

## How Colored Environmental Noise Affects Population Extinction

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Environmental noise can cause an exponential reduction in the mean time to extinction (MTE) of an isolated population. We study this effect on an example of a stochastic birth-death process with rates modulated by a colored (that is, correlated) Gaussian noise. A path integral formulation yields a transparent way of evaluating the MTE and finding the optimal realization of the environmental noise that determines the most probable path to extinction. The population-size dependence of the MTE changes from exponential in the absence of the environmental noise to a power law for a short-correlated noise and to no dependence for long-correlated noise. We also establish the validity domains of the white-noise limit and adiabatic limit.

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Extinction of a long-lived self-regulating population can occur as a large fluctuation resulting from the intrinsic discreteness of individuals and random nature of birth-death processes [1,2]. Extinction is a key negative factor in viability of small populations [3,4], whereas extinction of epidemic [3,5] is a favorable development. As a large fluctuation far from equilibrium, extinction is also of great interest to physics [1,2]. Population dynamics often occurs in time-varying environments. Understanding the impact of environmental noise on the mean time to extinction (MTE) of a population is both important [4] and interesting. Early models assumed that the environmental noise, which modulates the population birth-death rates, is delta-correlated in time [6,7]. More recently, numerous studies have focused on the effect of temporal autocorrelation, or color, of environmental noise on population extinction, see, e.g., Refs. [8]. Numerical simulations, performed by many population ecologists, provide only a partial insight into the complex and rich interplay between the nonlinear kinetics and intrinsic (demographic) stochasticity of the population on the one side and the magnitude and spectral and correlation properties of the environmental noise on the other.

In this Letter we formulate a theoretical framework for this problem by considering a prototypical example of a stochastic birth-death process with rates modulated by a positively correlated Gaussian noise with given magnitude and correlation time. We evaluate the MTE analytically and find that the qualitative and quantitative details of the exponential reduction of the MTE by the environmental noise are very sensitive to the noise color. It was discovered by Leigh [6,7] that white environmental noise changes the population-size dependence of the MTE from an exponential to a power-law with a large exponent. Here we show that noise color changes this exponent, reducing it at a fixed noise magnitude. For a long correlation time of the

environmental noise, where we develop an adiabatic theory, the MTE becomes independent of the population size for a strong enough noise. We also establish the validity domains of the white-noise limit and adiabatic limit.

The effect of the environmental noise on the MTE comes from special noise realizations which affect the birth and death rates in an optimal way. The optimization involves a statistical “cost” of a given reaction rate variation along with a “gain” due to a facilitated extinction. We find that the optimal realization of noise (ORN), which determines the most probable path to extinction, changes considerably with the noise correlation time. For a short-correlated noise the ORN has a form of a sudden “catastrophe”, reducing the reproduction rate, for a certain period of time, to a value which cannot sustain a steady population. For a long-correlated noise the ORN reduces the population size gradually. While not directly causing extinction, it makes a fatal demographic fluctuation much more probable. The ORNs in different intermediate regimes (depending on the rescaled noise magnitude and correlation time) can be found numerically.

To be specific, consider a continuous-time birth-death process of a population of  $n$  individuals with the birth rate  $\lambda_n$  and death rate  $\mu_n$  given by

$$\lambda_n = \frac{n}{2}(\mu + r - an), \quad \mu_n = \frac{n}{2}(\mu - r + an). \quad (1)$$

For time-independent rate constants  $\mu$ ,  $r$  and  $a$  (we assume  $r < \mu$ ), this is a symmetrized version of the logistic Verhulst model: a well-studied model of population dynamics, see, e.g., [9,10]. The terms linear in  $n$  describe the birth and death rates at small  $n$ , whereas the nonlinear terms describe, at  $a > 0$ , competition for resources which limits the exponential population growth. The pertinent rate equation  $\dot{n} = r\bar{n} - a\bar{n}^2$  predicts, at  $r > 0$ , a stable population of the average size  $\bar{n} = K \equiv r/a \gg 1$  which

sets in after the relaxation time  $t_r = 1/r$ . Demographic noise, however, makes this “stable” population metastable. The population actually goes extinct, as a large fluctuation ultimately brings it to the absorbing state  $n = 0$ . Large fluctuations are rare and therefore statistically independent. As a result, the long-time survival probability obeys Poisson’s law

$$\sum_{n=1}^{\infty} P_n(t) = 1 - P_0(t) = e^{-t/\tau_0}, \quad (2)$$

where  $P_n(t)$  is the probability to find  $n$  individuals at time  $t$ , and  $\tau_0$  is the MTE. It is a well-known result (that we will reproduce shortly) that  $\tau_0$  scales exponentially with  $K$ , see, e.g., [9,10]. In the limit of  $r \ll \mu$ , that we will be interested in, one obtains with exponential accuracy:

$$\tau_0 \propto \exp(rK/\mu), \quad (3)$$

where we have assumed  $rK/\mu \gg 1$ .

Environmental noise manifests itself as a time-modulation of the birth and death rates. We will assume a modulation of the parameter  $r$ :

$$r \rightarrow r(t) = r - \xi(t), \quad (4)$$

where  $\xi(t)$  is a “red” (positively correlated) Gaussian random process with zero mean, variance  $v \ll \mu^2$  and correlation time  $t_c$ . For convenience, we choose the Ornstein-Uhlenbeck noise defined by the correlator  $\langle \xi(t)\xi(t') \rangle = ve^{-|t-t'|/t_c}$ . The statistical weight of a given realization of this noise is  $\mathcal{P}[\xi(t)] \propto \exp\{-S[\xi(t)]\}$ , where

$$S[\xi(t)] = \frac{1}{4v} \int dt (t_c \dot{\xi}^2 + t_c^{-1} \xi^2). \quad (5)$$

The environmental noise does not change the Poisson character of the survival probability, Eq. (2). Unless the noise is too weak, however, it exponentially reduces the MTE. We found that the noise-reduced MTE  $\tau_\xi$  can be expressed in terms of the unperturbed MTE  $\tau_0$  and two dimensionless parameters: the rescaled noise variance  $V = vK/(r\mu)$  and the rescaled noise correlation time  $T = t_c/t_r = rt_c$ :

$$\ln \tau_\xi = F(V, T) \ln \tau_0, \quad (6)$$

where function  $F(V, T)$  describes different parameter regimes summarized in Fig. 1. Importantly, each of these regimes is also characterized by a different ORN which causes population extinction with the highest probability.

Our theory, which leads to Eq. (6), Fig. 1 and other results, starts from the master equation

$$\dot{P}_n = \lambda_{n-1}P_{n-1} - (\lambda_n + \mu_n)P_n + \mu_{n+1}P_{n+1}, \quad (7)$$

with the birth and death rates given by Eq. (1). One can show that, for  $K \gg 1$  and  $r \ll \mu$ , this master equation can be accurately approximated by the Fokker-Planck equation, derivable via the van Kampen system size expansion

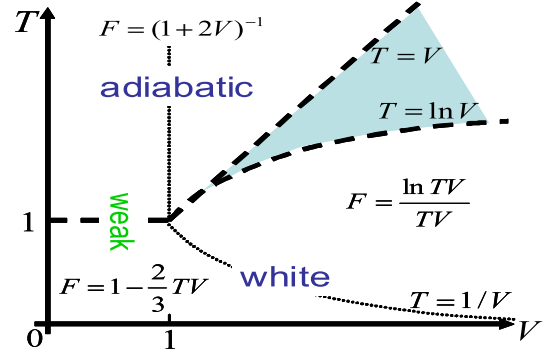


FIG. 1 (color online). Various regimes of extinction on the plane of rescaled parameters  $V$  and  $T$ . The dashed lines are schematic borders of the adiabatic, Eq. (16), and white-noise, Eq. (14) limits. The dotted line is the border of the weak-noise, Eq. (17), regime. The shaded area is a crossover region.

[1,2]. Switching to the continuous notation  $n \rightarrow q$ , one can write the Fokker-Planck equation as  $\hat{P} = \hat{H}P$ , with the linear differential operator

$$\hat{H}(q, \hat{p}) = \frac{\mu}{2} \hat{p}^2 q + \hat{p}(rq - aq^2). \quad (8)$$

Here  $\hat{p} = -\partial_q$  so that  $[q, \hat{p}] = 1$ . In the presence of environmental noise, see Eq. (4), one obtains the Hamiltonian  $\hat{H}_\xi(q, \hat{p}, t) = \hat{H}(q, \hat{p}) - \xi(t)\hat{p}q$ .

The evolution operator  $\hat{U}(q_f, t_f; q_i, t_i)$  of the Fokker-Planck equation can be represented as a path integral over time-dependent trajectories  $q(t)$  and  $p(t)$ . Below we specify the boundary conditions for such trajectories in the case of population extinction. Eventually the evolution operator must be averaged over realizations of the environmental noise, resulting in

$$\langle \hat{U} \rangle = \int \mathcal{D}\xi \mathcal{D}q \mathcal{D}p e^{-S[\xi] - \int dt [p\dot{q} - H(q, p) + \xi p q]}, \quad (9)$$

where  $p(t)$  and  $H(q, p)$  are understood as “classical” variables rather than operators.

Rare events in general, and population extinction in particular, are described by classical trajectories accumulating a large action (and therefore having exponentially small probabilities). For this reason the corresponding path integral can be evaluated via the saddle point approximation near the most probable trajectory describing a given rare event. To find the optimal trajectory one should consider the variation of the exponent in Eq. (9) over  $q(t)$ ,  $p(t)$  and  $\xi(t)$ . The variation over  $\xi$  yields the ORN which determines the most probable realization of a given rare event. Executing this program, one arrives at the following set of classical equations of motion for  $q(t)$ ,  $p(t)$ , and  $\xi(t)$ :

$$\dot{q} = \frac{\partial H}{\partial p} - \xi q, \quad \dot{p} = -\frac{\partial H}{\partial q} + \xi p, \quad (10)$$

$$t_c^2 \ddot{\xi} - \xi = 2vt_c p q. \quad (11)$$

The boundary conditions, corresponding to extinction of the metastable population of average size  $K$ , are  $q(t = -\infty) = K$ ,  $q(t = +\infty) = 0$ , and  $\xi(t = \pm\infty) = 0$ . The conditions for  $\xi$  follow from the fact that the ORN must have a finite duration. Indeed, there is no need in environmental variations well before a large fluctuation starts and well after the population goes extinct. With exponential accuracy, the extinction probability of the large fluctuation is given by the full action, see Eq. (9), calculated on the solution of Eqs. (10) and (11).

In the absence of environmental noise,  $\xi = 0$ , Eqs. (10) admit an integral of motion:  $H = \text{const}$ . Then it is easy to see that the trajectory obeying the proper boundary conditions has  $H = 0$  and is therefore implicitly given by the relation  $(\mu/2)p + r - aq = 0$ , see Eq. (8) and Fig. 2. Calculating the action along this trajectory one finds  $S = \int_K^0 pdq = r^2/(\mu a) = rK/\mu$  which yields  $\tau_0$  from Eq. (3). Solving for  $q(t)$  and  $p(t)$  for this trajectory, one finds the unperturbed optimal path to extinction:

$$q_0(t) = \frac{K}{e^{t/t_r} + 1}; \quad p_0(t) = \frac{-2r/\mu}{e^{-t/t_r} + 1}. \quad (12)$$

In what follows we analyze, in different limits, Eqs. (10) and (11) in the presence of environmental noise.

*Short-correlated noise.*—Here the term  $t_c^2 \ddot{\xi}(t)$  in Eq. (11) can be neglected, and the ORN becomes enslaved to the dynamics of  $q$  and  $p$ :  $\xi(t) \approx -2vt_c pq$ . As a result, Eqs. (10) become Hamiltonian equations of motion with the effective Hamiltonian

$$H_v(q, p) = H(q, p) + vt_c p^2 q^2. \quad (13)$$

The same result follows from a Gaussian integration over  $\mathcal{D}\xi$  in Eq. (9) with the white-noise action  $S[\xi] = \int dt \xi^2/(4vt_c)$ . Now,  $H_v$  is an integral of motion of Eqs. (10). By virtue of the boundary conditions  $H_v = 0$ . As a result, extinction proceeds along the line  $(\mu/2)p + r - aq + vt_c pq = 0$ ; see Fig. 2. Evaluating the action  $S = \int_K^0 pdq$  along this line, one arrives at Eq. (6) with

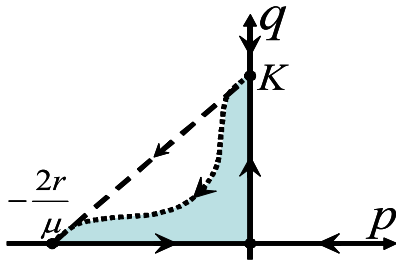


FIG. 2 (color online). Zero-energy trajectories of the Hamiltonian  $H$  (the dashed line), of  $H_v$  (the dotted line), and of both  $H$  and  $H_v$  (the solid lines). The shadowed area is the extinction action for the short-correlated environmental noise, leading to Eq. (14).

$$F(V, T) = \frac{1}{VT} \left[ \frac{1 + 2VT}{2VT} \ln(1 + 2VT) - 1 \right]. \quad (14)$$

As the (effectively) white noise is fully characterized by the product  $vt_c$ ,  $F$  only depends on the product  $VT$ .

For a weak noise,  $VT \ll 1$ , Eq. (14) yields  $F \approx 1 - 2VT/3$ . The corresponding reduction of the MTE is still exponentially large as, according to Eqs. (3) and (6),  $\tau_\xi = \tau_0 e^{-2vt_c r K^2/3\mu^2} \ll \tau_0$ . The most dramatic reduction of the MTE is predicted, in the spirit of the pure-white-noise result [6,7], in the strong-noise limit,  $VT \gg 1$ . Here  $F \approx \ln(VT)/(VT)$ , and one obtains

$$\tau_\xi \propto (vt_c K/\mu)^{r/(vt_c)}. \quad (15)$$

One can see that the exponential scaling of the MTE with the population size  $K$ , cf. Eq. (3), gives way to a power law with a large exponent. To clearly see the origin of this qualitative change in the MTE, let us find the ORN leading to Eq. (15). The logarithmic term in Eq. (14) comes from the hyperbolic part of the extinction trajectory, see Fig. 2, where  $vt_c pq \approx -r$ . Here  $\xi(t) \approx -2vt_c pq \approx 2r \approx \text{const}$ , and therefore  $\dot{q} \approx -rq$ . This equation describes the population size decay from the initial value  $K$  down to  $\mu/(vt_c)$ . At this population size [and at time  $\tilde{t} = t_r \ln(Kvt_c/\mu)$ ], the demographic noise takes over the environmental one; see Eq. (13). That is, the ORN of the short-correlated environmental noise is a catastrophic event, see Ref. [11], where the parameter  $r > 0$  suddenly drops to  $-r$  and keeps this value for a logarithmically long time  $\tilde{t} \gg t_r$ , see Fig. 3. The MTE (15) merely reflects the statistical weight of this ORN. This argument also shows that the validity of Eq. (14) requires a less restrictive condition than  $t_c \ll t_r$ . Indeed, it suffices to demand that  $t_c \ll \tilde{t} = t_r \ln(VT)$ ; see Fig. 1.

*Long-correlated noise.*—Here an adiabatic theory can be developed. The rare fluctuation, causing extinction, takes time about  $t_r$ ; see Fig. 3. As the environmental noise changes on a much longer time scale  $t_c$ , the extinction fluctuation samples an almost constant value of the noise  $\xi(0) = \xi_0$ , to be determined below. The effective parameter  $r$  is therefore equal to  $r - \xi_0 = \text{const}$ . The corresponding extinction rate is  $\sim \exp[-(r - \xi_0)^2/(\mu a)]$ , cf. Eq. (3).

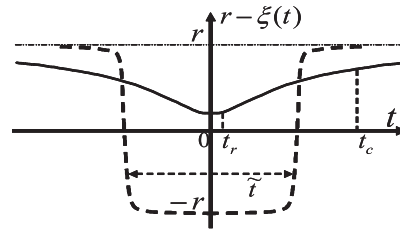


FIG. 3. Optimal realizations of the environmental noise in the limit of short (the dashed line) and long (the solid line) correlations of the noise. The duration of the catastrophe for the short-correlated noise is  $\tilde{t} \approx t_r \ln(Kvt_c/\mu)$ .

Now we notice that the right-hand side of Eq. (11) vanishes everywhere except in a narrow time window  $|t| \lesssim t_r \ll t_c$ . As a result, the solution of Eq. (11) for the ORN is  $\xi(t) \approx \xi_0 e^{-|t|/t_c}$ . Using it in Eq. (5), we find the statistical weight of the ORN to be  $\sim \exp[-\xi_0^2/(2v)]$ . Finally, we need to find the optimal value of  $\xi_0$  by optimizing the extinction rate against the statistical weight of the ORN. This is done by finding the minimum of  $\xi_0^2/(2v) + (r - \xi_0)^2/(\mu a)$  which is achieved at  $\xi_0 = r[1 + \mu a/(2v)]^{-1}$ . The minimum action,  $r^2/(\mu a + 2v)$ , yields the logarithm of the MTE, which is therefore given by Eq. (6) with

$$F(V, T) = (1 + 2V)^{-1}. \quad (16)$$

Notice that, for a strong long-correlated noise,  $V \gg 1$  and  $T \gg 1$ , one obtains  $\ln \tau_\xi = r^2/2v$  which is independent of the population-size  $K$ .

When does Eq. (16) apply? It turns out that, for a strong long-correlated noise, the condition  $T \gg 1$  gives way to a more restrictive one. Indeed, when deriving Eq. (16) we assumed that  $r(t) \approx r - \xi_0 e^{-|t|/t_c}$  does not change during the relaxation time  $t_r$ . This requires  $r'(0)t_r \ll r(0)$  and leads to the condition  $T \gg \max(1, V)$ , shown in Fig. 1 as the border of the adiabatic regime.

*Weak noise.*—Here we solve Eqs. (10) and (11) perturbatively. This is equivalent to performing the integration in Eq. (9) over the unperturbed extinction trajectory, Eq. (12) [12]. The Gaussian integration over the noise is done by going to the frequency space, and we obtain

$$F(V, T) = 1 - 4V \int_{-\infty}^{\infty} \frac{d\omega}{2\pi} \frac{(\pi\omega)^2}{\sinh^2 \pi\omega} \frac{T}{1 + (\omega T)^2}. \quad (17)$$

For a short-correlated noise,  $T \ll 1$ , this expression yields  $F = 1 - 2VT/3$  in agreement with the limit of  $VT \ll 1$  of Eq. (14). For a long-correlated noise,  $T \gg 1$ , Eq. (17) yields  $F = 1 - 2V$  in agreement with Eq. (16) at  $V \ll 1$ . These arguments provide the border of the weak-noise result (17) shown in Fig. 1. We reiterate that even a relatively weak noise causes an exponentially large reduction of the MTE.

Equation (17) shows that, for a weak environmental noise, there is only one relevant scale for the noise correlation time:  $T \sim 1$ . The situation is more complicated for a strong noise,  $V \gg 1$ . As discussed above, the adiabatic regime holds when  $T \gg V$ , whereas the effectively white-noise regime holds for  $T \ll \ln V$ . In the crossover regime,  $\ln V \lesssim T \lesssim V$  (see Fig. 1), the function  $F$  changes by a numerical factor of order unity. Here the MTE can be found by solving Eqs. (10) and (11) numerically.

To conclude, we have evaluated the reduction of the mean time to extinction (MTE) of an isolated population caused by environmental noise. We have also established the validity domains of the white-noise limit and adiabatic limit. Even a relatively weak environmental noise causes an exponentially large reduction of the MTE. A strong noise brings about qualitative changes in the scaling of

the MTE with the metastable population-size  $K$ . In the absence of environmental noise (or if the environmental noise is weak), the MTE scales exponentially with  $K$ . This scaling changes to a power law in the limit of a strong short-correlated noise, and becomes  $K$ -independent in the limit of a strong long-correlated noise. The optimal realization of the environmental noise (ORN), which results in the population extinction with the highest probability, also differs qualitatively in these two limits. For a short-correlated noise the ORN is a sharp catastrophe which, for a logarithmically long time, interchanges the birth and death rates of the system. For a long-correlated noise the ORN is a slow suppression of the birth rate down to a positive value. It is still debated in population biology “whether and under which conditions red noise increases or decreases extinction risk compared with uncorrelated (white) noise”, as put by Schwager *et al.* in Ref. [8]. We hope that the analysis presented here will help resolve this and related issues.

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