

Stochastic replicator dynamics and evolutionary stabilityTian-Jiao Feng,^{1,2} Cong Li,³ Xiu-Deng Zheng^{1,*}, Sabin Lessard,^{4,†} and Yi Tao^{1,3,5,‡}¹Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China²University of Chinese Academy of Sciences, Beijing 100049, China³School of Ecology and Environment, Northwestern Polytechnical University, Xi'an 710072, China⁴Department of Mathematics and Statistics, University of Montreal, Montreal H3C 3J7, Canada⁵Institute of Biomedical Research, Yunnan University, Kunming 650091, China

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To develop the concept of evolutionary stability in a stochastic environment, we investigate the continuous-time dynamics of a two-phenotype linear evolutionary game with generally correlated random payoffs in pairwise interactions. By using the Gram-Schmidt orthogonalization procedure and Itô's formula, we deduce a stochastic differential equation for the phenotype frequencies that extends the replicator equation, called the stochastic replicator equation. We give conditions for stochastic stability of a fixation state or a constant interior equilibrium point with respect to the stochastic dynamics of the two phenotypes. We show that, if a fixation state is stochastically stable, then the pure strategy corresponding to this fixation state must be stochastically evolutionarily stable with respect to mixed strategies. However, this is not the case for a mixed strategy that corresponds to a stochastically stable constant interior equilibrium point with respect to the two phenotypes.

DOI: [10.1103/PhysRevE.105.044403](https://doi.org/10.1103/PhysRevE.105.044403)**I. INTRODUCTION**

Since Maynard Smith's monograph entitled *Evolution and the Theory of Games* was published in 1982 [1], evolutionary game theory has been not only extensively developed and successfully applied to explain the evolution of animal behavior but also widely used in ecology, economics, and social science [1–7]. Evolutionary game theory started with the concept of an evolutionarily stable strategy (ESS) introduced by Maynard Smith and Price [8], which has become one of the main tools for predicting evolutionary outcomes under natural selection. An ESS is a strategy such that, if all members of a population adopt it, then no mutant strategy could successfully invade the population under the effect of natural selection [1,9]. On the other hand, the replicator equation developed by Taylor and Jonker [2] (see also Ref. [5]), which describes the continuous-time dynamics for strategy frequencies in an infinite population, provides a fundamental mathematical framework for understanding the relationship between evolutionary stability and evolutionary game dynamics. In particular, an ESS in a linear game with a constant payoff matrix is necessarily an asymptotically stable equilibrium with respect to the corresponding pure-strategy game dynamics.

One key assumption in classical evolutionary game theory is that the results of interactions between individuals are not influenced by stochastic environmental fluctuations. For a

linear game with pairwise interactions, this implies a constant payoff matrix. However, this assumption cannot be always true since environmental conditions are usually changing over time. The effect of environmental stochasticity on population and community dynamics has long been recognized in theoretical ecology [10–19]. For instance, 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, to a greater or lesser degree, exhibit random fluctuations. Therefore, the effect of environmental stochasticity on the evolution of animal behavior, and more specifically on evolutionary game dynamics, should also be a very important issue.

In a recent study, the stochastic dynamics of a discrete-time two-phenotype linear game with random payoffs in pairwise interactions was investigated [20,21]. This study provided conditions for stochastic stability of constant equilibrium points that can be used to explore evolutionary stability of animal behavior in a stochastic environment. Here, a constant equilibrium point is an equilibrium state of the game dynamics that does not depend on the randomness of the payoffs [20], and such an equilibrium is stochastically stable if there is convergence to this state with probability as close to 1 as we wish starting from any state close enough to the equilibrium. Moreover, a strategy is said to be stochastically evolutionarily stable (SES) if the fixation state of this strategy is stochastically stable against the introduction of any other nearby strategy. This means that, once fixed in the population, this strategy can resist invasion by at least any slightly perturbed strategy in small enough initial frequency with probability as close to 1 as we wish under the effects of

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random payoffs [20,21]. This is a direct extension of the concept of evolutionary stability in a constant environment with deterministic payoffs [1,5,8].

Environmental stochasticity caused by random fluctuations in selection parameters must be distinguished from demographic stochasticity caused by random variations in population, deme, or brood size as well as random drift as a result of sampling effects in a finite population. For an evolutionary game in a population of fixed size N , Nowak *et al.* [22] proposed the concept of ESS_N for a fixed strategy, which involves two conditions: (i) a single mutant of any other strategy must have a lower fitness; and (ii) the fixation probability of any other strategy introduced as a single mutant is less than the neutral threshold probability, $1/N$. See, e.g., Refs. [23,24] and references therein for further developments.

A theoretical framework for analyzing stochastic stability and stochastic evolutionary stability in continuous-time models for evolutionary games with random payoffs is certainly of interest. Foster and Young [25] are among the first to have proposed such a framework by directly adding a stochastic perturbation to the deterministic replicator equation for the rate of change in the frequency of any strategy (see Ref. [26] for applications and Refs. [27–30] for other studies on effects of stochastic fluctuations in evolutionary game theory). In this stochastic dynamics, a set of states S was said to be stochastically stable if, in the long run, it is nearly certain that the system lies within every open set containing S as the strength of the stochastic perturbations tends to zero. Although a stochastically stable set is always nonempty and minimizes a suitably defined potential function, it is by no means equivalent to the set of evolutionarily stable strategies in the deterministic dynamics even when the latter exists [25,26].

Fudenberg and Harris [31] pointed out that stochastic fluctuations in continuous-time evolutionary game dynamics should act on the growth rates of the different strategies, which correspond to their payoffs, rather than on the rates of change in their frequencies. Specifically, if there are m possible phenotypes or pure strategies used in random pairwise interactions in a well-mixed population, then the stochastic differentials of their numbers at time $t \geq 0$, represented by $n_i(t)$ for $i = 1, \dots, m$, should be given by the equations $dn_i(t) = n_i(t)[(\mathbf{A}\mathbf{x}(t))_i + \sigma_i dw_i(t)]$ for $i = 1, \dots, m$, where $\mathbf{x}(t) = (n_1(t), n_2(t), \dots, n_m(t)) / \sum_{j=1}^m n_j(t)$ is the vector of phenotype frequencies at time $t \geq 0$ and \mathbf{A} denotes a constant payoff matrix. Here, $(\mathbf{A}\mathbf{x}(t))_i$ represents the average payoff of phenotype i at time $t \geq 0$ for $i = 1, \dots, m$, while $(w_1(t), w_2(t), \dots, w_m(t))$ stands for a m -dimensional Wiener process. Using these stochastic differential equations and Ito's formula, Fudenberg and Harris [31] deduced a stochastic replicator equation for strategy frequencies. Imhof [32] investigated this equation to find conditions for the existence of a stationary probability distribution when an interior ESS exists with respect to the game matrix \mathbf{A} , as well as conditions for the asymptotic stochastic stability of a fixation state that corresponds to a strict Nash equilibrium for \mathbf{A} . However, this stochastic replicator equation actually describes a special case since the stochastic perturbations are applied on the average payoffs of the different strategies, not on the payoffs of the individuals using these strategies, and they are assumed to

be independent. See also Ref. [33] for a stochastic partial differential equation describing the joint dynamics of abundance densities and continuous trait values in evolutionary ecology.

In this study, we develop a generalized stochastic replicator equation for a two-phenotype linear evolutionary game in continuous time by considering stochastic perturbations on the payoffs in pairwise interactions. These payoffs are assumed to be generally correlated and stochastic evolutionary properties of equilibrium points are studied. In Sec. II, we not only develop the general theoretical framework for the stochastic replicator equation, but also analyze the stochastic stability of equilibrium points. We first extend the classical deterministic replicator equation to a stochastic replicator equation by using the Gram-Schmidt orthogonalization procedure and Itô's formula. Then, we deduce conditions for stochastic stability of a fixation state or a constant interior equilibrium point by using the stability theory of stochastic differential equations (SDE, see e.g., Ref. [34]). More specifically, by analyzing the stochastic stability of the zero solution of the linear approximation (or the Taylor expansion) of the stochastic replicator equation about a given constant equilibrium point, we can obtain conditions for stochastic stability of this equilibrium. In Sec. III, we apply the concept of stochastic evolutionary stability (SES) to the stochastic replicator equation. Our main goal is to provide a general theoretical framework for studying the significance of stochastic fluctuations in the replicator dynamics.

II. STOCHASTIC REPLICATOR EQUATION

We consider a two-phenotype evolutionary game in an infinite population in continuous time. The two phenotypes (or pure strategies) are denoted by R_1 and R_2 , respectively. Their payoffs in pairwise interactions at time $t \geq 0$ are assumed to be random variables. These are given by the entries of the payoff matrix

$$\mathbf{A}(t) = \begin{pmatrix} a_{11}(t) & a_{12}(t) \\ a_{21}(t) & a_{22}(t) \end{pmatrix} = \bar{\mathbf{A}} + \begin{pmatrix} \xi_1(t) & \xi_2(t) \\ \xi_3(t) & \xi_4(t) \end{pmatrix}, \quad (1)$$

where $a_{ij}(t)$ denotes the payoff to strategy R_i against strategy R_j for $i, j = 1, 2$. Here, $\bar{\mathbf{A}} = (\bar{a}_{ij})_{2 \times 2}$ represents the expected payoff matrix, while $\xi(t) = (\xi_1(t), \xi_2(t), \xi_3(t), \xi_4(t))^T$ for $t \geq 0$ is a multivariate Gaussian white noise with $\langle \xi_i(t) \rangle = 0$ and $\langle \xi_i(t) \xi_j(t') \rangle = 2\lambda_{ij} \sqrt{D_i D_j} \delta(t - t')$ for $i, j = 1, 2, 3, 4$, where $\lambda_{ij} = 1$ if $i = j$. Moreover, the variance-covariance matrix $\mathbf{C} = \langle \xi(t) \xi(t)^T \rangle$ is positive definite, and then invertible, so that $\xi_1(t)$, $\xi_2(t)$, $\xi_3(t)$, and $\xi_4(t)$ are linearly independent random variables. Note that, for $t, s \geq 0$ with $t \neq s$, the random vectors $\xi(t)$ and $\xi(s)$ are independent so that their components satisfy $\langle \xi_i(t) \xi_j(s) \rangle = 0$ for $i, j = 1, 2, 3, 4$.

Using the Gram-Schmidt orthogonalization procedure [35], the random variables

$$\eta_i(t) = \xi_i(t) - \sum_{k=1}^{i-1} \frac{\langle \xi_i(t) \eta_k(t) \rangle}{\langle \eta_k(t)^2 \rangle} \eta_k(t) \quad \text{for } i = 1, 2, 3, 4, \quad (2)$$

are Gaussian with $\langle \eta_i(t) \rangle = 0$ and $\langle \eta_i(t) \eta_j(t) \rangle = 0$ if $i \neq j$ for $i, j = 1, 2, 3, 4$, which implies that $\eta_1(t)$, $\eta_2(t)$,

$\eta_3(t)$, and $\eta_4(t)$ are independent. Moreover, the random vector $\eta(t) = (\eta_1(t), \eta_2(t), \eta_3(t), \eta_4(t))^T$ is independent of $\eta(s) = (\eta_1(s), \eta_2(s), \eta_3(s), \eta_4(s))^T$ for $s \neq t$.

Introducing the quantities $\psi_{ij} = \langle \xi_i(t)\eta_j(t) \rangle / \langle \eta_j(t)^2 \rangle$ for $i, j = 1, 2, 3, 4$ with $i > j$, and $2D_{\eta_i} = \langle \eta_i(t)^2 \rangle$ for $i = 1, 2, 3, 4$, we have the expressions

$$\psi_{i1} = \lambda_{1i} \sqrt{\frac{D_i}{D_1}}, \quad \text{for } i = 2, 3, 4, \tag{3a}$$

$$\psi_{i2} = \frac{\lambda_{2i} - \lambda_{12}\lambda_{1i}}{1 - \lambda_{12}^2} \sqrt{\frac{D_i}{D_2}}, \quad \text{for } i = 3, 4, \tag{3b}$$

$$\psi_{43} = \frac{(\lambda_{34} - \lambda_{13}\lambda_{14})(1 - \lambda_{12}^2) - (\lambda_{23} - \lambda_{12}\lambda_{13})(\lambda_{24} - \lambda_{12}\lambda_{14})}{1 - \lambda_{13}^2 - \lambda_{12}^2 - \lambda_{23}^2 + 2\lambda_{12}\lambda_{13}\lambda_{23}} \sqrt{\frac{D_4}{D_3}}, \tag{3c}$$

and

$$D_{\eta_1} = D_1, \tag{4a}$$

$$D_{\eta_2} = D_2(1 - \lambda_{12}^2), \tag{4b}$$

$$D_{\eta_3} = D_3 \left[1 - \lambda_{13}^2 - \frac{(\lambda_{23} - \lambda_{12}\lambda_{13})^2}{1 - \lambda_{12}^2} \right], \tag{4c}$$

$$D_{\eta_4} = D_4 \left[1 - \lambda_{14}^2 - \frac{(\lambda_{24} - \lambda_{12}\lambda_{14})^2}{1 - \lambda_{12}^2} - \frac{[(\lambda_{34} - \lambda_{13}\lambda_{14})(1 - \lambda_{12}^2) - (\lambda_{23} - \lambda_{12}\lambda_{13})(\lambda_{24} - \lambda_{12}\lambda_{14})]^2}{[(1 - \lambda_{13}^2)(1 - \lambda_{12}^2) - (\lambda_{23} - \lambda_{12}\lambda_{13})^2](1 - \lambda_{12}^2)} \right]. \tag{4d}$$

Note that $\eta_i(t)/\sqrt{2D_{\eta_i}} = d\omega_i(t)/dt$ for $t \geq 0$ and $i = 1, 2, 3, 4$ are independent standard white noises, where the random vector $(\omega_1(t), \omega_2(t), \omega_3(t), \omega_4(t))$ for $t \geq 0$ is a multivariate Wiener process, that is, a multivariate Brownian motion with independent components satisfying $\langle \omega_i(t) \rangle = 0$ and $\langle \omega_i(t)\omega_j(s) \rangle = \min(t, s)$ for $t, s \geq 0$ for $i = 1, 2, 3, 4$. Moreover, from (2) and (3), the random payoff matrix at time $t \geq 0$ can be rewritten as

$$\mathbf{A}(t) = \bar{\mathbf{A}} + \mathbf{\Pi}(t), \tag{5}$$

where $\mathbf{\Pi}(t)$ is given by

$$\begin{pmatrix} \eta_1(t) & \psi_{21}\eta_1(t) + \eta_2(t) \\ \sum_{j=1}^2 \psi_{3j}\eta_j(t) + \eta_3(t) & \sum_{j=1}^3 \psi_{4j}\eta_j(t) + \eta_4(t) \end{pmatrix}. \tag{6}$$

In the case of independent payoffs, that is, $\lambda_{ij} = 0$ for $i \neq j$, we have $\eta_i = \xi_i$ with $D_{\eta_i} = D_i$ for $i = 1, 2, 3, 4$, and $\psi_{ij} = 0$ for $i, j = 1, 2, 3, 4$ with $i > j$.

Let $x(t)$ be the frequency of strategy R_1 and, similarly, $1 - x(t)$ be the frequency of strategy R_2 , both at time $t \geq 0$. Assuming random pairwise interactions, the average payoffs to R_1 and R_2 at this time are given by

$$\pi_1(t) = x(t)\bar{a}_{11} + [1 - x(t)]\bar{a}_{12} + x(t)\eta_1(t) + [1 - x(t)][\psi_{21}\eta_1(t) + \eta_2(t)], \tag{7a}$$

$$\pi_2(t) = x(t)\bar{a}_{21} + [1 - x(t)]\bar{a}_{22} + x(t) \left[\sum_{i=1}^2 \psi_{3i}\eta_i(t) + \eta_3(t) \right] + [1 - x(t)] \left[\sum_{i=1}^3 \psi_{4i}\eta_i(t) + \eta_4(t) \right], \tag{7b}$$

respectively. Note that $x(t) = N_1(t)/[N_1(t) + N_2(t)]$, where $N_1(t)$ denotes the number of individuals using strategy R_1 and, similarly, $N_2(t)$ the number of individuals using strategy R_2 , both at time $t \geq 0$. Owing to the interpretation of payoffs as growth rates [2], the stochastic differential equations (SDE) for these numbers are given by

$$dN_1(t) = N_1(t)[\{x(t)\bar{a}_{11} + [1 - x(t)]\bar{a}_{12}\}dt + \{x(t) + [1 - x(t)]\psi_{21}\}\sqrt{2D_{\eta_1}}d\omega_1(t) + [1 - x(t)]\sqrt{2D_{\eta_2}}d\omega_2(t)], \tag{8a}$$

$$\begin{aligned} dN_2(t) = & N_2(t)[\{x(t)\bar{a}_{21} + [1 - x(t)]\bar{a}_{22}\}dt + \{x(t)\psi_{31} + [1 - x(t)]\psi_{41}\}\sqrt{2D_{\eta_1}}d\omega_1(t) \\ & + \{x(t)\psi_{32} + [1 - x(t)]\psi_{42}\}\sqrt{2D_{\eta_2}}d\omega_2(t) + \{x(t) + [1 - x(t)]\psi_{43}\}\sqrt{2D_{\eta_3}}d\omega_3(t) \\ & + [1 - x(t)]\sqrt{2D_{\eta_4}}d\omega_4(t)]. \end{aligned} \tag{8b}$$

Then, using the rules $(dt)^2 = 0$, $dt dw_i(t) = 0$, $[dw_i(t)]^2 = dt$, and $dw_i(t)dw_j(t) = 0$ if $i \neq j$ for $i, j = 1, 2, 3, 4$ in Itô's stochastic calculus (see Ref. [34]), the stochastic differential of $x(t)$ can be expressed as

$$dx(t) = \sum_{i=1}^2 \left[\frac{\partial x(t)}{\partial N_i(t)} dN_i(t) + \frac{1}{2} \frac{\partial^2 x(t)}{\partial N_i(t)^2} [dN_i(t)]^2 \right] + \frac{\partial^2 x(t)}{\partial N_1(t) \partial N_2(t)} dN_1(t) dN_2(t). \quad (9)$$

After calculations, the stochastic dynamics of $x(t)$ is found to be described by the equation

$$\begin{aligned} dx(t) = & x(t)[1 - x(t)]\{[(\bar{a}_{11} - \bar{a}_{12} - \bar{a}_{21} + \bar{a}_{22})x(t) + (\bar{a}_{12} - \bar{a}_{22})]dt \\ & + [(1 - \psi_{21} - \psi_{31} + \psi_{41})x(t) + (\psi_{21} - \psi_{41})]\sqrt{2D_{\eta_1}} d\omega_1(t) \\ & + [(1 - \psi_{42}) - (1 + \psi_{32} - \psi_{42})x(t)]\sqrt{2D_{\eta_2}} d\omega_2(t) - [(1 - \psi_{43})x(t) + \psi_{43}]\sqrt{2D_{\eta_3}} d\omega_3(t) \\ & - [1 - x(t)]\sqrt{2D_{\eta_4}} d\omega_4(t)\}, \end{aligned} \quad (10)$$

where

$$\begin{aligned} S(x(t)) = & -x(t)\{[(1 - \psi_{21})x(t) + \psi_{21}]^2 2D_{\eta_1} + [1 - x(t)]^2 2D_{\eta_2}\} \\ & + [1 - x(t)]\{[(\psi_{21} - \psi_{41})x(t) + \psi_{41}]^2 2D_{\eta_1} + [(\psi_{32} - \psi_{42})x(t) + \psi_{42}]^2 2D_{\eta_2} \\ & + [(1 - \psi_{43})x(t) + \psi_{43}]^2 2D_{\eta_3} + [1 - x(t)]^2 2D_{\eta_4}\} \\ & + [2x(t) - 1]\{[(1 - \psi_{21})x(t) + \psi_{21}][(\psi_{31} - \psi_{41})x(t) + \psi_{41}] 2D_{\eta_1} \\ & + [1 - x(t)][(\psi_{32} - \psi_{42})x(t) + \psi_{42}] 2D_{\eta_2}\}. \end{aligned} \quad (11)$$

Equation (10) above is a stochastic replicator equation that extends the deterministic replicator equation in classical evolutionary game theory [2,5]. Here, the payoffs in pairwise interactions are random variables that may be generally correlated.

Note that, if we assume $\xi_1(t) = \xi_2(t)$ and $\xi_3(t) = \xi_4(t)$ with $\xi_1(t)$ and $\xi_3(t)$ being independent of each other for all $t \geq 0$, then it can be shown in a similar way that $x(t)$ obeys the stochastic differential equation

$$\begin{aligned} dx(t) = & x(t)[1 - x(t)]\{[(\bar{a}_{11} - \bar{a}_{12} - \bar{a}_{21} + \bar{a}_{22})x(t) + \bar{a}_{12} \\ & - \bar{a}_{22}]dt + \{[1 - x(t)]2D_{\eta_3} - x(t)2D_{\eta_1}\}dt \\ & + \sqrt{2D_{\eta_1}} dw_1(t) - \sqrt{2D_{\eta_3}} dw_3(t)\}. \end{aligned} \quad (12)$$

This equation corresponds exactly to the stochastic replicator equation obtained by Fudenberg and Harris [31] (see also Ref. [32]) under the assumption that the phenotypes have average payoffs that are independent random variables.

III. STOCHASTIC STABILITY

Let x^* represents a constant equilibrium of Eq. (10), that is, an equilibrium of Eq. (10) that does not depend on the randomness of the payoff matrix $\mathbf{A}(t)$. This is clearly the case for both $x^* = 0$ and $x^* = 1$, called the fixation states or the boundary equilibria. This may also be the case for a constant equilibrium x^* with $0 < x^* < 1$, called a constant interior equilibrium.

A constant equilibrium x^* of Eq. (10) is said to be stochastically (asymptotically) stable if, with probability as close to 1 as we want, not only $x(t)$ stays as close to x^* as we want, but $x(t)$ tends to x^* , as soon as $x(0)$ is close enough to x^* . Otherwise, x^* is said to be stochastically (asymptotically) unstable. Throughout the paper, stochastic stability or instability will be understood in these senses. See the Appendix or Refs. [34,36]

for more technical details on these stability concepts in the theory of stochastic differential equations.

A. Fixation states

When $x(t)$ is close enough to the fixation state $x^* = 0$, Eq. (10) can be approximated as

$$\begin{aligned} dx(t) \approx & x(t)\{(\bar{a}_{12} - \bar{a}_{22} + 2[\psi_{41}(\psi_{41} - \psi_{21})D_{\eta_1} \\ & + \psi_{42}(\psi_{42} - 1)D_{\eta_2} + \psi_{43}^2 D_{\eta_3} + D_{\eta_4}]\}dt \\ & + (\psi_{21} - \psi_{41})\sqrt{2D_{\eta_1}} d\omega_1(t) \\ & + (1 - \psi_{42})\sqrt{2D_{\eta_2}} d\omega_2(t) - \psi_{43}\sqrt{2D_{\eta_3}} d\omega_3(t) \\ & - \sqrt{2D_{\eta_4}} d\omega_4(t)\}. \end{aligned} \quad (13)$$

Using stochastic stability conditions for the zero solution of a SDE (see the Appendix), the fixation state $x^* = 0$ is stochastically stable if

$$\begin{aligned} & \bar{a}_{12} - \bar{a}_{22} + (3\psi_{41}^2 + \psi_{21}^2 - 4\psi_{21}\psi_{41})D_{\eta_1} \\ & + (1 + 3\psi_{42}^2 - 4\psi_{42})D_{\eta_2} + 3\psi_{43}^2 D_{\eta_3} + 3D_{\eta_4} < 0. \end{aligned} \quad (14)$$

This result shows how environmental noise may affect the evolutionary dynamics of strategy R_2 when most individuals in the population display R_2 . In the particular case of independent payoffs [that is, independent random variables $\xi_1(t)$, $\xi_2(t)$, $\xi_3(t)$, and $\xi_4(t)$ for $t \geq 0$], the above condition for the fixation state $x^* = 0$ to be stochastically stable reduces to $\bar{a}_{12} - \bar{a}_{22} + D_2 + 3D_4 < 0$. Similarly, the fixation state $x^* = 1$ is stochastically stable if

$$-\bar{a}_{11} + \bar{a}_{21} + (1 - \psi_{31})(3 - \psi_{31})D_{\eta_1} + \psi_{32}^2 D_{\eta_2} + D_{\eta_3} < 0, \quad (15)$$

which reduces to $-\bar{a}_{11} + \bar{a}_{21} + 3D_1 + D_3 < 0$ when the payoffs are independent. On the other hand, the fixation states may be stochastically unstable if the inequalities are reversed.

As an example, we consider an additive Prisoner's dilemma with random cost $c(t)$ and random benefit $b(t)$ for cooperation at time $t \geq 0$ leading to a payoff matrix in the form

$$\begin{pmatrix} b(t) - c(t) & -c(t) \\ b(t) & 0 \end{pmatrix} = \begin{pmatrix} \bar{b} - \bar{c} & -\bar{c} \\ \bar{b} & 0 \end{pmatrix} + \begin{pmatrix} \xi_b(t) - \xi_c(t) & -\xi_c(t) \\ \xi_b(t) & 0 \end{pmatrix}. \quad (16)$$

Here, $\bar{b} > \bar{c} > 0$ so that the mean payoff matrix above corresponds to a standard deterministic Prisoner's dilemma [1,5], while $\xi_b(t)$ and $\xi_c(t)$ for $t \geq 0$ are two independent white noises with $\langle \xi_b(t) \rangle = \langle \xi_c(t) \rangle = 0$, $\langle \xi_b(t)^2 \rangle = 2D_b$, $\langle \xi_c(t)^2 \rangle = 2D_c$, and $\langle \xi_b(t)\xi_c(t) \rangle = 0$. In this stochastic Prisoner's dilemma, we use R_C and R_D to denote strategy 1 (cooperation) and strategy 2 (defection), respectively. Then, the frequency of R_C at time $t \geq 0$, denoted by $x(t)$, obeys the stochastic differential equation

$$dx(t) = x(t)[1 - x(t)][-\bar{c} + 2D_c x(t)]dt - \sqrt{2D_c} d\omega_c(t), \quad (17)$$

where $d\omega_c(t)/dt = \xi_c(t)/\sqrt{2D_c}$. When $x(t)$ is close enough to 0, we have the approximation

$$dx(t) \approx -x(t)[\bar{c}dt + \sqrt{2D_c} d\omega_c(t)]. \quad (18)$$

$$\begin{pmatrix} \bar{a}_{11} & \bar{a}_{12} \\ \bar{a}_{21} & u(\bar{a}_{11} - \bar{a}_{21}) + \bar{a}_{12} \end{pmatrix} + \begin{pmatrix} \eta_1(t) \\ \psi_{31}\eta_1(t) + \psi_{32}\eta_2(t) + \eta_3(t) \end{pmatrix} \begin{pmatrix} \psi_{21}\eta_1(t) + \eta_2(t) \\ (u - u\psi_{31} + \psi_{21}\eta_1(t) + (1 - u\psi_{32})\eta_2(t) - u\eta_3(t)) \end{pmatrix}, \quad (20)$$

and the corresponding stochastic replicator equation as

$$dx(t) = x(t)[1 - x(t)][(1 + u)x(t) - u][\bar{a}_{11} - \bar{a}_{21} + H(t)]dt + (1 - \psi_{31})\sqrt{2D_{\eta_1}} d\omega_1(t) - \psi_{32}\sqrt{2D_{\eta_2}} d\omega_2(t) - \sqrt{2D_{\eta_3}} d\omega_3(t), \quad (21)$$

where

$$H(t) = -2(1 - \psi_{31})\{x(t) + [1 - x(t)]\psi_{21} - (1 - \psi_{31})[1 - x(t)][(1 + u)x(t) - u]\}D_{\eta_1} + 2\psi_{32}[1 - x(t)]\{1 + \psi_{32}[(1 + u)x(t) - u]\}D_{\eta_2} + 2[1 - x(t)][(1 + u)x(t) - u]D_{\eta_3}. \quad (22)$$

In this case, not only the fixation states $x^* = 0$ and $x^* = 1$, but also $x^* = u/(1 + u)$ with $0 < x^* < 1$, are constant equilibrium points.

As in the previous section, it can be shown that the fixation states $x^* = 0$ and $x^* = 1$ are stochastically stable if

$$\bar{a}_{21} - \bar{a}_{11} + (1 - \psi_{31})[3u(1 - \psi_{31}) + 2\psi_{21}]D_{\eta_1} - \psi_{32}(2 - 3u\psi_{32})D_{\eta_2} + 3uD_{\eta_3} < 0 \quad (23)$$

and

$$\bar{a}_{21} - \bar{a}_{11} + (1 - \psi_{31})(3 - \psi_{31})D_{\eta_1} + \psi_{32}^2 D_{\eta_2} + D_{\eta_3} < 0, \quad (24)$$

respectively. Moreover, if the inequalities are reversed, then the fixation states may be stochastically unstable. In the particular case where $\xi_1(t)$, $\xi_2(t)$, and $\xi_3(t)$ are independent random variables, the fixation states $x^* = 0$ and $x^* = 1$ are stochastically stable if $\bar{a}_{21} - \bar{a}_{11} + 3u(D_1 + D_3) < 0$ and $\bar{a}_{21} - \bar{a}_{11} + 3D_1 + D_3 < 0$, respectively.

This equation implies that the fixation state $x^* = 0$ is stochastically stable if $\bar{c} > D_c$, and may be stochastically unstable if the inequality is reversed. Similarly, when $x(t)$ is close enough to 1, we have the approximation

$$dx(t) \approx -[1 - x(t)][(\bar{c} + 2D_c)dt + \sqrt{2D_c} d\omega_c(t)]. \quad (19)$$

This equation shows that the fixation state $x^* = 1$ may be stochastically unstable since $\bar{c} + 3D_c > 0$. All these results show that, under the influence of environmental noise, the stochastic instability of R_D fixation is possible, but the stochastic stability of R_C fixation is impossible. These also strongly suggest that environmental stochastic fluctuations may lead to the persistence of cooperation in the population.

B. Constant interior equilibrium

We now consider random payoffs satisfying the equation $u[a_{11}(t) - a_{21}(t)] = a_{22}(t) - a_{12}(t)$ at every time $t \geq 0$, where u is a positive constant. Here, we assume that the three random variables $\xi_1(t)$, $\xi_2(t)$, and $\xi_3(t)$ in the payoff matrix $\mathbf{A}(t)$ are linearly independent. Then, this random payoff matrix can be expressed as

On the other hand, the stochastic differential equation for $y(t) = x(t) - u/(1 + u)$ near 0, which corresponds to the constant interior equilibrium $x^* = u/(1 + u)$ for $x(t)$ in Eq. (21), can be approximated as

$$dy(t) \approx \frac{u}{1 + u} y(t) \left[\left(\bar{a}_{11} - \bar{a}_{21} - \frac{2(1 - \psi_{31})(\psi_{21} + u)}{1 + u} D_{\eta_1} + \frac{2\psi_{32}}{1 + u} D_{\eta_2} \right) dt + (1 - \psi_{31})\sqrt{2D_{\eta_1}} d\omega_1(t) - \psi_{32}\sqrt{2D_{\eta_2}} d\omega_2(t) - \sqrt{2D_{\eta_3}} d\omega_3(t) \right]. \quad (25)$$

The zero solution of this equation, i.e., the constant interior equilibrium $x^* = u/(1 + u)$, is stochastically stable if

$$\bar{a}_{11} - \bar{a}_{21} - \frac{(1 - \psi_{31})(2\psi_{21} + u\psi_{31} + u)}{1 + u} D_{\eta_1} + \frac{(2 + u\psi_{32})\psi_{32}}{1 + u} D_{\eta_2} + \frac{u}{1 + u} D_{\eta_3} < 0, \quad (26)$$

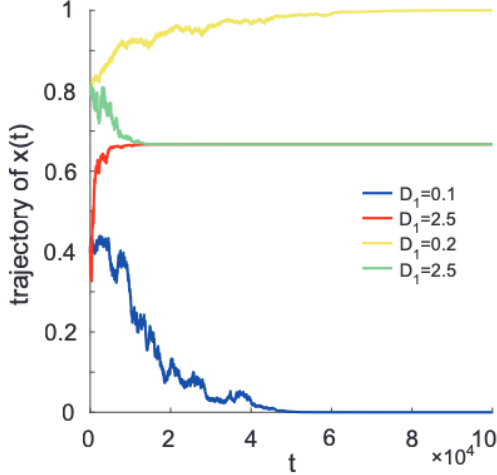


FIG. 1. Simulation results for a stochastic evolutionary game in the case of two strategies, R_1 and R_2 , with random payoff matrix $\begin{pmatrix} 1+\xi_1(t) & 0 \\ 0 & 2+2\xi_1(t) \end{pmatrix}$. Here, $\xi_1(t)$ is a Gaussian white noise with $\langle \xi_1(t) \rangle = 0$ and $\langle \xi_1(t)\xi_1(t') \rangle = 2D_1\delta(t-t')$ for $t, t' \geq 0$. The blue and red curves show the time evolution of $x(t)$, the frequency of R_1 , for $D_1 = 0.1$ and $D_1 = 2.5$, respectively, and initial value $x(0) = 0.4$; the yellow and green curves show the evolution for $D_1 = 0.2$ and $D_1 = 2.5$, respectively, and initial value $x(0) = 0.8$.

and may be stochastically unstable if the inequality is reversed. The above condition reduces to $\bar{a}_{11} - \bar{a}_{21} + u(D_3 - D_1)/(1+u) < 0$ in the case where $\xi_1(t)$, $\xi_2(t)$, and $\xi_3(t)$ are independent random variables.

As an example, consider the random payoff matrix

$$\mathbf{A}(t) = \begin{pmatrix} 1 & 0 \\ 0 & u \end{pmatrix} + \begin{pmatrix} \xi_1(t) & 0 \\ 0 & u\xi_1(t) \end{pmatrix} \quad (27)$$

for two strategies R_1 and R_2 , where u is a positive constant and $\xi_1(t)$ is a white noise with $\langle \xi_1(t) \rangle = 0$ and $\langle \xi_1(t)\xi_1(t') \rangle =$

$2D_1\delta(t-t')$. In this case, the mean payoff matrix

$$\bar{\mathbf{A}} = \begin{pmatrix} 1 & 0 \\ 0 & u \end{pmatrix}$$

determines a coordination game [37,38]. For the frequency of R_1 at time $t \geq 0$, we have the stochastic replicator equation

$$\begin{aligned} dx(t) = & x(t)[1-x(t)][(1+u)x(t)-u][(1-2x(t)) \\ & - [1-x(t)][(1+u)x(t)-u]]D_1 dt \\ & + \sqrt{2D_1} d\omega_1(t). \end{aligned} \quad (28)$$

Obviously, $x^* = u/(1+u)$ is a constant interior equilibrium. From Eqs. (23) and (24), the fixation states $x^* = 0$ and $x^* = 1$ are stochastically stable if $D_1 < 1/(3u)$ and $D_1 < 1/3$, respectively. Furthermore, from Eq. (26), the constant interior equilibrium $x^* = u/(1+u)$ is stochastically stable if $D_1 > (1+u)/u$. Simulation results for parameter values given by $u = 2$ and $D_1 = 0.1, 0.2, 2.5$ are shown in Fig. 1. These simulation results are in agreement with the theoretical predictions that the fixation state $x^* = 0$ (or $x^* = 1$) is stochastically stable if $D_1 < 1/6$ (or $D_1 < 1/3$) and the constant interior equilibrium $x^* = 2/3$ is stochastically stable if $D_1 > 3/2$. Therefore, in this case, an increase in the intensity of stochastic fluctuations will promote the stochastic stability of the constant interior equilibrium. This result is not only in agreement with previous results on stochastic evolutionary recurrence dynamics [20], but also in support of the potential importance of environmental stochasticity in shaping diversity in animal behavior.

IV. STOCHASTIC EVOLUTIONARY STABILITY

Let us recall that a mixed strategy represented by a frequency vector $\mathbf{x}^* = (x^*, 1-x^*)$ is stochastically evolutionarily stable (SES) with respect to the random payoff matrix $\mathbf{A}(t)$ in (1) for $t \geq 0$ if \mathbf{x}^* fixation is stochastically stable against any mixed strategy $\mathbf{x} = (x, 1-x) \neq \mathbf{x}^*$ close enough to \mathbf{x}^* [20,21]. We consider two cases.

Case I. With $\mathbf{x}^* = (0, 1)$ (i.e., pure strategy R_2), the payoffs to $\mathbf{x} = (x, 1-x) \neq \mathbf{x}^*$ and \mathbf{x}^* in pairwise interactions at time $t \geq 0$ are given by the entries of the matrix

$$\begin{pmatrix} \mathbf{x} \cdot \mathbf{A}(t)\mathbf{x} & \mathbf{x} \cdot \mathbf{A}(t)\mathbf{x}^* \\ \mathbf{x}^* \cdot \mathbf{A}(t)\mathbf{x} & \mathbf{x}^* \cdot \mathbf{A}(t)\mathbf{x}^* \end{pmatrix} = \begin{pmatrix} x^2 a_{11}(t) + x(1-x)[a_{12}(t) + a_{21}(t)] + (1-x)^2 a_{22}(t) & x a_{12}(t) + (1-x) a_{22}(t) \\ x a_{21}(t) + (1-x) a_{22}(t) & a_{22}(t) \end{pmatrix}. \quad (29)$$

If \mathbf{x} and \mathbf{x}^* have respective frequencies $z(t)$ and $1-z(t)$ at time $t \geq 0$, then their average payoffs in random pairwise interactions are given by

$$\begin{aligned} \pi_{\mathbf{x}}(t) = & \bar{a}_{11}x^2z(t) + \bar{a}_{12}x[1-xz(t)] + \bar{a}_{21}x(1-x)z(t) + \bar{a}_{22}(1-x)[1-xz(t)] \\ & + [x^2z(t) + \psi_{21}x[1-xz(t)] + \psi_{31}x(1-x)z(t) + \psi_{41}(1-x)[1-xz(t)]]\eta_1(t) \\ & + [x[1-xz(t)] + \psi_{32}x(1-x)z(t) + \psi_{42}(1-x)[1-xz(t)]]\eta_2(t) \\ & + [x(1-x)z(t) + \psi_{43}(1-x)[1-xz(t)]]\eta_3(t) + (1-x)[1-xz(t)]\eta_4(t), \end{aligned} \quad (30a)$$

$$\begin{aligned} \pi_{\mathbf{x}^*}(t) = & \bar{a}_{21}xz(t) + \bar{a}_{22}[1-xz(t)] + [\psi_{31}xz(t) + \psi_{41}[1-xz(t)]]\eta_1(t) + [\psi_{32}xz(t) + \psi_{42}[1-xz(t)]]\eta_2(t) \\ & + [xz(t) + \psi_{43}[1-xz(t)]]\eta_3(t) + [1-xz(t)]\eta_4(t), \end{aligned} \quad (30b)$$

respectively. Proceeding as for Eq. (10), the stochastic dynamics of $z(t)$ is described by the differential equation

$$dz(t) = xz(t)[1 - z(t)]\{[(\bar{a}_{11} - \bar{a}_{12} - \bar{a}_{21} + \bar{a}_{22})xz(t) + (\bar{a}_{12} - \bar{a}_{22}) + K(t)]dt + [(1 - \psi_{21} - \psi_{31} + \psi_{41})xz(t) + \psi_{21} - \psi_{41}]\sqrt{2D_{\eta_1}}d\omega_1(t) + [1 - \psi_{42} - (1 + \psi_{32} - \psi_{42})xz(t)]\sqrt{2D_{\eta_2}}d\omega_2(t) + [(\psi_{43} - 1)xz(t) - \psi_{43}]\sqrt{2D_{\eta_3}}d\omega_3(t) + [xz(t) - 1]\sqrt{2D_{\eta_4}}d\omega_4(t)\}, \tag{31}$$

where

$$K(t) = -2[(1 - \psi_{21} - \psi_{31} + \psi_{41})xz(t) + \psi_{21} - \psi_{41}] \times [(1 - \psi_{21} - \psi_{31} + \psi_{41})x^2z(t)^2 + (\psi_{31} - 2\psi_{41} + \psi_{21})xz(t) + \psi_{41}]D_{\eta_1} + 2[(1 + \psi_{32} - \psi_{42})xz(t) + \psi_{42} - 1][(1 + \psi_{32} - \psi_{42})xz(t) + \psi_{42}][1 - xz(t)]D_{\eta_2} + 2[1 - xz(t)][(1 - \psi_{43})xz(t) + \psi_{43}]^2D_{\eta_3} + 2[1 - xz(t)]^2D_{\eta_4}. \tag{32}$$

Near the zero solution $z(t) = 0$, the above differential equation can be approximated by

$$dz(t) \approx z(t)x\{[\bar{a}_{12} - \bar{a}_{22} - 2\psi_{41}(\psi_{21} - \psi_{41})D_{\eta_1} + 2\psi_{42}(\psi_{42} - 1)D_{\eta_2} + 2\psi_{43}^2D_{\eta_3} + 2D_{\eta_4}]dt + (\psi_{21} - \psi_{41})\sqrt{2D_{\eta_1}}d\omega_1(t) + (1 - \psi_{42})\sqrt{2D_{\eta_2}}d\omega_2(t) - \psi_{43}\sqrt{2D_{\eta_3}}d\omega_3(t) - \sqrt{2D_{\eta_4}}d\omega_4(t)\}. \tag{33}$$

Therefore, \mathbf{x}^* fixation is stochastically stable if

$$\bar{a}_{12} - \bar{a}_{22} + (\psi_{21} - \psi_{41})[(\psi_{21} - \psi_{41})x - 2\psi_{41}]D_{\eta_1} + (1 - \psi_{42})[(1 - \psi_{42})x - 2\psi_{42}]D_{\eta_2} + (2 + x)\psi_{43}^2D_{\eta_3} + (2 + x)D_{\eta_4} < 0. \tag{34}$$

Note also that the left-hand of this inequality is an increasing function of x . Therefore, for all possible $\mathbf{x} \neq \mathbf{x}^*$, the strategy $\mathbf{x}^* = (0, 1)$ is stochastically evolutionarily stable if the inequality in Eq. (14) holds. This implies that the stochas-

tic evolutionary stability of strategy R_2 is equivalent to the stochastic stability of R_2 fixation in Eq. (10). Obviously, this property is also in agreement with the corresponding one in the deterministic evolutionary game dynamics [5].

Case 2. Here, we use the random payoff matrix $\mathbf{A}(t)$ in (20) whose entries satisfy $u[a_{11}(t) - a_{21}(t)] = a_{22}(t) - a_{12}(t)$ for a constant $u > 0$. Then, the payoffs to the mixed strategies $\mathbf{x} = (x, 1 - x) \neq \mathbf{x}^*$ and $\mathbf{x}^* = (x^*, 1 - x^*)$ in pairwise interactions at time $t \geq 0$, where $x^* = u/(1 + u)$, are given by the entries of the matrix

$$\begin{pmatrix} \mathbf{x} \cdot \mathbf{A}(t)\mathbf{x} & \mathbf{x} \cdot \mathbf{A}(t)\mathbf{x}^* \\ \mathbf{x}^* \cdot \mathbf{A}(t)\mathbf{x} & \mathbf{x}^* \cdot \mathbf{A}(t)\mathbf{x}^* \end{pmatrix} = \begin{pmatrix} [x^2 + u(1 - x)^2]a_{11}(t) + (1 - x)\{a_{12}(t) + [(1 + u)x - u]a_{21}(t)\} & \frac{ua_{11}(t) + a_{12}(t)}{1 + u} \\ \frac{ua_{11}(t) + [(1 + u)x - u]a_{21}(t) + (1 + u)(1 - x)a_{12}(t)}{1 + u} & \frac{ua_{11}(t) + a_{12}(t)}{1 + u} \end{pmatrix}, \tag{35}$$

and the average payoffs to these strategies by

$$\pi_{\mathbf{x}}(t) = \bar{a}_{11} \left\{ [x^2 + u(1 - x)^2]z(t) + \frac{[1 - z(t)]u}{1 + u} \right\} + \bar{a}_{12} \left[(1 - x)z(t) + \frac{1 - z(t)}{1 + u} \right] + \bar{a}_{21}(1 - x)[(1 + u)x - u]z(t) + \left\{ [x^2 + u(1 - x)^2]z(t) + \frac{[1 - z(t)]u}{1 + u} + \psi_{21} \left[(1 - x)z(t) + \frac{1 - z(t)}{1 + u} \right] + \psi_{31}(1 - x)[(1 + u)x - u]z(t) \right\} \eta_1(t) + \left\{ (1 - x)z(t) + \frac{1 - z(t)}{1 + u} + \psi_{32}(1 - x)[(1 + u)x - u]z(t) \right\} \eta_2(t) + (1 - x)[(1 + u)x - u]z(t)\eta_3(t), \tag{36a}$$

$$\pi_{\mathbf{x}^*}(t) = \bar{a}_{11} \frac{u}{1 + u} + \bar{a}_{12} \left[\frac{1 - z(t)}{1 + u} + (1 - x)z(t) \right] + \bar{a}_{21} \left[x - \frac{u}{1 + u} \right] z(t) + \left[\frac{u}{1 + u} + \psi_{21} \left(\frac{1 - z(t)}{1 + u} + (1 - x)z(t) \right) + \psi_{31} \left(x - \frac{u}{1 + u} \right) z(t) \right] \eta_1(t) + \left[\frac{1 - z(t)}{1 + u} + (1 - x)z(t) + \psi_{32} \left(x - \frac{u}{1 + u} \right) z(t) \right] \eta_2(t) + \left[x - \frac{u}{1 + u} \right] z(t)\eta_3(t), \tag{36b}$$

where $z(t)$ and $1 - z(t)$ are the frequencies of \mathbf{x} and \mathbf{x}^* , respectively, at time $t \geq 0$. This leads to a stochastic dynamics of $z(t)$ given by the differential equation

$$dz(t) = z(t)^2 [1 - z(t)] \frac{[(1+u)x - u]^2}{1+u} \left\{ (\bar{a}_{11} - \bar{a}_{21}) dt + 2(\psi_{31} - 1) \left((1 - \psi_{31}) \frac{z(t)^2}{1+u} [(1+u)x - u]^2 + \frac{u + \psi_{21}}{1+u} \right. \right. \\ \left. \left. + (\psi_{31} - \psi_{21}) \left[x - \frac{u}{1+u} \right] z(t) \right) D_{\eta_1} dt + \frac{2\psi_{32}}{1+u} [(1+u)x - u] \{-\psi_{32}[(1+u)x - u]z(t) + \psi_{32} - 1\} z(t) + 1 \right) D_{\eta_2} dt \\ + \frac{2z(t)}{1+u} [(1+u)x - u] \{1 - [(1+u)x - u]z(t)\} D_{\eta_3} dt \\ \left. + (1 - \psi_{31}) \sqrt{2D_{\eta_1}} d\omega_1(t) - \psi_{32} \sqrt{2D_{\eta_2}} d\omega_2(t) - \sqrt{2D_{\eta_3}} d\omega_3(t) \right\}. \quad (37)$$

Near the zero solution $z(t) = 0$, this differential equation can be approximated by

$$dz(t) \approx z(t)^2 \frac{[(1+u)x - u]^2}{1+u} \left[\left(\bar{a}_{11} - \bar{a}_{21} + \frac{2(u + \psi_{21})(\psi_{31} - 1)}{1+u} D_{\eta_1} + \frac{2\psi_{32}}{1+u} D_{\eta_2} \right) dt \right. \\ \left. + (1 - \psi_{31}) \sqrt{2D_{\eta_1}} d\omega_1(t) - \psi_{32} \sqrt{2D_{\eta_2}} d\omega_2(t) - \sqrt{2D_{\eta_3}} d\omega_3(t) \right]. \quad (38)$$

Here, $z(t) \geq 0$ for $t \geq 0$, and the functions in front of dt and $d\omega_i(t)$ for $i = 1, 2, 3$, as well as their first derivatives with respect to $z(t)$, vanish at $z(t) = 0$. In this case, as shown in the Appendix, the zero solution $z(t) = 0$ is stochastically stable if the second derivative of the function in front of dt evaluated at $z(t) = 0$ is negative, which is equivalent to

$$\bar{a}_{11} - \bar{a}_{21} + \frac{2(u + \psi_{21})(\psi_{31} - 1)}{1+u} D_{\eta_1} + \frac{2\psi_{32}}{1+u} D_{\eta_2} < 0 \quad (39)$$

for all possible $x \neq x^*$. This is the condition for the mixed strategy \mathbf{x}^* to be stochastically evolutionary stable. As a special case, if $\xi_1(t)$, $\xi_2(t)$, and $\xi_3(t)$ are independent of each other, then only D_1 comes into play in Eq. (39) and \mathbf{x}^* is stochastically evolutionarily stable if $\bar{a}_{11} - \bar{a}_{21} - 2x^* D_1 < 0$. This implies that an increase of D_1 will promote the stochastic evolutionary stability of \mathbf{x}^* . However, we can see that the conditions for stochastic evolutionary stability of \mathbf{x}^* are not the same as the conditions for the constant interior equilibrium $x^* = u/(1+u)$ of Eq. (21) to be stochastically stable, contrary to what occurs in the deterministic evolutionary game dynamics [5].

V. DISCUSSION

The replicator equation introduced by Taylor and Jonker [2] provides an excellent framework to understand the relationship between evolutionary games dynamics in a deterministic environment and stability properties of equilibrium states [5]. When environmental stochasticity is introduced into the continuous-time dynamics of evolutionary games, we are faced with two challenging questions. The first one is how to reasonably construct a stochastic replicator equation that takes into account all stochastic effects. The second one is to describe the stochastic effects on the evolutionary dynamics. Of particular interest is the extension of the classical concept

of evolutionary stability introduced by Maynard Smith and Price [8]. Such an extension in the context of discrete-time linear games with random payoffs can be found in Zheng *et al.* [20,21].

Assuming that disturbances caused by stochastic fluctuations in the environment should be added directly to the growth rates of subpopulations corresponding to different phenotypes and using Itô's formula, Fudenberg and Harris [31] developed a stochastic replicator equation to describe the stochastic dynamics of phenotype frequencies (see also Imhof [32]). However, this model can only be regarded as a special case since it is assumed that the stochastic disturbances depend only on the phenotypes of the individuals, not on the phenotypes of the individuals interacting with them. In this paper, in order to develop a more general theoretical framework, we have considered a linear game for two phenotypes with random payoffs in pairwise interactions that are generally correlated. Note that a similar model was considered previously [20,21], but in a discrete-time framework. For the continuous-time evolutionary dynamics, we have derived a stochastic replicator equation using the Gram-Schmidt orthogonalization procedure [35] and Itô's formula [34]. The stochastic replicator equation is not only a natural extension of deterministic equation developed by Taylor and Jonker [2] (see also Ref. [5]), but also provides a fundamental theoretical framework for understanding evolutionary game dynamics and evolutionary stability in a stochastic environment.

As for the stochastic stability analysis of the stochastic replicator dynamics, we have focused on fixation states and constant interior equilibrium points when they exist. We have shown how conditions for their stochastic stability extend conditions in the deterministic case and how they can be used to define evolutionary stability of mixed strategies in a stochastic environment in agreement with Zheng *et al.* [20] that extends the definition in the deterministic case [1,5,8].

We have shown that, if the fixation state $x^* = 0$ of Eq. (10), which corresponds to extinction of phenotype R_1 against phenotype R_2 , is stochastically stable, then the pure strategy $\mathbf{x}^* = (0, 1)$ must be stochastically evolutionary stable against all mixed strategies $\mathbf{x} = (x, 1 - x)$ for $0 < x \leq 1$, where x and $1 - x$ are the probabilities of exhibiting the phenotypes R_1 and R_2 , respectively. On the other hand, if $u[a_{11}(t) - a_{21}(t)] = a_{22}(t) - a_{12}(t)$ where u is a positive constant, then $x^* = u/(1 + u)$ is a constant interior equilibrium of Eq. (10). However, we have shown that the condition for $x^* = u/(1 + u)$ to be stochastically stable does not exactly match the condition for the mixed strategy $\mathbf{x}^* = (x^*, 1 - x^*)$ to be stochastically evolutionarily stable against all possible mixed strategies $\mathbf{x} = (x, 1 - x) \neq \mathbf{x}^*$. This result implies that the relationship between stochastic stability and stochastic evolutionary stability based on the deterministic replicator equation [5] may not hold in a stochastic setting.

The concept of stochastic evolutionary stability as developed in Zheng *et al.* [20] is a core concept to understand the evolutionary game dynamics in a stochastic environment. Our results have not only revealed how stochastic evolutionary stability of equilibrium points is influenced by environmental noise but also shown that environmental noise can create a discrepancy between stochastic evolutionary stability of an interior equilibrium point and evolutionary stability of the corresponding mixed strategy once fixed in the population.

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APPENDIX: CONDITIONS FOR STOCHASTIC STABILITY

Let $x(t)$ for $t \geq 0$ be a continuous-time real stochastic process defined in a neighborhood of the origin 0, which is a fixed point called the zero solution.

The zero solution of $x(t)$ for $t \geq 0$ is said to be stochastically (asymptotically) stable if

(i) for any $r > 0$ and any ϵ in $(0, 1)$, there exists $\delta > 0$ such that

$$\mathbb{P}(|x(t)| < r \text{ for } t \geq 0) \geq 1 - \epsilon \tag{A1}$$

as soon as $|x(0)| < \delta$, and

(ii) for any ϵ in $(0, 1)$, there exists $\delta_0 > 0$ such that

$$\mathbb{P}\left(\lim_{t \rightarrow \infty} x(t) = 0\right) \geq 1 - \epsilon \tag{A2}$$

as soon as $|x(0)| < \delta_0$. Otherwise, the zero solution is said to be stochastically (asymptotically) unstable.

Now suppose that the one-dimensional process $x(t)$ for $t \geq 0$ obeys the Itô stochastic differential equation (SDE)

$$dx(t) = f(x(t))dt + \sum_{i=1}^m g_i(x(t))d\omega_i(t), \tag{A3}$$

where $(w_1(t), \dots, w_m(t))$ for $t \geq 0$ is a multivariate Wiener process, while f and g_i are smooth enough real functions with $f(0) = 0$ and $g_i(0) = 0$ such that

$$f(x(t)) = f'(0)x(t) + o(|x(t)|), \tag{A4a}$$

$$g_i(x(t)) = g'_i(0)x(t) + o(|x(t)|), \tag{A4b}$$

for $i = 1, \dots, m$ near $x(t) = 0$.

Let $V(x(t)) \geq 0$ for $t \geq 0$, with equality to 0 if and only if $x(t) = 0$, be a Lyapunov-candidate function for the zero solution. As shown on page 36 of Ref. [34], Itô's formula yields

$$dV(x(t)) = LV(x(t))dt + V'(x(t)) \sum_{i=1}^m g_i(x(t))d\omega_i(t), \tag{A5}$$

where the drift function is given by

$$LV(x(t)) = V'(x(t))f(x(t)) + \frac{1}{2}V''(x(t)) \sum_{i=1}^m g_i(x(t))^2, \tag{A6}$$

with V' and V'' denoting the first and second derivatives of V with respect to x . Taking $V(x(t)) = x(t)^2$ and using Eq. (A4), we have

$$LV(x(t)) = Mx(t)^2 + o(|x(t)|^2), \tag{A7}$$

where

$$M = 2f'(0) + \sum_{i=1}^m g'_i(0)^2. \tag{A8}$$

Note that, if M is negative, then

$$LV(x(t)) \leq M|x(t)|^2 + o(|x(t)|^2) \leq \frac{M}{2}|x(t)|^2 \tag{A9}$$

for $|x(t)|$ small enough. Similarly, if M is positive, then

$$LV(x(t)) \geq M|x(t)|^2 + o(|x(t)|^2) \geq \frac{M}{2}|x(t)|^2 \tag{A10}$$

for $|x(t)|$ small enough.

The above properties ensure the following result (see Ref. [34], page 116): the zero solution of the SDE (A3) is stochastically stable if M in Eq. (A8) is negative. On the other hand, if M is positive, the zero solution can be stochastically unstable and we may expect this to be true if M is large enough.

Similarly, if $M = 0$ with $f'(0) = 0$ and $g'_i(0) = 0$ for $i = 1, 2, \dots, m$ so that

$$f(x(t)) = \frac{f''(0)}{2}x(t)^2 + o(|x(t)|^2), \tag{A11a}$$

$$g_i(x(t)) = \frac{g''_i(0)}{2}x(t)^2 + o(|x(t)|^2), \tag{A11b}$$

for $i = 1, \dots, m$, then the stochastic differential equation (A3) can be approximated as

$$dx(t) \approx \frac{1}{2}x(t)^2 \left[f''(0)dt + \sum_{i=1}^m g''_i(0)d\omega_i(t) \right] \tag{A12}$$

near $x(t) = 0$. In this case, for $V(x(t)) = x(t)^2$, we have

$$LV(x(t)) = x(t)^3 \left[f''(0) + \frac{1}{4} x(t) \sum_{i=1}^m (g_i''(0))^2 \right]. \quad (\text{A13})$$

If $x(t) \geq 0$ is small enough for $t \geq 0$, then

$$LV(x(t)) \leq \frac{f''(0)}{2} |x(t)|^3 \quad (\text{A14})$$

in the case where $f''(0) < 0$, while

$$LV(x(t)) \geq \frac{f''(0)}{2} |x(t)|^3 \quad (\text{A15})$$

in the case where $f''(0) > 0$. We can conclude as previously that the zero solution of the SDE (A3) with $x(t) \geq 0$ for $t \geq 0$ is stochastically stable if $f''(0)$ is negative, and may be stochastically unstable if $f''(0)$ is positive and large enough.

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