PHYSICAL REVIEW LETTERS **122,** 108102 (2019)

Phase Diagram for Logistic Systems under Bounded Stochasticity

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(Received 12 September 2018; published 15 March 2019)

Extinction is the ultimate absorbing state of any stochastic birth-death process; hence, the time to extinction is an important characteristic of any natural population. Here we consider logistic and logisticlike systems under the combined effect of demographic and bounded environmental stochasticity. Three phases are identified: an inactive phase where the mean time to extinction T increases logarithmically with the initial population size, an active phase where T grows exponentially with the carrying capacity N, and a temporal Griffiths phase, with a power-law relationship between T and N. The system supports an exponential phase only when the noise is bounded, in which case the continuum (diffusion) approximation breaks down within the Griffiths phase. This breakdown is associated with a crossover between qualitatively different survival statistics and decline modes. To study the power-law phase we present a new WKB scheme, which is applicable both in the diffusive and in the nondiffusive regime.

DOI: 10.1103/PhysRevLett.122.108102

Noise and fluctuations are ubiquitous features of living systems. In particular, the reproductive success of individuals is affected by many random factors. Some of these factors, like the local density of nutrients or accidental encounter with predators, act on the level of a single individual. Others, like fluctuations in temperature and precipitation rates, affect many individuals coherently. The corresponding theory distinguishes between *demographic* stochasticity (shot noise), i.e., those aspects of noise that influence individuals in an uncorrelated manner, and *environmental* stochasticity, which acts on entire populations [1,2].

For a population of size n, demographic noise yields $\mathcal{O}(\sqrt{n})$ abundance fluctuations, while environmental stochasticity leads to $\mathcal{O}(n)$ variations. Accordingly, for large populations, environmental stochasticity is the dominant mechanism. A few recent analyses of empirical studies confirm this prediction [3–6]. However, the demographic noise controls the low-density states and must be taken into account for calculations of extinction times or fixation probabilities. Consequently, the study of models that combine deterministic effects, temporal environmental stochasticity, and demographic noise received considerable attention during the last years [7–13].

Almost any model of population dynamics includes two basic ingredients: exponential growth and resource competition. In particular, in the famous logistic equation

$$\frac{dn}{dt} = r_0 n - \beta n^2, \tag{1}$$

r_0 is the basic reproductive number (low-density growth rate) and the β-term reflects a density-dependent crowding effect, so the per-capita growth rate declines linearly with n.

A wide variety of similar models include the θ-logistic equation (where the growth rate declines like n^θ), ceiling models (growth rate is kept fixed, but the population cannot grow above a given carrying capacity), Ricker dynamics, and so on. All these models support a transcritical bifurcation at $r_0 = 0$: when $r_0 < 0$ the extinction point $n = 0$ is stable, while for $r_0 > 0$ it becomes unstable and the system admits a finite population stable state at n^* [e.g., $n^* = r_0/\beta$ for the logistic equation (1)].

Since the actual number of individuals in a population is always an integer, equations like (1) can only be interpreted as the deterministic limit of an underlying stochastic process. For any process with demographic noise, the empty state $n = 0$ is the only absorbing state, so each population must reach extinction in the long run. Under purely demographic noise, the bifurcation point separates two qualitatively different behaviors of the mean time to extinction T. When $r_0 < 0$, the extinction time is logarithmic in the initial population size, while for $r_0 > 0$ the time to extinction grows exponentially with n^* [2,14–16].

To understand the lifetime of empirical populations, one would like to study a logistic system under the influence of both demographic and environmental stochasticity. This problem was considered by a few authors [1,17–19] for the case where the strength of the environmental fluctuations is *unbounded*, e.g., when the state of the environment undergoes an Ornstein-Uhlenbeck process. In such a case, there are always rare periods of time in which the net growth rate is negative, and (as we shall see below) these periods dominate the asymptotic behavior of the extinction times. As a result, the system admits only two phases: an inactive (logarithmic) phase for $r_0 < 0$ and a temporal Griffiths phase [20], where T scales like a power law with n^*, for $r_0 > 0$.

Here we would like to consider another scenario, a system under *bounded* environmental variations. Since the noise is bounded, for large enough r_0 the growth rate is

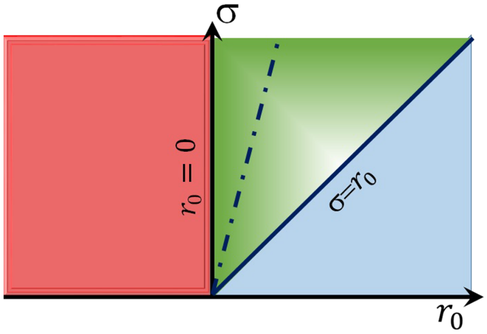

FIG. 1. A phase diagram for a logistic system under bounded stochasticity, presented in the $r_0 - \sigma$ plane. In the inactive phase ($r_0 < 0$, red), the time to extinction scales like $\ln n$ where N plays no role. In the active phase $r_0 > \sigma$ (blue), the extinction time grows exponentially with N. Under pure demographic noise (along the $\sigma = 0$ axis), the transition occurs at $r_0 = 0$. When $\sigma > 0$, the logarithmic and the exponential phases are separated by a finite power-law region (temporal Griffiths phase, green). The dashed-dotted line indicates the failure of the continuum (diffusive) approximation and the crossover from soft to sharp decline.

always positive, so the system allows for three phases: logarithmic, power law (temporal Griffiths phase), and exponential (see Fig. 1). This insight allows one to identify the failure of the standard analytic tool, the diffusion (continuum) approximation, inside the temporal Griffiths phase. To overcome that, we provide an alternative WKB analysis that is valid all over the power-law region. Our analysis reveals a crossover between two qualitatively different extinction dynamics. This distinction, in turn, may be relevant to several key concepts in the modern theory of viability and coexistence [21–23]. These connections will be expanded upon towards the end of the Letter.

Our model system, chosen to facilitate the numerical calculations, involves two "species" (types, alleles) competition in a finite community with one-sided mutation [24]. In this system, the number of individuals N is always fixed, where n of them belong to species A and $N - n$ to species B. At each elementary step, two individuals are chosen at random for a duel, the loser dies, and the winner produces a single offspring [25]. The possible outcomes of the duels (expressions above arrows represent probabilities) are

$$\begin{aligned} &B+B\xrightarrow{1}2B \qquad A+A\xrightarrow{1-\nu}2A \qquad A+A\xrightarrow{\nu}A+B \\ &A+B\xrightarrow{1-P_A}2B \qquad A+B\xrightarrow{P_A(1-\nu)}2A \qquad A+B\xrightarrow{\nu P_A}A+B, \end{aligned} \tag{2}$$

where ν is the chance of a mutation event, in which the offspring of an A is a B.

An A individual wins an interspecific duel with probability $P_A = 1/2 + s(t)/4$, where $s(t) = s_0 + \eta(t)$ and $\eta(t)$ is a zero-mean random process. Following [12] we consider a system with dichotomous (telegraphic) environmental noise, so $\eta = \pm\sigma$ (see [26] and Supplemental Material, Sec. II [27]). After each elementary step η may switch (from $\pm\sigma$ to $\mp\sigma$) with probability $1/N\tau$, so the persistence time of the environment is taken from a geometric distribution with mean τ generations, where a generation is defined as N elementary duels.

As required, this process supports an absorbing attractive fixed point at $n^* = 0$ when $r \equiv s(t) - \nu < 0$ [more accurately, the condition is $\tilde{s} \equiv s(1 - \nu/2) < \nu$]. In what follows, we neglect this tiny factor and use s for $\tilde{s}$ and an active attractive fixed point at $n^* = N[1 - \nu/s(t)]$ when $r > 0$.

Using the procedure described in [10], one may derive a discrete backward Kolmogorov equation (BKE) for this stochastic process. The BKE may be solved numerically, by inverting the corresponding matrix, to obtain $T(n)$, the mean time to extinction for a system with n A-type individuals. The mean is taken over both histories and the initial state of the system (plus or minus σ). The numerical results presented below were obtained from the BKE using this technique. For large-N systems we implemented, instead of direct inversion of a matrix, a transfer matrix approach that allows us to increase the numerical accuracy.

If $N \gg 1$ and the diffusion approximation is applicable, n may be replaced by the fraction $x = n/N$ and $n \pm 1$ by $x \pm 1/N$. Expanding all the relevant quantities to second order in $1/N$ and using the dominant balance analysis presented in [10], it can be shown that $T(x)$ satisfies

$$\left(s_0-\frac{\nu}{1-x}+g(1-2x)\right)\frac{\partial T(x)}{\partial x}+\left(\frac{1}{N}+gx(1-x)\right)\frac{\partial^2 T(x)}{\partial x^2} = -\frac{1}{x(1-x)}, \qquad T(0)=0, \qquad \left.\frac{\partial T(x)}{\partial x}\right|_{x=1}=\frac{1}{\nu}, \tag{3}$$

where $g \equiv \sigma^2\tau/2$ is the diffusion constant along the log-abundance axis. We solved Eq. (3) separately in the inner region $x \ll 1$ and in the outer region $x \gg 1/Ng$, using asymptotic matching to obtain, for $1/Ng \ll x \ll 1$,

$$T(x) = ([Ng]^{r_0/g} - x^{-r_0/g})\frac{\Gamma(r_0/g)}{r_0}\left(\frac{g}{\nu}\right)^{r_0/g} - \frac{\ln Ngx}{r_0}. \tag{4}$$

Accordingly, the time to extinction is logarithmic in $n = Nx$ when r_0 is negative (red region in Fig. 1). If r_0 is positive, the mean lifetime, for *any* initial conditions, grows like $N^{r_0/g}$, since the chance of a small population (even a single individual) to grow and reach the carrying capacity is N independent. These results are in complete agreement with former studies [1,17–19] of different logisticlike models, indicating the universality of the large-N behavior for all the systems that support a transcritical bifurcation.

However, for bounded noise, this continuum approximation must fail somewhere inside the power-law phase. Equation (4) suggests a power-law dependence of T on N for any $r_0 > 0$, but this cannot be the case for $r_0 > \sigma$

(light blue region of Fig. 1), where even in the pure $(-\sigma)$ state the time to extinction grows exponentially with N [2,14–16] and occasional jumps to the $+\sigma$ state can only increase stability.

To study the system when the continuum approximation fails, we adopt a version of the WKB analyses presented and discussed in [16,28]. We shall neglect the demographic noise and replace it (as in [1,12,29]) by an absorbing boundary condition at $x = 1/N$. The abundance dynamics is given by $\dot{x} = (r_0 \pm \sigma)x - \beta x^2$, where the environment stays in the same state (plus or minus σ) for $\tilde{\tau}$ generations and then switches, with probability $1/2$, to the other state (minus or plus σ).

Under this dynamics, if the system reaches x at certain time t, then one time increment before, at $t - \tilde{\tau}$, it was either at $x_+(x)$ or at $x_-(x)$. Equivalently, one may define $y \equiv \ln x$ and $y_\pm \equiv \ln x_\pm$. The probability to find the system at the log-density y at time t, $P(y,t)$, satisfies the master equation

$$\frac{dP(y,t)}{dt} = \frac{1}{2}[-2P(y) + P(y_+) + P(y_-)]. \tag{5}$$

At long times, $P(y,t)$ converges to its quasisteady state for which $dP/dt \approx 0$ [16]. Given $P(y)$, the N dependence of the mean time to extinction is inversely proportional to the rate of extinction, which is the probability to find the system with less than one individual $(0 < x < 1/N)$, so

$$\text{rate} \sim \int_{-\infty}^{-\ln N} P(y)dy. \tag{6}$$

When x is vanishingly small $x_\pm \approx x e^{-\tilde{\tau}(r_0 \pm \sigma)}$. Accordingly, in the extinction zone, the quasisteady state satisfies

$$P(y - \tilde{\tau}[r_0 + \sigma]) + P(y - \tilde{\tau}[r_0 - \sigma]) = 2P(y). \tag{7}$$

Instead of expanding $P(y_\pm)$ to second order in $\tilde{\tau}$ (this yields the continuum Fokker-Planck equation and the power law of the continuum limit), we assume that $P(y) = e^{S(y)}$ and implement the continuum approximation for S, replacing $S(y + \Delta y)$ by $S(y) + \Delta y S'(y)$, so $S'(y)$ is obtained as a solution of the transcendental equation

$$\exp(-\tilde{\tau} r_0 S') \cosh(\tilde{\tau}\sigma S') = 1. \tag{8}$$

This equation does not depend on y, so $S' = q$ and $S \sim qy$, where q is some constant. Accordingly, $P \sim \exp(qy)$ and $\text{rate} \sim N^{-q}$, so the time to extinction behaves like $T \sim N^q$.

In the limit $r_0 \ll \sigma$ one expects $q \ll 1$. In that case, both $q\tilde{\tau}r_0$ and $q\tilde{\tau}\sigma$ are small numbers and Eq. (8) yields

$$q = \frac{2r_0}{(\sigma^2 + r_0^2)\tilde{\tau}} \approx \frac{2r_0}{\sigma^2 \tilde{\tau}}, \tag{9}$$

where the last approximation reflects a self-consistency requirement for $q\tilde{\tau}r_0 \ll 1$. On the other hand, if $q\tilde{\tau}\sigma$ is large,

$$q = \frac{\ln 2}{\tilde{\tau}(\sigma - r_0)}. \tag{10}$$

The case (9) corresponds to the regime where the continuum approximation holds. In that case, the typical extinction trajectory is a random walk excursion in the log-abundance space (see below). Since the variance of M random numbers, picked independently from an exponential distribution with mean τ and alternating signs, is equal to the variance of the sum of M random steps of length $\tilde{\tau}$, $\tilde{\tau} = \tau$ and

$$T \sim N^{r_0/g}, \tag{11}$$

in agreement with the large-N asymptotics of (4).

In the other extreme (10), extinction occurs due to a (rare) long sequence of bad years, so $\tilde{\tau}$ must be compared with the tail of the corresponding exponential distribution, in which case $\tilde{\tau} = \tau \ln 2$; hence, in this regime

$$T \sim N^{1/[\tau(\sigma - r_0)]}. \tag{12}$$

This result indicates that the diffusion approximation indeed fails (the result depends on τ and σ separately, not on g) and that the power diverges when $r_0 \to \sigma$, i.e., at the transition between the temporal Griffiths phase and the exponential phase.

Beside these limits, the transcendental equation (8) has to be solved numerically. In Fig. 2 these numerical solutions are compared with the results obtained from a numerical solution of the BKE and with the asymptotic expressions (11) and (12).

As discussed in length in the Supplemental Material, Sec. I [27], our WKB analysis provides more evidence for the universality of all logisticlike (transcritical) systems. The only features that were used to establish Eq. (8) are the existence of an upper bound and the linearity of the growth rate at small x.

In the Supplemental Material (Sec. III) [27], we also show that the qualitative features of the extinction process change along the power-law phase, together with the functional form of the survival probability function $Q(t)$ (the chance of the system to survive until t).

Deep inside the temporal Griffiths phase (and in the exponential phase), the system spent most of its time fluctuating around x^* (the point where the mean of $\dot{x}$ vanishes, when the average is taken over the two signs of σ). Extinction reflects a rare event, an improbable series of bad years, and/or excess deaths (see [30], Fig. 5). Accordingly, the decline time (roughly speaking, the duration of the last excursion from x^* to extinction) scales like $\ln N$ [1] and is negligible with respect to the lifetime T [see Fig. 3(b)]. In that "sharp decline" case, the system has no memory: during each segment of time, either the catastrophe occurs or not. Accordingly, $Q(t) \sim \exp(t/T)$, where T is the mean time to extinction calculated above. As discussed in the Supplemental Material [27], this

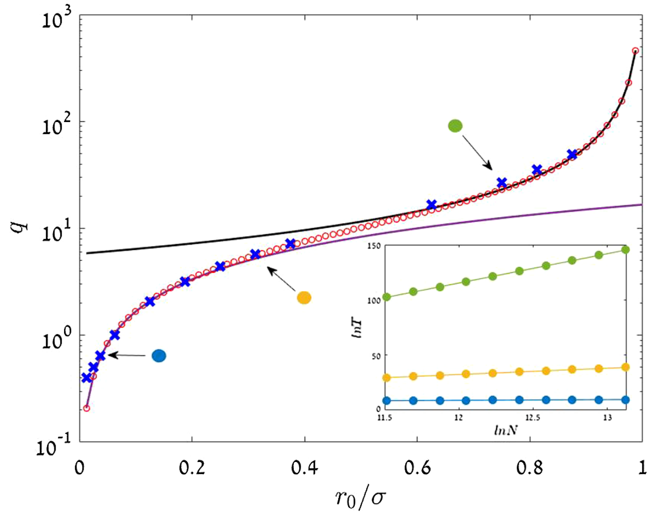

FIG. 2. In the temporal Griffiths phase $T \sim N^q$. The main figure shows q vs r_0/σ as obtained from the numerical solution of Eq. (8) (red open circles), in comparison with the asymptotic expressions for the diffusive regime [Eq. (11), purple line] and in the large-r_0 regime [Eq. (12), black line]. (Inset) Results for $T(N)$ as obtained from the numerical solution of the exact backward Kolmogorov equation for $r_0 = 0.003$ (blue circles), 0.025 (yellow), and 0.06 (green). By fitting these numerical results (full lines), one obtains the actual power q, and the outcomes are represented by blue Xs in the main figure (the Xs that correspond to the three specific cases depicted in the inset are marked by arrows). In general, the WKB predictions fit the numerical outcomes quite nicely, and the slight deviations in the low-r_0 region are due to the prefactors of the power law [in these cases, the numerical $T(N)$ graph fits perfectly the predictions of Eq. (4)]. All the results here were obtained for $\sigma = 0.08$, $\tau = 3/2, \nu = 0.04$.

behavior is associated with a gap in the spectrum of the corresponding Markov matrix.

In the diffusive regime, close to the extinction phase, the spectral gap closes down and the associated survival probability is $Q(t) \sim \exp(t/t_0)/t^{1/\rho}$, where ρ is related to the dispersion relation of the Markov matrix and T is proportional to t_0. In that case, the decline time is relatively long ["soft decline", Fig. 3(a)] and an excursion to extinction is a typical first passage trajectory of a random walker along the log-abundance axis.

Our results seems to be relevant to two important issues in population and community ecology: modern coexistence theory and the assessment of population viability.

Modern coexistence theory (MCT) has gained a lot of attention in recent years [22,23]. In MCT "coexistence" is declared if the steady-state probability distribution function is normalizable [21]. For the system considered here, close to zero $P \sim e^{qy} \sim x^{q-1}$, so the MCT persistence criteria is satisfied if $q > 0$, i.e., for any $r_0 > 0$.

However, the main factor that determines ecological stability and species turnover rates is the mean time to extinction. Given Eq. (6), one realizes that the coexistence criteria of MCT only guarantees that the time to extinction diverges with N, but this divergence may be as slow as N^ϵ for arbitrary small ϵ if $g = \epsilon r_0$. Accordingly, we believe that an instructive classification of populations' stability properties must use phase diagrams like Fig. 1, instead of being focused on (co)existence. In particular, for populations in the exponential phase, extinction risk is usually negligible, while in the sharp decline region extinction occurs due to rare events, so our predictive ability is quite limited. On the other hand, in the inactive and soft decline regions, extinction risk is high and is strongly related to the observed dynamics, so one may identify risk factors (like grazing or habitat loss) and try to avoid them.

Practically, in empirical studies of birds and plant populations, an initial abundance n_0 was measured and the survival probability Q was examined after a fixed time interval t [31,32]. If n_0 may be taken as a proxy for the carrying capacity, the results seem to indicate that these systems are in the power-law phase (see Supplemental

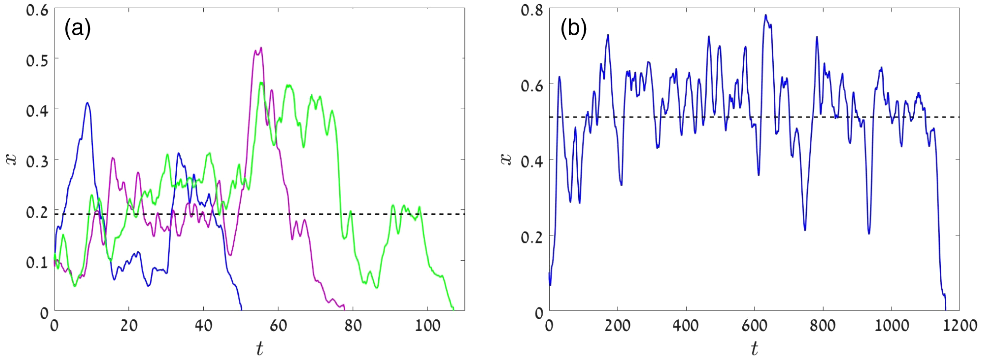

FIG. 3. Typical trajectories (frequency vs time) for a system with $\tau = 1$, $\sigma = 0.11$, and $\nu = 0.1$, where (a) $r_0 = 0.02$ and (b) $r_0 = 0.105$. The dashed line corresponds to x^*, the point where the mean (over environmental conditions) growth rate is zero. In (b) The population fluctuates most of its lifetime in a relatively narrow band around x^*, extinction happens due to the accumulation of rare sequences of bad years, and the decline time is logarithmic in N (sharp decline). As r_0 becomes smaller (a), the fluctuations are comparable with x^*; hence, the decline time becomes a finite fraction of the lifetime (soft decline).

Material, Sec. IV [27], where the empirical results are reproduced and analyzed). However, a single observation of n_0 cannot provide a reliable estimation of the carrying capacity in the soft decline regime. Large-scale empirical studies of $Q(t)$ (like those presented in [33,34]) suggest an exponentially truncated power law. If one likes to interpret these results as reflecting purely local dynamics under environmental stochasticity, it implies that the decline in these systems is indeed soft.

In spatially extended systems, the correlation length of environmental fluctuations plays an important role. When the linear size of the system is much smaller than the correlation length, temporal fluctuations are global. This case was examined recently in [35] and is expected to show similarities to the dynamics of a local population. On the other hand, when the correlation length is shorter than the population range, migration tends to average out the stochastic effects, so the effective strength of stochasticity decreases and T increases. Such an increase was reported in [34].

We acknowledge many helpful discussions with David Kessler. This research was supported by the ISF-NRF Singapore joint research program (Grant No. 2669/17).

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