Evolutionary game dynamics describes the evolution of phenotypical traits [1,2]. Evolution is based on birth and death processes, which are most adequately described by stochastic models [3]. Most such models study a fixed population size [4–8]. An important issue in biological systems is the loss of phenotypical traits [1,2]. Evolution is based on birth and death fluctuations [24]. To capture the extinction portrait in reaction extinction properties because it is not valid for large fluctuations. We investigate the most probable extinction trajectory under such fluctuations by mapping a stochastic evolutionary model to a problem of classical mechanics using the Wentzel-Kramers-Brillouin (WKB) approximation. Our results show that more abundant types in a coexistence may be more likely to go extinct first, in good agreement with previous results. The distance between the coexistence and extinction points is not a good predictor of extinction either. Instead, the WKB method correctly predicts the type going extinct first.

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Extinction dynamics from metastable coexistences in an evolutionary game

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Deterministic evolutionary game dynamics can lead to stable coexistences of different types. Stochasticity, however, drives the loss of such coexistences. This extinction is usually accompanied by population size fluctuations. We investigate the most probable extinction trajectory under such fluctuations by mapping a stochastic evolutionary model to a problem of classical mechanics using the Wentzel-Kramers-Brillouin (WKB) approximation. Our results show that more abundant types in a coexistence may be more likely to go extinct first, in good agreement with previous results. The distance between the coexistence and extinction points is not a good predictor of extinction either. Instead, the WKB method correctly predicts the type going extinct first.

Evolutionary game dynamics describes the evolution of phenotypical traits [1,2]. Evolution is based on birth and death processes, which are most adequately described by stochastic models [3]. Most such models study a fixed population size [4–8]. An important issue in biological systems is the loss of types [9,10]. Consequently, persistence of phenotypes and the probability that an invader takes over a population have been explored. However, there is still a lack of understanding of the effect of population size fluctuations on extinction dynamics, especially for an evolutionary game with population size fluctuations.

There is increasing evidence that fluctuations of population sizes caused by ecological processes can also affect evolutionary dynamics [11–20]. Accordingly, understanding the effect of population size fluctuations becomes more important. Stochastic models as reaction systems with accompanying population size fluctuations have a long tradition in mathematical biology [21]. Recently, a stochastic model [22,23] was proposed that directly connects evolutionary game dynamics to reaction rules by designing rates of death from interaction as a function of game payoffs. We examine the persistence of types in this system under the influence of population size changes. When population size is bounded, the population eventually goes to extinction due to stochasticity. Before extinction of the whole population, the population loses individual types. We examine single-type extinction from the coexistence of two types.

Though the associated noise can be well approximated by the Fokker-Planck approach, normally it fails to capture extinction properties because it is not valid for large fluctuations [24]. To capture the extinction portrait in reaction systems, we use the method developed in [24–27]. With this powerful tool, extinction dynamics for various systems has been described [26–36]. This method reformulates a master equation into a Hamilton-Jacobi equation form by using the Wentzel-Kramers-Brillouin (WKB) approximation. An effective Hamiltonian that arises from the reformulated equation yields equations of motion and eventually the most probable extinction trajectory and its properties.

Typically in our model, one type is more likely to go extinct first, while the other becomes more abundant. Interestingly, in some cases a more abundant type in the coexistence is more likely to go extinct first, consistent with known results for the extinction dynamics in two-type populations [34]. We use the same birth process, but a slightly different death process compared to [34]. The main differences are the death process from competition and the interpretation of its rate. We interpret these terms as arising from game interactions, which are naturally connected to the competitive Lokta-Volterra dynamics in the deterministic limit [37,38]. For our system, we show that the distance from the coexistence to the extinction point is a better predictor for the type going extinct first than the abundances in the coexistence. However, only the WKB method gives the right answer for the first extinction type.

Following [22], we consider three processes that trigger population size changes: reproduction, spontaneous death, and death from competition. We focus on two types, $X$ and $Y$. The reproduction process can be described by the reactions

$$X \rightarrow X + X, \quad Y \rightarrow Y + Y,$$

with corresponding constant rate $\lambda_b$. Individuals die at a constant rate $\lambda_d(< \lambda_b)$,

$$X \rightarrow 0, \quad Y \rightarrow 0.$$

Due to the limitation of resources, individuals compete with each other. There are four such reactions resulting in the death of one individual each,

$$X + X \rightarrow X, \quad Y + Y \rightarrow Y,$$

$$X + Y \rightarrow X, \quad X + Y \rightarrow Y,$$

where the corresponding rates are determined by interactions between individuals. Inspired by evolutionary games, where the outcome of interactions between individuals is represented by the payoff matrix $A$,

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

we assume four positive rate parameters: $a$, $b$, $c$, and $d$,

$$\lambda_{XX\rightarrow X} = \frac{1}{aM}, \quad \lambda_{YY\rightarrow Y} = \frac{1}{dM},$$

$$\lambda_{XY\rightarrow X} = \frac{1}{cM}, \quad \lambda_{Xy\rightarrow Y} = \frac{1}{bM}.$$

The element $A_{ij}$ of the payoff matrix captures the payoff of the type $i$ from interaction with type $j$. The individual with a smaller payoff dies with higher probability in a direct competition [22]. The parameter $M$ controls total population size in the
and thus the population grows at a constant rate, \( \lambda_b \). This rate is much smaller than \( \lambda_d \). The background color indicates the magnitude of change (a darker color represents faster changes). Dots are the fixed points of Eq. (6) \((n, m) = (0, 0), (0, d\lambda M), (a\lambda M, 0), \) and \( \lambda M / b \approx [a(c(b - d), bd(c - a))]. \) The fixed point \((0, 0)\) is unstable, and two fixed points on the axes are saddles. For \( a < c \) and \( d < b \), the fixed point where \( X \) and \( Y \) coexist is stable (see Fig. 1) in the deterministic model.

In the stochastic model, all reactions occur with constant rates with a Poisson process. Hence, abundances fluctuate around the coexistence point (Fig. 1) until eventually one type goes extinct. The discrepancy between deterministic dynamics and stochastic dynamics arises from the consecutive random events in each realization of the process. We are interested in the most probable extinction trajectory starting from a coexistence state that is stable in the deterministic case \((a < c \) and \( d < b)\). Stochastic systems are described by the probability \( P_{n,m}(t) \) that the system is in state \((n, m)\) at time \( t \). The probability \( P_{n,m}(t) \) changes according to the master equation,

\[
\frac{dP_{n,m}}{dt} = \lambda_b [(n + 1)P_{n+1,m} - n(n - 1)P_{n,m}] + \lambda_d [(m + 1)P_{n,m+1} - (n + m)P_{n,m}]
\]

where the effective Hamiltonian operator \( \hat{H} \) can be expressed by ladder operators for \( P_{n,m} \) \((\hat{a}^\dagger P_{n,m} = P_{n+1,m} \) and \( \hat{b}^\dagger P_{n,m} = P_{n,m+1}) \). The probabilities become zero for all negative indices. Note that \( P_{0,0}(\infty) = 1 \), because extinction of both types is the final absorbing state in the stochastic model with a bounded population size. The initial distribution quickly converges to the quasisteady state, which is peaked at the coexistence point. Subsequently, the probability leaks slowly into the absorbing states. Moreover, extinction from the coexistence to a single-type population occurs much faster than the collapse of the whole population. Since we focus on \( 1 \ll t \ll t_e \), where \( t_e \) is a characteristic time for the collapse of the whole population, the probability leakage from the coexistence can be expressed with the characteristic time scale \( \tau \),

\[
P_{n,m} = e^{-t/\tau} \psi_{n,m} \quad \text{for} \quad n, m > 0,
\]

where \( \psi_{n,m} \) is an eigenstate of \( \hat{H} \) with eigenvalue \(-1/\tau\), corresponding to the quasistationary distribution.

Next, we obtain an effective Hamiltonian using the WKB method. We start from the Eikonal ansatz with leading order,

\[
\psi_{n,m} = e^{-MS(x,y)},
\]

where \( S \) is a smooth function of the relative abundances \( x = n/M \) and \( y = m/M \). For large \( M \), the Taylor expansion \( S(x \pm 1/M, y) \approx S(x, y) \pm 1/M \partial_x S \) gives

\[
\hat{a}^\dagger P_{n,m} = P_{n+1,m} \approx e^{-t/\tau} e^{-MS(x + 1/M, y)} \approx P_{n,m} e^{\pm \partial_x S}.
\]

Inserting Eq. (8) into Eq. (7), we obtain in the leading order for large \( M \),

\[
1/\tau + M H(x, y, p_x, p_y) = 0,
\]

with the effective Hamiltonian \( H \) given by

\[
H = \lambda_b [x(e^{p_x} - 1) + y(e^{p_y} - 1)] + \lambda_d [x(e^{-p_x} - 1) + y(e^{-p_y} - 1)] + \frac{1}{a} [xx^2(e^{-p_x} - 1) + \frac{1}{b} [xy(e^{p_x} - 1)] + \frac{1}{c} [xy(e^{-p_x} - 1) + \frac{1}{d} [y^2(e^{-p_x} - 1)].
\]

where \( p_x = \partial_x S \) and \( p_y = \partial_y S \). It may seem surprising that the reaction system can be mapped into a Hamiltonian system. In fact, the situation that is described by the master Eq. (7) can be interpreted as a particle in a potential well with noise. As shown in Fig. 1(b), the speed of changing abundances depends on \( n \) and \( m \). If the abundances change fast, we can interpret this as the existence of a large potential gradient. Fast changes of abundances give short waiting time, implying small \( P_{n,m} \). As a result, we can imagine a potential well with a minimum at the
coexistence point. This potential landscape captures features of the probability \( P_{x,m} \). Therefore, the momenta are related to the gradient of probabilities \( P_{x,m} \).\(^{[24]} \)

Because the first extinction time \( \tau \) is exponentially large in \( M \)\(^{[33,34]} \), we can set \( 1/\tau \) to zero for large \( M \). Therefore, the most probable extinction trajectories are captured by the effective Hamiltonian with zero energy. From the derivatives of the effective Hamiltonian, we derive the equations of motion in the phase space\(^{[39]} \),

\[
\dot{x} = x(\lambda_b e^{\rho_x} - \lambda_d e^{\rho_y}), \quad \dot{y} = y(\lambda_b e^{\rho_y} - \lambda_d e^{\rho_x}), \quad \dot{\rho}_x = \lambda_b (1 - e^{\rho_x}) + \lambda_d (1 - e^{\rho_y}), \\
\dot{\rho}_y = \lambda_b (1 - e^{\rho_y}) + \lambda_d (1 - e^{\rho_x}),
\]

\(^{(13)}\)

For \( \rho_x = \rho_y = 0 \), the deterministic equations are recovered. Since we are interested in the trajectory to extinction from the coexistence quasisteady state, the system initially starts from the coexistence with \( (x, y, \rho_x, \rho_y) = \left(\frac{\dot{\lambda}_b}{\dot{\lambda}_d}, \frac{\dot{\lambda}_d}{\dot{\lambda}_b}, -\dot{\lambda}_b, -\dot{\lambda}_d\right) \). There are eight fixed points of Eq. (13) related to extinction states \( (x = 0, y = 0) \) with zero energy. Three of these points describe deterministic trajectories and are thus of no further interest here. Two of the points describe single populations. One fixed point describes extinction of both species almost at the same time, which occurs with negligible probability. Hence, we focus on the two extinction fixed points, \( (a, 0) \) and \( (0, b) \), \( \dot{x}, \dot{y} \leq 0 \), while momenta are set to the final values at the extinction point. Note that we need a long time sequence to capture extinction trajectories\(^{[26]} \). After setting the values, momenta are updated using the equations of motion backward in time for fixed coordinates. Using these updated momenta, coordinates are updated forward in time. As momenta may diverge during numerical integration, we update each momentum in turn. After many iterations, the trajectory remains unchanged.

To address which type is more likely to go extinct first, we compute the transition rates from the coexistence to the single-type populations. As \( M \) increases, the effective potential becomes steeper and extinction takes longer. As a result, almost every extinction occurs along the most probable trajectories for large \( M \). Hence, the extinction rates \( R_x \) and \( R_y \) of species \( X \) and \( Y \) can be calculated from

\[
R_x \propto \exp(-MS[T_x]), \quad R_y \propto \exp(-MS[T_y]).
\]

\(^{(14)}\)
is not determined by these factors—instead, it depends on the trajectory from quasistationary coexistence to extinction with zero energy. A compelling example is given in Fig. 3, where extinction happens, perhaps counterintuitively, most likely to the more abundant type, which is farther away from the extinction state.

We consider a stochastic model in which pairwise interactions are reflected in death rates. For coexistence games, two types coexist in populations for a long time. Due to stochasticity, however, extinctions always occur after a sufficiently long time. Our focus is the most probable trajectory to extinction from the coexistence of two types. By mapping our reaction system to the effective Hamiltonian system using the WKB method, we extract the rare event information, and we get the most probable trajectory to extinction. Mainly, we analyze which type is more likely to go extinct first between two types. Because of the pathway to extinction, there is a tendency that the type closer to its quasisteady state of the single-type population is more likely to go to extinction first. However, there is a region where distance fails to predict the first extinction type—only the WKB method makes a correct prediction in this case.

We apply a Hamiltonian framework to evolutionary game dynamics. Although reaction systems have already been used for describing biological populations [21,34] and ecological systems [41], our model can be directly applied within stochastic evolutionary game dynamics, leading to results that are out of reach without this approach.

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