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Non-Gaussian fluctuations arising from finite populations: Exact results for the evolutionary Moran process

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The appropriate description of fluctuations within the framework of evolutionary game theory is a fundamental unsolved problem in the case of finite populations. The Moran process recently introduced into this context in Nowak *et al.*, [Nature (London) **428**, 646 (2004)] defines a promising standard model of evolutionary game theory in finite populations for which analytical results are accessible. In this paper, we derive the stationary distribution of the Moran process population dynamics for arbitrary 2×2 games for the finite-size case. We show that a nonvanishing background fitness can be transformed to the vanishing case by rescaling the payoff matrix. In contrast to the common approach to mimic finite-size fluctuations by Gaussian distributed noise, the finite-size fluctuations can deviate significantly from a Gaussian distribution.

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Theoretical studies of coevolutionary dynamics usually assume infinite populations, as the replicator dynamics [1,2] or the Lotka-Volterra equations [3,4]. The limit of infinite populations leading to deterministic differential equations is an idealization motivated mainly by mathematical convenience. Only in a few cases will the population be large enough to justify the assumption of infinite populations.

In finite populations, crucial differences can appear. Population states that cannot be invaded by a small fraction of mutants in infinite population, so-called evolutionary stable strategies [1], can be invaded by a single mutant [5]. In addition, a certain inherent stochasticity is always present in finite populations. In multipopulation interactions, such fluctuations can possibly be exploited [6]. In this paper, we quantify the inherent fluctuations arising from finite populations. As a starting point, we investigate the classical Moran process [7] that was recently transferred to frequency dependent selection [5,8]. In a Moran process, in each time step one agent is replicated and one agent is eliminated. Thus the total size of the population is strictly conserved. This process can be considered as a standard model for game dynamics in finite populations. Although a strictly fixed population size will be fulfilled only in systems with hard resource limitations, e.g., a fixed number of academic positions, it is a widely common default, especially in spatial games [9–13]. From a systematic point of view, the dynamics within this process and the nature of the fluctuations have to be understood before a generalization to variable population sizes on solid grounds is possible.

In [14] we have shown that the Moran process introduced in [5] can be derived as a mean-field approximation of the finite population game dynamics. In mean-field theories of evolutionary game theory [15–18] not only the spatial degrees of freedom are neglected; but the limit of infinite populations also implies a transition from a stochastic system to a deterministic equation of motion. While the average effect of mutations can often be lumped in a deterministic term [15,21], different ways to incorporate external stochasticity have been proposed, e.g., by a Langevin term of Gaussian distributed noise [6,19,20] or stochastic payoffs [22]. Consequently, one could also approximate the intrinsic noise of the finite system by Gaussian noise reintroduced into the continuum equations. But a *priori* it is not clear, in which situation this approximation is justified. Especially in small populations, the inherent stochasticity may significantly exceed any external noise. In a finite-round Prisoner's Dilemma game, the broadness of the distribution of cooperators recently was found to promote cooperation [23]. Further, the distribution decay of fluctuations is known to be of substantial impact both in genetic evolutionary dynamics [24] and in evolutionary optimization [25].

To clarify the nature of inherent fluctuations of evolutionary dynamics in a Moran process is the scope of this paper. We quantify the deviations from the mean value by explicitely calculating the stationary distribution of strategies for general 2×2 games and provide a transformation for the case of nonvanishing background fitness. The process is illustrated with two qualitatively representative kinds of games, and the exact solution, also for the more realistic situation of a nonvanishing background fitness, is provided.

Moran evolution dynamics in 2×2 *games*. We consider a finite population of N agents of two different types, A and B, interacting in a game with the payoff matrix

$$P=\begin{pmatrix} a & b \\ c & d \end{pmatrix}. \tag{1}$$

Each agent interacts with a certain number of randomly chosen partners. The A individual s obtains the fitness

$$\pi_s^A = 1 - w + w\frac{n_s^A a + n_s^B b}{n_s^A + n_s^B}, \tag{2}$$

where $n_s^A (n_s^B)$ is the number of interactions with A (B) individuals. $0 \leqslant w \leqslant 1$ measures the contribution of the game to the fitness, $1-w$ is the background fitness. An equivalent equation holds for B agents. Occasionally, the payoff of a

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randomly chosen individual s is compared with the payoff of another randomly chosen agent, u. With probability $\pi_s/(\pi_s+\pi_u)$, a copy of agent s replaces agent u. With probability $\pi_u/(\pi_s+\pi_u)$, agent s is replaced by a copy of u. The probability that an agent reproduces is hence proportional to its payoff. The payoff depends on the type of the individual and on the kind of its interactions. This approach is frequently used in simulations of multiagent systems [26–29], genetic algorithms [30,31], and evolutionary game theory [16].

The averaged dynamics of this model can be computed from a mean-field theory [14]. If every agent interacts with a representative sample of the population, the average payoff of A and B individuals will be, respectively,

$$\pi^A(i) = 1 - w + w\frac{a(i-1) + b(N-i)}{N-1},$$

$$\pi^B(i) = 1 - w + w\frac{ci + d(N-1-i)}{N-1}, \tag{3}$$

where i is the number of A individuals. We explicitly excluded self-interactions. An individual is selected for reproduction with a probability proportional to its payoff, as described above. It replaces an individual that is chosen at random. This reduces the process to a Moran process [7], which was recently transfered to a game theoretic context [5,8]. The corresponding mean-field dynamics is given by a Markov process with the transition probabilities [14]

$$T_{i\to i+1} = \frac{\pi^A(i)i}{\pi^A(i)i + \pi^B(i)(N-i)}\frac{N-i}{N},$$

$$T_{i\to i-1} = \frac{\pi^B(i)(N-i)}{\pi^A(i)i + \pi^B(i)(N-i)}\frac{i}{N},$$

$$T_{i\to i} = 1 - T_{i\to i+1} - T_{i\to i-1}. \tag{4}$$

All other transition probabilities are zero. The states $i=0$ and $i=N$ are absorbing, while the remaining states are transient. Conveniently, a small mutation can be introduced to allow for an escape from the absorbing states [32].

The general case of nonvanishing background fitness. For a nonvanishing background fitness $1-w>0$ the transition properties obtained directly from Eqs. (3) and (4) become quite lengthy. A more elegant way is to rescale the payoff matrix of a given 2×2 game according to

$$\begin{pmatrix} a' & b' \\ c' & d' \end{pmatrix} = \begin{pmatrix} 1+(a-1)w & 1+(b-1)w \\ 1+(c-1)w & 1+(d-1)w \end{pmatrix}. \tag{5}$$

With this rescaled payoff matrix, a vanishing background fitness can be assumed in (3) without loss of generality.

Fluctuations around the average strategy. In order to quantify the deviations from the average strategy of the system, we compute the stationary distribution P_i for this system. We assume a small mutation probability μ. For $\mu \ll 1$, mutations affect the system only in the states that are absorbing for $\mu=0$. In this case, the strategy distribution is generated only by the inherent stochasticity of the finite population. The stationary probability can be computed in the interior independently from the boundaries, the correct normalization can then be found analyzing the transitions from the boundaries to the interior, i.e., $P_0\mu = P_1 T_{1\to 0}$.

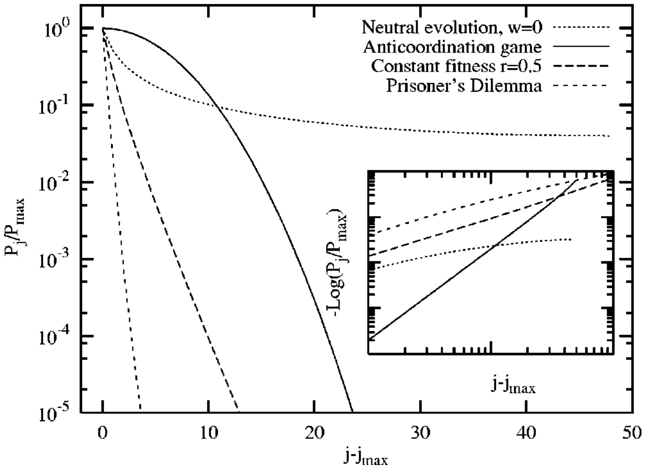

FIG. 1. Stationary probability distribution for different evolutionary dynamics depending on the distance to the maximum ($N=100$). For comparison, also the slow decay for neutral evolution is shown. The decay of the distribution can be fitted by a stretched exponential $\exp(-bx^\gamma)$ with $\gamma=2.06$ (anticoordination game), $\gamma=0.87$ (constant fitness), and $\gamma=0.63$ (Prisoner's Dilemma). The inset shows the same data where both axes are logarithmized, thus stretched exponentials appear as straight lines. The decay deviates significantly from a Gaussian distribution for constant fitness and Prisoner's Dilemma, corresponding to a random motion in an anharmonic potential.

Let us first consider the *neutral evolution* limit of $w=0$, where the fitness is constant and independent of the type. The payoffs are $\pi^A(i)=\pi^B(i)=1$. This implies

$$T_{i\to i+1} = T_{i\to i-1} = \frac{i(N-i)}{N^2}. \tag{6}$$

From $P_i T_{i\to i+1} = P_{i+1} T_{i+1\to i}$ we find in equilibrium for $0<i<N$,

$$P_i \propto \frac{1}{(N-i)i}, \tag{7}$$

which has a minimum at $i=N/2$. The equilibrium distribution arises from a neutral evolution of two types, as known from population genetics [33].

Constant fitness. The simplest case for $w>0$ is the case of constant fitness, i.e., $a=b<c=d=1$. The evolutionary dynamics drifts towards the type B, which has higher fitness. We find for the stationary probability distribution $(0<i<N-1)$,

$$\frac{P_{i+1}}{P_i} = r\frac{r(i+1) + N - i - 1}{ri + N - i}\frac{i}{i+1}\frac{N-i}{N-i-1}, \tag{8}$$

where $r=1-w+wa<1$. Far from the borders (at $i=0$, N), P_{i+1}/P_i converges to r implying an exponential decay of the stationary probability distribution.

Internal Nash equilibrium. For frequency dependent fitness and $w>0$, the game can have an internal Nash equilib-

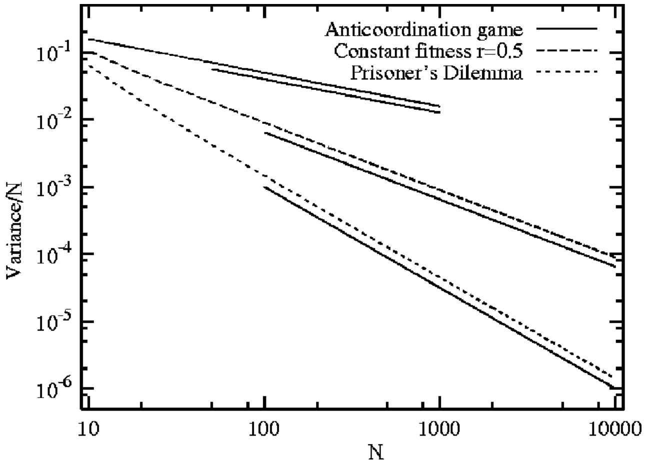

FIG. 2. Scaling of the variance, normalized by N, of the finite-size fluctuations for anticoordination game (slope $-1/2$), constant fitness (slope -1), and Prisoner's dilemma (slope $-3/2$). For neutral evolution (not shown) the variance increases faster than N.

rium or an equilibrium in one of the absorbing states.

As a simple example with an internal Nash equilibrium we choose a simple "anticoordination" game with $w=1$,

$$P = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}. \tag{9}$$

For the transition probabilities, we find

$$T_{i\to i+1} = \frac{N-i}{2N},$$

$$T_{i\to i-1} = \frac{i}{2N}, \tag{10}$$

which describes a random walk with a drift towards the deterministic fixed point $i=N/2$. In equilibrium, we have $P_i T_{i\to i+1} = P_{i+1} T_{i+1\to i}$ for every i, which leads to

$$P_{i+1} = P_0 \prod_{j=0}^{i} \frac{N-j}{j+1} = P_0 \binom{N}{i+1}, \tag{11}$$

where P_0 is determined by normalization. P_i is a binomial distribution around the equilibrium of the replicator dynamics at $i=N/2$, $P_i = 2^{-N}\binom{N}{i}$.

Prisoner's Dilemma: Nash equilibrium at the border. The Prisoner's Dilemma [34] is a standard model, where mutual cooperation leads to the highest payoff in the iterated game. It is motivated by the situation where two prisoners can reduce their time in prison by witnessing the other's guilt ("defect"). On the other hand, if both "cooperate" and refrain from blaming the other, both receive a reduction of punishment. This is described with parameters fulfilling $c > a > d > b$; the dilemma situation originates from the temptation $c > a$, defection yields a higher payoff if the opponent cooperates. In its standard parameters, the Prisoner's Dilemma is defined by the payoff matrix

$$P = \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix}, \tag{12}$$

which has a Nash equilibrium for mutual defection, i.e., $i=0$. As $b=0$, also the state $i=1$ is absorbing for $w=1$ (two cooperators are needed to promote cooperation). Thus a small mutation rate μ has to be assumed also for $T_{1\to 2}$. Alternatively, one could assume $w<1$. The transition probabilities are given by

$$T_{i\to i+1} = \frac{3i-3}{-i^2-2i+3iN+N(N-1)} \frac{i(N-i)}{N},$$

$$T_{i\to i-1} = \frac{4i+N-1}{-i^2-2i+3iN+N(N-1)} \frac{i(N-i)}{N}. \tag{13}$$

From this, a closed form of the probability distribution can be derived, (see below for a derivation with arbitrary payoff matrix). A comparison between different stationary distributions is shown in Fig. 1. The finite-size scaling of the variance is shown for the same cases in Fig. 2.

Stationary distribution for an arbitrary payoff matrix. For the ratio of the transition probabilities between i and $i+1$ we find with $w=1$, cf. Eq. (4),

$$\begin{aligned} \frac{T_{i\to i+1}}{T_{i+1\to i}} &= \frac{\pi^A(i)}{i\pi^A(i)+(N-i)\pi^B(i)} \frac{(i+1)\pi^A(i+1)+(N-i-1)\pi^B(i+1)}{\pi^B(i+1)} \frac{i(N-i)}{(i+1)(N-i-1)} \\ &= \frac{a(i-1)+b(N-i)}{c(i+1)+d(N-i-2)} \frac{i(N-i)[(i+1)^2(a-b-c+d)+(i+1)(-a+bN+cN+d-2dN)+N(N-1)d]}{(i+1)(N-i-1)[i^2(a-b-c+d)+i(-a+bN+cN+d-2dN)+N(N-1)d]} \\ &= \frac{a-b}{c-d} \frac{i-N_5}{i-N_6} \frac{i(N-i)}{(i+1)(N-i-1)} \frac{(i-N_1)(i-N_3)}{(i-N_2)(i-N_4)}. \end{aligned} \tag{14}$$

Here $N_1 \cdots N_4$ are the roots of the quadratic expressions in i and $N_5 = (a-bN)/(a-b)$, $N_6 = [c+d(N-2)]/(d-c)$. We have excluded the special cases $a-b=0$, $c-d=0$ discussed above in (8) and $(a-b)/(c-d)=1$, where some factors do not depend on i and part of the expression simplifies. For $N-1 > k \geq j > 1$, the density of the stationary state can be solved explicitly giving rising factorials (Pochhammer symbols), or equivalently, quotients of gamma functions,

$$\frac{P_k}{P_j} = \prod_{i=j}^{k-1} \frac{T_{i\to i+1}}{T_{i+1\to i}} = \left(\frac{a-b}{c-d}\right)^{k-j} \frac{j(N-j)}{k(N-k)} \frac{\Gamma(k-N_5)\Gamma(j-N_6)\Gamma(k-N_1)\Gamma(j-N_2)\Gamma(k-N_3)\Gamma(j-N_4)}{\Gamma(j-N_5)\Gamma(k-N_6)\Gamma(j-N_1)\Gamma(k-N_2)\Gamma(j-N_3)\Gamma(k-N_4)}, \tag{15}$$

which yields, after calculating P_N/P_{N-1} and P_1/P_0 explicitly, and after normalization, the total density of the stationary state. Equations (5) and (15) cover the general case of 2×2 games including nonvanishing background fitness. The previously discussed examples are included as special cases.

To conclude, the distribution of the fluctuations around a Nash equilibrium can be nontrivially broadened in realistic models of evolutionary game theory. We analyzed the effect of internal noise stemming from the inherent evolutionary update fluctuations in a finite population. In general, internal noise and externally imposed stochastic forces can follow qualitatively different distributions. In our paper, we concentrated on the important case of a Moran process, which can be considered as a standard model of evolutionary game dynamics in finite populations. For the Moran process, the effect of the finite size of the population can be accessed directly. Neglecting external noise, we have shown that the stationary distribution of the Moran process of evolutionary 2×2 games can be calculated analytically and yields different decay tails of the distributions. Depending on the payoff matrix and the location of the Nash equilibrium, the finite-size fluctuations may deviate significantly from a Gaussian distribution.

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