if the the point  $(\bar{\eta}, \sigma_\eta^2)$  is in the range between the black and red curves; and, conversely, for  $\bar{\eta} > \eta_0$ , all of  $\hat{x} = 0$ ,  $\hat{x} = 1$  and  $\hat{x} = 1/2$  are SLU if the the point  $(\bar{\eta}, \sigma_\eta^2)$  is in the range between the black and red curves. (b) The simulation results, where  $\hat{u} = 1$  and  $\eta_t = -0.16$  and  $0.2$  with same probability  $0.5$  so that  $\bar{\eta} = 0.02$  and  $\sigma_\eta^2 = 0.0324$ . Four trajectories of  $x_t$ , the frequency of strategy 1, are illustrated starting with  $x_0 = 0.2, 0.3, 0.7, 0.8$ : two converge to  $\hat{x} = 1/2$ , one to  $\hat{x} = 0$ , and one to  $\hat{x} = 1$ . Here three equilibrium states  $\hat{x} = 0$ ,  $\hat{x} = 1$ , and  $\hat{x} = 1/2$  are SLS.

$\sigma_\eta^2 = 2(2 + \bar{\eta})^2 \log(1 + \bar{\eta}/2)$  (red curve) are plotted on the  $(\bar{\eta}, \sigma_\eta^2)$  plane [Fig. 2(a)]. Let  $\eta_0$  denote the intersection of the two curves. Then, for  $\bar{\eta} < \eta_0$  (or  $\bar{\eta} > \eta_0$ ), all of  $\hat{x} = 0$ ,  $\hat{x} = 1$ , and  $\hat{x} = 1/2$  are SLS (or SLU) if the the point  $(\bar{\eta}, \sigma_\eta^2)$  is in the range between the black and red curves. Furthermore, the simulation results are shown in Fig. 2(b), where we take  $\hat{u} = 1$ , and  $\eta_t = -0.16$  and  $0.2$  with same probability  $0.5$  such that  $\bar{\eta} = 0.02$  and  $\sigma_\eta^2 = 0.0324$ . It is easy to see that for four trajectories of  $x_t$ , the frequency of strategy 1, with initial states  $x_0 = 0.2, 0.3, 0.7, 0.8$ , two converge to  $\hat{x} = 1/2$ , one to  $\hat{x} = 0$ , and one to  $\hat{x} = 1$ . Obviously, the simulation results strongly support the theoretical predictions.

#### IV. STOCHASTIC EVOLUTIONARY STABILITY AND STOCHASTIC CONVERGENCE STABILITY

Extending the standard definition of an evolutionarily stable strategy (ESS) in a constant environment [2] to a variable environment, a *stochastically evolutionarily stable* (SES) strategy can be defined as a strategy such that, if all the members of the population adopt it, then the probability for at least any slightly perturbed strategy to invade the population under the influence of natural selection is arbitrarily low. More specifically, a strategy represented by a frequency vector  $\hat{\mathbf{x}}$  is SES if  $\hat{\mathbf{x}}$  fixation is SLS against any other strategy  $\mathbf{x} \neq \hat{\mathbf{x}}$  at least nearby enough.

Similarly, the notion of a continuous stable strategy (CSS) introduced in Eshel and Motro [16] (see also Ref. [17]) and renamed later on convergence stable strategy [18,19] can be extended to a context of a variable environment. So a strategy represented by a two-dimensional frequency vector  $\hat{\mathbf{x}} = (\hat{x}, 1 - \hat{x})$  can be said to be *stochastically convergence stable* (SCS) if the fixation state of any nearby strategy  $\tilde{\mathbf{x}} = (\tilde{x}, 1 - \tilde{x})$  is SLU against a strategy  $\mathbf{x} = (x, 1 - x)$  if and

only if  $\mathbf{x}$  is in the direction of  $\hat{\mathbf{x}}$  with respect to  $\tilde{\mathbf{x}}$ . This means that  $\text{sgn}(x - \tilde{x}) = \text{sgn}(\hat{x} - \tilde{x})$ .

In this section, assume a positive stochastic game matrix at each time step  $t \geq 0$  in the form

$$\begin{aligned} \mathbf{A}(t) &= \begin{pmatrix} a_{11}(t) & a_{12}(t) \\ a_{21}(t) & a_{22}(t) \end{pmatrix} \\ &= \begin{pmatrix} \bar{a}_{11} & \bar{a}_{12} \\ \bar{a}_{21} & \bar{a}_{22} \end{pmatrix} + \begin{pmatrix} b_{11}(t) & b_{12}(t) \\ b_{21}(t) & b_{22}(t) \end{pmatrix} \\ &= \bar{\mathbf{A}} + \mathbf{B}(t). \end{aligned} \quad (24)$$

Here  $\bar{\mathbf{A}}$  is a constant matrix with all positive entries, while the entries of  $\mathbf{B}(t)$  are stochastic with mean equal to 0. The payoff matrix at time step  $t \geq 0$  for two mixed strategies,  $\mathbf{x} = (x, 1 - x)$  and  $\hat{\mathbf{x}} = (\hat{x}, 1 - \hat{x})$  in this order, is then given by

$$\begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix} = \begin{pmatrix} \mathbf{x}\mathbf{A}(t)\mathbf{x} & \mathbf{x}\mathbf{A}(t)\hat{\mathbf{x}} \\ \hat{\mathbf{x}}\mathbf{A}(t)\mathbf{x} & \hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}} \end{pmatrix}. \quad (25)$$

We are now ready to state our next two results.

Consider the positive stochastic game matrix Eq. (24) where  $b_{ij}(t)$  for  $i, j = 1, 2$  are independent random variables of variances  $\sigma_{ij}^2$  for  $i, j = 1, 2$ , respectively, while all higher-order centered moments are functions  $o(\sigma^2)$  where  $\sigma^2 = \max\{\sigma_{ij}^2 : i, j = 1, 2\}$ . With the assumption that  $\sigma^2$  is small enough and under generic conditions, the pure strategy  $\hat{\mathbf{x}} = (0, 1)$  is stochastically evolutionarily stable against any nearby mixed strategy  $\mathbf{x} = (x, 1 - x)$  if and only if

$$\sigma_{22}^2 < \left( \frac{\bar{a}_{22}}{\bar{a}_{12}} - 1 \right) \bar{a}_{22}^2. \quad (26)$$

This is also the necessary and sufficient condition for  $\hat{\mathbf{x}} = (0, 1)$  to be stochastically convergence stable. By symmetry, the pure strategy  $\hat{\mathbf{x}} = (1, 0)$  is stochastically evolutionarily stable against any nearby mixed strategy  $\mathbf{x} = (x, 1 - x)$  and stochastically convergence stable in generic cases under the condition that  $\sigma^2$  is small enough if and only if

$$\sigma_{11}^2 < \left( \frac{\bar{a}_{11}}{\bar{a}_{21}} - 1 \right) \bar{a}_{11}^2 \quad (27)$$

(Result 4, proved in Appendix A 4).

Consider the positive stochastic game matrix Eq. (24) where  $a_{11}(t) = a_{21}(t) + z(t)$  and  $a_{22}(t) = a_{12}(t) + \hat{u}z(t)$  for some constant  $\hat{u} = \hat{x}/(1 - \hat{x}) > 0$ , with  $a_{21}(t)$ ,  $a_{12}(t)$ , and  $z(t)$  being independent random variables of means and variances given by  $\bar{a}_{21}$ ,  $\bar{a}_{12}$ ,  $\bar{z}$  and  $\sigma_{21}^2$ ,  $\sigma_{12}^2$ ,  $\sigma_z^2$ , respectively, while all higher-order centered moments are functions  $o(\sigma^2)$ , where  $\sigma^2 = \max\{\sigma_{21}^2, \sigma_{12}^2, \sigma_z^2\}$ . With the assumption that  $\sigma^2$  is small enough and under generic conditions, the constant mixed strategy  $\hat{\mathbf{x}} = (\hat{x}, 1 - \hat{x})$  is stochastically evolutionarily stable against any mixed strategy  $\mathbf{x} = (x, 1 - x)$  if and only if

$$\bar{z}\bar{d}^2 + \bar{z}\sigma_{21}^2\hat{x}^2 + \bar{z}\sigma_{12}^2(1 - \hat{x})^2 - \bar{d}\sigma_z^2\hat{x} < 0, \quad (28)$$

where

$$\bar{d} = \bar{z}\hat{x} + \bar{a}_{21}\hat{x} + \bar{a}_{12}(1 - \hat{x}) > 0. \quad (29)$$

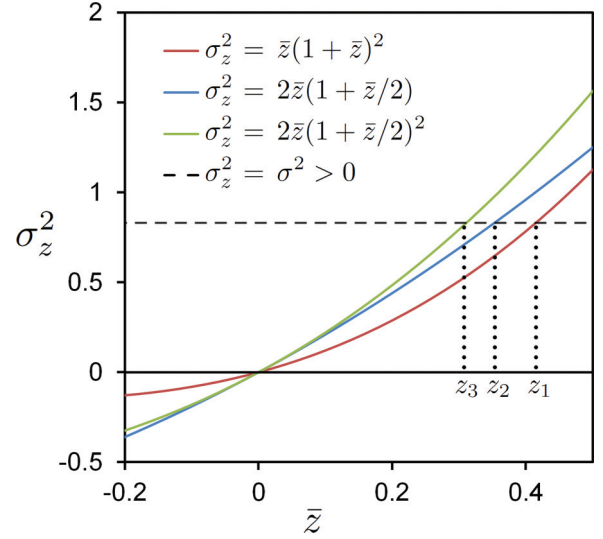


FIG. 3. Stochastic evolutionary stability and stochastic convergence stability. For the positive stochastic payoff matrix  $\begin{pmatrix} 1+z(t) & 1 \\ 1 & 1+z(t) \end{pmatrix}$  with a constant interior equilibrium  $\hat{x} = 1/2$ , if  $\sigma_z^2$  is small, then both pure strategies  $(0, 1)$  and  $(1, 0)$  are SES and SCS when  $\bar{z} > z_1$ , and the constant mixed strategy  $(1/2, 1/2)$  is SES when  $\bar{z} < z_2$  and SCS when  $\bar{z} < z_3$ .

On the other hand, it is stochastically convergence stable under the same assumption and conditions if and only if

$$\bar{z}\bar{d}^2 + \bar{z}\sigma_{21}^2\hat{x}^2 + \bar{z}\sigma_{12}^2(1 - \hat{x})^2 + \bar{z}\hat{x}^2\sigma_z^2 - \bar{d}\sigma_z^2\hat{x} < 0 \quad (30)$$

(Result 5, proved in Appendix A 5).

Consider, for instance, a positive stochastic game matrix

$$\mathbf{A}(t) = \begin{pmatrix} 1 + z(t) & 1 \\ 1 & 1 + \hat{u}z(t) \end{pmatrix},$$

where  $\hat{u} = \hat{x}/(1 - \hat{x}) > 0$  and  $z(t)$  is a random variable of mean  $\bar{z}$  and variance  $\sigma_z^2$  such that  $\bar{d} = \bar{z}\hat{x} + 1 > 0$  and  $\sigma_z^2$  is small enough. Owing to Result 4, conditions Eqs. (26)–(27) for the pure strategies  $(0, 1)$  and  $(1, 0)$  to be SES and SCS are

$$\hat{u}\sigma_z^2 < \bar{z}(1 + \hat{u}\bar{z})^2$$

and

$$\sigma_z^2 < \bar{z}(1 + \bar{z})^2,$$

respectively. On the other hand, conditions Eqs. (28) and (30) for the constant mixed strategy  $\hat{\mathbf{x}} = (\hat{x}, 1 - \hat{x})$  where  $\hat{x} = \hat{u}/(1 + \hat{u})$  to be SES and SCS reduce to

$$\hat{x}\sigma_z^2 > \bar{z}(1 + \hat{x}\bar{z})$$

and

$$\hat{x}\sigma_z^2 > \bar{z}(1 + \hat{x}\bar{z})^2,$$

respectively. Figure 3 illustrates the corresponding regions in the case  $\hat{u} = 1$  which corresponds to  $\hat{x} = 1/2$ . In the limit of a deterministic game matrix, that is,  $\sigma_z^2 = 0$ , both pure strategies are SES and SCS when  $\bar{z} > 0$ , while the mixed strategy is SES and SCS when  $\bar{z} < 0$ . In the presence of stochastic perturbations on the game matrix, that is,  $\sigma_z^2 = \sigma^2 > 0$  (where  $\sigma^2$  is small), there exist three threshold values  $z_1 > z_2 > z_3 > 0$

such that both pure strategies are SES and SCS when  $\bar{z} > z_1$  [where  $z_1$  is a positive solution of  $\sigma_z^2 = \bar{z}(1 + \bar{z})^2$ ], while the mixed strategy is SES when  $\bar{z} < z_2$  (where  $z_2$  is a positive solution of  $\sigma_z^2 = 2\bar{z}[1 + \bar{z}/2]$ ) and SCS when  $\bar{z} < z_3$  [where  $z_3$  is a positive solution of  $\sigma_z^2 = 2\bar{z}(1 + \bar{z}/2)^2$ ].

**V. DISCUSSION**

Evolutionary concepts such as that of an evolutionarily stable strategy (ESS) [2] and that of a convergence stable strategy (CSS) [16,19] were originally introduced for infinite populations in a deterministic environment. Therefore, they were initially stated in terms of conditions that ensure local (actually, asymptotic) stability of a resident strategy against any mutant strategy, or local instability (actually, initial invasion) of any resident strategy close enough to a given population strategy following the introduction of any mutant that brings the population strategy even closer.

In a stochastic environment, convergence to a constant equilibrium from any given initial state occurs with some probability. When this probability tends to 1 as the initial state tends to the equilibrium, then the equilibrium is said to be stochastically locally stable (SLS). On the other hand, when this probability is always 0 for any initial state different from the equilibrium, then the equilibrium is said to be stochastically locally unstable (SLU). These conditions were studied by Karlin and Liberman [20,21] in the framework of a one-locus two-allele viability model for a random mating diploid population undergoing discrete, nonoverlapping generations. This framework corresponds to a linear game model in discrete time with a symmetric payoff matrix for two pure strategies used in random pairwise interactions. We have extended the analysis to a general payoff matrix.

In the absence of stochastic perturbations on the payoffs, it is well known that a fixed resident strategy is locally stable against a mutant strategy introduced in small frequency if the payoff of the resident strategy against itself exceeds the payoff of the mutant strategy against the resident strategy, or in case of equality, if the payoff of the resident strategy against the mutant strategy exceeds the payoff of the mutant strategy against itself. In the presence of stochastic perturbations, it is expected values of functions of the payoffs that have to be compared for the resident strategy to be SLS, either the expected values of the logarithm of the payoffs against the resident strategy or, in case of equality of these payoffs, the expected values of the ratio of the payoffs against the mutant strategy over the common payoff against the resident strategy. Assuming small enough perturbations, these conditions can be expressed in terms of means, variances, and covariances of the payoffs.

Under conditions on the random payoffs for a constant interior equilibrium to exist, we have found a condition for this equilibrium to be SLS. We have shown that this equilibrium and both fixation states can be simultaneously SLS. This situation distinguishes game dynamics in a randomly fluctuating environment from game dynamics in a constant environment since, with constant payoffs, an interior equilibrium can be locally stable only if both fixation states are locally unstable [25].

In a constant environment, an evolutionarily stable strategy (ESS) and a convergence stable strategy (CSS) with respect to mixed strategies on two pure strategies correspond to a locally stable equilibrium with respect to the dynamics involving the two pure strategies. Both evolutionary concepts have been extended to take into account random perturbations on payoffs by using SLS and SLU conditions. We have shown that the condition for a pure strategy to be stochastically evolutionarily stable (SES) and stochastically convergence stable (SCS) is more stringent than in a constant environment, while the condition for a constant mixed strategy to be SES is less stringent than the condition to be SCS which is less stringent than the condition in a constant environment.

New phenomenons arise in game dynamics in a stochastic environment, and these make it not only more complex but also more interesting.

**ACKNOWLEDGMENTS**

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X.-D.Z. and C.L. contributed equally to this work.

**APPENDIX**

**1. Proof of Result 1**

We follow Karlin and Liberman [21] but with nonsymmetric fitness parameters given by the entries of the payoff matrix [Eq. (1)]. It is easy to check that Eq. (7) can be written in the form

$$\frac{u_{t+1}}{u_t} = \frac{b_t}{d_t} \left[ 1 + \frac{u_t(a_t d_t - b_t c_t)}{u_t b_t c_t + b_t d_t} \right], \tag{A1}$$

from which

$$\begin{aligned} \frac{1}{n}(\log u_n - \log u_0) &= \frac{1}{n} \sum_{t=0}^{n-1} \log \left( \frac{b_t}{d_t} \right) \\ &+ \frac{1}{n} \sum_{t=0}^{n-1} \log \left[ 1 + \frac{u_t(a_t d_t - b_t c_t)}{u_t b_t c_t + b_t d_t} \right], \end{aligned} \tag{A2}$$

for  $n \geq 1$ . Let

$$\mu = \mathbb{E} \left[ \log \left( \frac{b_t}{d_t} \right) \right] = \mathbb{E}(\log b_t) - \mathbb{E}(\log d_t), \tag{A3}$$

and define

$$E = \left\{ \frac{1}{n} \sum_{t=0}^{n-1} \log \left( \frac{b_t}{d_t} \right) \rightarrow \mu \right\}. \tag{A4}$$

The strong law of large numbers guarantees that  $\mathbb{P}(E) = 1$ . If  $u_t \rightarrow 0$ , then

$$\log \left[ 1 + \frac{u_t(a_t d_t - b_t c_t)}{u_t b_t c_t + b_t d_t} \right] \rightarrow 0, \tag{A5}$$

since  $a_t, b_t, c_t, d_t$  are assumed to be uniformly bounded below and above by positive constants. Under these conditions, Eq. (A2) implies that

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{t=0}^{n-1} \log \left( \frac{b_t}{d_t} \right) \leq 0 \quad (\text{A6})$$

if this limit exists. This is not possible in the set  $E$  if  $\mu > 0$ . In this case, we conclude that

$$\mathbb{P}(u_t \rightarrow 0) \leq \mathbb{P}(E^C) = 0. \quad (\text{A7})$$

This means that  $\hat{u} = 0$  is stochastically locally unstable if  $\mu > 0$ .

Now consider the case where  $\mu < 0$ . By the strong law of large numbers and Egorov's theorem, for any  $\epsilon > 0$ , there exists an integer  $N \geq 1$  such that the probability of the event

$$F = \left\{ \frac{1}{n} \sum_{t=0}^{n-1} \log \left( \frac{b_t}{d_t} \right) < \frac{\mu}{2}, \quad \forall n \geq N \right\} \quad (\text{A8})$$

satisfies

$$\mathbb{P}(F) \geq 1 - \epsilon. \quad (\text{A9})$$

On the other hand, using the assumption that  $A \leq a_t, b_t, c_t, d_t \leq B$  for some constants  $A, B > 0$ , there exists  $\delta > 0$  such that

$$\log \left[ 1 + \frac{u_t(a_t d_t - b_t c_t)}{u_t b_t c_t + b_t d_t} \right] < -\frac{\mu}{4} \quad (\text{A10})$$

as soon as  $u_t < \delta$ . Moreover, Eq. (7) leads to

$$u_{t+1} \leq u_t \left( \frac{u_t B + B}{u_t A + A} \right) = u_t \left( \frac{B}{A} \right) \leq u_0 \left( \frac{B}{A} \right)^{t+1}, \quad (\text{A11})$$

for  $t \geq 0$ . Therefore, there exists  $0 < \delta_0 < \delta$  such that  $u_t < \delta$  for  $t = 0, 1, \dots, N-1$  as soon as  $u_0 < \delta_0$ . As a consequence, Eq. (A2) for  $n = N$  and Eq. (A10) yield

$$\frac{1}{N} (\log u_N - \log u_0) < \frac{\mu}{2} - \frac{\mu}{4} = \frac{\mu}{4} < 0 \quad (\text{A12})$$

in the set  $F$  as soon as  $u_0 < \delta_0$ , which implies that

$$u_N < u_0 < \delta, \quad (\text{A13})$$

and by recurrence that  $u_n < \delta$  for all  $n \geq N$ .

It remains to show that  $u_n \rightarrow 0$  in  $F$  if  $u_0 < \delta_0$  as claimed in Karlin and Liberman [21], since then

$$P(u_n \rightarrow 0) \geq P(F) \geq 1 - \epsilon. \quad (\text{A14})$$

It suffices to notice that Eq. (A2) for all  $n \geq N$  under the above conditions gives

$$\frac{1}{n} (\log u_n - \log u_0) < \frac{\mu}{4} < 0, \quad (\text{A15})$$

from which

$$\log u_n < \log u_0 + \frac{n\mu}{4} \rightarrow -\infty. \quad (\text{A16})$$

This means that  $u_n \rightarrow 0$ , which completes the proof.

## 2. Proof of Result 2

Assuming  $b_t = d_t$ , the recurrence equation Eq. (7) with the change of variables  $v_t = 1/u_t$  becomes

$$v_{t+1} = v_t \left( \frac{c_t + d_t v_t}{a_t + d_t v_t} \right), \quad (\text{A17})$$

from which

$$v_{t+1} - v_t = \left( \frac{c_t}{d_t} - \frac{a_t}{d_t} \right) - \frac{\frac{a_t}{d_t} \left( 1 - \frac{a_t}{c_t} \right)}{\frac{a_t}{c_t} + \frac{d_t}{c_t} v_t} \quad (\text{A18})$$

for  $t \geq 0$ , and therefore

$$\frac{1}{n} (v_n - v_0) = \frac{1}{n} \sum_{t=0}^{n-1} \left( \frac{c_t}{d_t} - \frac{a_t}{d_t} \right) - \frac{1}{n} \sum_{t=0}^{n-1} \frac{\frac{a_t}{d_t} \left( 1 - \frac{a_t}{c_t} \right)}{\frac{a_t}{c_t} + \frac{d_t}{c_t} v_t} \quad (\text{A19})$$

for  $n \geq 1$ . Defining

$$E = \left\{ \frac{1}{n} \sum_{t=0}^{n-1} \left( \frac{c_t}{d_t} - \frac{a_t}{d_t} \right) \rightarrow \mu \right\}, \quad (\text{A20})$$

where

$$\mu = \mathbb{E} \left( \frac{c_t}{d_t} - \frac{a_t}{d_t} \right) = \mathbb{E} \left( \frac{c_t}{d_t} \right) - \mathbb{E} \left( \frac{a_t}{d_t} \right), \quad (\text{A21})$$

we conclude as in the proof of Result 1 that

$$\mathbb{P}(v_t \rightarrow +\infty) \leq \mathbb{P}(E^C) = 0 \quad (\text{A22})$$

if  $\mu < 0$ . On the other hand, if  $\mu > 0$ , then there exist an integer  $N \geq 1$  and a real number  $\Delta > 0$  such that

$$F = \left\{ \frac{1}{n} \sum_{t=0}^{n-1} \left( \frac{c_t}{d_t} - \frac{a_t}{d_t} \right) > \frac{\mu}{2}, \quad \forall n \geq N \right\} \quad (\text{A23})$$

satisfies  $\mathbb{P}(F) \geq 1 - \epsilon$  for any given  $\epsilon > 0$ , and

$$-\frac{\frac{a_t}{d_t} \left( 1 - \frac{a_t}{c_t} \right)}{\frac{a_t}{c_t} + \frac{d_t}{c_t} v_t} > -\frac{\mu}{4} \quad (\text{A24})$$

as soon as  $v_t > \Delta$ , which is the case for  $t = 0, 1, \dots, N-1$  as soon as  $v_0 > \Delta_0$  for some  $\Delta_0 > \Delta$  since

$$v_{t+1} \geq v_t \left( \frac{A + A v_t}{B + B v_t} \right) = v_t \left( \frac{A}{B} \right) > v_0 \left( \frac{A}{B} \right)^{t+1} > v_0 \left( \frac{A}{B} \right)^N. \quad (\text{A25})$$

Then, as in the proof of Result 1, it can be shown that we have  $v_n > \Delta$  for all  $n \geq N$  and  $v_n \rightarrow +\infty$  in  $F$  as soon as  $v_0 > \Delta_0$ , from which

$$P(v_n \rightarrow +\infty) \geq P(F) \geq 1 - \epsilon \quad (\text{A26})$$

as soon as  $v_0 > \Delta_0$ .

## 3. Proof of Result 3

With the payoffs given by the entries of the game matrix [Eq. (19)], the recurrence equation [Eq. (5)] can be written in the form

$$u_{t+1} = u_t \left( \frac{u_t c_t + u_t z_t + b_t}{u_t c_t + \hat{u} z_t + b_t} \right), \quad (\text{A27})$$



from which it is easy to get

$$\begin{aligned} u_{t+1} - \hat{u} &= (u_t - \hat{u}) \left( \frac{u_t c_t + u_t z_t + \hat{u} z_t + b_t}{u_t c_t + \hat{u} z_t + b_t} \right) \\ &= (u_t - \hat{u}) \left( \frac{u_t a_t + d_t}{u_t c_t + d_t} \right). \end{aligned} \quad (\text{A28})$$

In particular, this ensures that  $u_{t+1} - \hat{u} > 0$  if  $u_t - \hat{u} > 0$ , and  $u_{t+1} - \hat{u} < 0$  if  $u_t - \hat{u} < 0$ . Moreover, some algebraic manipulations lead to

$$\begin{aligned} \frac{u_t a_t + d_t}{u_t c_t + d_t} &= \left( \frac{\hat{u} a_t + d_t}{\hat{u} c_t + d_t} \right) \\ &\times \left[ 1 - \frac{d_t z_t (u_t - \hat{u})}{(\hat{u} a_t + d_t)(\hat{u} c_t + d_t + (u_t - \hat{u})c_t)} \right]. \end{aligned} \quad (\text{A29})$$

In order to conclude, it suffices to proceed as in the proof of Result 1 and to note that

$$\begin{aligned} \log \left( \frac{\hat{u} a_t + d_t}{\hat{u} c_t + d_t} \right) &= -\log \left( \frac{\hat{u} c_t + d_t}{\hat{u} a_t + d_t} \right) \\ &= -\log \left[ 1 - \frac{\hat{x} z_t}{\hat{x} a_t + (1 - \hat{x}) d_t} \right]. \end{aligned} \quad (\text{A30})$$

#### 4. Proof of Result 4

For  $\hat{\mathbf{x}} = (0, 1)$ ,  $\mathbf{x} = (x, 1 - x)$  and  $\mathbf{A}(t) = \bar{\mathbf{A}} + \mathbf{B}(t)$  as in Eq. (24), we find

$$\begin{aligned} \bar{d} &= \mathbb{E}[\hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}}] = \bar{a}_{22}, \\ \bar{b} &= \mathbb{E}[\mathbf{x}\mathbf{A}(t)\hat{\mathbf{x}}] = \bar{a}_{22} + x(\bar{a}_{12} - \bar{a}_{22}), \\ \sigma_d^2 &= \mathbb{E}[(\hat{\mathbf{x}}\mathbf{B}(t)\hat{\mathbf{x}})^2] = \sigma_{22}^2, \\ \sigma_b^2 &= \mathbb{E}[(\mathbf{x}\mathbf{B}(t)\hat{\mathbf{x}})^2] = (1 - x)^2 \sigma_{22}^2 + x^2 \sigma_{12}^2. \end{aligned} \quad (\text{A31})$$

Condition Eq. (12) for  $\hat{\mathbf{x}}$  fixation to be SLS against  $\mathbf{x}$  if the variances are small enough becomes

$$\begin{aligned} \log \left[ 1 + x \left( \frac{\bar{a}_{12} - \bar{a}_{22}}{\bar{a}_{22}} \right) \right] \\ < \frac{1}{2} \left\{ \frac{(1 - x)^2 \sigma_{22}^2 + x^2 \sigma_{12}^2}{[\bar{a}_{22} + x(\bar{a}_{12} - \bar{a}_{22})]^2} - \frac{\sigma_{22}^2}{\bar{a}_{22}^2} \right\}. \end{aligned} \quad (\text{A32})$$

This condition reduces to

$$x \left( \frac{\bar{a}_{12} - \bar{a}_{22}}{\bar{a}_{22}} \right) < -x \left( \frac{\bar{a}_{12} \sigma_{22}^2}{\bar{a}_{22}^3} \right) \quad (\text{A33})$$

for  $x > 0$  small enough. This condition is equivalent to

$$\bar{a}_{22}^2 (\bar{a}_{12} - \bar{a}_{22}) > \bar{a}_{12} \sigma_{22}^2, \quad (\text{A34})$$

which is the same as condition Eq. (26). The reversed inequality ensures that  $\hat{\mathbf{x}}$  fixation is SLU.

Next, we study stochastic convergence stability. Consider a strategy  $\tilde{\mathbf{x}} = (\tilde{x}, 1 - \tilde{x})$  with  $\tilde{x} > 0$  near the pure strategy  $\hat{\mathbf{x}} = (\hat{x}, 1 - \hat{x}) = (0, 1)$ . Given another strategy  $\mathbf{x} = (x, 1 - x)$ , the payoff matrix for  $\mathbf{x}$  and  $\tilde{\mathbf{x}}$  in this order is given by

$$\begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix} = \begin{pmatrix} \mathbf{x}\mathbf{A}(t)\mathbf{x} & \mathbf{x}\mathbf{A}(t)\tilde{\mathbf{x}} \\ \tilde{\mathbf{x}}\mathbf{A}(t)\mathbf{x} & \tilde{\mathbf{x}}\mathbf{A}(t)\tilde{\mathbf{x}} \end{pmatrix}, \quad (\text{A35})$$

where  $\mathbf{A}(t) = \bar{\mathbf{A}} + \mathbf{B}(t)$  as in Eq. (24). We find

$$\begin{aligned} \bar{d} &= \mathbb{E}[\tilde{\mathbf{x}}\mathbf{A}(t)\tilde{\mathbf{x}}] = \tilde{x}^2 \bar{a}_{11} + \tilde{x}(1 - \tilde{x})(\bar{a}_{12} + \bar{a}_{21}) + (1 - \tilde{x})^2 \bar{a}_{22}, \\ \bar{b} &= \mathbb{E}[\mathbf{x}\mathbf{A}(t)\tilde{\mathbf{x}}] = x\tilde{x}\bar{a}_{11} + x(1 - \tilde{x})\bar{a}_{12} + (1 - x)\tilde{x}\bar{a}_{21} \\ &\quad + (1 - x)(1 - \tilde{x})\bar{a}_{22}, \end{aligned} \quad (\text{A36})$$

and

$$\begin{aligned} \sigma_d^2 &= \mathbb{E}[(\tilde{\mathbf{x}}\mathbf{B}(t)\tilde{\mathbf{x}})^2] \\ &= \tilde{x}^4 \sigma_{11}^2 + \tilde{x}^2(1 - \tilde{x})^2 (\sigma_{12}^2 + \sigma_{21}^2) + (1 - \tilde{x})^4 \sigma_{22}^2, \\ \sigma_b^2 &= \mathbb{E}[(\mathbf{x}\mathbf{B}(t)\tilde{\mathbf{x}})^2] \\ &= x^2 \tilde{x}^2 \sigma_{11}^2 + x^2(1 - \tilde{x})^2 \sigma_{12}^2 + (1 - x)^2 \tilde{x}^2 \sigma_{21}^2 \\ &\quad + (1 - x)^2(1 - \tilde{x})^2 \sigma_{22}^2. \end{aligned} \quad (\text{A37})$$

Defining  $\Delta x = x - \tilde{x}$ , the above expressions lead to

$$\begin{aligned} \bar{b} - \bar{d} &= -g_1(\tilde{x})\Delta x, \\ \sigma_b^2 - \sigma_d^2 &= -2h_1(\tilde{x})\Delta x + o(\Delta x), \end{aligned} \quad (\text{A38})$$

where

$$g_1(\tilde{x}) = (\bar{a}_{22} - \bar{a}_{12}) + (\bar{a}_{21} - \bar{a}_{11} + \bar{a}_{12} - \bar{a}_{22})\tilde{x}, \quad (\text{A39})$$

$$\begin{aligned} h_1(\tilde{x}) &= -\tilde{x}^3 \sigma_{11}^2 - \tilde{x}(1 - \tilde{x}) \sigma_{12}^2 + \tilde{x}^2(1 - \tilde{x}) \sigma_{21}^2 \\ &\quad + (1 - \tilde{x})^3 \sigma_{22}^2. \end{aligned} \quad (\text{A40})$$

With small enough variances, strategy  $\tilde{\mathbf{x}}$  is SLU against strategy  $\mathbf{x}$  if

$$\log \left( \frac{\bar{b}}{\bar{d}} \right) > \frac{1}{2} \left( \frac{\sigma_b^2}{\bar{b}^2} - \frac{\sigma_d^2}{\bar{d}^2} \right), \quad (\text{A41})$$

where

$$\begin{aligned} \log \left( \frac{\bar{b}}{\bar{d}} \right) &= \log \left( 1 + \frac{\bar{b} - \bar{d}}{\bar{d}} \right) = \log \left[ 1 - \frac{g_1(\tilde{x})}{\bar{d}} \Delta x \right] \\ &= -\frac{g_1(\tilde{x})}{\bar{d}} \Delta x + o(\Delta x), \end{aligned} \quad (\text{A42})$$

while

$$\begin{aligned} \frac{1}{2} \left( \frac{\sigma_b^2}{\bar{b}^2} - \frac{\sigma_d^2}{\bar{d}^2} \right) &= \frac{\sigma_b^2}{2\bar{d}^2} \left[ \frac{1}{1 + (\bar{b} - \bar{d})/\bar{d}} \right]^2 - \frac{\sigma_d^2}{2\bar{d}^2} \\ &= \frac{\sigma_b^2}{2\bar{d}^2} \left[ 1 + \frac{g_1(\tilde{x})}{\bar{d}} \Delta x \right]^2 - \frac{\sigma_d^2}{2\bar{d}^2} + o(\Delta x) \\ &= \frac{\sigma_b^2 - \sigma_d^2}{2\bar{d}^2} + \frac{\sigma_b^2 g_1(\tilde{x})}{\bar{d}^3} \Delta x + o(\Delta x) \\ &= -\frac{h_1(\tilde{x})}{\bar{d}^2} \Delta x + \frac{\sigma_b^2 g_1(\tilde{x})}{\bar{d}^3} \Delta x + o(\Delta x). \end{aligned} \quad (\text{A43})$$

If  $\Delta x < 0$  and  $|\Delta x|$  small enough, then condition Eq. (A41) is equivalent to

$$(\bar{d}^2 + \sigma_d^2)g_1(\tilde{x}) > \bar{d}h_1(\tilde{x}). \quad (\text{A44})$$

For  $\tilde{\mathbf{x}}$  close enough to  $\hat{\mathbf{x}}$ , this condition reduces to

$$(\bar{a}_{22}^2 + \sigma_{22}^2)(\bar{a}_{22} - \bar{a}_{12}) > \sigma_{22}^2 \bar{a}_{22}, \quad (\text{A45})$$

which is equivalent to Eq. (26). On the contrary, if  $\Delta x > 0$ , then strategy  $\tilde{\mathbf{x}}$  is SLS against strategy  $\mathbf{x}$ .

### 5. Proof of Result 5

Dropping the mention of the time step to simplify the notation, let  $\mathbf{A} = (a_{ij})$  be a stochastic game matrix with  $a_{11} = a_{21} + z$  and  $a_{22} = a_{12} + \hat{u}z$  where  $\hat{u} = \hat{x}/(1 - \hat{x}) > 0$ . The payoff of the mixed strategy  $\mathbf{x} = (x, 1 - x)$  against  $\hat{\mathbf{x}} = (\hat{x}, 1 - \hat{x})$  is then given by

$$b = \mathbf{x}\mathbf{A}\hat{\mathbf{x}} = a_{21}\hat{x} + z\hat{x} + a_{12}(1 - \hat{x}), \quad (\text{A46})$$

which does not depend on  $\mathbf{x}$ . Therefore, it is the same as the payoff of  $\hat{\mathbf{x}}$  against itself, that is

$$d = \hat{\mathbf{x}}\mathbf{A}\hat{\mathbf{x}} = b. \quad (\text{A47})$$

On the other hand, the payoff of  $\hat{\mathbf{x}} = (\hat{x}, 1 - \hat{x})$  against  $\mathbf{x} = (x, 1 - x)$  is

$$c = \hat{\mathbf{x}}\mathbf{A}\mathbf{x} = \hat{\mathbf{x}}\mathbf{A}(\mathbf{x} - \hat{\mathbf{x}}) + \hat{\mathbf{x}}\mathbf{A}\hat{\mathbf{x}} = \hat{\mathbf{x}}\mathbf{A}\boldsymbol{\delta} + d, \quad (\text{A48})$$

where  $\boldsymbol{\delta} = (\delta, -\delta) = (x - \hat{x}, \hat{x} - x) = \mathbf{x} - \hat{\mathbf{x}}$ , while the payoff of  $\mathbf{x} = (x, 1 - x)$  against itself is

$$\begin{aligned} a &= \mathbf{x}\mathbf{A}\mathbf{x} = (\mathbf{x} - \hat{\mathbf{x}})\mathbf{A}(\mathbf{x} - \hat{\mathbf{x}}) + \hat{\mathbf{x}}\mathbf{A}(\mathbf{x} - \hat{\mathbf{x}}) + \mathbf{x}\mathbf{A}\hat{\mathbf{x}} \\ &= \boldsymbol{\delta}\mathbf{A}\boldsymbol{\delta} + \hat{\mathbf{x}}\mathbf{A}\boldsymbol{\delta} + d = \boldsymbol{\delta}\mathbf{A}\boldsymbol{\delta} + c. \end{aligned} \quad (\text{A49})$$

Note that

$$\boldsymbol{\delta}\mathbf{A}\boldsymbol{\delta} = \delta^2(a_{11} - a_{12} - a_{21} + a_{22}) = \delta^2(1 + \hat{u})z. \quad (\text{A50})$$

Therefore,

$$\mathbb{E}\left(\frac{a}{d} - \frac{c}{d}\right) = \mathbb{E}\left(\frac{\boldsymbol{\delta}\mathbf{A}\boldsymbol{\delta}}{d}\right) = \delta^2(1 + \hat{u})\mathbb{E}\left(\frac{z}{d}\right). \quad (\text{A51})$$

According to Result 2,  $\hat{\mathbf{x}}$  fixation is SLS if

$$\mathbb{E}\left(\frac{z}{d}\right) < 0, \quad (\text{A52})$$

and SLU if this inequality is reversed.

Let us write

$$a_{12} = \bar{a}_{12} + \eta_{12}, \quad a_{21} = \bar{a}_{21} + \eta_{21}, \quad z = \bar{z} + \zeta, \quad (\text{A53})$$

where  $\eta_{21}$ ,  $\eta_{12}$ , and  $\zeta$  are independent random variables of mean 0 and variances  $\sigma_{21}^2$ ,  $\sigma_{12}^2$ , and  $\sigma_z^2$ , respectively, while all higher-order centered moments are  $o(\sigma^2)$  where  $\sigma^2 = \max\{\sigma_{21}^2, \sigma_{12}^2, \sigma_z^2\}$ . Then we find

$$\begin{aligned} \mathbb{E}\left(\frac{z}{d}\right) &= \frac{1}{\bar{d}}[\bar{z}\bar{d}^2 + \bar{z}\sigma_{21}^2\hat{x}^2 + \bar{z}\sigma_{12}^2(1 - \hat{x})^2 - \bar{d}\sigma_z^2\hat{x}] \\ &\quad + o(\sigma^2), \end{aligned} \quad (\text{A54})$$

where

$$\bar{d} = \bar{z}\hat{x} + \bar{a}_{21}\hat{x} + \bar{a}_{12}(1 - \hat{x}). \quad (\text{A55})$$

In the case where  $\sigma^2$  is small enough, we conclude that  $\hat{\mathbf{x}}$  fixation is SLS if

$$\bar{z}\bar{d}^2 + \bar{z}\sigma_{21}^2\hat{x}^2 + \bar{z}\sigma_{12}^2(1 - \hat{x})^2 - \bar{d}\sigma_z^2\hat{x} < 0, \quad (\text{A56})$$

and SLU if this inequality is reversed. This gives the condition for  $\hat{\mathbf{x}}$  to be a stochastically evolutionarily stable strategy (SESS).

For stochastic convergence stability (SCS) of  $\hat{\mathbf{x}}$ , we consider a strategy  $\tilde{\mathbf{x}} = (\tilde{x}, 1 - \tilde{x})$  near  $\hat{\mathbf{x}} = (\hat{x}, 1 - \hat{x})$ . Given another strategy  $\mathbf{x} = (x, 1 - x)$ , the payoff matrix for  $\mathbf{x}$  and  $\tilde{\mathbf{x}}$  in this order is, again, given by Eq. (A35). Therefore, the means of the variables  $b$  and  $d$ ,  $\bar{b}$  and  $\bar{d}$ , have the same expressions as in Eq. (A36), but with  $\bar{a}_{11} = \bar{a}_{21} + \bar{z}$  and  $\bar{a}_{22} = \bar{a}_{12} + \hat{u}\bar{z}$ . Defining  $\Delta x = x - \tilde{x}$  and  $\Delta\hat{x} = \hat{x} - \tilde{x}$ , the difference of the means is found to be

$$\bar{b} - \bar{d} = -g_2(\tilde{x})\Delta x, \quad (\text{A57})$$

where

$$g_2(\tilde{x}) = \bar{z}[\hat{u} - (1 + \hat{u})\tilde{x}] = (1 + \hat{u})\Delta\hat{x}. \quad (\text{A58})$$

On the other hand, since

$$\begin{aligned} d &= \tilde{x}^2(a_{21} + z) + \tilde{x}(1 - \tilde{x})(a_{12} + a_{21}) + (1 - \tilde{x})^2(a_{12} + \hat{u}z) \\ &= (1 - \tilde{x})a_{12} + \tilde{x}a_{21} + [\tilde{x}^2 + \hat{u}(1 - \tilde{x})^2]z, \\ b &= x\tilde{x}(a_{21} + z) + x(1 - \tilde{x})a_{12} + \tilde{x}(1 - x)a_{21} \\ &\quad + (1 - x)(1 - \tilde{x})(a_{12} + \hat{u}z) \\ &= (1 - \tilde{x})a_{12} + \tilde{x}a_{21} + [x\tilde{x} + \hat{u}(1 - x)(1 - \tilde{x})]z, \end{aligned} \quad (\text{A59})$$

where  $a_{12}$ ,  $a_{21}$ , and  $z$  are independent random variables, the variances of  $b$  and  $d$  are given by

$$\begin{aligned} \sigma_d^2 &= (1 - \tilde{x})^2\sigma_{12}^2 + \tilde{x}^2\sigma_{21}^2 + [\tilde{x}^2 + \hat{u}(1 - \tilde{x})^2]^2\sigma_z^2, \\ \sigma_b^2 &= (1 - \tilde{x})^2\sigma_{12}^2 + \tilde{x}^2\sigma_{21}^2 + [x\tilde{x} + \hat{u}(1 - x)(1 - \tilde{x})]^2\sigma_z^2. \end{aligned} \quad (\text{A60})$$

Writing  $x = \tilde{x} + \Delta x$  and  $\tilde{x} = \hat{x} - \Delta\hat{x}$ , the difference of the variances is found to be

$$\sigma_b^2 - \sigma_d^2 = -2h_2(\tilde{x})\Delta x + o(\Delta x), \quad (\text{A61})$$

where

$$\begin{aligned} h_2(\tilde{x}) &= \sigma_z^2[\tilde{x}^2 + \hat{u}(1 - \tilde{x})^2][\hat{u}(1 - \tilde{x}) - \tilde{x}] \\ &= \sigma_z^2[\hat{x}^2 + \hat{u}(1 - \hat{x})^2]\Delta\hat{x} + o(\Delta\hat{x}) \\ &= \sigma_z^2(1 + \hat{u})\hat{x}\Delta\hat{x} + o(\Delta\hat{x}). \end{aligned} \quad (\text{A62})$$

Analogously to the conclusion drawn in the proof of Result 4, if  $\Delta x$  in absolute value and the variances are small enough, then strategy  $\tilde{\mathbf{x}}$  is SLU against strategy  $\mathbf{x}$  if

$$(\bar{d}^2 + \sigma_d^2)g_2(\tilde{x})\Delta x < \bar{d}h_2(\tilde{x})\Delta x, \quad (\text{A63})$$

where

$$\sigma_d^2 = (1 - \hat{x})^2\sigma_{12}^2 + \hat{x}^2\sigma_{21}^2 + \hat{x}^2\sigma_z^2 + O(\Delta\hat{x}). \quad (\text{A64})$$

If  $\Delta\hat{x}$  is small enough and such that  $(\Delta x)(\Delta\hat{x}) > 0$ , which means that  $\text{sgn}(x - \tilde{x}) = \text{sgn}(\hat{x} - \tilde{x})$ , then Eq. (A63) reduces to

$$\bar{z}\bar{d}^2 + \bar{z}\sigma_{21}^2\hat{x}^2 + \bar{z}\sigma_{12}^2(1 - \hat{x})^2 + \bar{z}\hat{x}^2\sigma_z^2 - \bar{d}\sigma_z^2\hat{x} < 0. \quad (\text{A65})$$

If either  $\Delta\hat{x}$  or  $\Delta x$  changes sign, then the reverse inequality is obtained, which means that strategy  $\tilde{\mathbf{x}}$  is SLS against strategy  $\mathbf{x}$ .

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