Cooperation Dilemma in Finite Populations under Fluctuating Environments

Michael Assaf,[1] Mauro Mobilia,[2] and Elijah Roberts[3]
[1]*Racah Institute of Physics, Hebrew University of Jerusalem, Jerusalem 91904, Israel*
[2]*Department of Applied Mathematics, School of Mathematics, University of Leeds, Leeds LS2 9JT, United Kingdom*
[3]*Department of Biophysics, Johns Hopkins University, Baltimore, Maryland 21218, USA*
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We present a novel approach allowing the study of rare events like fixation under fluctuating environments, modeled as extrinsic noise, in evolutionary processes characterized by the dominance of one species. Our treatment consists of mapping the system onto an auxiliary model, exhibiting metastable species coexistence, that can be analyzed semiclassically. This approach enables us to study the interplay between extrinsic and demographic noise on the statistics of interest. We illustrate our theory by considering the paradigmatic prisoner's dilemma game, whose evolution is described by the probability that cooperators fixate the population and replace all defectors. We analytically and numerically demonstrate that extrinsic noise may drastically enhance the cooperation fixation probability and even change its functional dependence on the population size. These results, which generalize earlier works in population genetics, indicate that extrinsic noise may help sustain and promote a much higher level of cooperation than static settings.

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Understanding the origin of cooperative behavior and how it is influenced by the population's intrinsic properties and by environmental factors are major scientific puzzles [1] that are suitably investigated in the framework of evolutionary game theory (EGT) [2]. In EGT, successful species with a high reproductive potential (fitness) spread, and the optimization of the fitness at an individual level can result in the reduction of the population's overall fitness, a phenomenon suggestively captured by the prisoner's dilemma (PD) game [1,2]. While in EGT the dynamics is traditionally studied in terms of differential equations, demographic fluctuations—intrinsic noise (IN)—are known to affect the evolution in finite populations. In this case, the dynamics is often described by a Markov chain and characterized by the fixation probability of a given trait (or "pure strategy"), which is the probability that the trait invades the entire population [3]. For the classic PD (with IN only), the cooperation fixation probability (CFP) vanishes exponentially with the population size (see, e.g., [4]), and defection prevails, leading to a cooperation dilemma. This prediction, at odds with many experimental observations, has motivated the investigation of various mechanisms that can promote and sustain cooperation [5].

Besides IN, an important source of fluctuations in such systems is extrinsic noise (EN) mostly due to the inherent environmental fluctuations and from being coupled to other fluctuating systems. Such EN can be aptly modeled in the form of random fluctuations in one or more interaction parameters. In theoretical population genetics [3,6–8], ecology [9–11], and cellular biology [12], it has been shown that the combined effect of IN and EN can significantly affect the lifetime of the long-lived metastable coexistence state the system dwells in prior to escape. In this work, we go beyond these and other works that focused on systems exhibiting metastability and present a novel approach that allows us to analyze the combined influence of IN and EN, with arbitrary correlation time, magnitude, and statistics, in systems characterized by the dominance of one species instead of metastability. This is done by a suitable mapping onto an auxiliary model possessing a long-lived metastable state and by treating the latter semiclassically. We illustrate our approach on the prototypical example of the PD game. We show that EN can drastically enhance the CFP and may even change its functional dependence on the population size. These results may be interpreted as the evolutionary signature of noisy environments on population diversity [13].

The paradigm of social dilemma is provided by the classic PD, whose main features are captured by assuming that the pairwise interaction between cooperators and defectors is described in terms of the benefit b and cost c of cooperation, with $b > c > 0$ [2]. Here, mutual cooperation leads to a payoff $b - c > 0$ and mutual defection gives a payoff 0, while when one player defects and the other cooperates, the former gets a payoff b and the latter gets $-c$. The quantity $r \equiv c/b$ is the cost-to-benefit ratio [2], and the dilemma arises from the fact that, while $r < 1$ and mutual cooperation enhances the population overall payoff, each individual is better off defecting.

We consider a finite and well-mixed population of size $N \gg 1$, with n cooperators and $N - n$ defectors. At the mean field level ($N \to \infty$), defection always prevails and the fraction $x \equiv n/N$ of cooperators evolves to extinction, $x = 0$, according to the replicator rate equation $(d/dt)x \equiv \dot{x} \propto x(1-x)[\Pi_C(x) - \Pi_D(x)]$. $\Pi_C = bx - c$

and $\Pi_{\mathsf{D}} = bx$ are the cooperator and defector average payoffs, respectively [2], and we assume that $b, c = \mathcal{O}(1)$.

When the population size is finite, demographic fluctuations always drive the system to either of the absorbing states $n = 0$ or $n = N$, and the stochastic dynamics is described by the master equation $\dot{P}_n = T^+_{n-1}P_{n-1} + T^-_{n+1}P_{n+1} - (T^+_n + T^-_n)P_n$, where T^+_n and T^-_n are the respective birth and death rates. As often, these are given in terms of the Moran model [2,4,14,15]: $T^+_n = [f_{\mathsf{C}}(n)/\bar{f}(n)]n(N - n)/N^2$ and $T^-_n = [f_{\mathsf{D}}(n)/\bar{f}(n)]n(N - n)/N^2$, where the cooperator and defector fitnesses are

$$f_{\mathsf{C}}(n) = 1 + s[bn/N - c] \quad \text{and} \quad f_{\mathsf{D}}(n) = 1 + sbn/N, \quad (1)$$

and the population average fitness is $\bar{f} = 1 + s(b - c)n/N$. In Eq. (1), the term 1 accounts for a baseline fitness contribution, and the selection strength is denoted by $s > 0$ [2,15,16]. While our approach applies to arbitrary selection strength, throughout the Letter we focus on the biologically relevant limit of weak selection, $s \ll 1$ [3,15], which ensures that $f_{\mathsf{C}/\mathsf{D}} > 0$ in Eq. (1).

Furthermore, it is convenient to work in the regime where $s \ll N^{-1/2}$. In this regime, one can accurately approximate the master equation by a Fokker-Planck equation (FPE) [16,17] for the probability $P(x, t)$ of having cooperator density x at time t [3,18]:

$$\partial_t P(x, t) = -\partial_x[A(x)P(x, t)] + 1/(2N)\partial_x^2[B(x)P(x, t)], \quad (2)$$

where $A(x) = T^+(x) - T^-(x) \sim O(s)$, giving a relaxation time $\propto s^{-1}$, $B(x) = T^+(x) + T^-(x)$, and $T^{\pm}(x) = T^{\pm}_n$.

An important notion to characterize evolutionary dynamics is the CFP $\phi_{\mathsf{C}}(x_0)$—the probability that cooperation fixates starting from an initial fraction x_0 of cooperators. In the absence of EN, $\phi_{\mathsf{C}}(x_0)$ can be calculated exactly [4,19], and one finds in the leading exponential order $\phi_{\mathsf{C}}(x_0) \sim e^{-Nsc(1-x_0)}$. Here, we purposely adopt another route and show how to asymptotically calculate $\phi_{\mathsf{C}}(x_0)$ via an auxiliary problem. For this, we consider the modified model obtained by supplementing the original PD system with a reflecting boundary at $n_0 = Nx_0$ by imposing $T^-_{n=n_0} = 0$. Hence, the only absorbing state of the modified model is the state $n = N$. Therefore, as $\dot{x} = A(x) < 0$ for any $0 < x < 1$, a quasistationary distribution (QSD) peaked at x_0 (for any value of x_0) forms after an $\mathcal{O}(s^{-1})$ relaxation time. This metastable state, however, slowly decays due to a slow leakage of probability into the absorbing state at $x = 1$, with a rate given by the inverse of the cooperation mean fixation time (MFT).

By employing the metastable ansatz $P(x, t) \simeq \pi(x)e^{-t/\tau}$ in Eq. (2), where $\pi(x)$ is the QSD, the MFT τ of the auxiliary model can be computed by using the semiclassical ansatz $\pi(x) \sim e^{-NS(x)}$. Here $S(x)$ is called the action function, while $p_x(x) \equiv S'(x)$ is the momentum [20,21]. This yields a stationary Hamilton-Jacobi equation, $H(x, p_x) = 0$, with Hamiltonian $H(x, p_x) = p_x A(x) + (p_x^2/2)B(x)$. Fixation occurs along the zero-energy trajectory $p_x(x) = -2A(x)/B(x)$, where $p_x(x) \sim \mathcal{O}(s) \ll 1$. This gives $S(x) = \int p_x dx = (c/b)\ln(2 - cs + 2bsx)$, from which the QSD at $x > x_0$, $\pi(x) \sim e^{-N[S(x)-S(x_0)]}$, is found. Since $\tau \sim \pi(1)^{-1}$, we have [20,22]

$$\ln\tau \simeq N[S(1) - S(x_0)] \simeq Nsc(1 - x_0), \quad (3)$$

where this result is valid when $Ns \gg 1$, which ensures a long-lived metastable state [16]. Importantly, we find that for $N^{-1} \ll s \ll N^{-1/2}$ the MFT τ of the modified problem (3) coincides to leading order with the inverse of the CFP in the original PD model [4,18]. We now use this finding to study the CFP in the presence of EN.

To this end, we incorporate EN in the form of one or more fluctuating parameters. For concreteness we take a fluctuating selection strength $s \to s(t) = s_0 + \xi(t)$. By directly affecting the fitness of C/D individuals, this choice is particularly relevant in population genetics [3,6–8,23], ecology [24], and cellular biology [13]. Here, ξ is taken as an Ornstein-Uhlenbeck process with mean zero, variance $\langle\xi(t)\xi(t')\rangle = \sigma^2 e^{-|t-t'|/\tau_c}$, and correlation time $\tau_c > 0$ [19,25]. We assume that σ is arbitrary so that $s(t)$ can become negative for $\sigma = \mathcal{O}(s_0)$. The Ornstein-Uhlenbeck process satisfies the following Langevin equation:

$$\dot{\xi} = -\xi/\tau_c + \sqrt{2\sigma^2/\tau_c}\,\eta(t), \quad (4)$$

where $\eta(t)$ is white Gaussian noise $\langle\eta(t)\eta(t')\rangle = \delta(t - t')$ [26].

We now proceed as in the absence of EN and compute τ of the modified PD model supplemented with a reflecting boundary at x_0. We have numerically confirmed (see Supplemental Material [27] for details) that, for $Ns_0 \gg 1$, $\phi_{\mathsf{C}}(x_0)$ and τ^{-1} exhibit the same asymptotic behavior in the original and modified models also *in the presence of EN*; see Fig. 1.

To account for the joint effects of IN and EN, we couple Eq. (4) with FPE (2) and arrive at the following *bivariate* FPE for the probability $P(x, \xi, t)$ to find cooperator density x and selection strength $s = s_0 + \xi$ at time t:

$$\begin{aligned}\partial_t P(x, \xi, t) = {} & [-\partial_x A + \partial_\xi(\xi/\tau_c)]P(x, \xi, t) \\ & + (2N)^{-1}[\partial_x^2 B + (2V/\tau_c)\partial_\xi^2]P(x, \xi, t). \quad (5)\end{aligned}$$

Here, $A = A(x, \xi) = T^+(x, \xi) - T^-(x, \xi)$ and $B = B(x, \xi) = T^+(x, \xi) + T^-(x, \xi)$ read, for $s \ll 1$,

$$\begin{aligned}A(x, \xi) &\simeq -x(1 - x)c(s_0 + \xi)[1 - (b - c)(s_0 + \xi)x], \\ B(x, \xi) &\simeq 2x(1 - x)[1 + c(s_0 + \xi)(x - 1/2)], \quad (6)\end{aligned}$$

and we have defined $V \equiv N\sigma^2$. For $N \gg 1$, we can use the semiclassical ansatz for the QSD $\pi(x, \xi) \sim e^{-NS(x,\xi)}$ in

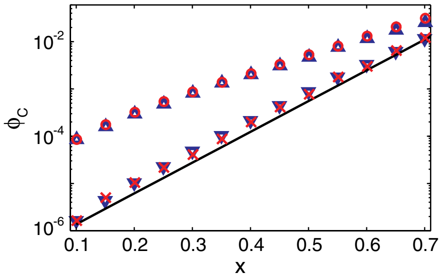

FIG. 1 (color online). ϕ_C versus $\alpha\tau^{-1}$ for intermediate EN, $\sigma/s_0 = 0.3$ (cross and downward triangle), and strong EN, $\sigma/s_0 = 1$ (open circle and upward triangle). The solid line is the analytical result for ϕ_C with IN only. Here $s_0 = 0.01$, $b = 1.25$, $c = 1$, $N = 1500$, and $\tau_c = 20$. The proportionality factor α varies slowly with the model parameters (35.3 for intermediate and 55.1 for strong EN).

Eq. (5), which yields the Hamilton-Jacobi equation $H(x, \xi, p_x, p_\xi) = 0$ with Hamiltonian

$$H = p_x A(x, \xi) - p_\xi \xi/\tau_c + (p_x^2/2)B(x, \xi) + (V/\tau_c)p_\xi^2, \tag{7}$$

where we have defined $p_x = \partial_x S$ and $p_\xi = \partial_\xi S$. The corresponding Hamilton equations are

$$\begin{aligned} \dot{x} &= \partial_{p_x} H = A + p_x B, \\ \dot{p}_x &= -\partial_x H = -p_x[\partial_x A + (p_x/2)\partial_x B], \\ \ddot{\xi} &= \xi/\tau_c^2 - 2(V/\tau_c)p_x \partial_\xi A(x, \xi), \end{aligned} \tag{8}$$

where the third equation has been obtained by combining the equations for $\dot{\xi}$ and $\dot{p}_\xi$ into a single equation and by keeping terms up to $\mathcal{O}(p_x) = \mathcal{O}(s_0)$; see below. The solution to the Hamilton-Jacobi equation for generic EN (with arbitrary τ_c) is found by solving numerically Eq. (8), yielding the action function $S(x, \xi) = \int p_x(x, \xi)dx + \int p_\xi(x, \xi)d\xi$ [28]. Here, we focus on two important and analytically amenable regimes: *short-correlated* (white) EN, when $\tau_c \ll s_0^{-1}$, and *long-correlated* (adiabatic) EN, when $\tau_c \gg s_0^{-1}$.

For short-correlated EN, $\tau_c \ll s_0^{-1}$, we find that $\ddot{\xi}$ is negligible in the third of Eq. (8) [29], yielding the effective noise strength $\xi \simeq \xi_{\text{eff}} \simeq -2cV\tau_c p_x x(1 - x)$ [10,12,30]. Since $p_x > 0$ (see below), $\xi_{\text{eff}} < 0$; thus, EN is exploited to enhance the CFP by decreasing the selection strength.

Substituting ξ_{eff} into the first of Eq. (8), one finds $\dot{x} = -x(1 - x)[cs_0 - 2p_x\{1 + c^2\tau_c Vx(1 - x) + \mathcal{O}(s_0)\}]$. It appears that EN markedly affects the dynamics when its magnitude satisfies $V\tau_c \gg \mathcal{O}(s_0)$. In this regime the corresponding effective white-noise Hamiltonian is $H(x, p_x) \simeq -x(1 - x)p_x[cs_0 - p_x\{1 + c^2\tau_c Vx(1 - x)\}]$. Solving $H = 0$, we find $p_x = cs_0/[1 + c^2\tau_c Vx(1 - x)]$. This yields the MFT in the modified model and, therefore, the CFP of the original PD model:

$$\ln\phi_C(x_0) \simeq -N\int_{x_0}^{1} \frac{cs_0 du}{1 + c^2 V\tau_c u(1 - u)} = -\frac{Ns_0}{c\tau_c V\gamma} \times \ln\left\{[1 + c^2\tau_c V(1 + \gamma)/2]\left(\frac{\gamma + 1 - 2x_0}{\gamma - 1 + 2x_0}\right)\right\}, \tag{9}$$

where $\gamma = \sqrt{1 + 4/(c^2\tau_c V)}$. In Fig. 2, we compare Eq. (9) with numerical simulations as a function of the relative EN strength σ/s_0 and find a very good agreement for both $x_0 = \mathcal{O}(1)$ (left panel) and $x_0 \ll 1$ (right panel). One can clearly see that EN, by effectively decreasing the selection strength s, enhances the CFP compared to the IN-only case with $\sigma = 0$ (see also Fig. 3 and Fig. S2 of [27], where we respectively plot the CFP versus N and τ_c).

For a given short-correlated EN, $\tau_c \ll s_0^{-1}$, there are two interesting limits to (9): (i) strong and (ii) weak EN. (i) The most striking effect of EN appears in the limit of strong EN, $V\tau_c \gg 1$, which yields $\gamma \to 1$. Here, for finite values of $x_0 > 0$, the dependence of $\phi_C(x_0)$ on N becomes a power law, and Eq. (9) gives way to $\phi_C(x_0) \sim [N(\sigma c)^2\tau_c(1 - x_0)/x_0]^{-(s_0/\sigma^2)/(c\tau_c)}$. This result is confirmed by numerical simulations; see Fig. 3. (ii) For weak EN, $V\tau_c \ll 1$, Eq. (9) can be approximated as $\ln\phi_C(x_0) \simeq -Ns_0c(1 - x_0)[1 - (1/6)c^2V\tau_c(1 - x_0)(2x_0 + 1)]$, which coincides with the IN-only result to leading order.

The behavior of Eq. (9) for a small initial density of C's ($x_0 \ll 1$) is particularly relevant in EGT [2]. In this case, for arbitrary EN strength and $x_0 \to 0$, the CFP is

$$\ln\phi_C^{(0)} \simeq -[2Ns_0/(c\tau_c V\gamma)]\ln\{1 + c^2\tau_c V(1 + \gamma)/2\}. \tag{10}$$

Again, for strong EN, $V\tau_c \gg 1$, Eq. (10) becomes a power law $\phi_C^{(0)} \simeq [N(\sigma c)^2\tau_c]^{-2(s_0/\sigma^2)/(c\tau_c)}$ [31].

Note that, while Eq. (9) has been formally derived in the regime $s \ll N^{-1/2}$, its predictions also hold when $Ns_0^2 = \mathcal{O}(1)$ with $s_0 \ll 1$, as illustrated by the numerical results in

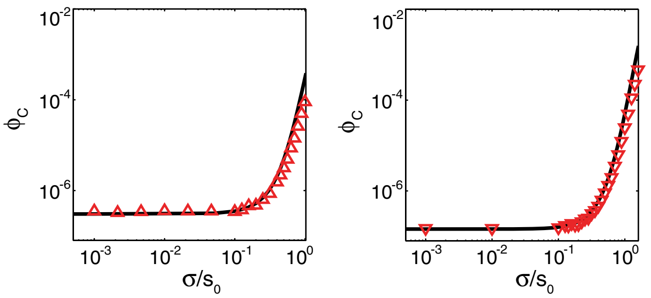

FIG. 2 (color online). ϕ_C versus relative EN strength σ/s_0 in the short-correlated EN regime. The solid line is from Eq. (9), and the symbols are numerical simulations. Here, $s_0 = 0.01$, $b = 1.25$, and $c = 1$, and $N = 2000$, $\tau_c = 25$, and $x_0 = 0.25$ in the left panel, while $N = 1750$, $\tau_c = 20$, and $x_0 = 0.1$ in the right panel. The agreement slightly improves from the left to right panels as the inequalities $Ns_0^2 \ll 1$ and $\tau_c s_0 \ll 1$ are better satisfied.

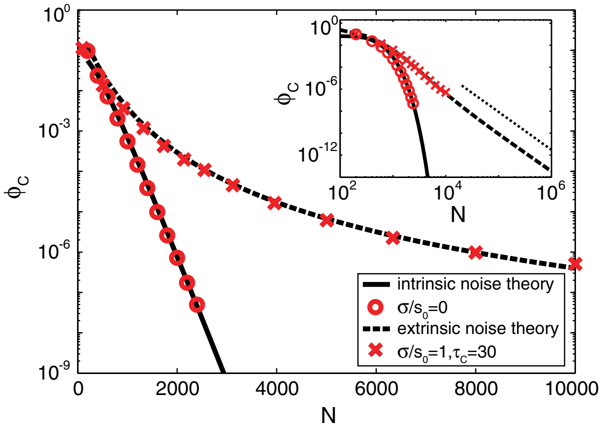

FIG. 3 (color online). ϕ_{C} versus N under short-correlated EN: Lines are theoretical results, while crosses and open circles are simulation results with and without EN, respectively; see the legend. Parameters are $s_0 = 0.01$, $b = 1.25$, $c = 1$, and $x_0 = 0.25$. IN-only results display exponential dependence on N, whereas for strong EN, $V\tau_c \gg 1$ (see the text), ϕ_{C} exhibits a power-law dependence on N. Inset: ϕ_{C} versus N on the log-log scale. Results of the theory and simulations are compared to $N^{-3.4}$ (dotted line). The power law $\phi_{\mathrm{C}} \sim N^{-10/3}$ predicted by (9) is approached when $N \to \infty$.

Fig. 3. This is because the leading correction to $\phi_{\mathrm{C}}(x_0)$ due to EN is independent of s_0 when $V\tau_c \gg \mathcal{O}(s_0)$ [see the denominator of the integrand of (9)]. Thus, our results due to EN are applicable as long as $s_0 \ll 1$ and are expected to hold also in the non-FPE regime where $Ns_0^2 \gtrsim \mathcal{O}(1)$ [27].

The case of long-correlated EN, $\tau_c \gg s_0^{-1}$, is investigated in the Supplemental Material [27]. In this case, for weak EN, $V < s_0$, we find that $\ln\phi_{\mathrm{C}}(x_0) \simeq -Ncs_0(1 - x_0)[1 - (c/s_0)V(1 - x_0)]$. Under strong EN, $V > s_0$, the intrinsic fluctuations are negligible [12] and $\phi_{\mathrm{C}}(x_0)$ is solely governed by Eq. (4), yielding $\phi_{\mathrm{C}}(x_0) \sim \tau_c^{-1}$; see Supplemental Material [27] for the details. In addition, the latter contains a summary of the various EN parameter regimes for fluctuating $s(t)$ and a parameter diagram; see Fig. S1 in [27].

For completeness, we have also considered the case of external fluctuations in the cost-to-benefit ratio $r = c/b$, with $r \to r(t) = r_0 + \xi(t)$ and $r_0 < 1$ [where $r_0 \sim \mathcal{O}(1)$]. In this case, the dynamics of ξ is given by (4) with $\langle\xi(t)\xi(t')\rangle = \sigma_r^2 e^{-|t-t'|/\tau_c}$, where $V_r \equiv N\sigma_r^2$. In addition, we assume $\sigma_r \ll r_0$ to guarantee $0 < r(t) < 1$ and that b is fixed so that $c(t) = br(t)$ fluctuates. Performing the calculations along the same lines as for fluctuating $s(t)$, we find for short-correlated EN, $\tau_c \ll s^{-1}$:

$$\ln\phi_{\mathrm{C}}(x_0) \simeq -N\int_{x_0}^{1}\frac{sbr_0du}{1 + (sb)^2V_r\tau_c u(1 - u)}. \tag{11}$$

Similarly as before, for strong EN, $s^2V_r\tau_c \gg 1$, Eq. (11) also predicts that $\phi_{\mathrm{C}}(x_0)$ decays algebraically with N.

Our approach generalizes earlier works in population genetics where the combined role of IN and EN was investigated by considering a fluctuating selection strength; see, e.g., [3,6–8,23]. In these studies the dynamics was implemented with the Wright-Fisher model with discrete time and nonoverlapping generations [3]. In such a setting, a diffusion theory was devised in the weak selection limit to account for IN and *time-uncorrelated* (white) EN by averaging separately on the two sources of noise [3,6–8]. When $N\sigma^2 \lesssim Ns_0^2 \ll 1$, the results of this approach coincide with Eq. (9) for $\tau_c = 1$ and $N \to N/2$ [32]. Yet, our approach is more general, since it allows us to study EN with arbitrary correlation time and statistics, as well as in the presence of frequency-dependent selection.

In this work, we have analyzed the fixation properties of evolutionary processes characterized by the dominance of one species. Our approach relies on a semiclassical treatment applied to an auxiliary model exhibiting metastability. This allows us to study how fixation is affected by the interplay between intrinsic and extrinsic noise. Our theory is general in the sense that it can deal with EN of arbitrary statistics, correlation time, and magnitude, with one or multiple fluctuating parameters, and can be also used for systems exhibiting metastable coexistence. Using the prototypical prisoner's dilemma game, we have shown that EN is exploited to effectively reduce the selection strength and, thereby, to drastically enhance cooperation, whose fixation probability is otherwise vanishingly small. This indicates that EN may be vital in sustaining a certain level of cooperation and population diversity by effectively opposing single-type dominance, as reported in recent microbial experiments [13]. Therefore, EN may contribute to reconcile the theoretical predictions with observed examples of cooperative behaviors.

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[25] Other non-Gaussian statistics are possible. Yet, without specific knowledge of the EN properties, we chose the Ornstein-Uhlenbeck noise, which is arguably the simplest form of EN with Gaussian statistics and arbitrary correlation time.

[26] $\eta(t)$ is the time-continuous limit ($dt \to 0$) of a temporally uncorrelated normal random variable with mean 0 and variance $1/dt$ [19].

[27] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.111.238101 for the following: the different results for the CFP are summarized in a diagram, the various EN parameter regimes are discussed, the CFP under weak and strong adiabatic EN is derived, and a description of our numerical method is given.

[28] D. M. Roma, R. A. O'Flanagan, A. E. Ruckenstein, A. M. Sengupta, and R. Mukhopadhyay, Phys. Rev. E **71**, 011902 (2005).

[29] Using the expression of ξ_{eff} together with Eqs. (6) and (8), one finds *a posteriori* that $\ddot{\xi} = \mathcal{O}(V\tau_c s_0^3) \ll Vs_0/\tau_c$ which is negligible in the third of Eq. (8).

[30] E. Y. Levine and B. Meerson, Phys. Rev. E **87**, 032127 (2013).

[31] It can be checked that Eq. (9) is well defined in the double limit of $V\tau_c \gg 1$ ($\gamma \to 1$) and $x_0 \to 0$.

[32] As time is discrete in the Wright-Fisher model and the EN between two successive generations is uncorrelated, the correspondence requires one to set $\tau_c = 1$ in Eq. (9). Also, a population of size $2N$ in the Wright-Fisher model maps onto a population of size N in the Moran model [3,16].