Stochastic evolutionary stability in matrix games with random payoffs

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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 behavior, but also widely used in economics and social sciences. Recently, in order to reveal the stochastic dynamical properties of evolutionary games in randomly fluctuating environments, the concept of stochastic evolutionary stability based on conditions for stochastic local stability for a fixation state was developed in the context of a symmetric matrix game with two phenotypes and random payoffs in pairwise interactions [Zheng *et al.*, Phys. Rev. E **96**, 032414 (2017)]. In this paper, we extend this study to more general situations, namely, multiphenotype symmetric as well as asymmetric matrix games with random payoffs. Conditions for stochastic local stability and stochastic evolutionary stability are established. Conditions for a fixation state to be stochastically unstable and almost everywhere stochastically unstable are distinguished in a multiphenotype setting according to the initial population state. Our results provide some alternative perspective and a more general theoretical framework for a better understanding of the evolution of animal behavior in a stochastic environment.

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I. INTRODUCTION

Forty years ago, Maynard Smith's *Evolution and the Theory of Games* was published [1]. This monograph provided a fundamental theoretical framework, called evolutionary game theory, for understanding the evolution of animal behavior (see also [2]). Since then, this theory has been very successful not only in biology but also in economics and social sciences [2,3].

Evolutionary game theory started with the concept of *evolutionarily stable strategy* (ESS) introduced by Maynard Smith and Price [4]. This concept has become one of the principal tools for analyzing the evolutionary dynamics in biological populations. Let us recall that an ESS is defined as a strategy such that, if all the members of a population adopt it, then no mutant strategy can successfully invade the population under the effect of natural selection [1,5]. This concept can explain the evolutionary stability of animal behaviors.

In the context of symmetric pairwise interactions, for instance, let $E(\mathbf{x},\mathbf{y})$ denote the payoff to strategy $\mathbf{x}$ against strategy $\mathbf{y}$. Then a strategy $\mathbf{x}$ is an ESS if (i) the payoff to $\mathbf{x}$ against itself is larger or equal to the payoff to any other strategy $\mathbf{y}$ against $\mathbf{x}$, that is, $E(\mathbf{x},\mathbf{x}) \geqslant E(\mathbf{y},\mathbf{x})$ for any $\mathbf{y} \neq \mathbf{x}$, and (ii) the payoff to $\mathbf{x}$ against $\mathbf{y}$ exceeds the payoff to $\mathbf{y}$ against itself in the case of an equality in (i), that is, $E(\mathbf{x},\mathbf{y}) > E(\mathbf{y},\mathbf{y})$ if $E(\mathbf{x},\mathbf{x}) = E(\mathbf{y},\mathbf{x})$ [1,2]. It can be shown that 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 and pairwise interactions occur at random.

On the other hand, in the context of asymmetric pairwise interactions (where the interacting individuals are distinguished by their positions, I and II; these could be, for instance, the male or female functions) [1,2], let $\hat{\mathbf{u}}$ and $\mathbf{u}$ denote two strategies in position I, and $\hat{\mathbf{v}}$ and $\mathbf{v}$ two strategies in position II. Then the strategy pair $(\hat{\mathbf{u}},\hat{\mathbf{v}})$ is said to be a *Nash equilibrium* (NE) if $\hat{\mathbf{u}}$ is a best reply to $\hat{\mathbf{v}}$, while $\hat{\mathbf{v}}$ a best reply to $\hat{\mathbf{u}}$, that is, $E(\mathbf{u},\hat{\mathbf{v}}) \leqslant E(\hat{\mathbf{u}},\hat{\mathbf{v}})$ for any $\mathbf{u} \neq \hat{\mathbf{u}}$ and $E(\mathbf{v},\hat{\mathbf{u}}) \leqslant E(\hat{\mathbf{v}},\hat{\mathbf{u}})$ for any $\mathbf{v} \neq \hat{\mathbf{v}}$ [2]. Moreover, the strategy pair $(\hat{\mathbf{u}},\hat{\mathbf{v}})$ is said to be a strict NE if $E(\mathbf{u},\hat{\mathbf{v}}) < E(\hat{\mathbf{u}},\hat{\mathbf{v}})$ for any $\mathbf{u} \neq \hat{\mathbf{u}}$ and $E(\mathbf{v},\hat{\mathbf{u}}) < E(\hat{\mathbf{v}},\hat{\mathbf{u}})$ for any $\mathbf{v} \neq \hat{\mathbf{v}}$ [2,6].

It is also known that the evolutionary game dynamics in an infinite population is described by the *replicator equation* [1,2,7]. For the symmetric matrix game with n possible pure strategies $S_1,\dots,S_n$ and random pairwise interactions, the replicator equation is given by $\dot{x}_i = x_i((\mathbf{A}\mathbf{x})_i - \mathbf{x}\cdot\mathbf{A}\mathbf{x})$ for $i = 1,2,\dots,n$, where $\mathbf{x} = (x_1,x_2,\dots,x_n)$ is a strategy frequency vector that represents the population state. Here x_i is the frequency of strategy S_i for $i = 1,2,\dots,n$ with $\sum_{i=1}^n x_i = 1$, and $\mathbf{A} = (a_{ij})_{n\times n}$ is the payoff matrix, with a_{ij} being the payoff to strategy S_i against strategy S_j for $i,j = 1,2,\dots,n$ [2]. Therefore, the term $(\mathbf{A}\mathbf{x})_i = \sum_{j=1}^n x_j a_{ij}$ is the expected payoff to strategy S_i for $i = 1,2,\dots,n$, while the term $\mathbf{x}\cdot\mathbf{A}\mathbf{x} = \sum_{i,j=1}^n x_i x_j a_{ij}$ is the mean payoff in the population. The most

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important property of the replicator equation is that if $\hat{\mathbf{x}} = (\hat{x}_1, \hat{x}_2, \ldots, \hat{x}_n)$ is an ESS, then it must be an asymptotically stable equilibrium of the replicator equation [2].

In a similar way, the dynamics of an asymmetric matrix game in an infinite population with m pure strategies $U_1, \ldots, U_m$ in position I and n pure strategies $V_1, \ldots, V_n$ in position II in random pairwise interactions is described by $\dot{u}_i = u_i((\mathbf{Bv})_i - \mathbf{u} \cdot \mathbf{Bv})$ and $\dot{v}_j = v_j((\mathbf{Cu})_j - \mathbf{v} \cdot \mathbf{Cu})$ for $i = 1, 2, \ldots, m$ and $j = 1, 2, \ldots, n$, where (i) $\mathbf{u} = (u_1, u_2, \ldots, u_m)$ with u_i being the frequency of strategy U_i in position I, and $\mathbf{v} = (v_1, v_2, \ldots, v_n)$ with v_j being the frequency of strategy V_j in position II; (ii) $\mathbf{B} = (b_{ij})_{m\times n}$ with b_{ij} being the payoff to strategy U_i in position I against strategy V_j in position II, while $\mathbf{C} = (c_{ji})_{n\times m}$ with c_{ji} being the payoff to strategy V_j in position II against strategy U_i in position I; and (iii) $(\mathbf{Bv})_i$ and $(\mathbf{Cu})_j$ are the expected payoffs to strategies U_i and V_j in positions I and II, respectively, while $\mathbf{u} \cdot \mathbf{Bv}$ and $\mathbf{v} \cdot \mathbf{Cu}$ are the mean payoffs of individuals in positions I and II, respectively [2]. As for the stability of equilibrium states in an asymmetric matrix game, it has been shown that an interior equilibrium cannot be asymptotically stable, while a fixation state is asymptotically stable if and only if it is a strict NE [2,8] (it is necessary to point out that a strict NE is also called an ESS by some authors [8,9]).

One key assumption in the classical matrix games is that the payoff matrices are constant, and this supposes that the environmental conditions do not change over time. However, as pointed out in Zheng *et al.* [10,11], the surrounding environment of a population is actually subject to stochastic fluctuations, and these in turn entail fluctuations in the occurrence of interactions between individuals and, more importantly, fluctuations in the payoffs received by interacting individuals. The importance of the effects of environmental random noise on population and community ecology has been stressed by many authors [12–19]. May [12], for instance, pointed out that, since real environments stochastically vary over time, 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, and that these must be taken into account in studying biological evolution. Therefore, in evolutionary matrix games, unless stochastic fluctuations of environmental conditions are so small that their effects can be neglected, there is no *priori* reason to assume that the payoff matrices are constant. But, then, how can we extend evolutionary stability concepts to evolutionary games with random payoff matrices? By analogy with an ESS in a constant environment, a strategy in a random environment could be said *stochastically evolutionarily stable* (SES) if this strategy is probabilistically favored by selection once fixed in the population. The impact of payoff fluctuations on evolutionary game dynamics has already been considered in some previous studies [20–23]. For instance, Stollmeier and Nagler [23] divided payoff fluctuations into two types, namely, deterministic periodic fluctuations and stochastic fluctuations, and then investigated the long-term behavior of a two-phenotype evolutionary game dynamics using the concept of geometric mean payoff (or fitness) and numerical simulations.

Recently, Zheng *et al.* [10,11] investigated a two-phenotype evolutionary game in an infinite population with discrete, nonoverlapping, generations, in which the payoffs in random pairwise interactions over succession generations are independent identically distributed random variables. Based on the concept of stochastic local stability (SLS), which was introduced in a population genetics framework by Karlin and Liberman [24–26], the concepts of *stochastic evolutionary stability* (SES) as described above and *stochastic convergence stability* (SCS) about the direction of evolution were developed [10]. These concepts allow us to better understand the effects of a random environment on evolutionary outcomes and, in particular, to study conditions on the variances of the payoffs that could favor the evolution of cooperation. Note that the evolutionary game dynamics with fluctuations in payoffs in a finite population has also aroused some research interest [27–30]. In particular, Li and Lessard [30] analyzed thoroughly the stochastic dynamics of a two-phenotype evolutionary game with a random payoff matrix in a finite population.

In this study, our goal is to extend the results on evolutionary stability in Zheng *et al.* [10] to more general situations, namely, symmetric as well as asymmetric matrix games with multiple phenotypes under the effects of random payoffs.

II. SYMMETRIC MATRIX GAME WITH RANDOM PAYOFFS

We first consider a symmetric evolutionary game in an infinite population with discrete, nonoverlapping generations and with n phenotypes (or pure strategies), denoted by $S_1, S_2, \ldots, S_n$. As in Zheng *et al.* [10], the payoffs in pairwise interactions at time step $t \geqslant 0$ are given by the game matrix

$$\mathbf{A}(t) = (a_{ij}(t))_{n\times n} = \begin{pmatrix} a_{11}(t) & a_{12}(t) & \ldots & a_{1n}(t) \\ a_{21}(t) & a_{22}(t) & \ldots & a_{2n}(t) \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}(t) & a_{n2}(t) & \ldots & a_{nn}(t) \end{pmatrix}, \quad (1)$$

where $a_{ij}(t)$ is the payoff to strategy S_i against strategy S_j for $i, j = 1, 2, \ldots, n$. 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 $B > A > 0$ such that $A \leqslant a_{ij}(t) \leqslant B$ for $i, j = 1, 2, \ldots, n$ and $t \geqslant 0$. Moreover, the probability distributions of $a_{ij}(t)$ for $i, j = 1, 2, \ldots, n$ do not depend on $t \geqslant 0$. The means, variances, and covariances of these random payoffs are denoted by $\langle a_{ij}(t)\rangle = \bar{a}_{ij}$, $\langle (a_{ij}(t) - \bar{a}_{ij})^2\rangle = \sigma_{ij}^2$ for $i, j = 1, 2, \ldots, n$, and $\langle (a_{ij}(t) - \bar{a}_{ij})(a_{kl}(t) - \bar{a}_{kl})\rangle = \sigma_{ij,kl}$ for $i, j, k, l = 1, 2, \ldots, n$ with $(i, j) \neq (k, l)$. As for $s \neq t$, the payoffs $a_{ij}(s)$ and $a_{kl}(t)$ are assumed to be independent of each other such that $\langle (a_{ij}(s) - \bar{a}_{ij})(a_{kl}(t) - \bar{a}_{kl})\rangle = 0$ for $i, j, k, l = 1, 2, \ldots, n$. A further assumption is that the variances σ_{ij}^2 for $i, j = 1, 2, \ldots, n$ are small.

Let $x_{i,t}$ be the frequency of strategy S_i at time step $t \geqslant 0$ for $i = 1, 2, \ldots, n$ with $\sum_{i=1}^n x_{i,t} = 1$. Assuming random pairwise interactions, the expected payoff to strategy S_i at time step $t \geqslant 0$, denoted by $\pi_{i,t}$, is given by $\pi_{i,t} = \sum_{j=1}^n x_{j,t} a_{ij}(t) = (\mathbf{A}(t)\mathbf{x}_t)_i$ for $i = 1, 2, \ldots, n$, where $\mathbf{x}_t = (x_{1,t}, x_{2,t}, \ldots, x_{n,t})$ denotes the population state at time step $t \geqslant 0$ [2]. This is a strategy frequency vector that belongs to the simplex $\Delta_n = \{\mathbf{p} = (p_1, p_2, \dots, p_n)\colon p_i \geqslant 0, i = 1, 2, \dots, n, \sum_{i=1}^n p_i = 1\}$. Then, the mean payoff in the population at time step $t \geqslant 0$, denoted by $\bar{\pi}_t$, is $\bar{\pi}_t = \sum_{i=1}^n x_{i,t}\pi_{i,t} = \mathbf{x}_t \cdot \mathbf{A}(t)\mathbf{x}_t$ [2]. Finally, the frequency of strategy S_i at time step $t+1$ is given by the recurrence equation

$$x_{i,t+1} = \frac{x_{i,t}\pi_{i,t}}{\bar{\pi}_t} = \frac{x_{i,t}\left(\mathbf{A}(t)\mathbf{x}_t\right)_i}{\mathbf{x}_t \cdot \mathbf{A}(t)\mathbf{x}_t} \tag{2}$$

for $i = 1, 2, \dots, n$ [2,10]. If the payoff matrix is a constant matrix, this equation is a deterministic recurrence equation which is a discrete-time version of the continuous-time replicator equation as shown by Hofbauer and Sigmund [2]. The two equations are related by a time change. Note, however, that the stochastic replicator equation has extra terms [20,31].

A. Stochastic local stability in a symmetric matrix game

We are interested in the asymptotic (or long-run) behavior of the process $\{\mathbf{x}_t\}$ for $t \geqslant 0$, and, therefore, we look at its equilibrium structure. Let $\hat{\mathbf{x}}$ represent a constant (nonrandom) equilibrium of this process, that is, an equilibrium of Eq. (2) that does not depend on the randomness of the payoff matrix $\mathbf{A}(t)$. This is clearly the case for each of the vertices in the simplex Δ_n, that is, $\mathbf{e}_i$ with 1 in the ith entry and 0 elsewhere for $i = 1, 2, \dots, n$. These are called the *fixation states*. They are on the boundary of the simplex Δ_n. We may also have a constant polymorphic equilibrium $\hat{\mathbf{x}} = (\hat{x}_1, \hat{x}_2, \dots, \hat{x}_n)$ (with at least two $\hat{x}_i$ such that $0 < \hat{x}_i < 1$) that may correspond to an interior point of Δ_n (if all $\hat{x}_i$ are such that $0 < \hat{x}_i < 1$) or a point on the boundary of Δ_n (if at least two $\hat{x}_i$ are such that $0 < \hat{x}_i < 1$ but at least one $\hat{x}_j = 0$). However, the existence of a constant polymorphic equilibrium strongly depends on the structure of the random payoff matrix $\mathbf{A}(t)$, which must be very peculiar. In this paper, we focus our attention on the stochastic stability of the fixation states.

Following Karlin and Liberman [24–26] (see also Zheng *et al.* [10]), a constant equilibrium $\hat{\mathbf{x}}$ is said to be *stochastically locally stable* (SLS) if for any $\epsilon > 0$ there exists δ_0 such that $\mathbb{P}(\mathbf{x}_t \to \hat{\mathbf{x}}) \geqslant 1 - \epsilon$ as soon as $|\mathbf{x}_0 - \hat{\mathbf{x}}| < \delta_0$ where $|\cdot|$ denotes the Euclidian norm or any equivalent norm. This means that $\mathbf{x}_t$ tends to $\hat{\mathbf{x}}$ as $t \to \infty$ with probability arbitrarily close to 1 (but different from 1) if the initial state $\mathbf{x}_0$ is sufficiently near $\hat{\mathbf{x}}$. Note, however, that no matter how close $\mathbf{x}_0$ is to $\hat{\mathbf{x}}$ (but different from $\hat{\mathbf{x}}$), it is not ascertained that $\mathbf{x}_t$ will converge to $\hat{\mathbf{x}}$. Stochastic fluctuations could cause $\mathbf{x}_t$ to depart sharply from $\hat{\mathbf{x}}$, but this will occur with small probability if $\mathbf{x}_0$ is close enough to $\hat{\mathbf{x}}$ and $\hat{\mathbf{x}}$ is SLS.

On the other hand, a constant equilibrium $\hat{\mathbf{x}}$ is said to be *stochastically unstable* (SU) if $\mathbb{P}(\mathbf{x}_t \to \hat{\mathbf{x}}) = 0$ as soon as $|\mathbf{x}_0 - \hat{\mathbf{x}}| > 0$ [24,25]. This means that, if $\hat{\mathbf{x}}$ is SU, then $\hat{\mathbf{x}}$ cannot be reached with probability 1 from any initial state different from $\hat{\mathbf{x}}$.

More generally, we will say that a constant equilibrium $\hat{\mathbf{x}}$ is *almost everywhere stochastically unstable* (a.e. SU) if the condition $\mathbb{P}(\mathbf{x}_t \to \hat{\mathbf{x}}) = 0$ holds for almost every initial state $\mathbf{x}_0$. For a fixation state $\mathbf{e}_i$ for $i = 1, 2, \dots, n$, for instance, it suffices to have the condition for $\mathbf{x}_0 = (x_{1,0}, x_{2,0}, \dots, x_{n,0})$ with $x_{j,0} > 0$ for all $j \neq i$.

We first consider the stochastic local stability of the fixation state corresponding to the vertex $\mathbf{e}_1$ with 1 in the first entry and 0 in all the others. Note that $x_{1,t} = 1 - \sum_{j=2}^n x_{j,t}$ at any time step $t \geqslant 0$. Then the expected payoff to S_i at time step $t \geqslant 0$ can be rewritten as

$$\pi_{i,t} = a_{i1}(t) + \sum_{j=2}^{n} x_{j,t}(a_{ij}(t) - a_{i1}(t)) \quad \text{for} \quad i = 1, 2, \dots, n, \tag{3}$$

and, similarly, the mean payoff in the population at the same time step as

$$\begin{aligned} \bar{\pi}_t &= \pi_{1,t} + \sum_{j=2}^{n} x_{j,t}(\pi_{j,t} - \pi_{1,t}) \\ &= a_{11}(t) + \sum_{j=2}^{n} x_{j,t}(a_{1j}(t) - a_{11}(t)) + \sum_{j=2}^{n} x_{j,t}(\pi_{j,t} - \pi_{1,t}). \end{aligned} \tag{4}$$

Therefore, for $i = 2, 3, \dots, n$ and every time step $T \geqslant 1$, Eq. (2) yields

$$x_{i,T} = x_{i,0} \prod_{t=0}^{T-1} \left(\frac{a_{i1}(t)}{a_{11}(t)}\right) Q_{i,t}, \tag{5}$$

where

$$Q_{i,t} = \frac{1 + \sum_{j=2}^n x_{j,t}(a_{ij}(t) - a_{i1}(t))/a_{i1}(t)}{1 + \left[\sum_{j=2}^n x_{j,t}(a_{1j}(t) - a_{11}(t)) + \sum_{j=2}^n x_{j,t}(\pi_{j,t} - \pi_{1,t})\right]/a_{11}(t)}. \tag{6}$$

Assuming $x_{i,0} > 0$, this leads to

$$\lim_{T\to\infty} \frac{1}{T} \log\left(\frac{x_{i,T}}{x_{i,0}}\right) = \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log\left(\frac{a_{i1}(t)}{a_{11}(t)}\right) + \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log Q_{i,t}, \tag{7}$$

where $\log Q_{i,t} \to 0$ as $\mathbf{x}_t \to \mathbf{e}_1$. This is the case since all $a_{ij}(t)$ for $i, j = 1, 2, \dots, n$ are assumed to be uniformly bounded below and above by positive constants. It can be shown by the strong law of large numbers and Egorov's theorem that the vertex $\mathbf{e}_1$ is SLS if

$$\left\langle \log\left(\frac{a_{i1}(t)}{a_{11}(t)}\right)\right\rangle = \langle \log a_{i1}(t)\rangle - \langle \log a_{11}(t)\rangle < 0 \quad \text{for} \quad i = 2, 3, \dots, n. \tag{8}$$

On the other hand, $\mathbf{e}_1$ is a.e. SU if at least one of the above inequalities is reversed, and SU if they are all reversed. (The detailed mathematical proof of these claims is given in the Appendix.)

Furthermore, let us assume that the random payoffs are close enough to their means so that Taylor's theorem leads to the approximations

$$\langle \log a_{ij}(t) \rangle \approx \log \bar{a}_{ij} - \frac{\sigma_{ij}^2}{2\bar{a}_{ij}^2} \quad \text{for } i, j = 1, 2, \ldots, n. \tag{9}$$

Thus, the conditions in Eq. (8) for the vertex $\mathbf{e}_1$ to be SLS reduce to

$$\log\left(\frac{\bar{a}_{11}}{\bar{a}_{i1}}\right) > \frac{1}{2}\left[\frac{\sigma_{11}^2}{\bar{a}_{11}^2} - \frac{\sigma_{i1}^2}{\bar{a}_{i1}^2}\right] \quad \text{for} \quad i = 2, 3, \ldots, n. \tag{10}$$

If at least one of the inequalities is reversed, then the vertex $\mathbf{e}_1$ is a.e. SU, while it is SU if they are all reversed. Therefore, the conditions for the vertex $\mathbf{e}_1$ to be SLS become less stringent as σ_{i1}^2 increases and more stringent as σ_{11}^2 decreases for $i = 2, 3, \ldots, n$.

More generally, under the same assumptions, the vertex $\mathbf{e}_k$ is SLS if

$$\log\left(\frac{\bar{a}_{kk}}{\bar{a}_{ik}}\right) > \frac{1}{2}\left[\frac{\sigma_{kk}^2}{\bar{a}_{kk}^2} - \frac{\sigma_{ik}^2}{\bar{a}_{ik}^2}\right] \quad \text{for } i = 1, 2, \ldots, n \text{ but } i \neq k, \tag{11}$$

a.e. SU if at least one of the inequalities is reversed, and SU if they are all reversed. For $n = 2$, the vertex $\mathbf{e}_1 = (1, 0)$ is SLS if $2\log(\bar{a}_{11}/\bar{a}_{21}) > \sigma_{11}^2/\bar{a}_{11}^2 - \sigma_{21}^2/\bar{a}_{21}^2$; and the vertex $\mathbf{e}_2 = (0, 1)$ is SLS if $2\log(\bar{a}_{22}/\bar{a}_{12}) > \sigma_{22}^2/\bar{a}_{22}^2 - \sigma_{12}^2/\bar{a}_{12}^2$ [10].

As an example, we consider a three-phenotype evolutionary game with the random payoff matrix

$$\mathbf{A}(t) = \begin{pmatrix} a_{11}(t) & a_{31}(t) & a_{21}(t) \\ a_{21}(t) & a_{11}(t) & a_{31}(t) \\ a_{31}(t) & a_{21}(t) & a_{11}(t) \end{pmatrix}, \tag{12}$$

where, at any time step $t \geqslant 0$, $a_{11}(t) = 1.9$ and 2.1 with the same probability 0.5 such that $\bar{a}_{11} = 2$ and $\sigma_{a_{11}}^2 = 0.01$; $a_{31}(t) = 1.4$ and 1.6 with the same probability 0.5 such that $\bar{a}_{31} = 1.5$ and $\sigma_{a_{31}}^2 = 0.01$; and the mean of $a_{21}(t)$ is taken as $\bar{a}_{21} = 3$. Here we will show how the size of the variance of $a_{21}(t)$, $\sigma_{a_{21}}^2$, affects the stochastic stability of the system. It is easy to see that $(1/3, 1/3, 1/3)$ is a constant interior equilibrium of the system, that is, it is independent of the randomness of the payoffs. It is also easy to see that the mean payoff matrix of $\mathbf{A}(t)$, denoted by $\bar{\mathbf{A}}$, exactly corresponds to a rock-scissors-paper game [2]. From the above theoretical analysis, we can see that the vertex $\mathbf{e}_k$ $(k = 1, 2, 3)$ is SLS if $\log(\bar{a}_{11}/\bar{a}_{21}) > \frac{1}{2}[\sigma_{a_{11}}^2/\bar{a}_{11}^2 - \sigma_{a_{21}}^2/\bar{a}_{21}^2]$ and $\log(\bar{a}_{11}/\bar{a}_{31}) > \frac{1}{2}[\sigma_{a_{11}}^2/\bar{a}_{11}^2 - \sigma_{a_{31}}^2/\bar{a}_{31}^2]$, that is, $\log(2/3) > \frac{1}{2}[0.01/4 - \sigma_{a_{21}}^2/9]$ and $\log(2/1.5) > \frac{1}{2}[0.01/4 - 0.01/2.25]$. More specifically, the vertex $\mathbf{e}_k$ $(k = 1, 2, 3)$ will lose its stability if $\sigma_{a_{21}}^2 < 7.32$. Moreover, the stochastic local stability analysis of the constant interior equilibrium $(1/3, 1/3, 1/3)$ is beyond the scope of this study, but it is similar to the one in Zheng *et al.* [10]. The simulation results are shown in Fig. 1, where we take $a_{21}(t) = 2.9$ and 3.1 with the same probability 0.5 such that $\sigma_{a_{21}}^2 = 0.01$ in Fig. 1(a), $a_{21}(t) = 1.5$ and 4.5 with the same probability 0.5 such that $\sigma_{a_{21}}^2 = 2.25$ in Fig. 1(b), and $a_{21}(t) = 0.2$ and 5.8 with the same probability 0.5 such that $\sigma_{a_{21}}^2 = 7.84$ in Fig. 1(c). We can see that the simulation results are consistent with the theoretical predictions.

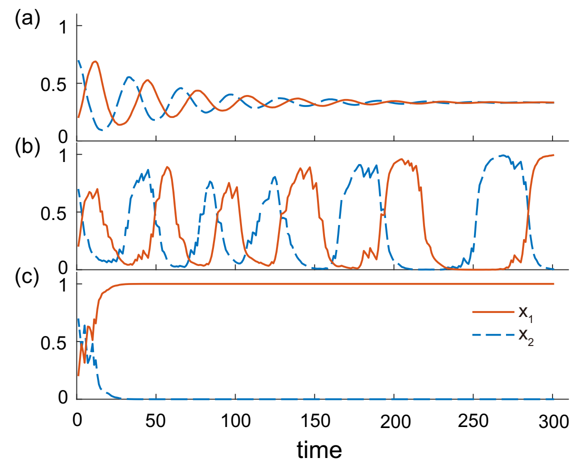

FIG. 1. Simulation results for the three-phenotype stochastic evolutionary game with the random payoff matrix given in Eq. (12). Here $x_{1,t}$ and $x_{2,t}$ denote the frequencies of strategies S_1 and S_2, respectively, at time step $t \geqslant 0$ (so that the frequency of strategy S_3 is $1 - x_{1,t} - x_{2,t}$). In panels (a), (b), and (c), the solid red and dashed blue curves represent the time evolution of $x_{1,t}$ and $x_{2,t}$, respectively, where the initial state is taken as $(x_{1,0}, x_{2,0}) = (0.2, 0.7)$. (a) Taking $a_{21}(t) = 2.9$ and 3.1 with the same probability 0.5 such that $\sigma_{a_{21}}^2 = 0.01$, the time evolution $(x_{1,t}, x_{2,t})$ converges to $(1/3, 1/3)$. (b) Taking $a_{21}(t) = 1.5$ and 4.5 with the same probability 0.5 such that $\sigma_{a_{21}}^2 = 2.25$, the time evolution of $(x_{1,t}, x_{2,t})$ periodically oscillates around $(1/3, 1/3)$. (c) Taking $a_{21}(t) = 0.2$ and 5.8 with the same probability 0.5 such that $\sigma_{a_{21}}^2 = 7.84$, the time evolution of $(x_{1,t}, x_{2,t})$ converges to (1,0).

Note that, in the degenerate case where $a_{ik}(t) = a_{kk}(t)$ for all $t \geqslant 0$ for some $i \neq k$, the conditions in Eq. (11) cannot be used to determine the stochastic local stability of $\mathbf{e}_k$. As an example, consider the case $n = 2$ with $a_{11}(t) = a_{21}(t)$ for all $t \geqslant 0$. Defining $v_t = x_{1,t}/x_{2,t}$ for $t \geqslant 0$, we have

$$v_{t+1} = v_t\left(\frac{v_t a_{11}(t) + a_{12}(t)}{v_t a_{21}(t) + a_{22}(t)}\right), \tag{13}$$

from which

$$v_{t+1} - v_t = \frac{a_{12}(t)}{a_{11}(t)} - \frac{a_{22}(t)}{a_{11}(t)} - \frac{a_{22}(t)[a_{12}(t) - a_{22}(t)]}{a_{21}(t)[v_t a_{11}(t) + a_{22}(t)]}. \tag{14}$$

Therefore, we get

$$\lim_{T\to\infty} \frac{1}{T}(v_T - v_0) = \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \left(\frac{a_{12}(t)}{a_{11}(t)} - \frac{a_{22}(t)}{a_{11}(t)}\right) - \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{a_{22}(t)[a_{12}(t) - a_{22}(t)]}{(a_{21}(t)[v_t a_{11}(t) + a_{22}(t)]}, \tag{15}$$

where

$$\frac{a_{22}(t)(a_{12}(t)-a_{22}(t))}{(a_{21}(t)[v_t a_{11}(t)+a_{22}(t)])} \to 0 \quad (16)$$

as $\mathbf{x}_t = (x_{1,t}, x_{2,t}) \to (1,0) = \mathbf{e}_1$, that is, $v_t \to \infty$. Using the strong law of large numbers and Egorov's theorem, it can be shown that the vertex $\mathbf{e}_1$ is SLS if

$$\left\langle \frac{a_{12}(t)}{a_{11}(t)} - \frac{a_{22}(t)}{a_{11}(t)} \right\rangle = \left\langle \frac{a_{12}(t)}{a_{11}(t)} \right\rangle - \left\langle \frac{a_{22}(t)}{a_{11}(t)} \right\rangle > 0, \quad (17)$$

and a.e. SU (actually SU) if the inequality is reversed (the mathematical proof is similar to one presented in Zheng *et al.* [10]).

Developing the random payoffs around their means and using the approximations

$$\left\langle \frac{a_{12}(t)}{a_{11}(t)} \right\rangle \approx \frac{\bar{a}_{12}}{\bar{a}_{11}} + \frac{\bar{a}_{12}\sigma_{11}^2}{\bar{a}_{11}^3} - \frac{\sigma_{11,12}}{\bar{a}_{11}^2} \quad (18)$$

and

$$\left\langle \frac{a_{22}(t)}{a_{11}(t)} \right\rangle \approx \frac{\bar{a}_{22}}{\bar{a}_{11}} + \frac{\bar{a}_{22}\sigma_{11}^2}{\bar{a}_{11}^3} - \frac{\sigma_{11,22}}{\bar{a}_{11}^2}, \quad (19)$$

the above condition for $\mathbf{e}_1$ to be SLS reduces to

$$\frac{\bar{a}_{12} - \bar{a}_{22}}{\bar{a}_{11}} > \frac{\sigma_{11,12} - \sigma_{11,22}}{\bar{a}_{11}^2 + \sigma_{11}^2}. \quad (20)$$

If the inequality is reversed, then $\mathbf{e}_1$ is a.e. SU (actually SU).

B. Stochastic evolutionary stability in a symmetric matrix game

We now extend the standard concept of an evolutionarily stable strategy (ESS) in a constant environment to a variable environment. A *stochastically evolutionarily stable* (SES) strategy is 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 as a result of selection is arbitrarily low [10]. More specifically, a mixed strategy represented by a frequency vector $\hat{\mathbf{x}} = (\hat{x}_1, \hat{x}_2, \dots, \hat{x}_n) \in \Delta_n$ is a SES strategy if the fixation of $\hat{\mathbf{x}}$ is SLS against any other strategy $\mathbf{x} = (x_1, x_2, \dots, x_n) \in \Delta_n$ with $\mathbf{x} \neq \hat{\mathbf{x}}$ close enough to $\hat{\mathbf{x}}$ [10].

Assuming payoffs for n pure strategies in pairwise interactions given by the random matrix $\mathbf{A}(t)$ at time step $t \geqslant 0$, the expected payoffs for two mixed strategies $\hat{\mathbf{x}}$ and $\mathbf{x}$ in pairwise interactions at the same time step are given by the game matrix

$$\begin{pmatrix} \hat{\mathbf{x}} \cdot \mathbf{A}(t)\hat{\mathbf{x}} & \hat{\mathbf{x}} \cdot \mathbf{A}(t)\mathbf{x} \\ \mathbf{x} \cdot \mathbf{A}(t)\hat{\mathbf{x}} & \mathbf{x} \cdot \mathbf{A}(t)\mathbf{x} \end{pmatrix}. \quad (21)$$

Here $\hat{\mathbf{x}} \cdot \mathbf{A}(t)\hat{\mathbf{x}}$ [or $\hat{\mathbf{x}} \cdot \mathbf{A}(t)\mathbf{x}$] is the expected payoff to strategy $\hat{\mathbf{x}}$ against strategy $\hat{\mathbf{x}}$ (or strategy $\mathbf{x}$), and $\mathbf{x} \cdot \mathbf{A}(t)\hat{\mathbf{x}}$ [or $\mathbf{x} \cdot \mathbf{A}(t)\mathbf{x}$] is the expected payoff to strategy $\mathbf{x}$ against strategy $\hat{\mathbf{x}}$ (or strategy $\mathbf{x}$). According to the conditions for the vertices of the simplex Δ_n to be SLS using approximations based on means, variances, and covariances of payoffs [see Eq. (10)], the mixed strategy $\hat{\mathbf{x}}$ is SES if

$$\log\left(\frac{\hat{\mathbf{x}} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}}}{\mathbf{x} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{\hat{\mathbf{x}}\cdot\mathbf{A}(t)\hat{\mathbf{x}}}}{(\hat{\mathbf{x}} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}})^2} - \frac{\sigma^2_{\mathbf{x}\cdot\mathbf{A}(t)\hat{\mathbf{x}}}}{(\mathbf{x} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}})^2}\right] \quad (22)$$

for $\mathbf{x} \neq \hat{\mathbf{x}}$ close enough to $\hat{\mathbf{x}}$. Here (i) $\bar{\mathbf{A}}$ denotes the mean of the random payoff matrix $\mathbf{A}(t) = (a_{ij}(t))_{n\times n}$, that is, $\bar{\mathbf{A}} = (\bar{a}_{ij})_{n\times n}$; (ii) $\hat{\mathbf{x}} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}}$ and $\mathbf{x} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}}$ are the means of the random variables $\hat{\mathbf{x}} \cdot \mathbf{A}(t)\hat{\mathbf{x}}$ and $\mathbf{x} \cdot \mathbf{A}(t)\hat{\mathbf{x}}$, respectively; and (iii) $\sigma^2_{\hat{\mathbf{x}}\cdot\mathbf{A}(t)\hat{\mathbf{x}}}$ and $\sigma^2_{\mathbf{x}\cdot\mathbf{A}(t)\hat{\mathbf{x}}}$ are the variances of the random variables $\hat{\mathbf{x}} \cdot \mathbf{A}(t)\hat{\mathbf{x}}$ and $\mathbf{x} \cdot \mathbf{A}(t)\hat{\mathbf{x}}$, respectively. These can be expressed as

$$\sigma^2_{\hat{\mathbf{x}}\cdot\mathbf{A}(t)\hat{\mathbf{x}}} = \langle(\hat{\mathbf{x}} \cdot \mathbf{A}(t)\hat{\mathbf{x}} - \hat{\mathbf{x}} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}})^2\rangle \quad (23)$$

and

$$\sigma^2_{\mathbf{x}\cdot\mathbf{A}(t)\hat{\mathbf{x}}} = \langle(\mathbf{x} \cdot \mathbf{A}(t)\hat{\mathbf{x}} - \mathbf{x} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}})^2\rangle. \quad (24)$$

In the case $n = 2$, for instance, $\hat{\mathbf{x}} = (1, 0)$ is SLS against $\mathbf{x} = (x, 1-x) \neq \hat{\mathbf{x}}$ close enough to $\hat{\mathbf{x}}$ if

$$\log\left(\frac{\bar{a}_{11}}{x\bar{a}_{11} + (1-x)\bar{a}_{21}}\right) > \frac{1}{2}\left[\frac{\sigma_{11}^2}{\bar{a}_{11}^2} - \frac{x^2\sigma_{11}^2 + 2x(1-x)\sigma_{11,21} + (1-x)^2\sigma_{21}^2}{(x\bar{a}_{11} + (1-x)\bar{a}_{21})^2}\right], \quad (25)$$

that is,

$$\bar{a}_{11}^2(\bar{a}_{11} - \bar{a}_{21}) > \bar{a}_{21}\sigma_{11}^2 - \bar{a}_{11}\sigma_{11,21}, \quad (26)$$

as shown in Zheng *et al.* [10]. This is the condition for $\hat{\mathbf{x}} = (1, 0)$ to be SES.

III. ASYMMETRIC MATRIX GAME WITH RANDOM PAYOFFS

We now consider an asymmetric matrix game, also known as a bimatrix game [1,2,32]. In pairwise interactions, players are in one of two possible positions, I or II. In position I, there are m phenotypes (or pure strategies), denoted by U_i for $i = 1, 2, \dots, m$; and in position II, n phenotypes, denoted by V_j for $j = 1, 2, \dots, n$. At time step $t \geqslant 0$, the payoffs to players in position I against players in position II are given by the game matrix

$$\mathbf{B}(t) = (b_{ij}(t))_{m\times n} = \begin{pmatrix} b_{11}(t) & b_{12}(t) & \dots & b_{1n}(t) \\ b_{21}(t) & b_{22}(t) & \dots & b_{2n}(t) \\ \vdots & \vdots & \ddots & \vdots \\ b_{m1}(t) & b_{m2}(t) & \dots & b_{mn}(t) \end{pmatrix}, \quad (27)$$

where $b_{ij}(t)$ is the payoff to strategy U_i against strategy V_j for $i = 1, 2, \dots, m$ and $j = 1, 2, \dots, n$; and the payoffs to players in position II against players in position I by

$$\mathbf{C}(t) = (c_{ji}(t))_{n\times m} = \begin{pmatrix} c_{11}(t) & c_{12}(t) & \dots & c_{1m}(t) \\ c_{21}(t) & c_{22}(t) & \dots & c_{2m}(t) \\ \vdots & \vdots & \ddots & \vdots \\ c_{n1}(t) & c_{n2}(t) & \dots & c_{nm}(t) \end{pmatrix}, \quad (28)$$

where $c_{ji}(t)$ is the payoff to V_j against U_i for $j = 1, 2, \dots, n$ and $i = 1, 2, \dots, m$. We assume that the payoffs are positive random variables that uniformly bounded below and above by two positive constants, that is, there exist real numbers $A, B > 0$ such that $A \leqslant b_{ij}(t), c_{ji}(t) \leqslant B$ for $i = 1, 2, \dots, m$ and $j = 1, 2, \dots, n$. The probability distributions of the payoffs do not depend on $t \geqslant 0$. The means, variances, and covariances of $b_{ij}(t)$ for $i = 1, 2, \dots, m$, $j = 1, 2, \dots, n$ and $t \geqslant 0$ are given by $\langle b_{ij}(t)\rangle = \bar{b}_{ij}$, $\langle(b_{ij}(t) - \bar{b}_{ij})^2\rangle = \sigma^2_{b_{ij}}$,

$\langle (b_{ij}(t)-\bar{b}_{ij})(b_{kl}(t)-\bar{b}_{kl})\rangle = \sigma_{b_{ij},b_{kl}}$, for all i,k,j,l with $(i,j)\neq(k,l)$, while $\langle (b_{ij}(s)-\bar{b}_{ij})(b_{kl}(t)-\bar{b}_{kl})\rangle = 0$ for all i,k,j,l and $s\neq t$, since payoffs at different time steps are assumed to be independent, and similarly for $c_{ji}(t)$. Moreover, $b_{ij}(t)$ and $c_{lk}(s)$ are independent of each other for all i,k,j,l and $t,s\geqslant 0$. Another assumption is that all variances are small.

At time step $t\geqslant 0$, the frequencies of strategy U_i in position I and strategy V_j in position II are denoted by $u_{i,t}$ and $v_{j,t}$, respectively, for $i=1,2,\dots,m$ and $j=1,2,\dots,n$ with $\sum_{i=1}^m u_{i,t}=1$ and $\sum_{j=1}^n v_{j,t}=1$, respectively. Assuming random pairwise interactions, the expected payoffs to U_i and V_j are given by

$$\phi_{i,t} = (\mathbf{B}(t)\mathbf{v}_t)_i = \sum_{j=1}^n v_{j,t} b_{ij}(t) \quad \text{for } i=1,2,\dots,m, \tag{29a}$$

$$\psi_{j,t} = (\mathbf{C}(t)\mathbf{u}_t)_j = \sum_{i=1}^m u_{i,t} c_{ji}(t) \quad \text{for } j=1,2,\dots,n, \tag{29b}$$

respectively, where $\mathbf{u}_t=(u_{1,t},u_{2,t},\dots,u_{m,t})\in\Delta_m$ and $\mathbf{v}_t=(v_{1,t},v_{2,t},\dots,v_{n,t})\in\Delta_n$ are frequency vectors that describe the current population state. The corresponding mean payoffs in positions I and II take the form

$$\bar{\phi}_t = \mathbf{u}_t\cdot\mathbf{B}(t)\mathbf{v}_t = \sum_{i=1}^m u_{i,t}\phi_{i,t}, \tag{30a}$$

$$\bar{\psi}_t = \mathbf{v}_t\cdot\mathbf{C}(t)\mathbf{u}_t = \sum_{j=1}^n v_{j,t}\psi_{j,t}, \tag{30b}$$

respectively [2]. As a result, the frequencies of strategies U_i and V_j at time step $t+1$ are given by

$$u_{i,t+1} = \frac{u_{i,t}(\mathbf{B}(t)\mathbf{v}_t)_i}{\mathbf{u}_t\cdot\mathbf{B}(t)\mathbf{v}_t} \quad \text{for } i=1,2,\dots,m, \tag{31a}$$

$$v_{j,t+1} = \frac{v_{j,t}(\mathbf{C}(t)\mathbf{u}_t)_j}{\mathbf{v}_t\cdot\mathbf{C}(t)\mathbf{u}_t} \quad \text{for } j=1,2,\dots,n, \tag{31b}$$

respectively [2].

A. Stochastic local stability in an asymmetric matrix game

Let $(\hat{\mathbf{u}},\hat{\mathbf{v}})\in\Delta_m\times\Delta_n$ represent a constant equilibrium of the process $\{\mathbf{u}_t,\mathbf{v}_t\}$ for $t\geqslant 0$, that is, an equilibrium of Eq. (31) that does not depend on the randomness of the payoff matrices $\mathbf{B}(t)$ and $\mathbf{C}(t)$. This is clearly the case for each of the points $(\mathbf{e}'_i,\mathbf{e}''_j)$ for $i=1,2,\dots,m$ and $j=1,2,\dots,n$, where $\mathbf{e}'_i$ denotes a vertex in the simplex Δ_m and $\mathbf{e}''_j$ a vertex in the simplex Δ_n. These are fixation states or boundary equilibria of Eq. (31). We will focus on the stochastic local stability (SLS) of these boundary equilibria.

According to the definitions introduced in the previous sections, a constant equilibrium $(\hat{\mathbf{u}},\hat{\mathbf{v}})$ of Eq. (31) is SLS if for any $\epsilon>0$ there exist $\delta'_0>0$ and $\delta''_0>0$ such that $\mathbb{P}((\mathbf{u}_t,\mathbf{v}_t)\to(\hat{\mathbf{u}},\hat{\mathbf{v}}))\geqslant 1-\epsilon$ as soon as $|\mathbf{u}_0-\hat{\mathbf{u}}|<\delta'_0$ and $|\mathbf{v}_0-\hat{\mathbf{v}}|<\delta''_0$. On the other hand, $(\hat{\mathbf{u}},\hat{\mathbf{v}})$ is a.e. SU if $\mathbb{P}((\mathbf{u}_t,\mathbf{v}_t)\to(\hat{\mathbf{u}},\hat{\mathbf{v}}))=0$ as soon as $|\mathbf{u}_0-\hat{\mathbf{u}}|>0$ or $|\mathbf{v}_0-\hat{\mathbf{v}}|>0$ and SU if $|\mathbf{u}_0-\hat{\mathbf{u}}|>0$ and $|\mathbf{v}_0-\hat{\mathbf{v}}|>0$.

Without loss of generality, we consider here only the stochastic local stability of the fixation state $(\mathbf{e}'_1,\mathbf{e}''_1)$. Note that $u_{1,t}=1-\sum_{i=2}^m u_{i,t}$ and $v_{1,t}=1-\sum_{j=2}^n v_{j,t}$. Then the expected payoffs to U_i and V_j can be reexpressed as

$$\phi_{i,t} = b_{i1}(t)+\sum_{j=2}^n v_{j,t}(b_{ij}(t)-b_{i1}(t)) \quad \text{for } i=1,2,\dots,m, \tag{32a}$$

$$\psi_{j,t} = c_{j1}(t)+\sum_{i=2}^m u_{i,t}(c_{ji}(t)-c_{j1}(t)) \quad \text{for } j=1,2,\dots,n, \tag{32b}$$

respectively, and the mean payoffs in positions I and II as

$$\begin{aligned}\bar{\phi}_t &= \phi_{1,t}+\sum_{i=2}^m u_{i,t}(\phi_{i,t}-\phi_{1,t})\\ &= b_{11}(t)+\sum_{j=2}^n v_{j,t}(b_{1j}(t)-b_{11}(t))+\sum_{i=2}^m u_{i,t}(\phi_{i,t}-\phi_{1,t}),\end{aligned} \tag{33a}$$

$$\begin{aligned}\bar{\psi}_t &= \psi_{1,t}+\sum_{j=2}^n v_{j,t}(\psi_{j,t}-\psi_{1,t})\\ &= c_{11}(t)+\sum_{i=2}^m u_{i,t}(c_{1i}(t)-c_{11}(t))+\sum_{j=2}^n v_{j,t}(\psi_{j,t}-\psi_{1,t}),\end{aligned} \tag{33b}$$

respectively. Therefore, iterating Eq. (31) leads to

$$u_{i,T} = u_{i,0}\prod_{t=0}^{T-1}\frac{b_{i1}(t)}{b_{11}(t)}G_{i,t} \quad \text{for } i=2,3,\dots,m, \tag{34a}$$

$$v_{j,T} = v_{j,0}\prod_{t=0}^{T-1}\frac{c_{j1}(t)}{c_{11}(t)}H_{j,t} \quad \text{for } j=2,3,\dots,n, \tag{34b}$$

where

$$G_{i,t} = \frac{1+\sum_{j=2}^n v_{j,t}(b_{ij}(t)-b_{i1}(t))/b_{i1}(t)}{1+\left[\sum_{j=2}^n v_{j,t}(b_{1j}(t)-b_{11}(t))+\sum_{i=2}^m u_{i,t}(\phi_{i,t}-\phi_{1,t})\right]/b_{11}(t)}, \tag{35a}$$

$$H_{j,t} = \frac{1+\sum_{i=2}^m u_{i,t}(c_{ji}(t)-c_{j1}(t))/c_{j1}(t)}{1+\left[\sum_{i=2}^m u_{i,t}(c_{1i}(t)-c_{11}(t))+\sum_{j=2}^n v_{j,t}(\psi_{j,t}-\psi_{1,t})\right]/c_{11}(t)}, \tag{35b}$$

respectively. Thus, for $i = 2, 3, \dots, m$ and $j = 2, 3, \dots, n$, we have

$$\lim_{T\to\infty} \frac{1}{T} \log\left(\frac{u_{i,T}}{u_{i,0}}\right) = \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log\left(\frac{b_{i1}(t)}{b_{11}(t)}\right) + \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log G_{i,t}, \tag{36a}$$

$$\lim_{T\to\infty} \frac{1}{T} \log\left(\frac{v_{j,T}}{v_{j,0}}\right) = \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log\left(\frac{c_{j1}(t)}{c_{11}(t)}\right) + \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log H_{j,t}, \tag{36b}$$

where $\log G_{i,t} \to 0$ and $\log H_{j,t} \to 0$ as $(\mathbf{u}_t, \mathbf{v}_t) \to (\mathbf{e}'_1, \mathbf{e}''_1)$. From there, proceeding as previously and using the same assumptions, it can be shown that the fixation state $(\mathbf{e}'_1, \mathbf{e}''_1)$ is SLS if

$$\log\left(\frac{\bar{b}_{11}}{\bar{b}_{i1}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{b_{11}}}{\bar{b}^2_{11}} - \frac{\sigma^2_{b_{i1}}}{\bar{b}^2_{i1}}\right] \quad \text{for } i = 2, 3, \dots, m, \tag{37a}$$

$$\log\left(\frac{\bar{c}_{11}}{\bar{c}_{j1}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{c_{11}}}{\bar{c}^2_{11}} - \frac{\sigma^2_{c_{j1}}}{\bar{c}^2_{j1}}\right] \quad \text{for } j = 2, 3, \dots, n, \tag{37b}$$

a.e. SU if at least one of these inequalities is reversed, and SU if they are all reversed (the mathematical proof is similar to the one in the case of a symmetric matrix game; see the Appendix).

By analogy, the fixation state $(\mathbf{e}'_k, \mathbf{e}''_l)$ for $k = 1, 2, \dots, m$ and $l = 1, 2, \dots, n$ is SLS if

$$\log\left(\frac{\bar{b}_{kl}}{\bar{b}_{il}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{b_{kl}}}{\bar{b}^2_{kl}} - \frac{\sigma^2_{b_{il}}}{\bar{b}^2_{il}}\right], \tag{38a}$$

$$\log\left(\frac{\bar{c}_{lk}}{\bar{c}_{jk}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{c_{lk}}}{\bar{c}^2_{lk}} - \frac{\sigma^2_{c_{jk}}}{\bar{c}^2_{jk}}\right], \tag{38b}$$

for $i = 1, 2, \dots, m$ but $i \neq k$ and $j = 1, 2, \dots, n$ but $j \neq l$, a.e. SU if at least one of these inequalities is reversed, and SU if they are all reversed.

In the special case $m = n = 2$, for instance, we conclude that $(\mathbf{e}'_1, \mathbf{e}''_1)$ is SLS if

$$2\log(\bar{b}_{11}/\bar{b}_{21}) > \sigma^2_{b_{11}}/\bar{b}^2_{11} - \sigma^2_{b_{21}}/\bar{b}^2_{21}, \tag{39a}$$

$$2\log(\bar{c}_{11}/\bar{c}_{21}) > \sigma^2_{c_{11}}/\bar{c}^2_{11} - \sigma^2_{c_{21}}/\bar{c}^2_{21}; \tag{39b}$$

$(\mathbf{e}'_2, \mathbf{e}''_2)$ is SLS if

$$2\log(\bar{b}_{22}/\bar{b}_{12}) > \sigma^2_{b_{22}}/\bar{b}^2_{22} - \sigma^2_{b_{12}}/\bar{b}^2_{12}, \tag{40a}$$

$$2\log(\bar{c}_{22}/\bar{c}_{12}) > \sigma^2_{c_{22}}/\bar{c}^2_{22} - \sigma^2_{c_{12}}/\bar{c}^2_{12}; \tag{40b}$$

$(\mathbf{e}'_1, \mathbf{e}''_2)$ is SLS if

$$2\log(\bar{b}_{12}/\bar{b}_{22}) > \sigma^2_{b_{12}}/\bar{b}^2_{12} - \sigma^2_{b_{22}}/\bar{b}^2_{22}, \tag{41a}$$

$$2\log(\bar{c}_{21}/\bar{c}_{11}) > \sigma^2_{c_{21}}/\bar{c}^2_{21} - \sigma^2_{c_{11}}/\bar{c}^2_{11}; \tag{41b}$$

and $(\mathbf{e}'_2, \mathbf{e}''_1)$ is SLS if

$$2\log(\bar{b}_{21}/\bar{b}_{11}) > \sigma^2_{b_{21}}/\bar{b}^2_{21} - \sigma^2_{b_{11}}/\bar{b}^2_{11}, \tag{42a}$$

$$2\log(\bar{c}_{12}/\bar{c}_{22}) > \sigma^2_{c_{12}}/\bar{c}^2_{12} - \sigma^2_{c_{22}}/\bar{c}^2_{22}. \tag{42b}$$

As an example, we consider a two-phenotype asymmetric evolutionary game with random payoff matrices

$$\mathbf{B}(t) = \begin{pmatrix} 2 & 6 \\ b_{21}(t) & 3.5 \end{pmatrix}, \tag{43a}$$

$$\mathbf{C}(t) = \begin{pmatrix} 2 & c_{12}(t) \\ 1 & 3.5 \end{pmatrix}, \tag{43b}$$

where $b_{21}(t) = c_{12}(t)$ and $\bar{b}_{21} = \bar{c}_{12} = 2.5$. The mean payoff matrices $\bar{\mathbf{B}}$ and $\bar{\mathbf{C}}$ correspond to the game known as the battle of the sexes [2]. From the above theoretical analysis, the vertex $(\mathbf{e}'_1, \mathbf{e}''_1)$ is SLS if $\log(\bar{b}_{11}/\bar{b}_{21}) > \frac{1}{2}[\sigma^2_{b_{11}}/\bar{b}^2_{11} - \sigma^2_{b_{21}}/\bar{b}^2_{21}]$ and $\log(\bar{c}_{11}/\bar{c}_{21}) > \frac{1}{2}[\sigma^2_{c_{11}}/\bar{c}^2_{11} - \sigma^2_{c_{21}}/\bar{c}^2_{21}]$, that is, $\log(2/2.5) > -\frac{1}{2}\sigma^2_{b_{21}}/6.25$ and $\log(2/1) > 0$. More specifically, the vertex $(\mathbf{e}'_1, \mathbf{e}''_1)$ is SLS (or a.e. SU) if $\sigma^2_{b_{21}} > 2.79$ (or $\sigma^2_{b_{21}} < 2.79$). The simulation results are shown in Fig. 2, and these results match the theoretical predictions.

B. Stochastic evolutionary stability in an asymmetric matrix game

Consider $(\hat{\mathbf{u}}, \hat{\mathbf{v}}) \in \Delta_m \times \Delta_n$ and $(\mathbf{u}, \mathbf{v}) \in \Delta_m \times \Delta_n$, where $\hat{\mathbf{u}}$ and $\mathbf{u}$ represent two mixed strategies in position I, and $\hat{\mathbf{v}}$ and $\mathbf{v}$ two mixed strategies in position II. At time step $t \geqslant 0$, the expected payoffs to $\hat{\mathbf{u}}$ or $\mathbf{u}$ against $\hat{\mathbf{v}}$ or $\mathbf{v}$, and vice versa, are given by the game matrices

$$\begin{pmatrix} \hat{\mathbf{u}} \cdot \mathbf{B}(t)\hat{\mathbf{v}} & \hat{\mathbf{u}} \cdot \mathbf{B}(t)\mathbf{v} \\ \mathbf{u} \cdot \mathbf{B}(t)\hat{\mathbf{v}} & \mathbf{u} \cdot \mathbf{B}(t)\mathbf{v} \end{pmatrix} \tag{44}$$

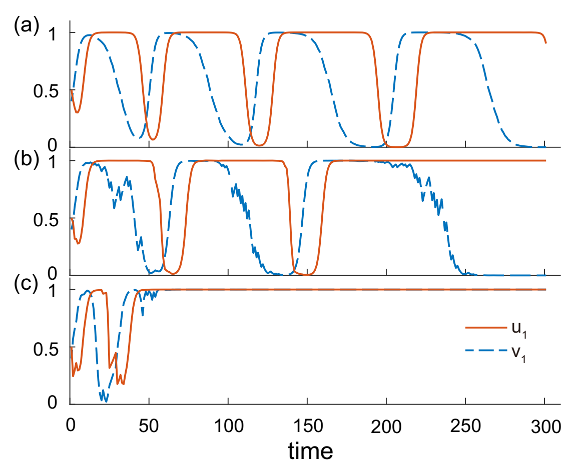

FIG. 2. Simulation results for the two-phenotype stochastic asymmetric evolutionary game with the random payoff matrices given in Eq. (43). Here $u_{1,t}$ and $v_{1,t}$ denote the frequencies of strategy U_1 in position I and strategy V_1 in position II, respectively, at time step $t \geqslant 0$. In panels (a), (b), and (c), the solid red and dashed blue curves represent the time evolution of $u_{1,t}$ and $v_{1,t}$, respectively, where the initial state is taken as $(u_{1,0}, v_{1,0}) = (0.5, 0.4)$. (a, b) Taking $b_{21} = 2.4$ and 2.6 with the same probability 0.5 such that $\sigma^2_{b_{21}} = 0.01$, and taking $b_{21} = 1.5$ and 3.5 with the same probability 0.5 such that $\sigma^2_{b_{21}} = 1$, the time evolution of $(u_{1,t}, v_{1,t})$ periodically oscillates between the boundaries. (c) Taking $b_{21} = 0.5$ and 4.5 with the same probability 0.5 such that $\sigma^2_{b_{21}} = 4$, the time evolution of $(u_{1,t}, v_{1,t})$ converges to the vertex $(\mathbf{e}'_1, \mathbf{e}''_1)$.

and

$$\begin{pmatrix} \hat{\mathbf{v}} \cdot \mathbf{C}(t)\hat{\mathbf{u}} & \hat{\mathbf{v}} \cdot \mathbf{C}(t)\mathbf{u} \\ \mathbf{v} \cdot \mathbf{C}(t)\hat{\mathbf{u}} & \mathbf{v} \cdot \mathbf{C}(t)\mathbf{u} \end{pmatrix}, \tag{45}$$

respectively. If both $\mathbf{B}(t)$ and $\mathbf{C}(t)$ are constant payoff matrices, denoted by $\mathbf{B}$ and $\mathbf{C}$, respectively, then the strategy pair $(\hat{\mathbf{u}}, \hat{\mathbf{v}})$ is known to be a Nash equilibrium if $\hat{\mathbf{u}}$ is the best reply to $\hat{\mathbf{v}}$, and vice versa, that is, $\mathbf{u} \cdot \mathbf{B}\hat{\mathbf{v}} \leqslant \hat{\mathbf{u}} \cdot \mathbf{B}\hat{\mathbf{v}}$ for all $\mathbf{u} \in \Delta_m$, and $\mathbf{v} \cdot \mathbf{C}\hat{\mathbf{u}} \leqslant \hat{\mathbf{v}} \cdot \mathbf{C}\hat{\mathbf{u}}$ for all $\mathbf{v} \in \Delta_n$ [2].

We now extend this concept to the situation where the payoff matrices $\mathbf{B}(t)$ and $\mathbf{C}(t)$ are random. The strategy pair $(\hat{\mathbf{u}}, \hat{\mathbf{v}})$ is said to be SES (stochastically evolutionarily stable) if the fixation state $(\hat{\mathbf{u}}, \hat{\mathbf{v}})$ is SLS against any other close enough strategy pair $(\mathbf{u}, \mathbf{v})$. From the previous analysis, this is the case if

$$\log\left(\frac{\hat{\mathbf{u}} \cdot \bar{\mathbf{B}}\hat{\mathbf{v}}}{\mathbf{u} \cdot \bar{\mathbf{B}}\hat{\mathbf{v}}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{\hat{\mathbf{u}}\cdot\mathbf{B}(t)\hat{\mathbf{v}}}}{(\hat{\mathbf{u}} \cdot \bar{\mathbf{B}}\hat{\mathbf{v}})^2} - \frac{\sigma^2_{\mathbf{u}\cdot\mathbf{B}(t)\hat{\mathbf{v}}}}{(\mathbf{u} \cdot \bar{\mathbf{B}}\hat{\mathbf{v}})^2}\right], \tag{46a}$$

$$\log\left(\frac{\hat{\mathbf{v}} \cdot \bar{\mathbf{C}}\hat{\mathbf{u}}}{\mathbf{v} \cdot \bar{\mathbf{C}}\hat{\mathbf{u}}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{\hat{\mathbf{v}}\cdot\mathbf{C}(t)\hat{\mathbf{u}}}}{(\hat{\mathbf{v}} \cdot \bar{\mathbf{C}}\hat{\mathbf{u}})^2} - \frac{\sigma^2_{\mathbf{v}\cdot\mathbf{C}(t)\hat{\mathbf{u}}}}{(\mathbf{v} \cdot \bar{\mathbf{C}}\hat{\mathbf{u}})^2}\right], \tag{46b}$$

where $\bar{\mathbf{B}} = (\bar{b}_{ij})_{m\times n}$ and $\bar{\mathbf{C}} = (\bar{c}_{ji})_{n\times m}$ are the mean payoff matrices, while $\sigma^2_{\hat{\mathbf{u}}\cdot\mathbf{B}(t)\hat{\mathbf{v}}}$, $\sigma^2_{\mathbf{u}\cdot\mathbf{B}(t)\hat{\mathbf{v}}}$, $\sigma^2_{\hat{\mathbf{v}}\cdot\mathbf{C}(t)\hat{\mathbf{u}}}$, and $\sigma^2_{\mathbf{v}\cdot\mathbf{C}(t)\hat{\mathbf{u}}}$ are the variances of $\hat{\mathbf{u}} \cdot \mathbf{B}(t)\hat{\mathbf{v}}$, $\mathbf{u} \cdot \mathbf{B}(t)\hat{\mathbf{v}}$, $\hat{\mathbf{v}} \cdot \mathbf{C}(t)\hat{\mathbf{u}}$, and $\mathbf{v} \cdot \mathbf{C}(t)\hat{\mathbf{u}}$, respectively.

In the case $m = n = 2$, for instance, the pure strategy pair $(\mathbf{e}'_1, \mathbf{e}''_1)$ is SES against any other close enough strategy pair $(\mathbf{u}, \mathbf{v}) \neq (\mathbf{e}'_1, \mathbf{e}''_1)$ if

$$\log\left(\frac{\bar{b}_{11}}{u\bar{b}_{11} + (1-u)\bar{b}_{21}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{b_{11}}}{\bar{b}^2_{11}} - \frac{u^2\sigma^2_{b_{11}} + 2u(1-u)\sigma_{b_{11},b_{21}} + (1-u)^2\sigma^2_{b_{21}}}{(u\bar{b}_{11} + (1-u)\bar{b}_{21})^2}\right], \tag{47a}$$

$$\log\left(\frac{\bar{c}_{11}}{v\bar{c}_{11} + (1-v)\bar{c}_{21}}\right) > \frac{1}{2}\left[\frac{\sigma^2_{c_{11}}}{\bar{c}^2_{11}} - \frac{v^2\sigma^2_{c_{11}} + 2v(1-v)\sigma_{c_{11},c_{21}} + (1-v)^2\sigma^2_{c_{21}}}{(v\bar{c}_{11} + (1-v)\bar{c}_{21})^2}\right], \tag{47b}$$

that is,

$$\bar{b}^2_{11}(\bar{b}_{11} - \bar{b}_{21}) > \bar{b}_{21}\sigma^2_{b_{11}} - \bar{b}_{11}\sigma_{b_{11},b_{21}}, \tag{48a}$$

$$\bar{c}^2_{11}(\bar{c}_{11} - \bar{c}_{21}) > \bar{c}_{21}\sigma^2_{c_{11}} - \bar{c}_{11}\sigma_{c_{11},c_{21}}. \tag{48b}$$

IV. CONCLUSION

As pointed out in the Introduction, environmental conditions are randomly changing over time, and those stochastic fluctuations in the surrounding environment of a population introduce random variations in the occurrence of interactions between individuals and, more importantly, random variations in the payoffs received by interacting individuals. On the other hand, evolutionary concepts such as those of evolutionary stability and convergence stability [33–36] were originally introduced for a large (virtually infinite) population 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 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. How can we extend such concepts for a population in a stochastic environment? This is the question that has been addressed in this paper.

We have investigated not only the concept of stochastic evolutionary stability in a general setting of a n-phenotype symmetric matrix game with random payoffs but also its extension to a multiphenotype asymmetric matrix game (or bimatrix game) with random payoff matrices. In addition, we have to point out that although, in general, our analysis does not require the assumption that the variances of the payoffs are small to get criteria for stochastic local stability and stochastic evolutionary stability [see Eqs. (8) and (36)], this assumption is just more convenient to understand how stochastic fluctuations in the payoffs affect the long-term behavior of the stochastic evolutionary game dynamics.

In the case of a symmetric matrix game with a random payoff matrix $\mathbf{A}(t) = (a_{ij}(t))_{n\times n}$ at every time $t \geqslant 0$, we have shown that the vertex $\mathbf{e}_k$ of the frequency simplex Δ_n, which corresponds to the fixation state of strategy S_k, for $k = 1, 2, \ldots, n$, is stochastically locally stable (SLS) if $2\log(\bar{a}_{kk}/\bar{a}_{ik}) > (\sigma^2_{kk}/\bar{a}^2_{kk} - \sigma^2_{ik}/\bar{a}^2_{ik})$ for all $i = 1, 2, \ldots, n$ but $i \neq k$. This result has been obtained under the assumption that the payoffs in pairwise interactions have variances small enough so that higher-order moments can be ignored. When the variances vanish, the result reduces to the well-known condition for local stability of $\mathbf{e}_k$ in the deterministic game dynamics [2]. Moreover, we have shown that a mixed strategy represented by the frequency vector $\hat{\mathbf{x}} = (\hat{x}_1, \hat{x}_2, \ldots, \hat{x}_n) \in \Delta_n$, so that the pure strategy S_i is used with probability $\hat{x}_i$ for $i = 1, 2, \ldots, n$, is stochastically evolutionarily stable (SES) if $2\log(\hat{\mathbf{x}} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}}/\mathbf{x} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}}) > [\sigma^2_{\hat{\mathbf{x}}\cdot\bar{\mathbf{A}}\hat{\mathbf{x}}}/(\hat{\mathbf{x}} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}})^2 - \sigma^2_{\mathbf{x}\cdot\bar{\mathbf{A}}\hat{\mathbf{x}}}/(\mathbf{x} \cdot \bar{\mathbf{A}}\hat{\mathbf{x}})^2]$, which means that $\hat{\mathbf{x}}$ is SLS against $\mathbf{x}$, for any close enough mixed strategy $\mathbf{x} \neq \hat{\mathbf{x}}$. This result extends the concept of evolutionary stability in a deterministic environment to a stochastic environment.

In the case of an asymmetric matrix game with random payoff matrices $\mathbf{B}(t) = (b_{ij}(t))_{m\times n}$ and $\mathbf{C}(t) = (c_{ji}(t))_{n\times m}$ at every time $t \geqslant 0$, a fixation state is represented by $(\mathbf{e}'_k, \mathbf{e}''_l)$ for $1 \leqslant k \leqslant m$ and $1 \leqslant l \leqslant n$, where $\mathbf{e}'_k$ represents a vertex of the simplex Δ_m and $\mathbf{e}''_l$ a vertex of the simplex Δ_n, for $k = 1, 2, \ldots, m$ and $l = 1, 2, \ldots, n$. Under the assumption that the payoffs in pairwise interactions have small enough variances, we have shown that a fixation state $(\mathbf{e}'_k, \mathbf{e}''_l)$ is SLS if $2\log(\bar{b}_{kl}/\bar{b}_{il}) > (\sigma^2_{b_{kl}}/\bar{b}^2_{kl} - \sigma^2_{b_{il}}/\bar{b}^2_{il})$ and $2\log(\bar{c}_{lk}/\bar{c}_{jk}) > (\sigma^2_{c_{lk}}/\bar{c}^2_{lk} - \sigma^2_{c_{jk}}/\bar{c}^2_{jk})$ for all $i = 1, 2, \ldots, m$ but $i \neq k$ and $j = 1, 2, \ldots, n$ but $j \neq l$. This result extends the concept of stochastic local stability in a symmetric matrix game to an asymmetric matrix game. As in the symmetric case, this result can be applied to mixed strategies to get conditions for stochastic evolutionary stability in the asymmetric case. The strategy pair $(\hat{\mathbf{u}}, \hat{\mathbf{v}}) \in \Delta_m \times \Delta_n$ (where $\hat{\mathbf{u}} = (\hat{u}_1, \hat{u}_2, \ldots, \hat{u}_m)$ represents a mixed strategy in position I, and $\hat{\mathbf{v}} = (\hat{v}_1, \hat{v}_2, \ldots, \hat{v}_n)$ a mixed strategy in position II) is SES if $2\log(\hat{\mathbf{u}} \cdot \bar{\mathbf{B}}\hat{\mathbf{v}}/\mathbf{u} \cdot \bar{\mathbf{B}}\hat{\mathbf{v}}) > [\sigma^2_{\hat{\mathbf{u}}\cdot\mathbf{B}(t)\hat{\mathbf{v}}}/(\hat{\mathbf{u}} \cdot \bar{\mathbf{B}}\hat{\mathbf{v}})^2 - \sigma^2_{\mathbf{u}\cdot\mathbf{B}(t)\hat{\mathbf{v}}}/(\mathbf{u} \cdot \bar{\mathbf{B}}\hat{\mathbf{v}})^2]$ and $2\log(\hat{\mathbf{v}} \cdot \bar{\mathbf{C}}\hat{\mathbf{u}}/\mathbf{v} \cdot \bar{\mathbf{C}}\hat{\mathbf{u}}) > [\sigma^2_{\hat{\mathbf{u}}\cdot\mathbf{C}(t)\hat{\mathbf{u}}}/(\hat{\mathbf{v}} \cdot \bar{\mathbf{C}}\hat{\mathbf{u}})^2 - \sigma^2_{\mathbf{v}\cdot\mathbf{C}(t)\hat{\mathbf{u}}}/(\mathbf{v} \cdot \bar{\mathbf{C}}\hat{\mathbf{u}})^2]$.

These extensions to concepts in deterministic matrix games [1,2] and random 2×2 symmetric matrix games [10] provide a theoretical framework to address questions related to evolution in a population in a stochastic environment with multiple phenotypes and asymmetric pairwise interactions.

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APPENDIX: STOCHASTIC LOCAL STABILITY IN A SYMMETRIC MATRIX GAME

The proof below for n types is an extension of an analysis for two types that can be found in Karlin and Liberman [24,25] and Zheng *et al.* [10].

Equation (5) can be rewritten as

$$\frac{x_{i,T}}{x_{i,0}} = \prod_{t=0}^{T-1} \left(\frac{a_{i1}(t)}{a_{11}(t)}\right) Q_{i,t}, \tag{A1}$$

which implies

$$\frac{1}{T}\log\left(\frac{x_{i,T}}{x_{i,0}}\right) = \frac{1}{T}\sum_{t=0}^{T-1}\log\left(\frac{a_{i1}(t)}{a_{11}(t)}\right) + \frac{1}{T}\sum_{t=0}^{T-1}\log Q_{i,t}, \tag{A2}$$

for every time step $T \geqslant 1$ and $i = 2, \ldots, n$ such that $x_{i,0} > 0$. Let

$$\mu_i = \left\langle \log\left(\frac{a_{i1}(t)}{a_{11}(t)}\right)\right\rangle \tag{A3}$$

and

$$E_i = \left\{\frac{1}{T}\sum_{t=0}^{T-1}\log\left(\frac{a_{i1}(t)}{a_{11}(t)}\right) \to \mu_i \text{ as } T \to \infty\right\}, \tag{A4}$$

for $i = 2, \ldots, n$. By the strong law of large numbers, we have that $\mathbb{P}(E_i) = 1$ for $i = 2, \ldots, n$. On the other hand, for $Q_{i,t}$ given in Eq. (6) with $a_{kl}(t)$ being assumed uniformly bounded below and above by positive constants for all $k, l = 1, \ldots, n$, we have $\log Q_{i,t} \to 0$ for $i = 2, \ldots, n$ when $1 - x_{1,t} = \sum_{j=2}^n x_{j,t} \to 0$. But then we conclude from Eq. (A2) that

$$\lim_{T\to\infty}\frac{1}{T}\sum_{t=0}^{T-1}\log\left(\frac{a_{i1}(t)}{a_{11}(t)}\right) \leqslant 0 \tag{A5}$$

if this limit exists and $x_{i,0} > 0$ for some $i = 2, \ldots, n$, since then

$$\log\left(\frac{x_{i,T}}{x_{i,0}}\right) \leqslant \log\left(\frac{1}{x_{i,0}}\right) < \infty \tag{A6}$$

for $i = 2, \ldots, n$ and all $T \geqslant 1$. This conclusion is not possible in the set E_i if $\mu_i > 0$ and $x_{i,0} > 0$ for some $i = 2, \ldots, n$, in which case

$$\mathbb{P}(x_{1,t} \to 1) \leqslant \mathbb{P}\left(E_i^C\right) = 0. \tag{A7}$$

This entails that the fixation state $\mathbf{e_1}$ is almost everywhere stochastically unstable (a.e. SU) if $\mu_i > 0$ for some $i = 2, \ldots, n$, and stochastically unstable (SU) if $\mu_i > 0$ for all $i = 2, \ldots, n$,

Now consider the case where $\mu_i < 0$ for all $i = 2, \ldots, n$. By the strong law of large numbers and Egorov's theorem, given any $\varepsilon > 0$, there exists an integer $T_i \geqslant 1$ such that the probability of the event

$$F_i = \left\{\frac{1}{T}\sum_{t=0}^{T-1}\log\left(\frac{a_{i1}(t)}{a_{11}(t)}\right) < \frac{\mu_i}{2} \text{ for all } T \geqslant T_i\right\} \tag{A8}$$

satisfies

$$\mathbb{P}(F_i) \geqslant 1 - \varepsilon/(n-1) \tag{A9}$$

for $i = 2, \ldots, n$, so that the event $F = \bigcap_{i=2}^n F_i$ satisfies

$$\mathbb{P}(F) \geqslant 1 - \varepsilon. \tag{A10}$$

On the other hand, using the assumption that $A \leqslant a_{kl}(t) \leqslant B$ for some constants $A, B > 0$ and for all $k, l = 1, \ldots, n$, there exists $\delta_i > 0$ such that

$$\log Q_{i,t} = \log\left(\frac{1 + \sum_{j=2}^n x_{j,t}(a_{ij}(t) - a_{i1}(t))/a_{i1}(t)}{1 + \left[\sum_{j=2}^n x_{j,t}(a_{1j}(t) - a_{11}(t)) + \sum_{j=2}^n x_{j,t}(\pi_{j,t} - \pi_{1,t})\right]/a_{11}(t)}\right) < -\frac{\mu_i}{4} \tag{A11}$$

as soon as $1 - x_{1,t} = \sum_{j=2}^n x_{j,t} < \delta_i$ for $i = 2, \ldots, n$. Moreover, if $1 - x_{1,t} = \sum_{j=2}^n x_{j,t} \leqslant \delta_1$ where $\delta_1 = \frac{A}{4(B-A)} > 0$, then Eq. (5) leads to

$$\begin{aligned} x_{i,t+1} &= x_{i,t}\left(\frac{a_{i1}(t) + \sum_{j=2}^n x_{j,t}(a_{ij}(t) - a_{i1}(t))}{a_{11}(t) + \left[\sum_{j=2}^n x_{j,t}(a_{1j}(t) - a_{11}(t)) + \sum_{j=2}^n x_{j,t}(\pi_{j,t} - \pi_{1,t})\right]}\right) \\ &\leqslant x_{i,t}\left(\frac{B + (B-A)\sum_{j=2}^n x_{j,t}}{A + 2(A-B)\sum_{j=2}^n x_{j,t}}\right) \leqslant x_{i,t}\left(\frac{5B}{2A}\right) \end{aligned} \tag{A12}$$

and, by recurrence,

$$x_{i,t+1} \leqslant x_{i,0}\left(\frac{5B}{2A}\right)^{t+1} \quad \text{(A13)}$$

for $i = 2, \ldots, n$, from which

$$1 - x_{1,t+1} = \sum_{i=2}^{n} x_{j,t+1} \leqslant \left(\sum_{i=2}^{n} x_{i,0}\right)\left(\frac{5B}{2A}\right)^{t+1} = (1 - x_{1,0})\left(\frac{5B}{2A}\right)^{t+1} \quad \text{(A14)}$$

for all $t \geqslant 0$. Therefore, there exists $0 < \delta_0 < \delta_1$ such that $1 - x_{1,t} < \check{\delta}$ for $t = 0, 1, \ldots, \hat{T} - 1$ as soon as $1 - x_{1,0} < \delta_0$, where $\check{\delta} = \min(\delta_2, \ldots, \delta_n)$ and $\hat{T} = \max(T_2, \ldots, T_n)$. Then in the set $F = \bigcap_{i=2}^{n} F_i$ as soon as $1 - x_{1,0} < \delta_0$, we have

$$\frac{1}{\hat{T}}(\log x_{i,\hat{T}} - \log x_{i,0}) < \frac{\mu_i}{2} - \frac{\mu_i}{4} = \frac{\mu_i}{4} < 0 \quad \text{(A15)}$$

for $i = 2, \ldots, n$, owing to Eqs. (A2), (A8), and (A11). This implies

$$1 - x_{1,\hat{T}} = \sum_{i=2}^{n} x_{i,\hat{T}} < \sum_{i=2}^{n} x_{i,0} < \check{\delta} \quad \text{(A16)}$$

and, by recurrence, $1 - x_{1,T} < \check{\delta}$ for all $T \geqslant \hat{T}$.

Since $P(F) \geqslant 1 - \varepsilon$, it remains to show that $1 - x_{1,T} \to 0$ as $T \to \infty$ in F as soon as $1 - x_{1,0} < \delta_0$. It suffices to notice that Eq. (A15) extends from $\hat{T}$ to all $T \geqslant \hat{T}$, from which

$$\log x_{i,T} < \log x_{i,0} + \frac{T\mu_i}{4} \to -\infty \quad \text{(A17)}$$

as $T \to \infty$ for $i = 2, \ldots, n$, and then

$$1 - x_{1,T} = \sum_{i=2}^{n} x_{i,T} \to 0 \quad \text{(A18)}$$

as $T \to \infty$. This completes the proof.

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