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 $2 \times 2$ 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 few cases the population will 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 [2]. In addition, a certain inherent stochasticity is always present in finite populations. In multipopulation interactions, such fluctuations can possibly be exploited [5]. 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 [8,9]. In a Moran process, in each time step one agent is replaced by a randomly chosen partner. The individual with the highest fitness is transferred to the next generation. By doing so, the population state is updated and the process is repeated. 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, it is known to be of substantial impact both in genetic evolution [23] and in evolutionary optimization [24].

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 explicitly calculating the stationary distribution of strategies for general $2 \times 2$ 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 $2 \times 2$ games.— We consider a finite population of $N$ agents of two different types, A and B, interacting in a game with the payoff matrix

$$P = \begin{pmatrix} a & b \\ c & d \end{pmatrix},$$

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

$$\pi^A_s = 1 - w + w \frac{n^A_a + n^B_b}{n^A_s + n^B_s},$$

where $n^A_s$ ($n^B_s$) is the number of interactions with A (B) individuals. $0 \leq w \leq 1$ 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 randomly chosen individual is compared with the payoff of another randomly chosen agent. With probability $\pi_u/(\pi_u + \pi_v)$, a copy of agent $s$ replaces agent $u$. With probability $\pi_u/(\pi_u + \pi_v)$, 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, 27, 28, 29], genetic algorithms [31, 32], 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,

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

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

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. The payoff matrix, $u$, is replaced by a copy of $u$. The probability that an agent reproduces is hence proportional to its payoff. The payoff of another randomly chosen agent is compared with the payoff of another randomly chosen agent. With probability $\pi_u/(\pi_u + \pi_v)$, a copy of agent $s$ replaces agent $u$. With probability $\pi_u/(\pi_u + \pi_v)$, 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, 27, 28, 29], genetic algorithms [31, 32], and evolutionary game theory [16].

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

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

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. The payoff of another randomly chosen agent is compared with the payoff of another randomly chosen agent. With probability $\pi_u/(\pi_u + \pi_v)$, a copy of agent $s$ replaces agent $u$. With probability $\pi_u/(\pi_u + \pi_v)$, 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, 27, 28, 29], genetic algorithms [31, 32], and evolutionary game theory [16].

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special cases

− size fluctuations for anticoordination game (slope on $i$ than $N$.

For neutral evolution (not shown) the variance increases faster than $N$.

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

$$T_{i \rightarrow i+1} = \frac{N - i}{2N} \tag{10}$$

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

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

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

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 is a standard model, where mutual cooperation leads to 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

$$P = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}. \tag{12}$$

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

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

$$T_{i \rightarrow i-1} = \frac{4i + N - 1}{-i^2 - 2i + 3iN + N(N-1)} \frac{i(N-i)}{N}. \tag{14}$$

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. (11),

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

$$= \frac{a(i+1) + b(N-i) - i(N-i)(i+1)^2(a-b-c+d) + (i+1)(-a+bN+cN+d-2dN) + N(N-1)d}{c(i+1) + d(N-i-2) (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} \frac{i(N-i)}{(i+1)(N-i-1)} \frac{i-N_4}{i-N_5} \frac{(i-N_5)(i-N_3)}{(i-N_2)(i-N_4)}.$$

Here $N_1 \cdots N_4$ are the roots of the quadratic expressions in $i$ and $N_5 = \frac{a-bN}{a-b}$, $N_6 = \frac{c+d(N-2)}{d-c}$. We have excluded the special cases $a-b = 0$, $c-d = 0$ discussed above in (5) 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,
\[
\frac{P_k}{P_j} = \prod_{i=j}^{k-1} \frac{T_{i\rightarrow i+1}}{T_{i+1 \rightarrow i+2}} = \left(\frac{a-b}{c-d}\right)^{k-j} \frac{j(N-j)}{k(N-k)} \frac{\Gamma(k-N_3)\Gamma(j-N_6)\Gamma(k-N_1)\Gamma(j-N_2)\Gamma(k-N_3)\Gamma(j-N_4)}{\Gamma(j-N_3)\Gamma(k-N_6)\Gamma(j-N_1)\Gamma(k-N_2)\Gamma(j-N_2)\Gamma(k-N_4)}
\]

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 16 and 17 cover the general case of 2\(\times\)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\(\times\)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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