Extinction Rate Fragility in Population Dynamics

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Population extinction is of central interest for population dynamics. It may occur from a large rare fluctuation. We find that, in contrast to related large-fluctuation effects like noise-induced interstate switching, quite generally extinction rates in multipopulation systems display fragility, where the height of the effective barrier to be overcome in the fluctuation depends on the system parameters nonanalytically. We show that one of the best-known models of epidemiology, the susceptible-infectious-susceptible model, is fragile to total population fluctuations.

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Extinction of a population is one of the major problems of population dynamics [1,2]. It may be caused by regular changes in the environment, but may also result from a large rare fluctuation. Such fluctuation can be an unlikely sequence of elementary birth-death events, for example, and then extinction can be visualized as overcoming an effective entropic barrier. Much work has been done on extinction for various models of population dynamics, and several fluctuation mechanisms have been explored [3–13].

A system of interacting populations can be thought of as a many-body system far from thermal equilibrium. Fluctuation-induced population extinction is closely related to a diverse group of other nonequilibrium physical phenomena that involve large fluctuations. A well-known example is switching between coexisting states, which is intensively studied in modulated Josephson junctions, nano- and micromechanical resonators, and nanomagnets [14–19]. Because large fluctuations are rare, the rates of extinction and switching are small. One can write the rate as $W_e \propto \exp(-\mathcal{Q})$ with $\mathcal{Q} \gg 1$. The rate exponent $\mathcal{Q}$ is of primary interest for theory and experiment. In systems close to thermal equilibrium it is known at least in principle, $\mathcal{Q} = R/k_BT$, where R is the free energy barrier and T is temperature [20], but finding it for nonequilibrium systems, and, in particular, for populations, remains a major challenge.

In this Letter we develop an optimal-fluctuation theory of extinction in multipopulation systems. We show that extinction displays a qualitative feature that does not generally occur in interstate switching. The extinction rate can be fragile. A small perturbation of the system can lead to an abrupt change of the rate exponent $\mathcal{Q}$. If the perturbation is proportional to a parameter μ, the value of $\mathcal{Q}$ for $\mu \to 0$ is smaller than for $\mu = 0$. Respectively, the extinction rate W_e is exponentially larger than for $\mu = 0$. Remarkably, the mean-field dynamics remains unchanged. We find a general condition for the onset of fragility and illustrate the effect with the broadly used susceptible-infectious-susceptible (SIS) model of epidemiology [2].

We consider extinction in a spatially uniform system of coupled populations (species). The system state is characterized by a vector $\mathbf{X}$ with integer components $X_1, X_2, \ldots$ equal to the size of different populations. The formulation applies also to autocatalytic stirred chemical and incapsulated biochemical systems including those discussed in the context of the origins of life [21], with $\mathbf{X}$ enumerating different molecular species.

Along with $\mathbf{X}$ it is convenient to consider a quasicontinuous vector $\mathbf{x} = \mathbf{X}/N$ where N is the characteristic total population N. We assume $N \gg 1$, in which case typical fluctuations in the system are small. If we disregard fluctuations, motion in $\mathbf{x}$ space is described by dynamical equations [2] [cf. Eq. (3) below], and quite generally the system has a stable state $\mathbf{x}_A$, which it approaches over a relaxation time t_r. For simplicity, we assume that the state $\mathbf{x}_A$ is stationary, although the results immediately extend to the case of periodic $\mathbf{x}_A$.

Extinction occurs as a result of a large fluctuation away from $\mathbf{x}_A$, in which one of the populations (labeled with an E) disappears, $x_E = 0$. If the extinction rate is $W_e \ll t_r^{-1}$, the probability of such a fluctuation is independent of time for $t_r \ll t \ll 1/W_e$. In analogy to the problem of switching and following Kramers [20], the rate W_e can be related to the probability current into the extinction hyperplane $x_E = 0$. This extinction current is also independent of time for $t_r \ll t \ll 1/W_e$.

The distinction from the switching problem comes from the facts that (i) the extinct population usually does not emerge again, i.e., fluctuations do not remove the system from the hyperplane $x_E = 0$, and (ii) the population size is non-negative. As a consequence, the extinction current terminates at $x_E = 0$. The population probability distribution accumulates in the hyperplane $x_E = 0$, whereas for $x_E > 0$ it is quasistationary for $t_r \ll t \ll 1/W_e$. These singular features have no analog in switching and ultimately lead to fragility of extinction rates.

We describe the multipopulation system by a master equation for the probability $\rho(\mathbf{X})$ to be in state $\mathbf{X}$,

$$\dot{\rho}(\mathbf{X}) = \sum_r [W(\mathbf{X}-\mathbf{r};\mathbf{r})\rho(\mathbf{X}-\mathbf{r}) - W(\mathbf{X};\mathbf{r})\rho(\mathbf{X})]. \tag{1}$$

Here, $W(\mathbf{X};\mathbf{r})$ is the rate of an elementary transition $\mathbf{X} \to \mathbf{X}+\mathbf{r}$ in which the populations change by $\mathbf{r} = (r_1, r_2, \ldots)$. The condition that the system does not leave the extinction hyperplane is

$$W(\mathbf{X};\mathbf{r}) = 0 \quad \text{for } X_E = 0, \qquad r_E \neq 0. \tag{2}$$

If fluctuations can be disregarded, from Eq. (1) we obtain for average scaled populations $\bar{\mathbf{x}}$ a mean-field equation,

$$\dot{\bar{\mathbf{x}}} = \sum_{\mathbf{r}} \mathbf{r} w(\bar{\mathbf{x}};\mathbf{r}), \tag{3}$$

where $w(\mathbf{x};\mathbf{r}) = W(N\mathbf{x};\mathbf{r})/N$ is a transition rate per individual. We assume that, along with an asymptotically stable solution $\mathbf{x}_A$, Eq. (3) has a stationary solution $\mathbf{x}_\mathcal{S}$ that lies in the extinction hyperplane $x_E = 0$ and is asymptotically stable with respect to $x_{i\neq E}$ but unstable for x_E. This is the extinction state, the system is ultimately brought there by fluctuations for $t \gtrsim W_e^{-1}$. For $t_r \ll t \ll W_e^{-1}$ the distribution $\rho(\mathbf{X})$ peaks at $\mathbf{X}_A = N\mathbf{x}_A$ if the system was close to $\mathbf{x}_A$ for $t = 0$.

The exponent $\mathcal{Q}$ in the extinction rate W_e can be found either by solving the mean first passage time problem for reaching extinction [3,4,7] or by calculating the small-X_E tail of $\rho(\mathbf{X})$, which determines the extinction current [9,10,12,13]. In both methods one looks for the optimal (most probable) fluctuation that leads to extinction, and the results coincide. Here we will study the quasistationary distribution. In the standard eikonal approximation, to leading order in $N^{-1} \ll 1$, Eq. (1) is transformed into equations

$$\rho(\mathbf{X}) = \exp[-Ns(\mathbf{x})], \qquad \dot{s} = -H(\mathbf{x}, \partial_\mathbf{x} s),$$
$$H(\mathbf{x},\mathbf{p}) = \sum_{\mathbf{r}} w(\mathbf{x};\mathbf{r})[\exp(\mathbf{pr}) - 1]. \tag{4}$$

We took into account that, typically, $|\mathbf{r}| \ll N$, and $W(\mathbf{X};\mathbf{r})$ depends on $\mathbf{X}$ polynomially, whereas ρ is exponential in $\mathbf{X}$. Therefore we expanded $\rho(\mathbf{X}+\mathbf{r}) \approx \rho(\mathbf{X})\exp(-\mathbf{r}\partial_\mathbf{x} s)$ and replaced $w(\mathbf{x}-\mathbf{r}/N;\mathbf{r}) \to w(\mathbf{x};\mathbf{r})$.

Equation (4) reduces the problem to classical dynamics of an auxiliary Hamiltonian system with equations of motion

$$\dot{\mathbf{x}} = \sum_{\mathbf{r}} \mathbf{r} w(\mathbf{x};\mathbf{r}) e^{\mathbf{pr}}, \qquad \dot{\mathbf{p}} = -\sum_{\mathbf{r}} \partial_\mathbf{x} w(\mathbf{x};\mathbf{r})(e^{\mathbf{pr}} - 1). \tag{5}$$

The distribution $\rho(\mathbf{X})$ is determined by the mechanical action of the auxiliary system $s(\mathbf{x})$. In the quasistationary regime $\dot{s} = 0$; i.e., $H = 0$ in Eq. (4). We notice that $\sum_\mathbf{r} w(\mathbf{x};\mathbf{r})\mathbf{r}\partial_\mathbf{x} s \leq 0$ for $H(\mathbf{x}, \partial_\mathbf{x} s) = 0$, and therefore $s(\mathbf{x})$ decreases if $\mathbf{x}$ shifts along a mean-field trajectory (3) (unless $\partial_\mathbf{x} s = \mathbf{0}$) [22,23]. Since the mean-field trajectories go to $\mathbf{x}_A$, action $s(\mathbf{x})$ is minimal at $\mathbf{x}_A$. Respectively, $\rho(\mathbf{X})$ is maximal for $\mathbf{X}_A = N\mathbf{x}_A$, as expected on physical grounds.

In the spirit of the method of optimal fluctuation [13,24–26], the extinction rate exponent is determined by the minimum of $s(\mathbf{x})$ in the extinction hyperplane. From the above arguments, the minimum is reached at the extinction state $\mathbf{x}_\mathcal{S}$. Therefore

$$\mathcal{Q} = N[s(\mathbf{x}_\mathcal{S}) - s(\mathbf{x}_A)] = N\int_{-\infty}^{\infty} dt \mathbf{p}\dot{\mathbf{x}}. \tag{6}$$

Equation (6) corresponds to the intuitive picture in which the most probable fluctuation leading to extinction starts from the stable state and brings the system to the extinction state. The respective optimal Hamiltonian trajectory, Eq. (5), goes from the Hamiltonian fixed point ($\mathbf{x}_A$, $\mathbf{p} = \mathbf{0}$) to the fixed point ($\mathbf{x}_\mathcal{S}$, $\mathbf{p}_\mathcal{S}$).

We now find the final momentum $\mathbf{p}_\mathcal{S}$. Since action $s(\mathbf{x})$ is minimal with respect to $x_{i\neq E}$ at $\mathbf{x}_\mathcal{S}$, $(p_\mathcal{S})_{i\neq E} = 0$. To find $(p_\mathcal{S})_E$ we note that if $w(\mathbf{x};\mathbf{r})$ smoothly vary with $\mathbf{x}$, as we presume, then from $H = 0$ for any small $|\mathbf{x} - \mathbf{x}_\mathcal{S}|$

$$\sum_{\mathbf{r}} w(\mathbf{x};\mathbf{r})\{\exp[(p_\mathcal{S})_E r_E] - 1\} = 0. \tag{7}$$

Equation (7) has a trivial solution $(p_\mathcal{S})_E = 0$. However, there are no Hamiltonian trajectories that would go from ($\mathbf{x}_A$, $\mathbf{p} = \mathbf{0}$) to ($\mathbf{x}_\mathcal{S}$, $\mathbf{p} = \mathbf{0}$). Indeed, using Eq. (3) one can show that trajectories that go to ($\mathbf{x}_\mathcal{S}$, $\mathbf{p} = \mathbf{0}$) lie on the manifold $x_E = 0$, $p_{i\neq E} = 0$ which does not contain ($\mathbf{x}_A$, $\mathbf{p} = \mathbf{0}$). This is a major difference from interstate switching in reaction systems, where the optimal trajectory goes to the saddle point and $\mathbf{p} = \mathbf{0}$ there [23].

The trajectory that gives the extinction exponent $\mathcal{Q}$ generically goes to ($\mathbf{x}_\mathcal{S}$, $\mathbf{p}_\mathcal{S}$) with $(p_\mathcal{S})_E \neq 0$. This was found earlier for specific models [7,9,12]. Near $\mathbf{x}_\mathcal{S}$ the quasistationary distribution ρ as a function of $\mathbf{x}$ steeply varies with x_E, $\rho \propto \exp[-N(p_\mathcal{S})_E x_E]$, but it is smooth with respect to $x_{i\neq E}$.

The above picture does not apply in some nongeneric yet important cases where population fluctuations are effectively constrained. For example, the system can have conservation laws so that variables x_E and $x_{i\neq E}$ are not independent, at least near $x_E = 0$. To gain intuition into the resulting change of the formulation and its dramatic effect on $\mathcal{Q}$ we will consider the problem of disease extinction in the SIS model. In this model the numbers of susceptible (S) and infected (I) individuals X_1 and X_2 change because of birth and death, with rates

$$W(\mathbf{X};(1,0)) = N\mu, \qquad W(\mathbf{X};(-1,0)) = \mu X_1,$$
$$W(\mathbf{X};(0,-1)) = \mu X_2, \tag{8}$$

and because of infection on contact and recovery, with those recovered immediately becoming susceptible [2]. The corresponding rates are

$$W(\mathbf{X};(-1,1)) = \beta X_1X_2/N, \qquad W(\mathbf{X};(1,-1)) = \varkappa X_2. \tag{9}$$

Disease extinction occurs where $X_2 \equiv X_E = 0$. For the infection reproductive rate $R_0 = \beta/(\mu + \varkappa) > 1$, the system has an endemic equilibrium $\mathbf{x}_A = \mathbf{X}_A/N = (R_0^{-1}, 1 - R_0^{-1})$. It coexists with the disease-free stationary state $\mathbf{x}_S = \mathbf{X}_S/N = (1, 0)$.

Much work has been done on the SIS model in the limit $\mu = 0$ where the total population does not fluctuate, $x_1 + x_2 = 1$ [2–4,6,10]. Here, the Hamiltonian system (5) has effectively 1 degree of freedom. A direct substitution shows that on the optimal trajectory $p_2 = 0$ and $p_1 = \ln(\beta x_1/\varkappa)$, which gives

$$\mathcal{Q}_{\mu=0} = N(\ln R_0 - 1 + R_0^{-1}). \tag{10}$$

In this case $(p_S)_E \equiv (p_S)_2 = 0$, whereas $(p_S)_1 = \ln R_0$. This is in contradiction with the general result for optimal extinction paths.

We now allow the total population to fluctuate, albeit slowly; i.e., we assume that the characteristic birth-death rate μ is nonzero but small, $\mu \ll \varkappa$. At the same time we assume that it is not exponentially small, $\mu \gg W_e$, so that the distribution is quasistationary. Then the Hamiltonian trajectory for extinction consists of three almost straight sections $T1$, $T2$, $T3$ shown in Fig. 1(b). Sections $T1$, $T3$ correspond to slow motion characterized by time μ^{-1}, whereas motion in section $T2$ is fast, with typical time $(\beta - \varkappa)^{-1}$. A direct substitution shows that motion in section $T1$ is described by equations

$$p_1 = p_2 = \ln[1 + e^{\mu(t-t_1)}], \qquad x_2 = e^{p_2} - R_0^{-1}, \tag{11}$$

while $|x_1 - R_0^{-1}| \lesssim \mu$ [t_1 in Eq. (11) is arbitrary].

Motion in section $T2$ can be described by setting $\mu = 0$ in Eqs. (5), (8), and (9). This gives

$$p_2 = \ln C, \qquad p_1 = \ln(CR_0x_1), \qquad x_1 + x_2 = C, \tag{12}$$

where $x_1 = (Cf + \varkappa)/(\beta + f)$ with $f = \exp[(\beta C - \varkappa) \times (t - t_2)]$ with arbitrary C, t_2. If we set $C = R_0^{-1/2}$, then $x_1 \to R_0^{-1/2}$, $x_2 \to 0$, and $p_1 \to 0$ with increasing $t - t_2$, and the trajectory approaches section $T3$ where

$$p_2 = -\ln(R_0x_1), \qquad x_1 = 1 - \exp[-\mu(t - t_3)], \tag{13}$$

while $|p_1|, x_2 \to 0$ for $\mu \to 0$. The solutions (11) and (12) match if at the end of section $T1$ and at the beginning of section $T2$ we have $p_1 = p_2 = -(\ln R_0)/2$.

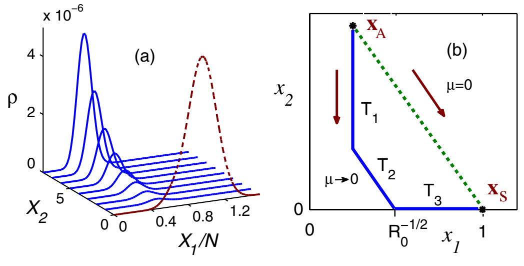

FIG. 1 (color online). (a) A snapshot of the probability $\rho(\mathbf{X})$ near the extinction plane $X_2 = 0$ for the SIS model; ρ is quasicontinuous in X_1/N. The data of simulations refer to $\mu t = 9$, $R_0 = 4$, $\mu' \equiv \mu/(\mu + \varkappa) = 0.1$. For $t = 0$ the system was at $\mathbf{X}_A$, and the total number of particles was $N = 50$. (b) Asymptotic optimal Hamiltonian trajectories for extinction for $\mu \to 0$ (solid line) and $\mu = 0$ (dashed line).

At the end of section $T3$ we have $\mathbf{x} \to \mathbf{x}_S = (1, 0)$ and $\mathbf{p} \to \mathbf{p}_S = (0, -\ln R_0)$, as expected from the analysis of a generic extinction problem. The extinction rate exponent is

$$\mathcal{Q}_{\mu\to 0} = N(R_0^{1/2} - 1)^2/R_0. \tag{14}$$

This value, which is obtained in the limit $\mu \to 0$, is smaller than $\mathcal{Q}$ for $\mu = 0$ [cf. Eq. (10)]. The discontinuity with respect to μ shows the fragility of the result obtained by disregarding fluctuations of the total population.

In Fig. 2 we compare the values of $\mathcal{Q}$ obtained for $\mu = 0$ and for $\mu \to 0$. Also shown are the results of numerical simulations obtained for $\mu = 0$ and for small nonzero μ. They are in excellent agreement with the analytical results. As illustrated in Fig. 1(a), for $W_et \ll 1$ the probability distribution accumulates (linearly in time) near $x_1 = X_1/N = 1$ in the extinction plane, $X_2 = 0$. Away from the extinction plane, for discrete $X_2 \geq 1$, the distribution is quasistationary. For small X_2 it has a peak along x_1 at $\approx R_0^{-1/2}$ where the asymptotic extinction path approaches the plane $x_2 = 0$.

The fragility in the SIS model occurs because the perturbation violates conservation of the total population in the unperturbed system. We now show that, generally in the extinction problem, a perturbation theory breaks down if in the unperturbed system population fluctuations in the extinction hyperplane are effectively constrained and the perturbation lifts the constraint. Formally, because of the constraint on fluctuations, on the optimal extinction trajectory $(p_S)_{i\neq E} \neq 0$ at least for one i.

A perturbation changes the elementary transition rates in Eq. (1), $W(\mathbf{X};\mathbf{r}) \to W(\mathbf{X};\mathbf{r}) + \mu W^{(1)}(\mathbf{X};\mathbf{r})$, with $\mu \ll 1$

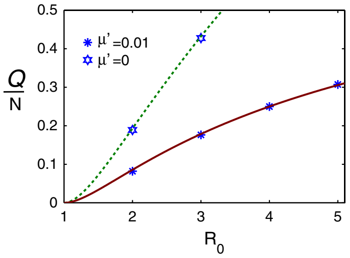

FIG. 2 (color online). The switching exponent $\mathcal{Q}$ for the SIS model of epidemics. The solid and dashed lines show the results for $\mu \to 0$ [Eq. (14)] and $\mu = 0$ [Eq. (10)], respectively. The data points are obtained from the numerical solution of the master equation for the total initial populations $N = 50$ and $N = 100$, which made it possible to directly extract the exponent $\mathcal{Q}$.

for a small perturbation. The eikonal Hamiltonian [Eq. (4)] is, respectively, modified, $H \rightarrow H + \mu H^{(1)}$. To first order in μ the resulting change of the extinction exponent $\mathcal{Q}^{(1)}$ can be calculated along the trajectory $\mathbf{x}(t)$, $\mathbf{p}(t)$ of the unperturbed Hamiltonian [27],

$$\begin{aligned} \mathcal{Q}^{(1)} &= -N\mu \int_{-\infty}^{\infty} dt H^{(1)}(\mathbf{x}(t), \mathbf{p}(t)), \\ H^{(1)}(\mathbf{x}, \mathbf{p}) &= \sum_{\mathbf{r}} w^{(1)}(\mathbf{x}; \mathbf{r})[\exp(\mathbf{pr}) - 1]. \end{aligned} \tag{15}$$

Because $\mathbf{p}(t)$ exponentially decays for $t \rightarrow -\infty$ (where $\mathbf{x} \rightarrow \mathbf{x}_A$), the integral over time in Eq. (15) does not diverge at the lower limit.

We assume that the perturbation weakly changes the mean-field dynamics and does not destroy the extinction state. Then $W^{(1)}$ must satisfy condition (2), and $w^{(1)} = W^{(1)}/N \rightarrow 0$ for $x_E \rightarrow 0$ and $r_E \neq 0$. Since on the optimal extinction trajectory $x_E(t)$ exponentially decays for $t \rightarrow \infty$, the terms with $r_E \neq 0$ in $H^{(1)}$ also decay, and the integral of these terms converges on the upper limit. However, if at the endpoint of the trajectory $p_{i \neq E} \neq 0$ for some i, and because generally

$$w^{(1)}(\mathbf{x}_S; \mathbf{r}) \neq 0 \quad \text{for } r_E = 0, \tag{16}$$

the term $H^{(1)}$ remains nonzero for $t \rightarrow \infty$ and overall the integral Eq. (15) diverges.

The divergence of $\mathcal{Q}^{(1)}$ means that the optimal extinction trajectory changes nonperturbatively, as does also the rate exponent $\mathcal{Q}$; i.e., the extinction rate is fragile with respect to the corresponding perturbation. Population fluctuations in the SIS model provide an example of such a perturbation, as seen from the comparison of Eqs. (8) and (16). We note that, in the problem of switching of reaction systems, the perturbation theory does not diverge, since on the optimal path $\mathbf{p} \rightarrow \mathbf{0}$ for $t \rightarrow \infty$ [23] and integral Eq. (15) remains finite.

In conclusion, we have considered fluctuation-induced extinction. We showed how to find the logarithm of the extinction rate $\mathcal{Q}$ for a system of coupled populations and how the formulation differs from the seemingly similar and extensively studied problem of the rate of interstate switching in nonequilibrium systems. An important consequence of this difference is the extinction rate fragility. A small perturbation ($\propto \mu$) can change the rate exponentially strongly; $\mathcal{Q}$ for $\mu \rightarrow 0$ differs from $\mathcal{Q}$ for $\mu = 0$. The fragility is related to the discontinuity of the quasistationary extinction current. A general condition for the onset of fragility is derived. Explicit results are obtained for the broadly used SIS model of epidemiology. It is shown that the model is fragile to fluctuations of the total population. This limits the applicability of the disease extinction rates obtained with the standard one-variable SIS model, where such fluctuations are disregarded. The analytical results are quantitatively confirmed by simulations.

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