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Stochastic Fluctuations Through Intrinsic Noise in Evolutionary Game Dynamics

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Abstract A one-step (birth–death) process is used to investigate stochastic noise in an elementary two-phenotype evolutionary game model based on a payoff matrix. In this model, we assume that the population size is finite but not fixed and that all individuals have, in addition to the frequency-dependent fitness given by the evolutionary game, the same background fitness that decreases linearly in the total population size. Although this assumption guarantees population extinction is a globally attracting absorbing barrier of the Markov process, sample trajectories do not illustrate this result even for relatively small carrying capacities. Instead, the observed persistent transient behavior can be analyzed using the steady-state statistics (i.e., mean and variance) of a stochastic model for intrinsic noise that assumes the population does not go extinct. It is shown that there is good agreement between the theory of these statistics and the simulation results. Furthermore, the ESS of the evolutionary game can be used to predict the mean steady state.

Keywords Intrinsic noise · ESS · Evolutionary games · Stochastic effects

1. Introduction

It is well known that one of the basic assumptions of standard evolutionary game theory developed by Maynard Smith (1982) (see also Taylor and Jonker, 1978; Lessard, 1984; Cressman, 1992; Hofbauer and Sigmund, 1998; Hofbauer and Sigmund, 2003) is that the population size is effectively infinite. In particular, the population size is sufficiently large so that stochastic effects can be ignored (Peck and Feldman, 1988) in the deterministic evolutionary dynamics based on expected payoffs through random pairwise interactions between individuals. However, for

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real populations, this assumption is not always valid, in which case stochastic effects due to finite populations (or other factors) may be important in the evolutionary outcome of the dynamics (Hastings, 2004).

Consider the standard deterministic single-species game-theoretic model (see Section 2), where each individual is characterized by its phenotype (or strategy) and its fitness is a function of the population's phenotypic distribution through the game's payoff matrix. As pointed out by Foster and Young (1990), this model does not account for stochastic terms that may arise from a variety of factors. First, there is variability due to differences between an individual's realized and expected payoffs resulting from random interactions with other individuals. Second, there is natural variability in the payoff matrix that results from environmental influences. Third, there is background mutation, and possibly immigration of individuals from other gene pools.

Each of these stochastic factors has been examined under the assumption that the population size is finite and fixed. For instance, a great deal of research analyzing the effect of rare but recurring mutations began with Foster and Young (1990), who showed that stable strategies in their stochastic model differ from both the traditional evolutionarily stable strategy (ESS) and the concept of an attractor in a deterministic dynamical system (see also Kandori et al., 1993). More recently, Broom (2005) analyzed the effect of variability in the payoff matrix on the ESS. The model of Taylor et al. (2004) is more directly relevant for our approach, since its assumptions of fixed payoff matrix and no mutation effects are the same as ours. Specifically, they analyzed stochastic evolutionary game dynamics with finite population size using a frequency-dependent Moran process 1962. This is a Markov process that assumes (1) the population size is a fixed constant; (2) at each time step, an individual is chosen for reproduction proportional to its fitness; (3) one identical offspring is produced, replacing another randomly chosen individual (see also Fogel et al., 1997, 1998; Ficici and Pollack, 2000).

In this paper, we also investigate stochastic fluctuations in evolutionary game dynamics. However, although our population is finite, its size varies according to a one-step birth–death process (Van Kampen, 1992) where, at each step, an individual either dies or reproduces an identical offspring. Thus, our Markov process is closer to models of intrinsic noise as used in the physical sciences to predict the appearance and disappearance of different types of particles under random interactions (Van Kampen, 1992). In our intrinsic noise model, particles are individuals exhibiting different strategies in the population and their numbers change according to their fitness (see Section 3). Recently, this approach to modelling stochastic fluctuations has gained interest in the biological literature (Swift, 2002; Tao, 2004; Tao et al., 2005) in other contexts as well.

In our model, species extinction is a globally attracting absorbing barrier of the Markov process but this is seldom observed in sample trajectories when the deterministic model has even a moderate equilibrium population size of 20 or more individuals. As argued by Hastings (2004), such circumstances are common when stochastic influences are included and it is then the transient dynamics that become "an essential explanatory aspect of understanding ecological systems." For this reason, we concentrate on analyzing the dynamics of the steady-state statistics (i.e., the mean and variance) of the conditional distribution assuming the population

does not go extinct. This is in contrast to the approach of Taylor et al. (2004), who focus instead on the conditions for selection to favor successful invasion and/or fixation of new phenotypes by calculating the corresponding barrier's absorption probability.

The basic evolutionary game model is from Maynard Smith (1982), but we assume that the individual's background fitness depends on the population size. Our main goal is to show how the population size affects the statistical properties of evolutionary game dynamics. The paper is organized as follows. In Section 2, the basic deterministic model for evolutionary game dynamics is briefly described and related to the static concept of an evolutionarily stable strategy. Section 3 develops our intrinsic noise model for the elementary two-phenotype matrix game model of Section 2. We then analyze this stochastic model when the equilibrium of the underlying deterministic system is monomorphic (Section 4) and when it is polymorphic (Section 5). The final section summarizes the results in relation to the ESS concept and the Appendices contain most of the longer calculations.

2. The deterministic model and evolutionarily stable strategies

In order to clearly illustrate the effect of intrinsic noise on the evolutionary dynamics, we will apply it to the case of a single species where each individual uses one of two possible (pure) strategies, R_1 and R_2. Suppose p_i is the proportion of the population using strategy R_i.

In the deterministic model, individuals interact in random pairwise contests and so those using strategy R_i receive an expected payoff of

$$f_i = \sum_{j=1}^{2} a_{ij} p_j \quad \text{for} \quad i = 1, 2 \tag{1}$$

where a_{ij} is the payoff to strategy (or phenotype) R_i when interacting with R_j. It is convenient to rewrite Eq. (1) in matrix notation (Cressman, 1992) as $f_i = e_i \cdot Ap$ where

$$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

is the 2×2 payoff matrix, $p \in \Delta^2 \equiv \{(p_1, p_2) : p_1 + p_2 = 1, p_i \geq 0\}$ is the frequency vector of strategy types in the population, e_i is the ith unit coordinate vector (e.g., $e_1 = (1, 0)$) corresponding to R_i, and $u \cdot Av \equiv \sum_{i,j=1}^{2} u_i a_{ij} v_j$ is the standard inner product.

We assume $a_{ij} \geq 0$ for all $1 \leq i, j \leq 2$. To include population size effects, we also assume the fitness of an individual using pure strategy R_i is given by

$$W_i = f_i + W_0$$

where W_0 is called the background fitness (Maynard Smith, 1982). That is, W_0 is the component of an individual's fitness that is not due to contests in the population. We assume that all individuals have the same background fitness which is given by

$$W_0(N) = 1 - \beta N$$

where N is the total population size, and the positive parameter $1/\beta$ can be thought of as the environmental carrying capacity. In particular, background fitness depends only on the population size and is independent of the strategy type.

With fitness interpreted as the reproductive success of an individual (who produces offspring with the same strategy), the continuous-time deterministic dynamics becomes

$$\frac{dn_1}{dt} = W_1 n_1 = n_1(e_1\, Ap + 1 - \beta N)$$

$$\frac{dn_2}{dt} = W_2 n_2 = n_2(e_2\, Ap + 1 - \beta N) \tag{2}$$

where $n_i = p_i N$ is the number of individuals with phenotype R_i. In particular, $N = n_1 + n_2$, since $p_2 = 1 - p_1$. Following Lessard (1984), (2) can be rewritten in terms of N and p_1 as

$$\frac{dp_1}{dt} = p_1(1 - p_1)(W_1 - W_2) = p_1(1 - p_1)(e_1\, Ap - e_2\, Ap) \tag{3}$$

$$\frac{dN}{dt} = N\overline{W} \tag{4}$$

where $\overline{W} = p_1 W_1 + (1 - p_1)W_2$ is the mean fitness of the population. Equation (3) is the replicator equation (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998) of evolutionary game theory when there are two strategies.

The equilibria (p^*, N^*) and their stability for the dynamics (3) and (4) can be understood in terms of the ESS structure of the game with payoff matrix A as outlined in the following paragraph. First, notice that common background fitness implies the one-dimensional dynamics (3) is independent of N and so its evolutionary outcome p^* can be determined and then substituted into (4) to find N^* (Cressman, 1992). Furthermore, the equilibrium $N^* = 0$ is unstable due to our assumption that all payoffs are nonnegative.

According to Maynard Smith (1982) definition, $S \in \Delta^2$ is an ESS if and only if for all $\widehat{S} \in \Delta^2$ different from S,

$$\text{either} \quad (\widehat{S} - S)AS < 0 \tag{5}$$

$$\text{or} \quad (\widehat{S} - S)AS = 0 \quad \text{and}(\widehat{S} - S)A\widehat{S} > 0. \tag{6}$$

To simplify comparisons to the ESS in our analysis of intrinsic noise starting in the following section, it is better to add 1 to all entries of the payoff matrix and define $b_{ij} \equiv a_{ij} + 1, 1 \le i, j \le 2$. This does not alter the ESS structure.

The monomorphic equilibrium with no individuals using strategy R_2 (i.e., the boundary point ($p^* = (1, 0)$, $N^* = b_{11}/\beta$)) is locally asymptotically stable for (3) and (4) if and only if $b_{11} > b_{21}$ if and only if $p^* = (1, 0)$ is an ESS.[1] Heuristically, stability follows, since the ESS strategy then has the higher payoff when it is common in the population. Likewise, ($p^* = (0, 1)$, $N^* = b_{22}/\beta$)) is locally asymptotically stable if and only if $b_{22} > b_{12}$ if and only if this p^* is an ESS. If both these monomorphic equilibria are ESSs, then there is an unstable polymorphic equilibrium (i.e., p^* is in the interior of Δ^2) that is not an ESS given by

$$p_1^* = \frac{b_{12} - b_{22}}{b_{12} - b_{22} + b_{21} - b_{11}} \tag{7}$$

$$N^* = \frac{1}{\beta} \frac{b_{12}b_{21} - b_{11}b_{22}}{b_{12} - b_{22} + b_{21} - b_{11}}. \tag{8}$$

This equilibrium separates the domain of attraction of the boundary ESSs. If exactly one monomorphic equilibrium is an ESS, it is globally asymptotically stable (and so there is no interior equilibrium).

Finally, if neither monomorphic equilibrium is an ESS (i.e., $b_{11} < b_{21}$ and $b_{22} < b_{12}$), then neither pure strategy has the higher payoff when it is common, suggesting the population evolves toward a polymorphism (i.e., a mixed strategy). In fact, the interior equilibrium (7) is an ESS and globally asymptotically stable in this case.

3. Intrinsic noise

Intrinsic noise is one of the most important stochastic processes in physics and chemistry. It is used there to describe the internal noise that is due to the system consisting of discrete particles (Van Kampen, 1992) by modelling stochastic effects as a one-step (birth–death) process. In the context of evolutionary games, we interpret each individual as a particle in the system. Thus, with this interpretation, the theory of one-step (birth–death) processes can be used to investigate stochastic noise due to random interactions between individuals. We begin with a short description about this process, as it applies to intrinsic noise in evolutionary games with finite population size.

Let $\Phi(n_1, n_2; t)$ denote the joint probability distribution that the numbers of R_1 and R_2 equal n_1 and n_2 at time t. As a one-step process, $\Phi(n_1, n_2; t)$ may jump to an adjacent state $n_1 \pm 1$ or $n_2 \pm 1$ in the time interval Δt with probability proportional to individual fitness. $\Phi(0, 0; t)$ is then an increasing function of t since $(n_1, n_2) = (0, 0)$ is an absorbing barrier. Moreover, every trajectory of this stochastic process will eventually be absorbed at $(n_1, n_2) = (0, 0)$ (i.e., $(n_1, n_2) = (0, 0)$ is a globally absorbing steady state) (see the following section).

Here, it is assumed that Δt is sufficiently small that at most one birth–death event occurs during this time interval. Following Swift (2002), we take the

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[1]Here we ignore the degenerate possibility that $b_{11} = b_{21}$ (in which case we would also need to compare b_{12} to b_{22}). We also assume $b_{12} \neq b_{22}$.

probability that n_i increases to $n_i + 1$ and that n_i decreases to $n_i - 1$ as Δt times the positive and negative terms on the right-hand side of (2) respectively. That is, n_i increases by 1 with probability $b_i n_i \Phi(n_1, n_2; t)\Delta t$ where $b_i \equiv e_i Ap + 1 = p_1 b_{i1} + p_2 b_{i2}$ and decreases by 1 with probability $n_i \beta N \Phi(n_1, n_2; t)\Delta t$. Thus, the population leaves state (n_1, n_2) with probability $(b_1 n_1 + b_2 n_2 + n_1 \beta N + n_2 \beta N)\Phi(n_1, n_2; t)\Delta t$ in the time interval from t to $t + \Delta t$. However, the population can also enter state (n_1, n_2) if it is in state $(n_1 + 1, n_2)$ at time t and one R_1-strategist is lost (this occurs with probability $(n_1 + 1)\beta(N + 1)\Phi(n_1 + 1, n_2; t)\Delta t$) or it is in state $(n_1 - 1, n_2)$ at time t and one R_1-strategist is gained etc. That is,

$$
\begin{aligned}
\frac{\Phi(n_1, n_2; t + \Delta t) - \Phi(n_1, n_2; t)}{\Delta t} \\
= (n_1 + 1)\beta(N + 1)\Phi(n_1 + 1, n_2; t) - n_1 \beta N \Phi(n_1, n_2; t) \\
+ (n_2 + 1)\beta(N + 1)\Phi(n_1, n_2 + 1; t) - n_2 \beta N \Phi(n_1, n_2; t) \\
+ b_1(n_1 - 1)\Phi(n_1 - 1, n_2; t) - b_1 n_1 \Phi(n_1, n_2; t) \\
+ b_2(n_2 - 1)\Phi(n_1, n_2 - 1; t) - b_2 n_2 \Phi(n_1, n_2; t) \\
= \sum_{i=1}^{2} \left((E_i^{+1} - 1)\beta N n_i \Phi + (E_i^{-1} - 1)b_i n_i \Phi \right)
\end{aligned}
\tag{9}
$$

where $E_i^{\pm 1}$ is the operator given by

$$
E_i^{\pm 1} g(n_1, n_2) = \begin{cases} g(n_1 \pm 1, n_2) & \text{if } i = 1 \\ g(n_1, n_2 \pm 1) & \text{if } i = 2 \end{cases}
$$

that shifts the population of R_i-strategists by $\pm$ one individual.

By taking the limit in (9) as Δt approaches zero, we obtain

$$
\frac{\partial \Phi(n_1, n_2; t)}{\partial t} = \sum_{i=1}^{2} \left((E_i^{+1} - 1)\beta N n_i \Phi + (E_i^{-1} - 1)b_i n_i \Phi \right).
\tag{10}
$$

This is the continuous-time master equation (Van Kampen, 1992) of $\Phi(n_1, n_2; t)$ corresponding to (2). Clearly, $(n_1, n_2) = (0, 0)$ remains an absorbing barrier of this continuous-time Markov process. Since we are more interested in the transient behavior of sample trajectories for the Markov process, it is the evolution of the conditional probability distribution of $\Phi(n_1, n_2; t)$ that assumes the population does not go extinct (i.e., either $n_1 \neq 0$ or $n_2 \neq 0$ or both) that is more important for us. For instance, when the population is monomorphic as in Section 4, this may evolve to the unique conditional equilibrium called the quasi-stationary distribution (Seneta, 1996; Pielou, 1977; Nasell, 2001). To investigate such questions in general, we approximate the evolution of the mean and variance of any initial conditional distribution by expanding the operators $E_i^{\pm 1}$ about equilibrium points (p^*, N^*) of the deterministic dynamics when p^* is either on the boundary

(Section 4) or the interior (Section 5) of Δ^2. In particular, we examine whether these evolve to a stable equilibrium.

4. Intrinsic noise for boundary equilibria

The theory of intrinsic noise is most straightforward when all individuals in the population are using the same strategy, say R_1. For the deterministic model, the dynamics (2) is now one-dimensional (since $n_2(t) = 0$ for all t) given by the logistic equation $\dot{n}_1 = n_1(a_{11} + 1 - \beta n_1) = n_1(b_{11} - \beta n_1)$ with globally asymptotically stable equilibrium $n_1^* = b_{11}/\beta$ corresponding to the boundary equilibrium $(p^* = (1, 0), N^* = b_{11}/\beta)$. We develop the corresponding model with intrinsic noise in the following section before returning to examine intrinsic noise near $(p^* = (1, 0), N^* = b_{11}/\beta)$ in the full dynamical system (2) in Section 4.2.

4.1. Internal steady-state statistics

In this section, we assume that $n_2 = 0$ initially (and so, from (9), $n_2 = 0$ for all time) and denote the probability distribution $\Phi(n_1, 0; t)$ that the number of R_1 individuals equals n_1 at time t by $\Phi(n_1; t)$ for convenience. Suppose one individual gives birth (to an offspring also using R_1) or dies per unit time with relative probabilities $n_1 b_{11}$ and βn_1^2 respectively. The discrete-time Markov process is then given by (if $n_1 \geq 1$)

$$\Phi(n_1; t + 1) = p_{n_1-1, n_1} \Phi(n_1 - 1; t) + p_{n_1+1, n_1} \Phi(n_1 + 1; t)$$

where the one-step transition probabilities from state n_1 to states $n_1 - 1$ and $n_1 + 1$ are

$$p_{n_1, n_1-1} = \frac{\beta n_1^2}{n_1 b_{11} + \beta n_1^2}$$

and

$$p_{n_1, n_1+1} = \frac{n_1 b_{11}}{n_1 b_{11} + \beta n_1^2}$$

respectively.

Clearly, $n_1 = 0$ is an absorbing barrier of this discrete-time Markov process. From Nasell (2001) (see also Seneta, 1996), every trajectory of the continuous-time Markov process corresponding to the logistic equation will eventually be absorbed at $n_1 = 0$ (i.e., $n_1 = 0$ is a globally absorbing steady state). For completeness, the proof of this statement for our discrete-time process is given in Appendix A. For instance, in Fig. 1a, where $\beta = 1$ and $a_{11} = 3$, the equilibrium size for the monomorphic population using strategy R_1 is $n_1^* = 4$. We see that within 200 time steps, the population has gone extinct for the sample path depicted.
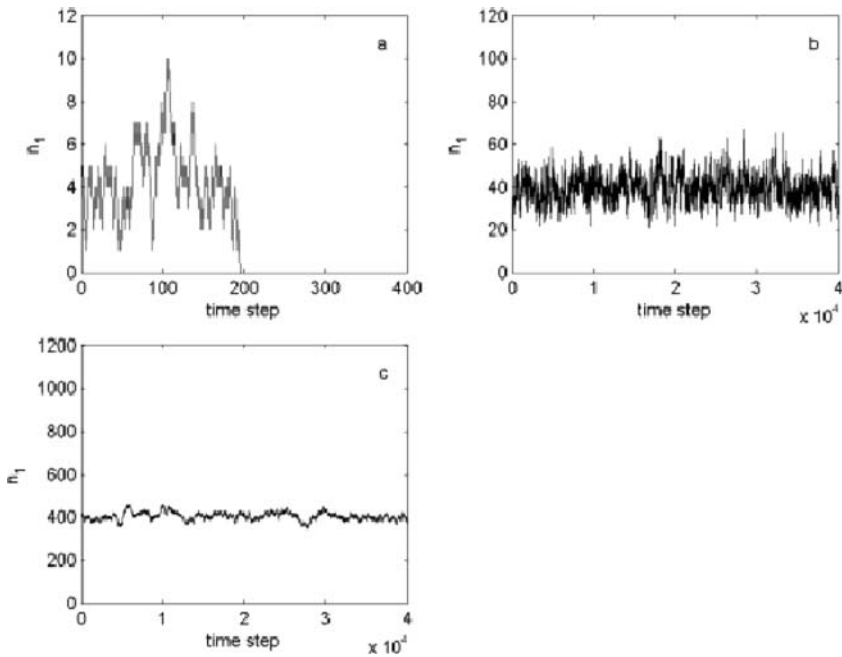
Fig. 1 Sample trajectories starting at the equilibrium population size n_1^* for the discrete-time one-step process corresponding to (11) with payoff parameter $a_{11} = 3$. (a) $\beta = 1$ and $n_1^* = 4$. (b) $\beta = 0.1$ and $n_1^* = 40$. (c) $\beta = 0.01$ and $n_1^* = 400$. For this process, the transition probabilities from state n to states $n - 1$ and $n + 1$ are $p_{n,n-1} = (\beta n^2)/(4n + \beta n^2)$ and $p_{n,n+1} = (4n)/(4n + \beta n^2)$, respectively.

However, from Fig. 1b and c, with $\beta = .1$ and $\beta = .01$, respectively (i.e., $n_1^* = 40$ and $n_1^* = 400$ respectively), there is no indication the population will go extinct for these sample paths even after 40,000 time steps. In fact, from simulations, observed sample paths rarely go extinct for moderate equilibrium sizes of $n_1^* \cong 20$. This is not surprising, since Nasell (2001) shows that the expected time to extinction in the continuous-time process grows exponentially as a function of n_1^* (he also shows that the quasi-stationary distribution near n_1^* will be close to normal when extinction time is large).

Let us assume that the equilibrium population size is large enough (e.g., $n_1^* \geq 20$) so that expected time to absorption at $n_1 = 0$ along observed sample paths is quite long. We investigate the transient behavior of the sample paths by making the following two continuous-time approximations to the discrete process.

First, the master equation (10) of $\Phi(n_1, 0; t)$ corresponding to (9) (cf. (2)) is now

$$\frac{\partial \Phi(n_1; t)}{\partial t} = \left(E_1^{+1} - 1\right)\beta n_1^2 \Phi + \left(E_1^{-1} - 1\right)b_{11}n_1 \Phi \tag{11}$$

where the step operator is $E_1^{\pm 1}g(n_1) = g(n_1 \pm 1)$. From the Taylor expansion $g(n_1 \pm 1) = g(n_1) \pm g'(n_1) + (1/2)g''(n_1) \pm (1/3!)g'''(n_1) + \cdots$ of g about n_1, the

step operator $E_1^{\pm 1}$ is given by

$$E_1^{\pm 1} = 1 \pm \frac{\partial}{\partial n_1} + \frac{1}{2}\frac{\partial^2}{\partial n_1^2} \pm \frac{1}{3!}\frac{\partial^3}{\partial n_1^3} + \cdots.$$

Hence, omitting all derivatives beyond second order, the Fokker–Planck approximation (Van Kampen, 1992) of the master equation is

$$\frac{\partial \Phi(n_1;t)}{\partial t} = -\frac{\partial}{\partial n_1}(b_{11} - \beta n_1)n_1 \Phi + \frac{1}{2}\frac{\partial^2}{\partial n_1^2}(b_{11} + \beta n_1)n_1 \Phi. \qquad (12)$$

The steady-state statistics (Van Kampen, 1992) at the boundary equilibrium $n_1^* = b_{11}/\beta$ refer to the mean and variance of the following approximation of (12). When n_1 is near this equilibrium n_1^*, let $x_1 \equiv n_1 - n_1^*$. By taking the Taylor expansions of $(b_{11} - \beta n_1)n_1$ and $(b_{11} + \beta n_1)n_1$ from (12) in terms of x_1 and retaining only the lowest nonzero terms, we obtain

$$\frac{\partial \Phi(x_1;t)}{\partial t} = b_{11}\frac{\partial}{\partial x}x_1 \Phi + \frac{b_{11}^2}{\beta}\frac{\partial^2}{\partial x_1^2}\Phi. \qquad (13)$$

The mean and variance of a solution $\Phi(x_1;t)$ for (13) are calculated through its first and second moments $\langle x_1 \rangle \equiv \int_{-\infty}^{\infty} x_1 \Phi(x_1;t)dx_1$ and $\langle x_1^2 \rangle \equiv \int_{-\infty}^{\infty} x_1^2 \Phi(x_1;t)dx_1$, respectively.

To determine how these moments evolve with time, boundary conditions must be added to (13) as x_1 (or n_1) becomes infinite. In fact, since there is no a priori reason $n_1 \geq 0$ (i.e., $x_1 \geq -n_1^*$) in this approximation, we need to impose boundary conditions as $x_1 \to \pm\infty$. Clearly, from Fig. 1, sample trajectories of our discrete-time process remain bounded. In particular, $\Phi(x_1;t)$ is identically zero when $|x_1|$ is sufficiently large. Since non trivial solutions of (13) cannot be identically zero for large $|x_1|$, we translate the biological fact of bounded population size into the mathematical condition that $\Phi(x_1;t)$ approaches zero asymptotically as $|x_1| \to \infty$ in the following sense. Specifically, we assume $\lim_{x_1 \to \pm\infty} \Phi(x_1;t) = 0$, $\lim_{x_1 \to \pm\infty} x_1 \Phi(x_1;t) = 0$, $\lim_{x_1 \to \pm\infty} (\partial \Phi(x_1;t))/(\partial x_1) = 0$, etc. (i.e., $\Phi(x_1;t)$ and its derivatives as functions of x_1 approach zero faster than any polynomial).

By substituting (13) and applying integration by parts, these boundary conditions imply

$$\frac{d\langle x_1 \rangle}{dt} = \int_{-\infty}^{\infty} x_1 \frac{\partial \Phi(x_1;t)}{\partial t}dx_1 = \int_{-\infty}^{\infty} x_1 \left(b_{11}\frac{\partial}{\partial x_1}x_1 \Phi + \frac{b_{11}^2}{\beta}\frac{\partial^2}{\partial x_1^2}\Phi\right)dx_1$$

$$= b_{11}x_1^2 \Phi \big|_{-\infty}^{\infty} - b_{11}\int_{-\infty}^{\infty} x_1 \Phi dx_1 + \frac{b_{11}^2}{\beta}\left[x_1\frac{\partial \Phi}{\partial x_1}\big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty}\frac{\partial \Phi}{\partial x_1}dx_1\right]$$

$$= -b_{11}\langle x_1 \rangle$$

$$\frac{d\langle x_1^2 \rangle}{dt} = \int_{-\infty}^{\infty} x_1^2 \frac{\partial \Phi(x_1;t)}{\partial t} dx_1 = \int_{-\infty}^{\infty} x_1^2 \left(b_{11} \frac{\partial}{\partial x_1} x_1 \Phi + \frac{b_{11}^2}{\beta} \frac{\partial^2}{\partial x_1^2} \Phi \right) dx_1$$

$$= b_{11} \left[x_1^3 \Phi \big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} 2x_1^2 \Phi dx_1 \right] + \frac{b_{11}^2}{\beta} \left[x_1^2 \frac{\partial \Phi}{\partial x_1} \big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} 2x_1 \frac{\partial \Phi}{\partial x_1} dx_1 \right]$$

$$= -2b_{11}\langle x_1^2 \rangle - \frac{2b_{11}^2}{\beta} \left[-\int_{-\infty}^{\infty} \Phi dx_1 \right]$$

$$= -2b_{11}\langle x_1^2 \rangle + \frac{2b_{11}^2}{\beta}.$$

That is, $\langle x_1 \rangle$ and $\langle x_1^2 \rangle$ evolve to 0 and b_{11}/β, respectively, under (13). In fact, Van Kampen (1992) shows that $\Phi(x_1;t)$ is a standard normal distribution with mean 0 and variance b_{11}/β for large t (cf. the quasi-stationary distribution of Nasell (2001) that is close to normal near n_1^* when this equilibrium size is large). Thus, for large t, the expectation and variance of n_1 near the equilibrium n_1^* are $\langle n_1 \rangle = \sigma_{n_1}^2 = b_{11}/\beta$. These are called the steady-state statistics of the dynamics (12) for the equilibrium n_1^*.

Since these theoretical steady-state statistics are based on two successive approximations, (12) and (13), of the one-step process (9), an immediate question is how accurate they are for the original equation. A naive test is to consider the mean and variance of the sample trajectories with 40,000 data points in Fig. 1b and c (i.e., when the population does not go extinct). For $\beta = 0.1$ (Fig. 1b), the mean and variance are 39.675 and 39.695, respectively, and for $\beta = 0.01$ (Fig. 1c) they are 395.458 and 396.012.[2] These are consistent with the theoretical values of 40 (Fig. 1b) and 400 (Fig. 1c), especially given that the linearized terms in x become less accurate as variance increases.

To test this accuracy further, we performed Monte Carlo simulations following Gillespie (1977) for (11) using the payoff matrix

$$\begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}$$

that has $b_{11} = 4$. As we can see from Fig. 2, there is surprisingly good agreement for the means and variances (for the range of values $\beta = 0.01$ to 0.09). Although not apparent from Fig. 2, it is clear from Fig. 1 that the relative fluctuation strength $\sigma_{n_1}/\langle x_1 \rangle$ (defined by the coefficient of variation which is given by the standard deviation divided by the mean) decreases as $n_1^* = b_{11}/\beta$ increases. These results are also related to the concept of Fano factor (see, for example, Thattai and van Oudenaarden, 2001; Tao, 2004; Tao et al., 2005) which is always 1 for our model.

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[2]Even for $\beta = 1$ (Fig. 1a), the mean and variance are 4.456 and 3.049 for the first 180 time steps (i.e., before the population goes extinct) and these are reasonably consistent with the theoretical values of 4.
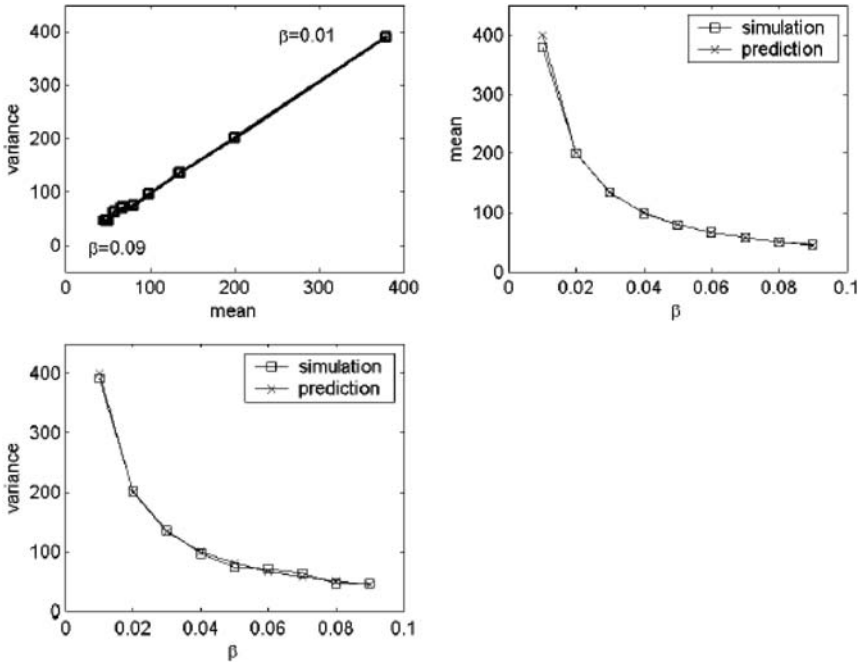
Fig. 2 The means and variances of sample trajectories of (11) compared with the theoretical steady-state statistics (i.e., the mean and variance) of (13). Payoff parameter is $a_{11} = 3$.

4.2. External steady-state statistics: Is it possible that a mutant strategy can invade the population through intrinsic noise?

The question we examine in this section is whether the distribution of individuals using pure strategy R_1 found in Section 4.1 through internal intrinsic noise can be successfully invaded by a mutant strategist using pure strategy R_2. For the deterministic system (2) (or equivalently (3) (4)), ($p^* = (1, 0)$, $N^* = b_{11}/\beta$) is asymptotically stable if and only if $b_{11} > b_{21}$ if and only if $p^* = (1, 0)$ is an ESS.

For this equilibrium, $n_1^* = b_{11}/\beta$ and $n_2^* = 0$. Let $x_1 = n_1 - n_1^*$ and $x_2 = n_2$. By using the same methods as in Section 4.1 (for details see Section 5), we obtain

$$\frac{d}{dt}\begin{pmatrix} \langle x_1 \rangle \\ \langle x_2 \rangle \end{pmatrix} = \begin{pmatrix} -b_{11} & b_{12} \\ 0 & b_{21} - b_{11} \end{pmatrix} \begin{pmatrix} \langle x_1 \rangle \\ \langle x_2 \rangle \end{pmatrix} \tag{14}$$

as the linear approximation to the master Eq. (10) for the evolution of the expected values of x_1 and x_2. We see that $\langle x_1 \rangle$ and $\langle x_2 \rangle$ evolve to 0 if and only if $b_{11} > b_{21}$. That is, $n_1^* = b_{11}/\beta$ and $n_2^* = 0$ is asymptotically stable if and only if $p^* = (1, 0)$ is an ESS. This agrees with the simulation results of Fig. 3 for the one-step process
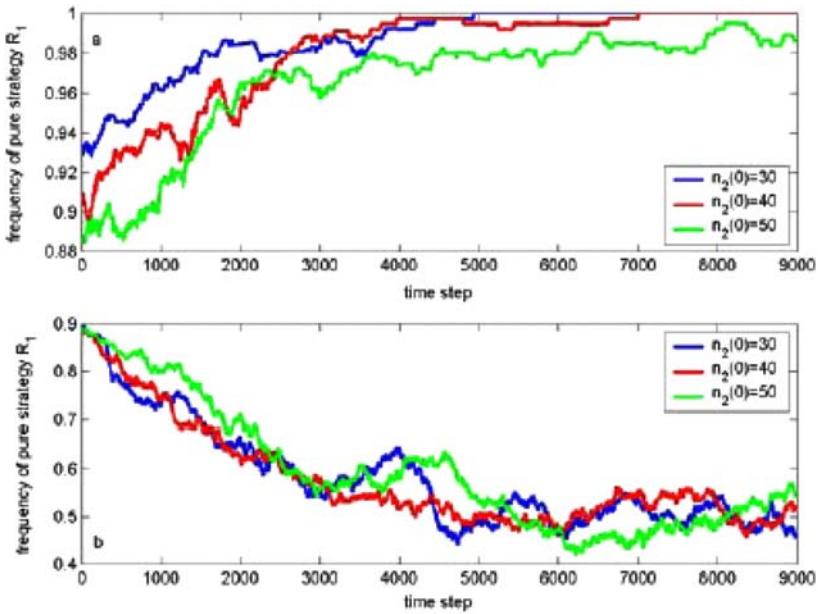
Fig. 3 Stochastic simulations are plotted where most of the individuals in the population are initially R_1-strategists. The parameter is taken as $\beta = 0.01$ and the payoff matrices are $\begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}$ and $\begin{bmatrix} 1 & 3 \\ 3 & 1 \end{bmatrix}$ in (a) and (b), respectively. The three curves in each figure correspond to three different initial conditions, which are $n_2(0) = 30, 40$, and 50 out of a total population size of 400. The simulations in (a) show that, if most of the individuals are R_1-strategists, the pure strategy R_2 will eventually go extinct. In (b), the population initially evolves toward the ESS proportion of 50% R_1-strategists and then oscillates around this stable equilibrium.

(9). That is, in Fig. 3a where the payoff matrix is

$$\begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}$$

with ESS $p^* = (1, 0)$, the simulations show R_2 cannot invade R_1 when the initial proportion of R_2 individuals is small (up to 10% in these simulations). On the other hand, when the payoff matrix is

$$\begin{bmatrix} 1 & 3 \\ 3 & 1 \end{bmatrix},$$

there is no ESS at $p^* = (1, 0)$ and Fig. 3b confirms R_2 does successfully invade R_1, since the proportion of R_2 individuals is increasing initially (as the population evolves towards the ESS $p^* = (\{1/2\}, \{1/2\})$). This latter situation is examined more closely in the following section.

In summary, stability of boundary equilibria based on the transient behavior due to internal and external intrinsic noise is the same as the deterministic system. In particular, these stochastic effects do not enhance the ability of the mutant strategy to invade. This contrasts with the limiting behavior of stochastic models with recurring mutations and fixed population size analyzed by Foster and Young (1990) (see also Kandori et al., 1993) where some ESSs were shown to be unstable.

5. Intrinsic noise for interior equilibria

We begin this section by giving the technical details of the linear expansion for the means and variances under the master equation. By omitting all derivatives beyond the second in the Taylor expansion $E_i^{\pm 1} = 1 \pm (\partial/\partial n_i) + (1/2)(\partial^2/\partial n_i^2) \pm (1/3)(\partial^3/\partial n_i^3) + \cdots$ of the step operators $E_i^{\pm 1}$, the Fokker–Planck approximation of the master Eq. (10) is now (cf. (12))

$$\frac{\partial \Phi(n_1, n_2; t)}{\partial t} = \sum_{i=1}^{2} \left(-\frac{\partial}{\partial n_i}(b_i - \beta N)n_i \Phi + \frac{1}{2}\frac{\partial^2}{\partial n_i^2}(b_i + \beta N)n_i \Phi \right). \quad (15)$$

When the systems (3) and (4) are near the interior (i.e., polymorphic) equilibrium (p^*, N^*) given by (7) and (8), we are interested in the steady-state statistics of (15). For this purpose, set $x_i = n_i - n_i^*$ $(i = 1, 2)$, substitute this in (15) and expand the coefficients in powers of x_i. By retaining only the lowest nonzero terms, we obtain

$$\frac{\partial \Phi(x_1, x_2; t)}{\partial t} = \sum_{i=1}^{2} \left(-\frac{\partial}{\partial x_i}(c_{i1}x_1 + c_{i2}x_2)\Phi + D_i \frac{\partial^2 \Phi}{\partial x_i^2} \right) \quad (16)$$

where $D_i \equiv \beta N^* n_i^*$ and $c_{ij} = (\partial/\partial n_j)(b_i - \beta N)n_i$ and these partial derivatives are evaluated at the equilibrium.[3] That is,

$$c_{11} = \left((b_{11} - b_{12})\frac{p_2^*}{N^*} - \beta \right) n_1^*, \qquad c_{12} = -\left((b_{11} - b_{12})\frac{p_1^*}{N^*} + \beta \right) n_1^*$$

$$c_{21} = \left((b_{21} - b_{22})\frac{p_2^*}{N^*} - \beta \right) n_2^*, \qquad c_{22} = -\left((b_{21} - b_{22})\frac{p_1^*}{N^*} + \beta \right) n_2^*.$$

Generalization of the zero boundary conditions given in Section 4.1 now leads to $d\langle x_i \rangle/dt = c_{i1}\langle x_1 \rangle + c_{i2}\langle x_2 \rangle$ for $i = 1, 2$ as the evolution of the first moments (see

---

[3]At the boundary equilibrium of Section 4.2, it is easy to verify that $c_{11} = -b_{11}, c_{12} = b_{12}, c_{21} = 0$, and $c_{22} = b_{21} - b_{11}$. This leads to (14) by following the same calculations that produce (17) at an interior equilibrium.

Appendix B). In matrix form, this is

$$\frac{d}{dt}\begin{pmatrix} \langle x_1 \rangle \\ \langle x_2 \rangle \end{pmatrix} = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix} \begin{pmatrix} \langle x_1 \rangle \\ \langle x_2 \rangle \end{pmatrix}. \tag{17}$$

A straightforward application (Appendix B) of the two-dimensional Routh–Hurwitz stability conditions (Pielou, 1977) shows that $(\langle x_1 \rangle, \langle x_2 \rangle) = (0, 0)$ is globally asymptotically stable for (17) if and only if p^* is an ESS. In this case, the expectations of n_1 and n_2 evolve to $\langle n_1 \rangle = p_1^* N^*$ and $\langle n_2 \rangle = p_2^* N^*$, respectively (i.e., (p^*, N^*) is globally asymptotically stable for (16)). On the other hand, if p^* is not an ESS, then (p^*, N^*) is unstable and we expect the population to evolve to one of the boundary equilibria of Section 4. For this reason, we assume p^* is an ESS for the remainder of this section.

In order that (16) is a good approximation of the master Eq. (10), it is important that the distribution $\Phi(n_1, n_2; t)$ is not too spread out from the equilibrium $n_i^* = p_i^* N^*$. That is, we need to analyze the dynamics for the variance and covariance of solutions of (16). As shown in Appendix B, this is given in matrix form by

$$\frac{d}{dt}\begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} = \begin{pmatrix} 2c_{11} & 2c_{12} & 0 \\ c_{21} & c_{11} + c_{22} & c_{12} \\ 0 & 2c_{21} & 2c_{22} \end{pmatrix} \begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} + \begin{pmatrix} 2D_1 \\ 0 \\ 2D_2 \end{pmatrix}. \tag{18}$$

It is also shown there that a (globally) asymptotically stable equilibrium for (18) exists with values

$$\begin{pmatrix} \langle x_1^2 \rangle \\ \langle x_1 x_2 \rangle \\ \langle x_2^2 \rangle \end{pmatrix} = \frac{1}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \begin{pmatrix} -(c_{11} + c_{22})c_{22}D_1 - c_{12}(c_{12}D_2 - c_{21}D_1) \\ c_{11}c_{12}D_2 + c_{21}c_{22}D_1 \\ -(c_{11} + c_{22})c_{11}D_2 - c_{21}(c_{21}D_1 - c_{12}D_2) \end{pmatrix}$$

if and only if p^* is an ESS.

Since $\langle x_i \rangle = 0$ at equilibrium, these equilibrium values are the (co)variances of the joint distribution $\Phi(n_1, n_2; t)$ for large t as well. That is,

$$\begin{aligned}
\sigma_{n_1}^2 &= -\frac{D_1(c_{11}c_{22} - c_{12}c_{21}) + D_1 c_{22}^2 + D_2 c_{12}^2}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \\
&= -\frac{\beta(N^*)^2\big(p_1^*(c_{11}c_{22} - c_{12}c_{21}) + p_1^* c_{22}^2 + p_2^* c_{12}^2\big)}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \\
\sigma_{n_2}^2 &= -\frac{D_2(c_{11}c_{22} - c_{12}c_{21}) + D_2 c_{11}^2 + D_1 c_{21}^2}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})} \\
&= -\frac{\beta(N^*)^2\big(p_2^*(c_{11}c_{22} - c_{12}c_{21}) + p_2^* c_{11}^2 + p_1^* c_{21}^2\big)}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})}
\end{aligned}$$

$$\mathrm{cov}(n_1, n_2) = \frac{D_1 c_{21} c_{22} + D_2 c_{11} c_{12}}{(c_{11} + c_{22})(c_{11} c_{22} - c_{12} c_{21})}$$

$$= \frac{\beta (N^*)^2 (p_1^* c_{21} c_{22} + p_2^* c_{11} c_{12})}{(c_{11} + c_{22})(c_{11} c_{22} - c_{12} c_{21})}.$$

Since c_{ij}, βN^*, p_1^*, and p_2^* are all independent of β, we see that $\langle n_1 \rangle$ and $\langle n_2 \rangle$ as well as $\sigma_{n_1}^2$, $\sigma_{n_2}^2$, $\mathrm{cov}(n_1, n_2)$ all grow linearly with respect to N^* (i.e., with respect to $1/\beta$) just as was the case for the steady-state statistics of the stable boundary equilibria considered in the previous section.

These results show that the fluctuations in the number of R_1-strategists will be less noticeable as the equilibrium population size N^* gets large (cf. Fig. 1b compared to Fig. 1c in Section 4). The transient dynamics for the discrete-time Markov process is then approximated well by the evolution of the means. Just as for the boundary equilibria of Section 4, it is then the ESS concept that predicts the eventual evolutionary outcome.

On the other hand, for deterministic evolutionary game dynamics, we are often more interested in the phenotypic frequency of strategy use than in the actual number using these strategies near any interior stable equilibrium. Thus, the steady-state statistics of this frequency are also of interest under stochastic fluctuations. To calculate these, notice that p_1 can be approximated as

$$p_1 - p_1^* = \frac{\partial}{\partial n_1} \left(\frac{n_1}{n_1 + n_2} \right) \Big|_{(n_1^*, n_2^*)} (n_1 - n_1^*) + \frac{\partial}{\partial n_2} \left(\frac{n_1}{n_1 + n_2} \right) \Big|_{(n_1^*, n_2^*)} (n_2 - n_2^*)$$

$$= \frac{p_2^*}{N^*} (n_1 - n_1^*) - \frac{p_1^*}{N^*} (n_2 - n_2^*)$$

if the system's state is near the stable fixed point (p^*, N^*). This approximation implies that the steady-state statistics of the frequency p_1 are

$$\langle p_1 \rangle = p_1^* + \frac{p_2^*}{N^*} (\langle n_1 \rangle - n_1^*) - \frac{p_1^*}{N^*} (\langle n_2 \rangle - n_2^*) = p_1^*$$

$$\sigma_{p_1}^2 = \frac{1}{(N^*)^2} ((p_2^*)^2 \sigma_{n_1}^2 + (p_1^*)^2 \sigma_{n_2}^2 - 2 p_1^* p_2^* \, \mathrm{cov}(n_1, n_2))$$

$$= -\frac{\beta}{(c_{11} + c_{22})(c_{11} c_{22} - c_{12} c_{21})}$$

$$\times \left(\begin{array}{c} (p_1^* p_2^*)(c_{11} c_{22} - c_{12} c_{21}) + (p_2^*)^2 (p_1^* c_{22}^2 + p_2^* c_{12}^2) \\ + (p_1^*)^2 (p_2^* c_{11}^2 + p_1^* c_{21}^2) + 2 p_1^* p_2^* (p_1^* c_{21} c_{22} + p_2^* c_{11} c_{12}) \end{array} \right)$$

$$= \frac{\beta}{b_{12} - b_{22} + b_{21} - b_{11}}$$

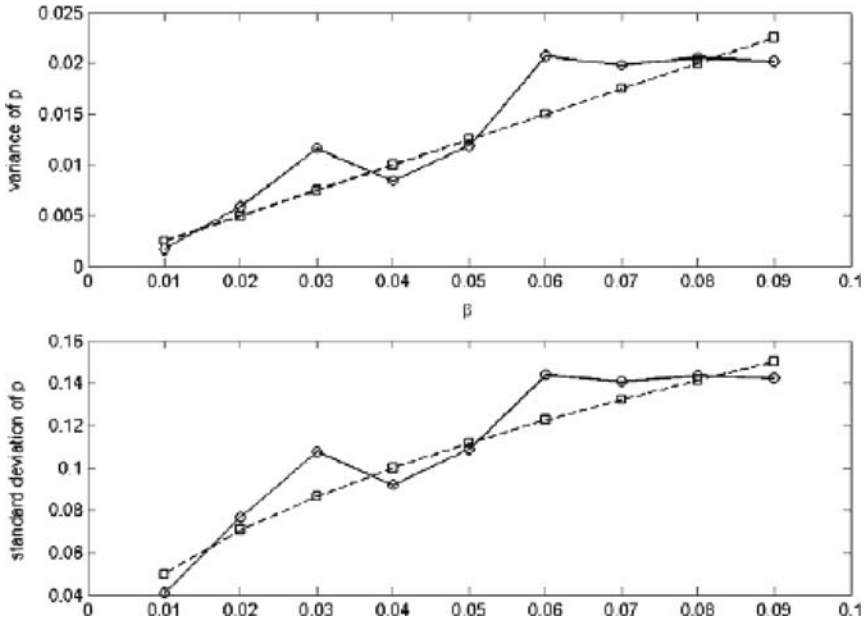$$= \frac{\beta}{a_{12} - a_{22} + a_{21} - a_{11}}$$

Fig. 4 A comparison between Monte Carlo simulations and theoretical predictions is plotted for different values of β taken from 0.01 to 0.09 when the payoff matrix is taken as $\begin{bmatrix} 1 & 3 \\ 3 & 1 \end{bmatrix}$. For the variance and standard deviation of phenotypic frequency p, the *empty circles* (connected by the *sold line segments*) indicate the results of the Monte Carlo simulation, and the *squares* (connected by the *broken curve*) denote the theoretical predictions.

This result shows clearly that, for a given two-phenotype payoff matrix with an interior ESS (i.e., $a_{12} > a_{22}$ and $a_{21} > a_{11}$), the variance of phenotypic frequency p_1 is an increasing linear function of the parameter β (i.e., the variance will decrease as the equilibrium population size N^* increases). That is, stochastic fluctuations are expected to become negligible for the frequency dynamics as population size becomes large and so the deterministic model can be used instead.

For a simple example, a comparison between the Monte Carlo simulations of (10) (the simulation algorithm is from Gillespie (1977)) and the theoretical predictions of the steady-state predictions from (16) for different values of the parameter β is plotted in Fig. 4, where the payoff matrix is given by

$$(a_{ij})_{2\times 2} = \begin{bmatrix} 1 & 3 \\ 3 & 1 \end{bmatrix}.$$

This figure again shows that the theoretical analysis is quite accurate.

6. Conclusion

In this paper, stochastic noise in a simple evolutionary game dynamics with two phenotypes is analyzed using the theory of one-step birth–death processes. We assume that the population size is finite but not fixed, and we mainly focus our attention on the statistics based on random interactions between individuals. This differs from other studies of stochastic effects due to finite populations in evolutionary game theory where population size is assumed to be fixed and interactions may be random (Taylor et al., 2004) or based on a structured population such as when interactions only occur between neighbors on an evolutionary graph (Ohtsuki et al., 2006). Moreover, this literature typically examines the long-term steady-state solution of the Markov process which, in our case, is of little interest since fitnesses that decrease in population size (i.e., logistic density effects) imply the population eventually goes extinct (i.e., the only steady state is the trivial solution $n_1 = n_2 = 0$). Instead, we examine the transient behavior (that assumes the population is not extinct) which can be quite long lasting (see Fig. 1b and c) for even moderate equilibrium population sizes of 40 individuals in the corresponding deterministic model. Since these transient probability distributions are analytically intractable for our one-step process, we approximate their steady-state statistics (i.e., their means and variances) through linearizing the master equation of the associated continuous-time process. We find good agreement between these latter analytic statistics and simulation results of the original one-step process (see Figs. 2 and 4).

Our main results show that the deterministic model of evolutionary game theory continues to predict the stochastic population means and that the stochastic effects on the variances become less important as the equilibrium population size increases. For two phenotypes with individual fitness given as a combination of pairwise interactions (through a payoff matrix) and a background fitness that is independent of phenotype, the deterministic model is fully understood by examining the ESSs of the payoff matrix. In particular, the frequencies of the two phenotypes approach the ESS proportions as the population size evolves to the N^* where logistic density effects exactly cancel the payoffs gained through pairwise interactions (Section 2). The same stable equilibrium occurs for the linearized master equation. Furthermore, stable equilibrium variances for the number of individuals using the two phenotypes can also be determined for this stochastic equation. In fact, these variances increase linearly in the equilibrium population size N^*. Thus, for large N^*, the frequency variance approaches zero. That is, stochastic effects become less and less relevant for large populations and only the deterministic model of evolutionary game theory need be considered to predict the evolution of phenotypic frequencies.

In conclusion, the issue raised by Hastings (2004) (i.e., that using deterministic approximations of stochastic models applied to complex ecological systems may give misleading predictions of the evolutionary outcome) is not a problem for two-phenotype evolutionary games when the (stable) equilibrium population size is quite large. That is, stochastic fluctuations can be ignored in these circumstances and standard game-theoretic deterministic dynamics can be legitimately used to predict population mean strategy and population size. In fact, these predictions

remain valid for a moderate equilibrium population size as well. In this latter case, the stochastic fluctuations about the mean become increasingly prominent. As we have seen, these can also be analyzed through deterministic evolutionary dynamics that predict stable variances (and covariances).

Appendix A

Here we show that every trajectory in Section 4.1 is eventually absorbed in the extinction state. A similar approach shows this is also true for the trajectories that start in the interior of the state space as in Sections 4.2 and 5. By the Mean Ergodic Theorem for discrete-time Markov processes (Bharucha-Reid, 1960),

$$\pi_{ij} \equiv \lim_{n \to \infty} \frac{1}{n} \sum_{\nu=0}^{n} p_{ij}^{(\nu)}$$

exists for all $0 \le i, j < \infty$ and satisfies $\sum_{j=0}^{\infty} \pi_{ij} \le 1$ and $\pi_{ij} = \sum_{k=0}^{\infty} \pi_{ik} p_{kj} = \sum_{k=0}^{\infty} p_{ik} \pi_{kj}$. Here, $p_{ij}^{(\nu)}$ is the transition probability from state i to state j in ν steps and $p_{ij} = p_{ij}^{(1)}$. For our one-step Markov chain, we have $p_{i,i-1} = \beta i^2/(4i + \beta i^2)$ and $p_{i,i+1} = 4i/(4i + \beta i^2)$ as the only nonzero transition probabilities. Thus,

$$p_{i,i-1} \pi_{i-1,0} + p_{i,i+1} \pi_{i+1,0} = \pi_{i0}$$

for $i \ge 1$ and the second-order recurrence relation becomes

$$\pi_{i+1,0} - \pi_{i0} = \frac{\beta i}{4} (\pi_{i0} - \pi_{i-1,0}).$$

From this, it is easy to show that $\pi_{i+1,0} - \pi_{i0} = 0$ for all i (otherwise we have the contradiction $\pi_{i0} < 0$ for i sufficiently large). Furthermore, $\pi_{00} = 1$ and $\pi_{0j} = 0$ if $j > 0$, since $i = 0$ is an absorbing barrier. Thus, $\pi_{i0} = 1$ for all $i \ge 0$ and, furthermore, $\pi_{ij} = 0$ if $j > 0$.

Since $p_{i0}^{(\nu)}$ is an increasing function of ν, $\pi_{i0} = 1$ implies $\lim_{\nu \to \infty} p_{i0}^{(\nu)} = 1$. In particular, the population goes extinct along every trajectory of (9).

Appendix B

This appendix provides the mathematical details that justify the results given in Section 5 for the evolution and stability of the first and second moments corresponding to Eq. (16).

Using the zero boundary conditions

$$\lim_{x_1, x_2 \to \pm\infty} \Phi(x_1, x_2; t) = 0, \quad \lim_{x_1, x_2 \to \pm\infty} x_i \Phi(x_1, x_2; t) = 0, \quad \lim_{x_1, x_2 \to \pm\infty} \frac{\partial \Phi(x_1, x_2; t)}{\partial x_i} = 0,$$

... for $i = 1, 2$, we obtain

$$
\begin{aligned}
\frac{d\langle x_1 \rangle}{dt} &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 \frac{\partial \Phi}{\partial t} dx_1 dx_2 \\
&= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 \left(-\frac{\partial}{\partial x_1} (c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial^2 \Phi}{\partial x_1^2} \right) dx_1 dx_2 \\
&\quad + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 \left(-\frac{\partial}{\partial x_2} (c_{21} x_1 + c_{22} x_2) \Phi + D_2 \frac{\partial^2 \Phi}{\partial x_2^2} \right) dx_1 dx_2 \\
&= \int_{-\infty}^{\infty} \left[x_1 \left(-(c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) \right] \Big|_{x_1 = -\infty}^{x_1 = \infty} dx_2 \\
&\quad - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \left(-(c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) dx_1 dx_2 \\
&\quad + \int_{-\infty}^{\infty} x_1 \left(-(c_{21} x_1 + c_{22} x_2) \Phi + D_2 \frac{\partial \Phi}{\partial x_2} \right) \Big|_{x_2 = -\infty}^{x_2 = \infty} dx_1 \\
&= c_{11} \langle x_1 \rangle + c_{12} \langle x_2 \rangle - \int_{-\infty}^{\infty} D_1 \Phi \Big|_{x_1 = -\infty}^{x_1 = \infty} dx_2 \\
&= c_{11} \langle x_1 \rangle + c_{12} \langle x_2 \rangle.
\end{aligned}
$$

This combines with a similar calculation for $d\langle x_2 \rangle / dt$ to yield (17). $(\langle x_1 \rangle, \langle x_2 \rangle) = (0, 0)$ is globally asymptotically stable if and only if the trace of

$$
\begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}
\tag{B.1}
$$

is negative and its determinant is positive. From the main text,

$$
c_{11} + c_{22} = (b_{11} - b_{12} + b_{22} - b_{21}) p_1^* p_2^* - \beta N^* = \frac{2 b_{12} b_{21} - b_{22} b_{21} - b_{12} b_{11}}{b_{11} - b_{12} + b_{22} - b_{21}} < 0
$$

for any interior equilibrium (p^*, N^*). Furthermore, $c_{11} c_{22} - c_{12} c_{21} = -\beta p_1^* p_2^* N^* (b_{11} - b_{12} + b_{22} - b_{21}) > 0$ if and only if the fixed interior equilibrium of (3) and (4) is globally asymptotically stable (i.e., p^* is an ESS).

For the second moments, we have

$$
\begin{aligned}
\frac{d\langle x_1^2 \rangle}{dt} &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1^2 \frac{\partial \Phi}{\partial t} dx_1 dx_2 \\
&= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1^2 \left(-\frac{\partial}{\partial x_1} (c_{11} x_1 + c_{12} x_2) \Phi + D_1 \frac{\partial^2 \Phi}{\partial x_1^2} \right) dx_1 dx_2
\end{aligned}
$$

$$+ \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1^2 \left(-\frac{\partial}{\partial x_2}(c_{21}x_1 + c_{22}x_2)\Phi + D_2 \frac{\partial^2 \Phi}{\partial x_2^2} \right) dx_1 d_2$$

$$= \int_{-\infty}^{\infty} \left[x_1^2 \left(-(c_{11}x_1 + c_{12}x_2)\Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) \right] |_{x_1=-\infty}^{x_1=\infty} dx_2$$

$$- \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} 2x_1 \left(-(c_{11}x_1 + c_{12}x_2)\Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) dx_1 dx_2$$

$$+ \int_{-\infty}^{\infty} x_1^2 \left(-(c_{21}x_1 + c_{22}x_2)\Phi + D_2 \frac{\partial \Phi}{\partial x_2} \right) |_{x_2=-\infty}^{x_2=\infty} dx_1$$

$$= 2c_{11}\langle x_1^2 \rangle + 2c_{12}\langle x_1 x_2 \rangle - 2D_1 \left[x_1 \Phi |_{x_1=-\infty}^{x_1=\infty} - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \Phi dx_1 dx_2 \right]$$

$$= 2c_{11}\langle x_1^2 \rangle + 2c_{12}\langle x_1 x_2 \rangle + 2D_1$$

and

$$\frac{d\langle x_1 x_2 \rangle}{dt} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 x_2 \frac{\partial \Phi}{\partial t} dx_1 dx_2$$

$$= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 x_2 \left(-\frac{\partial}{\partial x_1}(c_{11}x_1 + c_{12}x_2)\Phi + D_1 \frac{\partial^2 \Phi}{\partial x_1^2} \right) dx_1 dx_2$$

$$+ \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 x_2 \left(-\frac{\partial}{\partial x_2}(c_{21}x_1 + c_{22}x_2)\Phi + D_2 \frac{\partial^2 \Phi}{\partial x_2^2} \right) dx_1 dx_2$$

$$= \int_{-\infty}^{\infty} \left[x_1 x_2 \left(-(c_{11}x_1 + c_{12}x_2)\Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) \right] |_{x_1=-\infty}^{x_1=\infty} dx_2$$

$$- \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_2 \left(-(c_{11}x_1 + c_{12}x_2)\Phi + D_1 \frac{\partial \Phi}{\partial x_1} \right) dx_1 dx_2$$

$$+ \int_{-\infty}^{\infty} x_1 x_2 \left(-(c_{21}x_1 + c_{22}x_2)\Phi + D_2 \frac{\partial \Phi}{\partial x_2} \right) |_{x_2=-\infty}^{x_2=\infty} dx_1$$

$$- \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x_1 \left(-(c_{21}x_1 + c_{22}x_2)\Phi + D_2 \frac{\partial \Phi}{\partial x_2} \right) dx_1 dx_2$$

$$= c_{11}\langle x_1 x_2 \rangle + c_{12}\langle x_2^2 \rangle - D_1 \left[\int_{-\infty}^{\infty} x_2 \Phi |_{x_1=-\infty}^{x_1=\infty} dx_2 \right]$$

$$+ c_{21}\langle x_1^2 \rangle + c_{22}\langle x_1 x_2 \rangle - D_2 \left[\int_{-\infty}^{\infty} x_1 \Phi |_{x_1=-\infty}^{x_1=\infty} dx_1 \right]$$

$$= c_{21}\langle x_1^2 \rangle + (c_{11} + c_{22})\langle x_1 x_2 \rangle + c_{12}\langle x_2^2 \rangle.$$

Equation (18) results by combining these equations with a similar calculation for $d\langle x_2^2 \rangle/dt$.

Since the determinant of

$$
\begin{pmatrix}
2c_{11} & 2c_{12} & 0 \\
c_{21} & c_{11} + c_{22} & c_{12} \\
0 & 2c_{21} & 2c_{22}
\end{pmatrix}
$$

is $4(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21}) < 0$ at an interior ESS, Cramer's Rule implies the equilibrium of (18) is

$$
\begin{pmatrix}
\langle x_1^2 \rangle \\
\langle x_1 x_2 \rangle \\
\langle x_2^2 \rangle
\end{pmatrix}
= \frac{1}{(c_{11} + c_{22})(c_{11}c_{22} - c_{12}c_{21})}
\begin{pmatrix}
-(c_{11} + c_{22})c_{22}D_1 - c_{12}(c_{12}D_2 - c_{21}D_1) \\
c_{11}c_{12}D_2 + c_{21}c_{22}D_1 \\
-(c_{11} + c_{22})c_{11}D_2 - c_{21}(c_{21}D_1 - c_{12}D_2)
\end{pmatrix}.
$$

Furthermore, if

$$
\begin{pmatrix}
x \\
y
\end{pmatrix}
$$

is an eigenvector of

$$
\begin{pmatrix}
c_{11} & c_{12} \\
c_{21} & c_{22}
\end{pmatrix}
$$

with eigenvalue λ, then

$$
\begin{pmatrix}
x^2 \\
xy \\
y^2
\end{pmatrix}
$$

is an eigenvector of

$$
\begin{pmatrix}
2c_{11} & 2c_{12} & 0 \\
c_{21} & c_{11} + c_{22} & c_{12} \\
0 & 2c_{21} & 2c_{22}
\end{pmatrix}
$$

with eigenvalue 2λ. The third eigenvalue is $c_{11} + c_{22} < 0$ with eigenvector

$$
\begin{pmatrix}
2c_{12} \\
-c_{11} + c_{22} \\
-2c_{21}
\end{pmatrix}.
$$

Thus, the equilibrium is stable if and only if p^* is an ESS.

To assist with the notational complexity in the main text, the following table is provided. The subscripts i and j here take on the values of 1 and 2.

R_i	possible individual phenotypes (or strategies)
a_{ij}	payoff of an R_i-strategist in a pairwise contest with R_j
f_i	expected payoff to R_i-strategist
p_i	frequency of R_i-strategists
Δ^2	set of frequency vectors (p_1, p_2)
n_i	number of R_i-strategists
N	total population size (equal to $n_1 + n_2$)
β	logistic density parameter inversely related to carrying capacity
W_i	fitness of an R_i-strategist (equal to $f_i + 1 - \beta N$)
b_{ij}	adjusted payoff of an R_i-strategist (equal to $a_{ij} + 1$)
b_i	positive component of fitness of an R_i-strategist (equals $f_i + 1$)
$\Phi(n_1, n_2; t)$	probability that the number of R_i-strategists is n_i at time t if $n_2 = 0$, this is also denoted as $\Phi(n_1; t)$
$E_i^\pm$	operator that shifts the number of R_i-strategists by ± 1 individual
$p_{n,m}$	one-step transition probability from state n to state m
x_i	number of R_i-strategists relative to equilibrium n_i^* (equals $n_i - n_i^*$)
$\langle \text{arg} \rangle$	expected value of the argument arg
σ^2_{arg}	variance of the argument arg
$\text{cov}(n_1, n_2)$	covariance of n_1 and n_2

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