

## Population extinction on a random fitness seascape

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 (Received 23 July 2020; accepted 13 October 2020; published 4 November 2020)

We explore the role of stochasticity and noise in the statistical outcomes of commonly studied population dynamics models within a space-independent (mean-field) perspective. Specifically, we consider a distributed population with logistic growth at each location, subject to “seascape” noise, wherein the population’s fitness randomly varies with *location and time*. Despite its simplicity, the model actually incorporates variants of directed percolation, and directed polymers in random media, within a mean-field perspective. Probability distributions of the population can be computed self-consistently, and the extinction transition is shown to exhibit novel critical behavior with exponents dependent on the ratio of the strengths of migration and noise amplitudes. The results are compared and contrasted with the more conventional choice of demographic noise due to stochastic changes in reproduction.

DOI: [10.1103/PhysRevE.102.052106](https://doi.org/10.1103/PhysRevE.102.052106)

### I. INTRODUCTION

The growth of spatially distributed populations is of importance to ecology, evolutionary biology, epidemiology, among many other fields. One of the simplest models of a species or pathogen propagating in space is the *Fisher equation* [1–5], given by

$$\frac{dy(x, t)}{dt} = \mu y - ay^2 + D\nabla^2 y. \quad (1)$$

At each spatial coordinate  $x$ , the population size  $y(x, t)$  initially increases exponentially in time  $t$ , at a rate determined by the *fitness parameter*  $\mu > 0$ . This (logistic type) growth is eventually slowed down by the nonlinear term, describing resource limitations, with the population asymptoting to  $\mu/a$  (the capacity). Alternatively, for  $\mu < 0$ , the population decays to zero. The diffusion term  $D$  captures migration of the population to nearby points in space.

Such deterministic evolution is only valid if reproductive stochasticity is ignored. In particular, near extinction points where the population hits zero (such as when a species suffers ecological collapse or when a pathogen is without available hosts), the deterministic description does not capture the stochasticity of small number fluctuations. Transitioning from a model with a finite, discrete population into a continuum formulation results in a noise of amplitude proportional to the square root of the number of individuals. Including this so-called *demographic noise* [6–11] leads to the stochastic Fisher equation

$$dy = (\mu y - ay^2 + D\nabla^2 y)dt + \sigma_d \sqrt{y}dW, \quad (2)$$

with  $\sigma_d$  as the noise amplitude, and  $dW = dW(x, t)$  being a standard Wiener process. Models of this type have been studied in a number of contexts outside of population growth, thanks to connections to directed percolation [12–19] (with the onset of laminar turbulence for  $\mu = a = 0$  [17] as a

recent application). Indeed, extinction transitions are expected to generically belong to the directed percolation universality class [20,21].

The main focus of this paper is on a different form of noise. The implicit assumption of the Fisher equation is that the fitness  $\mu$  is an intrinsic property, uniform in time and the same across all locations. In reality, the growth rate is strongly influenced by external factors, such as nutrient level, light, etc. at different times and places. Generalizing from a static but position-dependent *fitness landscape*  $\mu(x)$ , a time-varying fitness  $\mu(x, t)$  is commonly referred to as a *seascape* [22–27]. Population growth on a random seascape is thus governed by

$$dy = (\mu y - ay^2 + D\nabla^2 y)dt + \sigma y dW, \quad (3)$$

with  $\sigma^2$  being the variance of the fitness noise, and  $dW = dW(x, t)$  a Wiener process as before. While there is natural relevance in having environmental variation to be spatially correlated [28–31], we will focus our efforts on the uncorrelated case. Note that for  $a = 0$ , the linear equation describes the evolving weight  $y(x, t)$  of a directed polymer in a quenched random energy landscape [ $\sigma dW(x, t)$ ], with  $\ln y(x, t)$  satisfying the Kardar-Parisi-Zhang equation, notable in the study of surface growth problems [32–40]. Indeed, the connection between the problem of directed polymers in random media (DPRM) and the Fisher equation under “multiplicative” seascape noise has been noted before, and subject to several numerical studies [14,41–43]. Multiplicative noise has also turned up in studies of symmetry breaking [44,45], theoretical ecology [8,46,47], and immunology [48].

While much studied, the problem of directed polymers in random media is largely unsolved in other than one dimension. Such limitations will necessarily extend to characterizing the effect of a random seascape on a population in two or more dimensions. We thus resort to replacing near-neighbor migrations with jumps of arbitrary length. This “mean-field” limit is reasonable for a well-mixed bacterial population, or

for a pathogen infecting an active city. An alternative description is to replace continuous space with a series of nodes indexed by  $k = 1, 2, \dots, N$ . If population  $y_k$  of each node can jump to any other node in the network at rate  $D/N$ , then (for  $N \gg 1$ ) evolution in a random seascape is described by

$$dy_k = \{\mu y_k - a y_k^2 + D(\bar{y} - y_k)\}dt + \sigma y_k dW_k, \quad (4)$$

and similarly for demographic noise we have

$$dy_k = \{\mu y_k - a y_k^2 + D(\bar{y} - y_k)\}dt + \sigma_d \sqrt{y_k} dW_k, \quad (5)$$

where  $\bar{y} = \frac{1}{N} \sum_k y_k$  is the spatial average, with  $dW_k = dW(k, t)$  being spatiotemporal noise. In a sense, the diffusion coefficient  $D$  now behaves like a mean-field coupling strength. The problem can be solved exactly in this case, as for  $N \rightarrow \infty$  the probability distribution for  $\bar{y}$  converges to a  $\delta$ -function, reducing the above equations to those of independent variables whose distributions can be obtained by standard methods. The important population average  $\bar{y}$  is then computed self-consistently.

We carry out this program below initially for seascape noise in three cases: neutral evolution ( $\mu = a = 0$ ) in Sec. II, decaying population ( $\mu < 0$ ) in Sec. III, and saturating growth ( $\mu > 0, a > 0$ ) in Sec. IV. For comparison, the cases of demographic noise, as well as mixed demographic and seascape noise, are studied Sec. V.

Despite the commonality in their deterministic parts, the two types of stochastic noise relate to two quite distinct universality classes, that of directed polymers in random media for Eq. (4) versus directed percolation for Eq. (5). As such, we might expect them to exhibit different behaviors in the all-important extinction regime. This is indeed the case: Near the extinction threshold, we show that seascape noise leads to a broadly distributed population, characterized by a tail falling off as a power-law. The power-law exponent varies continuously with  $\sigma^2/D$  such that, when the noise is large, fluctuations in the population much exceed the mean. The extinction transition no longer belongs to the (“mean-field”) directed percolation universality class. However, as we show in Sec. V, demographic noise restores the directed percolation universality class.

## II. NEUTRAL POPULATION FOR $\mu = a = 0$

Many subtleties of seascape noise can be gleaned by considering Eq. (4) in the “neutral” case, given by

$$dy_k = D(\bar{y} - y_k)dt + \sigma y_k dW_k. \quad (6)$$

The above equation can be interpreted as describing a form of synchronization: each  $y_k$  is being pulled toward the spatial mean  $\bar{y}$  with strength  $D$ , but they are forced apart by the noise  $\sigma y_k dW_k$ . The interplay between the two tendencies manifests in the population variance, with one limiting form being a “synchronized” population described by a tight distribution, and the other being an “incoherent” population that is broadly distributed [49,50].

While it would be interesting to analyze the case of a finite  $N$ , computations simplify in the thermodynamic limit of  $N \rightarrow \infty$  [51]. If we start with a uniform initial condition, say  $y_k(t=0) \equiv y_0$  for all  $k$ , then the evolving probability distributions of all individual members will be identical. Thus,

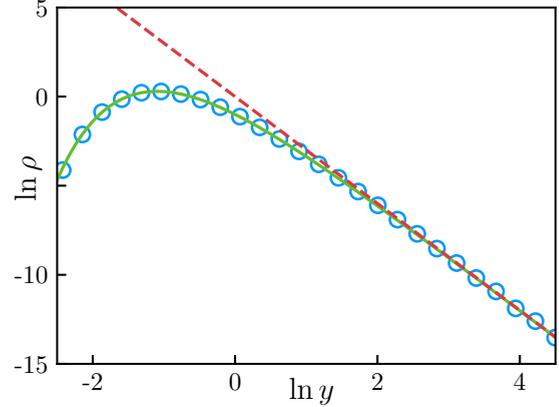


FIG. 1. Simulated vs predicted probability distribution in the steady state of Eq. (6). Circles show simulation results from  $5 \times 10^6$  runs of Eq. (7), the solid line shows the prediction of Eq. (10), while the dashed line emphasizes the large- $y$  behavior from Eq. (11). Simulation was run using the stochastic Runge-Kutta method, with  $y_0 = 1, D = 0.5, \sigma = 1.0$ , and  $\mu = a = 0$ . The simulation ran for 25 time units, with a time step of 0.01.

if there exists some long-time stationary distribution with finite mean, then this mean will be the same for each member. So by simply applying the law of large numbers and taking expectations, we obtain  $\bar{y} = \langle y \rangle = y_0$ . The second equality follows from the conservation of average population in the neutral limit, remaining at  $Ny_0$  at all times.

Therefore, the large- $N$  dynamics are captured by the single stochastic differential equation

$$dy = D(y_0 - y)dt + \sigma y dW, \quad (7)$$

independent of the spatial index  $k$ . From here, we can construct a Fokker-Plank equation for the evolution of the probability density function  $\rho(y, t)$ , namely

$$\partial_t \rho = -\partial_y \left[ D(y_0 - y)\rho - \frac{\sigma^2}{2} \partial_y (y^2 \rho) \right]. \quad (8)$$

A stationary distribution ( $\partial_t \rho \equiv 0$ ) is obtained by setting the probability current in the above square brackets to zero, leading to

$$0 = y^2 \rho' + (c_D + 2)y\rho - c_D y_0 \rho, \quad (9)$$

where we define  $c_D = 2D/\sigma^2$ . This is a solvable ordinary differential equation, with a properly normalized solution given by

$$\rho(y) = \frac{(c_D y_0)^{c_D+1}}{\Gamma(c_D+1)} y^{-2-c_D} e^{-c_D y_0/y}, \quad (10)$$

which is a scaled inverse chi-squared distribution with  $\nu = 2(c_D + 1)$  and  $\tau = y_0 c_D / (1 + c_D)$ . This prediction agrees with simulated infinite- $N$  dynamics depicted in Fig. 1.

An important characteristic of this solution is the behavior in the tail, where for large populations  $y$ , the density behaves as

$$\rho \propto y^{-2-c_D}; \quad (11)$$

this is confirmed in Fig. 2. Although stochastic population models have produced power laws before [8,48,52–56], this

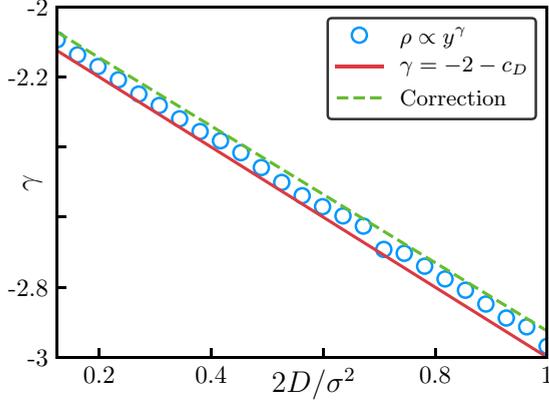


FIG. 2. Simulated vs predicted power-law decays of the tail of the probability distribution in the steady state of Eq. (6). Circles show numerically obtained decay exponents from simulating  $5 \times 10^6$  replications of Eq. (7); the solid line depicts the predicted decay exponent at large  $y$  from Eq. (11); and the dashed line shows the maximum error arising from measuring the exponent at finite  $y$ , as predicted via Eq. (10). The simulation was run using the stochastic Runge-Kutta method, with  $y_0 = 1$ ,  $D = 0.5$ ,  $\sigma = 1.0$ , and  $\mu = a = 0$ . The time step of integration was 0.01, with a total integration time of 25 units. Regression to identify the decay rate of the PDFs began at  $y^* \approx 13.34$ , and the final exponent was averaged over the final five time units with samples every 0.05 time units.

result is distinctive in that the exponent varies continuously with the migration rate  $D$  [57].

Even though the mean of the distribution stays at the initial value of  $y_0$ , the seascape fluctuations lead to a power-law tail, which results in a variance (and higher moments) that may either be finite or infinite. Specifically, we have

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} = \frac{2D}{2D - \sigma^2}, \quad (12)$$

such that the variance becomes infinite when  $c_D$  crosses 1, and the population distribution becomes broad compared to the mean. Parenthetically, we note that such a “transition” does not occur in the case of demographic noise as described later in the text.

### III. DECAYING POPULATION FOR $\mu < 0$

Now consider Eq. (4) in the presence of negative fitness  $\mu$ . The nonlinear term is now asymptotically irrelevant, as can be seen by the transformation to  $z = ye^{-\mu t}$ , such that the dynamics in this “moving frame” become

$$dz = [-az^2 e^{\mu t} + D(\bar{z} - z)]dt + \sigma z dW. \quad (13)$$

Since  $\mu < 0$ , the nonlinear term drops out at large times, leaving us with

$$dz = D(\bar{z} - z)dt + \sigma z dW, \quad (14)$$

which is simply the exact same dynamics as for  $\mu = 0$  in Eq. (6). Therefore, the same long-time results hold in these transformed coordinates. This includes the exact distribution predicted in Eq. (10) as well as the moment ratio in Eq. (12), as confirmed by the simulations depicted in Fig. 3. Therefore,

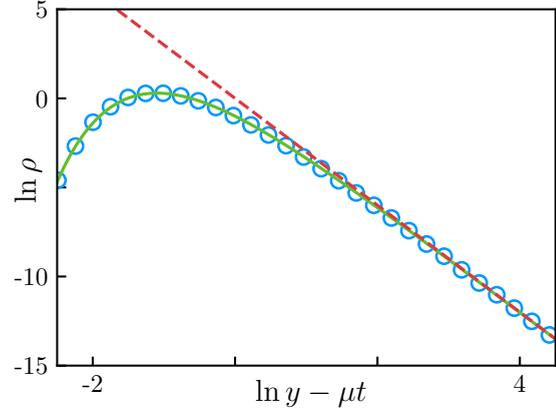


FIG. 3. Simulated vs predicted probability densities for the decaying population; note the time-dependent horizontal axis. Circles show simulation results from  $5 \times 10^6$  runs of Eq. (4), the solid line depicts the exact steady-state solution of Eq. (10), and the dashed line shows the predicted large- $y$  behavior from Eq. (11). Simulation was run using the stochastic Runge-Kutta method, with  $y_0 = 1$ ,  $D = 0.5$ ,  $\sigma = 1.0$ ,  $\mu = -0.1$ , and  $a = 1$ . The time step of integration was 0.01, with a total integration time of 100 units.

while the mean population size decays exponentially, the ratio

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} = \frac{2D}{2D - \sigma^2} \quad (15)$$

indicates that the mean ceases to be a good measure of the distribution for  $2D/\sigma^2 < 1$ .

### IV. GROWING POPULATION FOR $\mu > 0$

The most intricate case corresponds to when  $\mu$ ,  $a$ ,  $D$ , and  $\sigma$  are all strictly positive:

$$dy_k = \{\mu y_k - ay_k^2 + D(\bar{y} - y_k)\}dt + \sigma y_k dW_k. \quad (16)$$

The intricacy arises as the noise modifies the mean value of  $y$  from the bare value of  $\mu/a$ . In reality, the dynamics of the mean depend on the value of every higher moment. More intuitively, note that the restoring force of the logistic growth term is asymmetric, in that it “punishes” overly large values of  $y$  harder than small ones. Under the effect of noise, this biases  $y$  to smaller values, and we should expect the true value of  $\langle y \rangle$  to be smaller than  $\mu/a$ .

To properly analyze this case, we need to construct a self-consistent solution in the long-time, large- $N$  limit. Assuming a long-time stationary distribution exists, and given that every node has the same initial condition  $y_k(t = 0) = y_0$ , then the uniformity of their stochastic dynamics indicates that all nodes arrive to the same distribution  $\rho$ , for all  $k$ , i.e.,  $\bar{y} = \int y \rho(y) dy$ . The stationary distribution  $\rho(y)$  is obtained by examining the Fokker-Plank equation associated with the stochastic differential equation

$$dy = [\mu y - ay^2 + D(\bar{y} - y)]dt + \sigma y dW, \quad (17)$$

given by

$$\partial_t \rho = -\partial_y \left[ (\mu y - ay^2 + D(\bar{y} - y))\rho - \frac{\sigma^2}{2} \partial_y (y^2 \rho) \right]. \quad (18)$$

This move into simplifying the model via introducing a self-consistency condition is well-precedented in the study of stochastic PDEs [44,45,58,59]. It should also be noted that because the coefficient of  $dt$  depends on  $\rho$  (via  $\bar{y}$ ), this makes the SDE (17) be classified as a McKean-Vlasov equation, which should be expected considering the equation's origins in analyzing large numbers of weakly interacting particles [60–64].

Setting the probability current in Eq. (18) to zero leads to the ordinary differential equation

$$0 = y^2 \rho' + (2 + c_D - c_\mu) y \rho - c_D \bar{y} \rho + c_a \rho y^2, \quad (19)$$

where  $c_D = 2D/\sigma^2$ ,  $c_\mu = 2\mu/\sigma^2$ , and  $c_a = 2a/\sigma^2$ . This admits an unnormalized solution of the form

$$\hat{\rho}(y) = e^{-c_D \bar{y}/y} e^{-c_a y} y^{-2-c_D+c_\mu}. \quad (20)$$

Note that finite  $\bar{y}$  and  $a$  cut off power-law tails of the distribution for small and large  $y$ , respectively, so that all moments of the distribution are now finite.

To convert Eq. (20) to a proper PDF, we need the normalization factor

$$\begin{aligned} 1Z &= \int_0^\infty \hat{\rho}(y) dy \\ &= 2 \left( \frac{c_a}{c_D \bar{y}} \right)^{\frac{1+c_D-c_\mu}{2}} \mathcal{K}_{1+c_D-c_\mu}(2\sqrt{c_D c_a \bar{y}}), \end{aligned} \quad (21)$$

where  $\mathcal{K}_\gamma$  is a modified Bessel function of the second kind. The mean of the distribution is then given by

$$\begin{aligned} 1(y)Z &= \int_0^\infty y \hat{\rho}(y) dy \\ &= 2 \left( \frac{c_a}{c_D \bar{y}} \right)^{\frac{c_D-c_\mu}{2}} \mathcal{K}_{c_D-c_\mu}(2\sqrt{c_D c_a \bar{y}}), \end{aligned} \quad (22)$$

leading to the self-consistency equation

$$\bar{y} = \frac{c_D}{c_a} \left( \frac{\mathcal{K}_\beta(2x)}{\mathcal{K}_{\beta+1}(2x)} \right)^2, \quad (23)$$

where we define  $\beta = c_D - c_\mu$  and  $x = \sqrt{c_D c_a \bar{y}}$  for the sake of convenience. The above equation can be solved numerically; as depicted in Fig. 4, there is excellent agreement between the thus analytically constructed PDF and the result from numerical simulation.

### A. Asymptotic behavior

Going beyond the numerical solution of the self-consistency condition, we would like to gain analytic insight into the behavior of the population, particularly close to the extinction line. To do so, it is convenient to recast Eq. (23) as

$$x = c_D \frac{\mathcal{K}_\beta(2x)}{\mathcal{K}_{\beta+1}(2x)}. \quad (24)$$

The solution now explicitly depends on only two parameters, as  $x = f(\beta, c_D)$ , and it can be plotted as in Fig. 5. Notably, we focus on the region where  $x$  is small, hoping to construct perturbative forms for small  $x \propto \sqrt{\bar{y}}$ .

As depicted in Fig. 5, the small  $x$  region spans two segments: one corresponding to extinction as  $\mu \rightarrow 0$  along the

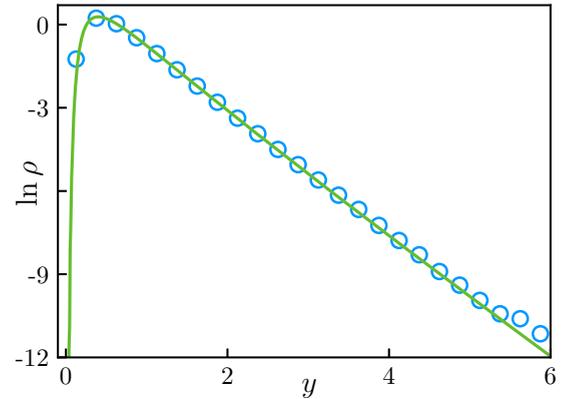


FIG. 4. Simulated vs predicted probability densities for Eq. (17). Circles show simulation results from  $5 \times 10^6$  runs; the solid line depicts the exact steady-state solution of Eq. (20). Simulation was run using the stochastic Runge-Kutta method, with  $D = 0.5$ ,  $\sigma = 1$ ,  $\mu = 1$ , and  $a = 1$ . The value of  $\bar{y}$  was numerically decided in order to obey the self-consistency condition in Eq. (23). The time step of integration was 0.01, with a total integration time of 25 units.

line  $c_D = \beta > 0$ , and another corresponding to  $c_D \rightarrow 0$  for  $\beta < 0$  corresponding to  $\bar{y} \rightarrow 0$  as  $a \rightarrow \infty$ . Only the former is of interest, and for which we need the asymptotic behavior of the right-hand side of Eq. (24) as  $x \rightarrow 0$ . Not surprisingly, given the power-law in Eq. (20), the expansion of  $\mathcal{K}_\beta/\mathcal{K}_{\beta+1}$  for  $\beta > 0$  is nonanalytic, and given by

$$\frac{\mathcal{K}_\beta(2x)}{\mathcal{K}_{\beta+1}(2x)} \simeq x \left( \frac{1}{\beta} + \frac{x^2}{\beta^2(1-\beta)} + \frac{\Gamma(-\beta)}{\Gamma(\beta+1)} x^{2\beta} \right). \quad (25)$$

The leading term in an expansion of Eq. (24) is thus  $c_D/\beta$ , indicating that a nonzero solution exists for  $c_D/\beta > 1$ . However, the next-order term can be either  $x^3$  or  $x^{1+2\beta}$  depending on  $\beta$ , setting up two distinct singular behaviors:

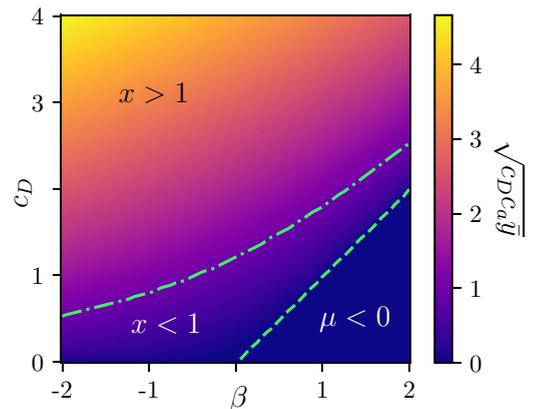


FIG. 5. “Heat map” depicting the dependence of the self-consistent mean  $\bar{y}$  from Eq. (23) on the parameters  $\beta$  and  $c_D$ . The dashed line marks the boundary of the region where  $\mu < 0$ , and the population goes extinct. The dash-dotted line shows where the quantity  $x = \sqrt{c_D c_a \bar{y}}$  is less than 1, denoting the region where a perturbative analysis may be appropriate. (The parameters  $a = 1$  and  $\sigma = 1$  were used for this plot.)

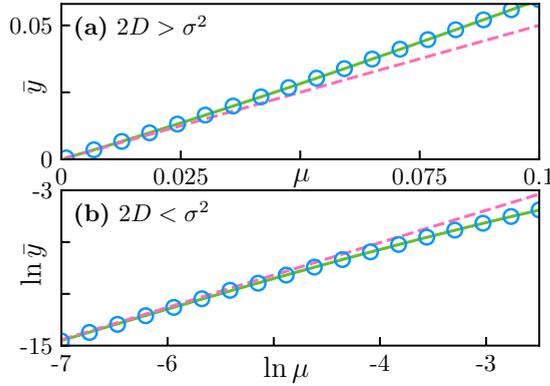


FIG. 6. Singular behavior close to extinction as  $\mu \rightarrow 0$ . The solid curve shows the predicted mean via root-finding on Eq. (23), and the circles depict the simulated means obtained from using these chosen values. The dashed curves show the small  $\mu$  asymptotics from Eq. (28) (exact prefactors given in Appendix A). Here,  $a = 1$ ,  $\sigma = 1$ , and  $\bar{y}$  is selected in line with the self-consistency condition of Eq. (23). In the top panel (a),  $D = 1.0$ , so  $2D > \sigma^2$ , while in (b),  $D = 0.2$ , so  $2D < \sigma^2$ . Numerical simulations used  $5 \times 10^4$  replications with  $dt = 0.01$  across 10 time units for (a) and 50 for (b), with the last 2.5 units being used for sampling.

(i) For  $\beta > 1$ , balancing of the cubic and linear terms leads to  $x^2 \simeq \beta(1 - \beta)c_\mu/c_D$ . As  $\mu \rightarrow 0$ , the mean population size thus vanishes as

$$\bar{y} = \frac{x^2}{c_D c_a} \simeq \frac{\mu}{a} \left(1 - \frac{\sigma^2}{2D}\right). \quad (26)$$

This is the usual “mean-field” singularity close to the (directed percolation) extinction transition for  $\mu \rightarrow 0$ , but with amplitude reduced by  $\sigma^2/2D$ .

(ii) For  $\beta < 1$ , the linear term must be balanced with the nonanalytical correction from  $x^{1+2\beta}$ , resulting in  $x^{2\beta} \propto c_\mu$ . Restoring the prefactors results in a leading singularity of the form

$$\bar{y} = \frac{x^2}{c_D c_a} \simeq \frac{\sigma^4}{4aD} \left( \frac{-\Gamma(c_D) \mu}{\Gamma(-c_D) D} \right)^{\frac{a}{2\beta}}. \quad (27)$$

This is very interesting in that seascape noise with  $\sigma^2 > 2D$  leads to a new universality class with the continuously varying extinction exponent of  $(\sigma^2/2D) > 1$ .

Thus, excluding the exceptional point at  $\beta = 1$ , the singular behavior of the mean is summarized by

$$1\bar{y} \propto \begin{cases} \mu, & 2D > \sigma^2; \\ \mu^{\sigma^2/(2D)}, & 2D < \sigma^2. \end{cases} \quad (28)$$

This is confirmed in Fig. 6, with one case having linear dependence and the other exhibiting a power-law singularity. To gain insight into this unusual scaling, note that averaging Eq. (16) over noise, and using  $\langle y \rangle = \bar{y}$  in the stationary regime, immediately yields

$$\mu\bar{y} = a\langle y^2 \rangle = \frac{\int_0^\infty y^2 \hat{\rho}(y) dy}{\int_0^\infty \hat{\rho}(y) dy} \propto \begin{cases} \bar{y}^2, & c_D > 1; \\ \bar{y}^{1+c_D}, & c_D < 1. \end{cases} \quad (29)$$

As noted before,  $\hat{\rho}(y)$  has a power-law form,  $y^{-2-c_D}$  (for  $\mu \rightarrow 0$ ), which is cut off by  $c_D \bar{y}$  at small  $y$  and  $(c_a)^{-1}$  at large

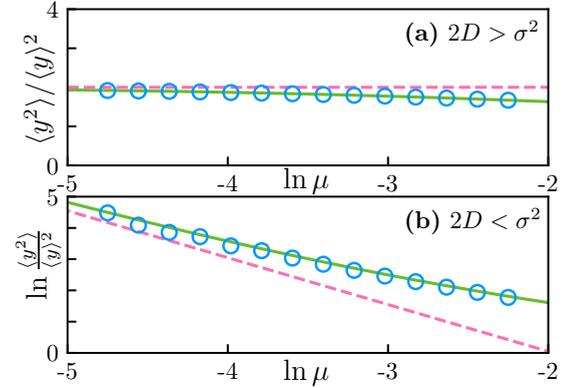


FIG. 7. The ratio of the second to squared-first moments near the extinction transition  $\mu \rightarrow 0$ . The solid curve shows the predicted moment ratio via root-finding on Eq. (23), and the circles depict the simulated ratios obtained from using these chosen values. The dashed curves show the small  $\mu$  asymptotics from Eq. (30) (exact prefactors given in Appendix A). Here,  $a = 1$ ,  $\sigma = 1$ , and  $\bar{y}$  is selected in line with the self-consistency condition of Eq. (23). In the top panel (a),  $D = 1.0$ , so  $2D > \sigma^2$ , while in (b),  $D = 0.2$ , so  $2D < \sigma^2$ . Numerical simulations used  $2 \times 10^6$  replications with  $dt = 0.01$  across 10 time units for (a) and 50 for (b), with the last 2.5 units being used for sampling.

$y$ . The denominator of Eq. (29) is dominated by the short-distance cutoff and scales as  $(c_D \bar{y})^{-1-c_D}$ , while the numerator may be governed by the small- or large- $y$  cutoff depending on whether  $1 - c_D$  is negative or positive. In the former case, the numerator scales as  $(c_D \bar{y})^{1-c_D}$ , while in the latter it scales as  $c_a^{c_D-1}$ , leading to the proportionalities indicated in Eq. (29). Solving for  $\bar{y}$  in the two cases then leads to the scalings in Eq. (28).

The ratio  $\langle y^2 \rangle / \langle y \rangle^2$  is a measure of the breadth of the distribution. Keeping track of prefactors, as shown in full in Appendix A, yields

$$\begin{aligned} \frac{\langle y^2 \rangle}{\langle y \rangle^2} &= \frac{2D}{2D - \sigma^2}, \quad 2D > \sigma^2; \\ \frac{\langle y^2 \rangle}{\langle y \rangle^2} &\propto \mu^{1-\sigma^2/(2D)}, \quad 2D < \sigma^2. \end{aligned} \quad (30)$$

Note that this behavior smoothly connects to that obtained previously for  $\mu \leq 0$ : For  $2D/\sigma^2 > 1$ , we obtain the same finite ratio of  $\langle y^2 \rangle / \langle y \rangle^2$  on both sides of the transition. For  $2D/\sigma^2 < 1$ , the moment ratio diverges as  $\mu \rightarrow 0$ , matching the infinite ratio from before. The difference in behavior is clearly confirmed in Fig. 7. This suggests that parameter space can be divided into two regions: one where the variance is large compared to the mean, and one where they are comparable. The line that separates these regions is set by the ratio of the coupling  $D$  to the seascape noise variance  $\sigma^2$ , and is schematically shown in Fig. 8. (Distinct singular behaviors for moments or cumulants is typically associated with multifractality, and it has been observed in the critical behavior of systems with quenched disorder [65,66].)

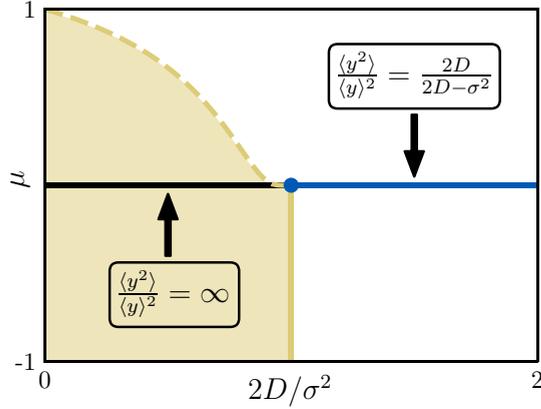


FIG. 8. Phase diagram of Eq. (4) in the large- $N$  limit. Extinction occurs as  $\mu \rightarrow 0$  (solid blue and black lines), with portions to the right and left of the blue dot exhibiting distinct critical behaviors. The vertical line extending from the dot to  $\mu < 0$  separates narrow and broad probability distributions. Broad distributions extend to the shaded region below the crossover (dashed) line, here obtained from the condition [see Eq. (30 b)]  $\mu^{1-\sigma^2/(2D)} \geq 1.5$ .

**V. DEMOGRAPHIC NOISE**

We may well ask if the extinction transition described above persists with the addition of demographic noise, i.e., for the equation

$$dy_k = \mu y_k - ay_k^2 + D(\bar{y} - y_k) + \sigma y_k dW_k + \sigma_d \sqrt{y_k} dW'_k. \tag{31}$$

We first consider demographic noise by itself (with  $\sigma = 0$ ), and then the mixed case ( $\sigma_d \neq 0$  and  $\sigma \neq 0$ ).

**A. Demographic noise with  $\mu = 0$**

For  $\mu = a = 0$ , because of the conserved form of the deterministic part,  $\bar{y} = \langle y \rangle = y_0$ , leading to the stochastic differential equation

$$dy = D(y_0 - y)dt + \sigma_d \sqrt{y} dW. \tag{32}$$

Then, following the same Fokker-Plank procedure as before, we find the exact distribution for  $y$  as

$$\rho(y) = \frac{c'_D c'_b y_0}{\Gamma(c'_D y_0)} e^{-c'_b y} y^{-1+c'_D y_0}, \tag{33}$$

with  $c'_D = 2D/\sigma_d^2$ . This is a so-called  $\Gamma$  distribution with a shape parameter  $k = c'_D y_0$  and a rate parameter  $\lambda = c'_D$ .

Note that the tail of this distribution at large  $y$  is exponential, as opposed to the power-law in the case of seascape noise. This leads to well-behaved moments, and the moment ratio

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} = 1 + \frac{1}{y_0} \frac{\sigma_d^2}{2D}. \tag{34}$$

As an aside, we note that for demographic noise the probability distribution is singular (albeit normalizable) for  $y \rightarrow 0$  (as may be seen in Fig. 9). Consequently, negative moments  $\langle y^{-m} \rangle$  are infinite for  $m > y_0 c_D$ .

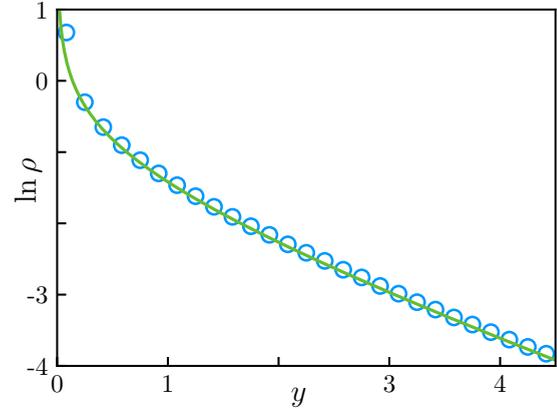


FIG. 9. Simulated vs predicted probability densities for demographic noise. Circles show simulation results from  $5 \times 10^6$  runs of Eq. (32); the solid line depicts the exact steady-state solution from Eq. (33). Simulation was run using the stochastic Runge-Kutta method, with  $y_0 = 1, D = 0.25, \sigma_2 = 1.0, \sigma_d = 0.5$ , and  $\mu = a = 0$ . The time step of integration was 0.01, with a total integration time of 25 units.

**B. Demographic noise with  $\mu < 0$**

Since the population decays to zero, we can ignore the quadratic term as before, and focus on the stochastic differential form

$$dy_k = D\bar{y}(t) - (D + |\mu|)y_k + \sigma_d \sqrt{y_k} dW, \tag{35}$$

with  $\bar{y}(t) = y_0 e^{-|\mu|t}$ . For  $D = 0$ , random fluctuations at a particular location can set  $y_k = 0$  (an absorbing state). At any time  $t$ , the global population is then composed of a heterogeneous set of extinct nodes, and nodes with nonzero  $y_k$ . The initial probability distribution thus develops a  $\delta$ -function at the origin that gradually grows to encompass the entire probability. A finite  $D$  acts as a source that feeds into the population at each location, removing the possibility of local extinction (say of an infection) [58,67,68]. This is despite the fact that this source (from the global population) is itself decaying exponentially. Unlike other extinction models (e.g., [69]), the overall population decay does not arise from individual subpopulations going extinct, but rather from all subpopulations decaying at an even pace. Moreover, while the global decay rate is  $|\mu|$ , Eq. (35) indicates that local nodes relax in response to global and noise fluctuations at a more rapid rate of  $(D + |\mu|)$ .

In the limit of  $D \gg |\mu|$  we can take advantage of the separation of timescales and assume local nodes arrive at a quasisteady state. Ignoring the slow time dependence of  $\bar{y}(t)$ , this quasisteady distribution is given by Eq. (33), with  $y_0$  replaced by  $\bar{y}(t)$ . A typical stochastic node trajectory can be constructed by setting the left-hand side of Eq. (35) to zero; the right-hand side admits a positive solution for  $\sqrt{y_k(t)}$  for any realization of noise, given  $\bar{y} > 0$ .

**C. Demographic noise with  $\mu > 0$**

For  $\mu > 0$ , we again assume uniformity and use the law of large numbers to assert  $\bar{y} = \langle y \rangle$ . This reduces the problem to

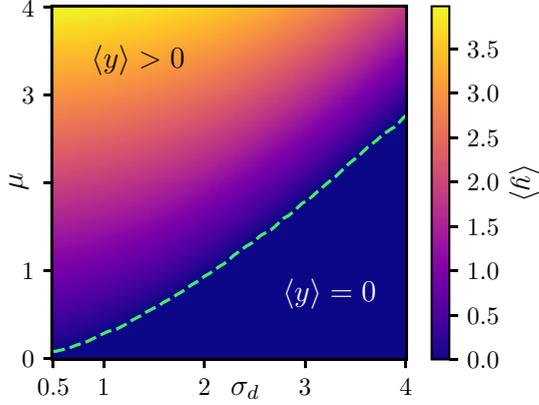


FIG. 10. “Heat map” depicting the dependence of the self-consistent mean  $\bar{y}$  for demographic noise. The shade of the color indicates the result for  $\bar{y}$  from Eq. (40). The dashed line indicates the critical value of  $\mu_c$  below which  $\bar{y} = 0$  exactly. (Root-finding was done with  $a = 1$  and  $D = 1.5$ .)

a single stochastic differential equation

$$dy = \{\mu y - ay^2 + D(\bar{y} - y)\}dt + \sigma_d \sqrt{y} dW. \quad (36)$$

The stationary state of the corresponding Fokker-Plank equation satisfies

$$0 = y\rho' + (c'_D - c'_\mu)y\rho + (1 - c'_D\bar{y})\rho + c'_a y^2 \rho, \quad (37)$$

where  $c'_a = 2a/\sigma_d^2$ . This admits an unnormalized solution of the form

$$\hat{\rho}(y) = y^{-1+c'_D\bar{y}} \exp\left[-(c'_D - c'_\mu)y - \frac{c'_a}{2}y^2\right]. \quad (38)$$

While the distribution still diverges as a power-law close to the origin, a finite  $\bar{y}$  renders the PDF normalizable.

To compute the normalization and moments of the distribution, we note the identity

$$\int y^m \hat{\rho}(y) dy = \frac{1}{2} \left(\frac{\sigma_d^2}{a}\right)^{z+\frac{m}{2}} \left[ \Gamma\left(z + \frac{m}{2}\right) {}_1F_1\left(z + \frac{m}{2}, \frac{1}{2}, r^2\right) + 2r\Gamma\left(\frac{1+m}{2} + z\right) {}_1F_1\left(\frac{1+m}{2} + z, \frac{3}{2}, r^2\right) \right], \quad (39)$$

where  $r = (c'_\mu - c'_D)/\sqrt{2c'_a}$  and  $z = c'_D\bar{y}/2$ , and  ${}_1F_1$  is the Kummer confluent hypergeometric function. While more cumbersome than in the seascape case, the mean can still be obtained from the self-consistency condition

$$\bar{y} = \frac{\int y \hat{\rho}(y) dy}{\int \hat{\rho}(y) dy} \quad (40)$$

by numerical and perturbative analysis, which is further detailed in Appendix B.

However, unlike the case of seascape noise, a finite solution for  $\bar{y}$  does not exist for all  $\mu > 0$ . Instead, a critical value of  $\mu_c$  should be exceeded for a finite mean, as depicted in Fig. 10. An implicit equation determining  $\mu_c$  is provided in Appendix C. In the limit of small noise, it leads to  $\mu_c \propto \sigma_d^2$ ,

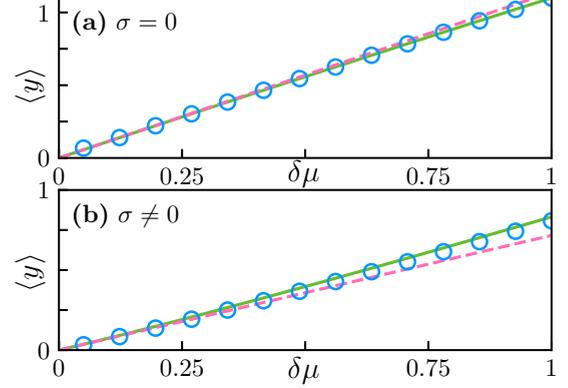


FIG. 11. Critical behavior close to extinction for both demographic noise [Eq. (36)] and mixed noise [Eq. (41)]. The solid curve shows the predicted mean via root-finding on the appropriate self-consistency equations, while the circles depict the simulated means from the stochastic differential equations. The dashed curves mark the predicted linear dependence close to the transition, with slopes given in Appendixes B and D. Here,  $a = 1$ ,  $D = 1$ , and  $\bar{y}$  is selected to be in line with the appropriate self-consistency condition. In panel (a),  $\sigma = 0$  and  $\sigma_d = 1$ ; in (b),  $\sigma = 1$  and  $\sigma_d = 0.25$ . Numerical simulations used  $5 \times 10^4$  replications with  $dt = 0.01$  across 10 time units for (a) and 50 for (b), with the last 2.5 units used for sampling.

while for large noise  $\mu_c \propto \sigma_d \sqrt{\ln \sigma_d}$ . To characterize critical behavior near the extinction transition, we consider  $\mu = \mu_c + \delta\mu$  for  $\delta\mu \ll \mu_c$ . As indicated in the Appendixes, the self-consistency condition of Eq. (40) yields an analytic expansion in the vicinity of  $\mu_c$ , which can be rearranged to yield  $\bar{y} \propto \delta\mu$ . This behavior is confirmed numerically in Fig. 11(a).

We may also inquire about the behavior of higher moments. From averaging the equations of motion, it is easy to check that  $\langle y^2 \rangle = \mu \langle y \rangle / a$ . It can also be checked that (unlike seascape noise) all moments vanish at criticality in the same manner, i.e.,  $\langle y^m \rangle \propto \langle y \rangle \propto (\delta\mu)$ . Consequently, the ratio  $\frac{\langle y^2 \rangle}{\langle y \rangle^2}$  diverges as  $1/(\delta\mu)$  on approaching  $\mu_c$ , as depicted in Fig. 12(a).

#### D. Combined demographic and seascape noise

The novel critical behaviors at extinction observed for seascape noise thus give way to standard behavior of directed percolation with demographic noise. It is thus important to inquire about the nature of the transition when both demographic and seascape noise are present. Since each noise component has an independent physical motivation, a mixed-noise model is quite realistic, and has appeared in a number of contexts [8,9,46,48,55]. The two noise elements can alternatively be represented by a single noise, which, after replacing  $\bar{y}$  for the population average, leads to the stochastic differential equation

$$1dy = \{\mu y - ay^2 + D(\bar{y} - y)\}dt + \sqrt{\sigma_d^2 y + \sigma^2 y^2} dW. \quad (41)$$

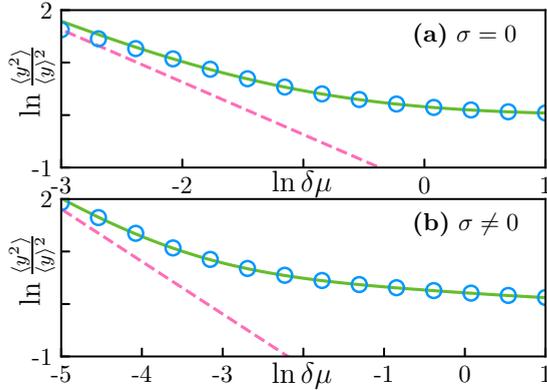


FIG. 12. Scaling of the moment ratio,  $\langle y^2 \rangle / \langle y \rangle^2$ , for both demographic noise [Eq. (36)] and mixed noise [Eq. (41)]. The solid curve shows the predicted moments via root-finding on the appropriate self-consistency equations, while the circles depict the simulation results. The dashed curves mark the predicted small  $\delta\mu$  scaling, with exponent  $-1$  and prefactors in Appendixes B and D. Here,  $a = 1$ ,  $D = 1.5$ , and  $\bar{y}$  is selected to be in line with the appropriate self-consistency condition. In panel (a),  $\sigma = 0$  and  $\sigma_d = 1$ ; in (b),  $\sigma = 1$  and  $\sigma_d = 0.25$ . Numerical simulations used  $2 \times 10^4$  replications with  $dt = 0.01$  across 10 time units for (a) and 50 for (b), with the last 2.5 units being used for sampling.

Analysis of the corresponding Fokker-Planck equation leads to a stationary distribution proportional to

$$\hat{\rho}(y) = y^{-1+\bar{y}c'_d} \left( y + \frac{\sigma_d^2}{\sigma^2} \right)^{-1-\bar{y}c'_d+c_\mu-c_D+q} e^{-c_a y}, \quad (42)$$

where  $q = 2a\sigma_d^2/\sigma^4$ . Note that the (integrable) divergence close to zero (proportional to  $y^{-1+\bar{y}c'_d}$ ) is identical to that of pure demographic noise. On the other hand, the exponential decay at large  $y$  is the same as that of seascape noise, although the subleading power-law is modified by an additional power of  $y^{1-\bar{y}c'_d+q}$ .

Since the extinction transition is dominated by the behavior for  $y$  close to zero, its critical behavior turns out to be the same as that of demographic noise. Indeed,  $\bar{y} = \langle y \rangle$  vanishes proportionately to  $\delta\mu$  [as seen in Fig. 11(b)], and the moment ratio,  $\langle y^2 \rangle / \langle y \rangle^2$ , still scales inversely with  $\delta\mu$  [as verified in Fig. 12(b)]. This is shown explicitly in Appendix D. Such scaling exists regardless of the ratio of  $\sigma_d$  to  $\sigma$ , indicating that any amount of demographic noise will destroy the unusual extinction transition observed in the seascape case. Thus the novel universality and broad distributions, characteristic of seascape noise close to an extinction transition, disappear in the presence of (expected) demographic noise.

## VI. DISCUSSION

Both seascape fluctuations and demographic noise have well-defined origins. The former arises from natural variations in population fitness and access to resources, whereas the latter is the result of moving from a discrete to a continuum description. Both are unavoidable in real-world systems, and neglecting one or the other can cause drastically incomplete

predictions of the breadth of a population. In particular, seascape fluctuations broaden the tail of the distribution at large values, while demographic stochasticity controls its behavior close to zero.

To understand the importance of seascape fluctuations, it is instructive to consider Eq. (3) in the limit of  $a = 0$  and  $D = 0$ . At each point  $\ln y$  now performs a random walk, resulting in broad log-normal distributions for which characterizing the population in terms of mean  $\langle y \rangle$  and variance  $\langle y^2 \rangle_c$  is inadequate. A finite diffusion coefficient (still with  $a = 0$ ) is expected to modify the log-normal distribution. The resulting behavior, in the universality class of directed polymers in random media (DPRM), is highly dependent on dimensionality: In one dimension it leads to the celebrated Tracy-Widom distribution [35,38,70], while in dimensions larger than 2 a critical value of  $D_c$  separates broad and narrow distributions [33,40,71]. To circumvent difficulties associated with spatial dimensionality, in this paper we consider a mean-field limit [Eq. (4)] in which the parameter  $D$  accounts for migration between any pair of sites, irrespective of their separation. In this case, seascape noise of strength  $\sigma$  generates a power-law tail in the distribution for large populations that falls off with exponent  $2 + 2D/\sigma^2$ . Much like the case of DPRM at high dimensions, this signals a transition from broad to narrow distributions for  $D > D_c = \sigma^2/2$ .

For  $a = 0$ , a finite  $\mu$  simply makes the mean,  $\bar{y}$ , time-dependent (proportional to  $e^{\mu t}$ ) without modifying the shape of the distribution. For  $\mu > 0$ , a finite  $a$  is needed to curtail the exponential growth of the population; a self-consistency requirement now enables computing a stationary  $\bar{y}$ . The finite  $a$  also leads to an exponential decay of the distribution at large values, resulting in well-behaved moments. The most interesting aspect of the problem is then the nature of the extinction transition as  $\mu \rightarrow 0$ : For  $D > D_c$ , the mean (and all other moments) vanish linearly with  $\mu$ , as expected for a mean-field extinction transition. However, for  $D < D_c$  the mean vanishes as  $\mu^{\sigma^2/(2D)}$ , with higher moments vanishing with other exponents (harking back to the broad distribution expected for  $\mu = 0$ ).

While the above unconventional critical behavior is an accurate description of Eq. (4) as  $\mu \rightarrow 0$ , its relevance to an actual species extinction must also account for demographic stochasticity. For  $D = 0$ , demographic noise in Eq. (5) is incompatible with a continuous probability distribution, with fluctuations causing local extinctions resulting in a growing  $\delta$ -function in the PDF at the absorbing point  $y = 0$ . A finite  $D$  removes the  $\delta$ -function by seeding new population at all sites through migration from other sites, resulting in the steady-state distribution of Eq. (33), with a normalizable divergence at the origin. (For  $|\mu| \ll D$ , the same distribution, albeit with a time-dependent  $\bar{y}(t)$ , can be used to describe growing or shrinking populations.) However, the boundary between growth and extinction is no longer at  $\mu = 0$  in the presence of demographic noise, and the self-consistency condition should be used to identify a critical value of  $\mu_c$ . The nature of the extinction transition at  $\mu_c$  is now conventional, belonging to the expected directed percolation universality class. Finally, we find that when both seascape and demographic noise are present, the resulting extinction transition (at a finite  $\mu_c$ ) is again conventional. This is not too surprising as extinction

characterizes behavior when  $y \rightarrow 0$ , where demographic fluctuations are paramount.

The overarching theme of this investigation is the emphasis on the need to characterize the full distribution of a population and not just its mean. In the course of this investigation, in the mean-field limit, we have encountered a few distributions of some repute: For seascape noise, a scaled inverse chi-squared distribution appears; for demographic noise, a  $\Gamma$  distribution shows up, and when both noises are mixed (for  $\mu = a = 0$ ), a rescaled  $\beta$  prime distribution manifests. The special functions characterizing these distributions are typically solutions of relatively simple differential equations. In our context, these equations appear naturally in computing steady states of Fokker-Planck equations, providing examples of their applicability.

The Covid-19 epidemic has motivated myriad current studies of spread and control of epidemics [72–75]. With notable exceptions (e.g., Ref. [69]), most studies follow a number of time-dependent quantities that are implicitly assumed to characterize the whole distribution. The approach of this paper can be used to examine actual distributions via the self-consistency condition in the mean-field limit, for multiple stochastic equations, generalizing Eq. (41). Even for a single quantity, we may generalize the exponent of the stabilizing nonlinear term from 2 to an arbitrary  $\alpha$ . This is not without motivation, since instead of an embedded logistic equation at every point in space, we would now have a *Richards' equation*. The Richards' equation acts as a generalization of logistic growth, and it has been used in a variety of ecological models [76,77]. Indeed, most results presented in this paper have natural generalizations for  $\alpha > 1$ , including corresponding distributions. The most notable complexity arises in the self-consistency equation for the mean, which requires numerical analysis and lacks closed forms.

Another interesting query is the applicability of the mean-field results to the finite dimensional extinction problem. There is a certain richness of dimensional dependence in directed percolation models, but we may nonetheless expect some qualitative behavior in the mean-field case to carry over to finite dimensions [18]. For example, in the important cases of one and two dimensions, the limiting distribution for  $a = 0$  arising from Eq. (3) is always broad. It would be interesting to investigate the nature of the extinction transition with seascape noise (with and without demographic noise) in these dimensions.

Finally, we note that certain predictions in this model may be experimentally replicable. Well-mixed microbial populations are often represented via a mean-field migration model, which we employ here. While tracking entire distributions is cumbersome (albeit not impossible), the mean and standard deviation of the population should be relatively easy to track. Our model predicts that the ratio of these quantities makes a dramatic change, passing from finite to very large as the

strength of seascape noise is increased above a threshold value. The fitness of a population can be controlled via the resources afforded to the microbes, and local fluctuations in this quantity can be constructed by randomizing access to resources (e.g., light levels). While the results presented in this paper may not be robust to various perturbations, an experiment probing the effects of seascape fluctuations in fitness should yield highly informative results.

## ACKNOWLEDGMENTS

This research was supported by James S. McDonnell Foundation Award No. 220020540 (B.O.-L.), as well as by NSF through Grants No. DMR-1708280 and No. PHY-2026995 (M.K.).

## APPENDIX A: MOMENTS FOR SEASCAPE NOISE

We will elaborate upon the case of seascape noise with positive fitness, that is,

$$dy = [\mu y - ay^2 + D(\bar{y} - y)]dt + \sigma y dW, \quad (\text{A1})$$

with  $\mu > 0$ . In the main body of the paper we find that, in the appropriate limit, the distribution of  $y$  is proportional to

$$\hat{\rho}(y) = e^{-cd\bar{y}/y} e^{-c_a y} y^{-2-\beta}, \quad (\text{A2})$$

where we used the law of large numbers to assert  $\bar{y} = \langle y \rangle$ . We further define  $c_D = 2D/\sigma^2$ ,  $c_a = 2a/\sigma^2$ , and  $\beta = 2(D - \mu)/\sigma^2$ .

To get the right normalization  $Z$  for the distribution, and to choose a self-consistent value of  $\bar{y}$ , we need to use the unnormalized moments

$$\int_0^\infty y^m \hat{\rho}(y) dy = 2 \left( \frac{c_a}{c_D \bar{y}} \right)^{(1+\beta)/2} \mathcal{K}_{\beta+1}(2\sqrt{c_D c_a \bar{y}}). \quad (\text{A3})$$

Therefore, we have that

$$\sqrt{\frac{c_a}{c_D}} \bar{y} = \frac{\mathcal{K}_\beta(2\sqrt{c_D c_a \bar{y}})}{\mathcal{K}_{\beta+1}(2\sqrt{c_D c_a \bar{y}})}, \quad (\text{A4})$$

as the self-consistent restriction on  $\langle y \rangle = \bar{y}$ .

Because we have assumed that  $\bar{y} = \langle y \rangle$  and  $\bar{y}$  is constant in time, we can take the expectation of both sides of the dynamics to get  $\mu \langle y \rangle = a \langle y^2 \rangle$ . Therefore, we have that

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} = \frac{\mu/a}{\langle y \rangle}. \quad (\text{A5})$$

So if we want to understand the ratio  $\langle y^2 \rangle / \langle y \rangle^2$  in the extinction limit, that is, as  $\mu \rightarrow 0$  and  $\bar{y} \rightarrow 0$ , then all we need to do is understand the asymptotics of (A4) alone.

For the sake of brevity we will define  $x = \sqrt{c_D c_a \bar{y}}$ . The most convenient form of  $\mathcal{K}$ , the modified Bessel function of the second kind, is

$$2\mathcal{K}_\beta(2x) = \frac{\pi/2}{\sin(\pi\beta)} \sum_{m=0}^{\infty} \frac{x^{2m-\beta}}{m! \Gamma(m-\beta+1)} - \frac{\pi/2}{\sin(\pi\beta)} \sum_{m=0}^{\infty} \frac{x^{2m+\beta}}{m! \Gamma(m+\beta+1)}. \quad (\text{A6})$$

Thus, limiting to the lowest-order terms in  $x$ , the right-hand side of Eq. (A4) becomes

$$\begin{aligned} \frac{\mathcal{K}_\beta(2x)}{\mathcal{K}_{\beta+1}(2x)} &\simeq (-1) \left( \frac{x^{-\beta}}{\Gamma(-\beta+1)} + \frac{x^{-\beta+2}}{\Gamma(-\beta+2)} - \frac{x^\beta}{\Gamma(\beta+1)} - \frac{x^{\beta+2}}{\Gamma(-\beta+2)} \right) \\ &\times \left( \frac{x^{-\beta-1}}{\Gamma(-\beta)} + \frac{x^{-\beta+1}}{\Gamma(-\beta+1)} - \frac{x^{\beta+1}}{\Gamma(\beta+2)} - \frac{x^{\beta+3}}{\Gamma(\beta+3)} \right)^{-1}. \end{aligned} \quad (\text{A7})$$

Disambiguating which terms are actually most relevant depends on the choice of  $\beta$ , with there being three regimes of note. We shall elaborate on each of these in turn.

### 1. $\beta > 1$

In this case, the  $x^{-\beta}$  and  $x^{-\beta+2}$  terms dominate the numerator of (A7), whereas the denominator is dominated by the  $x^{-\beta-1}$  and  $x^{-\beta+1}$  terms. Therefore, we find that

$$\frac{\mathcal{K}_\beta(2x)}{\mathcal{K}_{\beta+1}(2x)} \simeq \frac{x}{\beta} \left( 1 + \frac{x^2}{\beta(1-\beta)} \right). \quad (\text{A8})$$

Since  $x \propto \sqrt{\bar{y}}$ , the  $\sqrt{\bar{y}}$  on the left-hand side of Eq. (A4) cancels out the leading  $x$ , hence the need to include the second-order correction. From here, we can easily solve for  $\bar{y}$  to get

$$\bar{y} \simeq \frac{\mu}{D} \frac{\beta(\beta-1)}{c_D^2}. \quad (\text{A9})$$

Expanding  $\beta$  in the small- $\mu$  limit then leads to

$$\bar{y} \simeq \frac{\mu}{a} \left( 1 - \frac{\sigma^2}{2D} \right), \quad (\text{A10})$$

which is linear in  $\mu$ , as stated in the main text. Moreover, we get

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} = \frac{2D}{2D - \sigma^2} + O(\mu), \quad (\text{A11})$$

which is consistent with the results from the  $\mu = 0$  analysis for  $2D > \sigma^2$ .

### 2. $-1 < \beta < 1$

Here, the numerator of (A7) is dominated by the  $x^\beta$  and  $x^{-\beta}$  terms, and the only term from the denominator that survives is the  $x^{-\beta-1}$  term. So

$$\frac{\mathcal{K}_\beta(2x)}{\mathcal{K}_{\beta+1}(2x)} \simeq \frac{x}{\beta} \left( 1 + \frac{\Gamma(-\beta)}{\Gamma(\beta)} x^{2\beta} \right). \quad (\text{A12})$$

The leading  $x$  cancels out the  $\bar{y}$  on the left-hand side of (A4), leaving us with the mean being set by

$$\bar{y} \simeq \frac{1}{c_a c_D} \left( \frac{-\Gamma(\beta) \mu}{\Gamma(-\beta) D} \right)^{1/\beta}. \quad (\text{A13})$$

In the small  $\mu$  limit,  $\beta \rightarrow c_D$ , so the lowest-order behavior in  $\mu$  is given by

$$\bar{y} \simeq \frac{1}{c_a c_D} \left( \frac{-\Gamma(c_D) 1}{\Gamma(-c_D) D} \right)^{1/c_D} \mu^{1/c_D}. \quad (\text{A14})$$

So if  $|\beta| < 1$ , the mean goes as  $\mu^{\sigma^2/(2D)}$ . Moreover, the moment ratio is given by

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} \simeq c_D^{1+1/c_D} \left( \frac{-\Gamma(-c_D)}{\Gamma(c_D)} \right)^{1/c_D} c_\mu^{1-1/c_D}. \quad (\text{A15})$$

This provides all the prefactors neglected in the main body, Eq. (30).

### 3. $\beta < -1$

For this region, the numerator of (A7) is dominated by the  $x^\beta$  and  $x^{\beta+2}$  terms, and the denominator is dominated by the  $x^{\beta+1}$  and  $x^{\beta+3}$  terms. So

$$\frac{\mathcal{K}_\beta(2x)}{\mathcal{K}_{\beta+1}(2x)} \simeq \frac{-(\beta+1)}{x} \left( 1 + \frac{x^2}{(\beta+1)(\beta+2)} \right). \quad (\text{A16})$$

As before, the second-order expansion is required. Solving for  $\bar{y}$  gives us

$$\bar{y} = \frac{-(\beta+1)(\beta+2)}{c_a(\beta+2+c_D)}, \quad (\text{A17})$$

and therefore

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} = \frac{\beta}{\beta+1} \left( 1 + \frac{c_D}{\beta+2} \right)^2. \quad (\text{A18})$$

Unlike the previous two cases, there is no need to do a small- $\mu$  analysis here. The only way for  $\beta = c_D - c_\mu$  to be negative is for  $\mu$  to be greater than  $D$ . This is not possible in the limit of small  $\mu$ , so this regime is irrelevant for our purposes.

## APPENDIX B: MOMENTS FOR DEMOGRAPHIC NOISE

Here, we will show the extinction behavior of our mean-field model under demographic noise. In particular, we will look at

$$dy_k = [\mu y_k - a y_k^2 + D(\bar{y} - y_k)] dt + \sigma_d \sqrt{\bar{y}_k} dW_k. \quad (\text{B1})$$

As before, we use the law of large numbers to assert that the ensemble average, spatial average, and initial condition are identical. If this holds true, then there is some stationary density  $\rho$  that is identical for every  $y_k$ , and we can transform the above equation into a Fokker-Planck equation, where

$$0 = -\partial_t \rho = \partial_y \{ [\mu y - a y^2 + D(\bar{y} - y)] \rho \}. \quad (\text{B2})$$

This simplifies to

$$0 = y \rho' + (1 - c_D \bar{y}) \rho + (c_D - c_\mu) y \rho + c_a y^2 \rho, \quad (\text{B3})$$

with  $c'_D = 2D/\sigma_d^2$ ,  $c'_\mu = 2\mu/\sigma_d^2$ , and  $c'_a = 2a/\sigma_d^2$  as usual. This admits an unnormalized solution of the form

$$\hat{\rho}(y) = y^{-1+c'_D \bar{y}} \exp[-(c'_D - c'_\mu) y - (c'_a/2) y^2]. \quad (\text{B4})$$

To get the moments of  $y$ , it is expedient to define  $z = D\bar{y}/\sigma_d^2$  and  $r = (-D + \mu)/\sqrt{a\sigma_d^2}$ . Using these definitions, we find that

$$1\bar{y} = \frac{\int y\hat{\rho}(y)dy}{\int \hat{\rho}(y)dy} = \sqrt{\frac{2}{c'_a}} \frac{\Gamma(\frac{1}{2} + z) {}_1F_1(\frac{1}{2} + z, \frac{1}{2}, r^2) + 2r\Gamma(1 + z) {}_1F_1(1 + z, \frac{3}{2}, r^2)}{\Gamma(z) {}_1F_1(z, \frac{1}{2}, r^2) + 2r\Gamma(\frac{1}{2} + z) {}_1F_1(\frac{1}{2} + z, \frac{3}{2}, r^2)}, \quad (\text{B5})$$

where  ${}_1F_1$  is the Kummer confluent hypergeometric function.

We want our analysis to take place near  $\mu = \mu_c$ , so  $\bar{y}$  should be close to zero. The most practical way to analyze the extinction behavior is to look at both the numerator and denominator of the expression (B5) for  $\bar{y}$  in the limit of small  $z$ , since if  $\bar{y}$  is small, then so is  $z \propto \bar{y}$ . Specifically, we have

$$\bar{y} \simeq \sqrt{\frac{2}{c'_a}} \frac{A + Bz}{Ez^{-1} + F}, \quad (\text{B6})$$

where  $A$ ,  $B$ ,  $E$ , and  $F$  are constants obtained by expanding in  $z$ , with  $A$  and  $B$  given by

$$1A = e^{r^2} \sqrt{\pi} [1 + \text{erf}(r)], \quad (\text{B7})$$

$$B = -e^{r^2} \gamma_E \sqrt{\pi} \text{erf}(r) + \sqrt{\pi} {}_1F_1^{(1,0,0)}\left(\frac{1}{2}, \frac{1}{2}, r^2\right) + \sqrt{\pi} \Gamma_P(0, 1/2) e^{r^2} + 2r {}_1F_1^{(1,0,0)}\left(1, \frac{3}{2}, r^2\right), \quad (\text{B8})$$

and  $E$  and  $F$  are given by

$$1E = 1, \quad (\text{B9})$$

$$F = -\gamma_E + \pi \text{erfi}(r) + {}_1F_1^{(1,0,0)}\left(0, \frac{1}{2}, r^2\right), \quad (\text{B10})$$

with  $\Gamma_P$  being the polygamma,  $\text{erf}$  the error function,  $\text{erfi}$  the imaginary error function, and  $\gamma_E \approx 0.577$  is the Euler-Mascheroni constant.

Using these approximate forms, it is easy to see that

$$\bar{y} = \frac{-2c'_D A - \sqrt{2c'_a} E}{c'_D c'_D B - \sqrt{2c'_a} F}. \quad (\text{B11})$$

Let us assume that  $\mu_c$  is the critical value of  $\mu$  where  $\bar{y}$  goes from zero to nonzero. The above form allows us to obtain the critical  $\mu$ , since it implies that  $\mu_c$  must satisfy  $c'_D A = \sqrt{2c'_a}$ , or

$$\sqrt{\frac{a}{\pi}} \frac{\sigma_d}{D} = e^{r_c^2} [1 + \text{erf}(r_c)], \quad (\text{B12})$$

with  $r_c = (-D + \mu_c)/\sqrt{a\sigma_d^2}$ .

If we are instead interested in the behavior of the mean near zero, then we can substitute  $\mu = \mu_c + \delta\mu$  for infinitesimal  $\delta\mu$ , and find

$$\bar{y} = \frac{-2\delta A}{c'_D B - \sqrt{2c'_a} F} \delta\mu, \quad (\text{B13})$$

where

$$\delta A = \frac{2}{\sqrt{a\sigma_d}} - \frac{2\pi(D - \mu_c)}{a\sigma_d^2} e^{r_c^2} [1 - \text{erf}(-r_c)]. \quad (\text{B14})$$

This means that our predicted mean for demographic noise scales as  $\bar{y} \propto \delta\mu = \mu - \mu_c$  near extinction, with a slope that is exactly predictable from the above equation.

By taking the expectation of both sides of the dynamics, we attain  $\langle y^2 \rangle = (\mu/a)\langle y \rangle$ . So if we plug this into  $\langle y^2 \rangle / \langle y \rangle^2$  and only keep the lowest-order terms in  $\delta\mu$ , we get

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} = \frac{\mu_c + \delta\mu}{a\bar{y}} \propto \frac{1}{\delta\mu}. \quad (\text{B15})$$

Therefore, unlike in the case of seascape noise, the moment ratio always diverges as  $1/\delta\mu$ .

### APPENDIX C: $\mu_c$ FOR DEMOGRAPHIC NOISE

Here we will find approximate forms for the critical fitness  $\mu_c$ , at which the mean population goes from zero to nonzero. In the previous Appendix, we demonstrated that Eq. (B12) sets the condition for  $\mu_c$ . If we let  $r_\mu = \mu_c/(\sigma_d\sqrt{a})$  and  $r_D = D/(\sigma_d\sqrt{a})$ , then this condition can be written as

$$\frac{1}{r_D\sqrt{\pi}} = e^{(r_\mu - r_D)^2} [1 + \text{erf}(r_\mu - r_D)], \quad (\text{C1})$$

where  $\text{erf}$  is the error function. In the following, we examine separately the large and small noise limits of the above equation.

#### 1. $\sigma_d \gg 1$

Since  $r_D \propto 1/\sigma_d$ , we might expect this quantity to be small. Let us assume that  $r_\mu$  is large, and further that  $r_\mu r_D$  is small. These conditions can be checked for self-consistency at the end.

Taking these assumptions in hand, we have

$$1 \frac{1}{\sqrt{\pi} r_D} = e^{(r_\mu - r_D)^2} [1 + \text{erf}(r_\mu - r_D)] \simeq 2e^{r_\mu^2}. \quad (\text{C2})$$

By assumption, we were allowed to neglect the  $e^{-2r_\mu r_D}$  term, as well as approximate the error function by a constant. We now obtain  $r_\mu \simeq \sqrt{-\ln(2\sqrt{\pi} r_D)}$ , and therefore we obtain

$$\mu_c \simeq \sigma_d \sqrt{-\ln\left(2\sqrt{\frac{\pi}{a}} \frac{D}{\sigma_d}\right)}. \quad (\text{C3})$$

Notice that  $r_\mu \propto \sqrt{\ln(\sigma_d)}$  and  $r_\mu r_D \propto \ln(\sigma_d)/\sigma_d$ , making our initial assumptions self-consistent.

#### 2. $0 < \sigma_d \ll 1$

An efficient way to rewrite Eq. (C1) is

$$\frac{1}{r_D\sqrt{\pi}} = \text{erfcx}(r_D - r_\mu), \quad (\text{C4})$$

in terms of the scaled complementary error function,  $\text{erfcx}$ . Since  $\sigma_d$  is small,  $r_D$  is necessarily large. If we assume  $r_\mu$  is small, then we can take the first-order Taylor series of  $\text{erfcx}$  to get

$$\begin{aligned} 1/r_\mu &= \frac{-(\sqrt{\pi}r_D)^{-1} + \text{erfcx}(r_D)}{\text{erfcx}'(r_D)} \\ &= \frac{-(\sqrt{\pi}r_D)^{-1} + \text{erfcx}(r_D)}{-2/\sqrt{\pi} + 2r_D\text{erfcx}(r_D)} \\ &= \frac{1}{2r_D}. \end{aligned} \quad (\text{C5})$$

Since  $r_D$  is large,  $r_\mu$  is small and self-consistent, leading to

$$\mu_c = a \frac{\sigma_d^2}{2D}. \quad (\text{C6})$$

Another way to prove this case is by using the fact that  $c'_D$  is large, so we can approximate the unnormalized distribution (B4) by

$$\hat{\rho}(y) \simeq y^{-1+c'_D\bar{y}} e^{-c'_D y}. \quad (\text{C7})$$

The second moment is exactly solvable here, with  $\langle y^2 \rangle = \bar{y}^2 + \bar{y}/c'_D$ . If we then take the expectation of both sides of the dynamics (B1) and plug in the second moment, we find that

$$\partial_t \bar{y} = \left( \mu - \frac{a}{c'_D} \right) \bar{y} - a \bar{y}^2. \quad (\text{C8})$$

$$\bar{y} = \frac{s \sin(\pi t) \Gamma(t) \Gamma(1+z') {}_1\mathcal{F}_1(1+z', 1-t, q) + q^t \Gamma(-t) \Gamma(1+t+z') {}_1\mathcal{F}_1(1+t+z', 1+t, q)}{\pi \left[ -\Gamma(z') {}_1\mathcal{F}_1^R(z', -t, q) + q^{1+t} \Gamma(1+t+z') {}_1\mathcal{F}_1^R(1+t+z', 2+t, q) \right]}, \quad (\text{D3})$$

with  ${}_1\mathcal{F}_1$  being the Kummer hypergeometric function and  ${}_1\mathcal{F}_1^R$  being its regularized version. In the extinction limit,  $\bar{y}$  must be small, and so  $z'$  should be too. In such a limit, we find

$$\bar{y} \simeq \frac{s \sin(\pi t)}{\pi} \frac{A' + B' z'}{E' / z' + F'}, \quad (\text{D4})$$

which simplifies into

$$\bar{y} \simeq \frac{-\sigma_d^2}{2D} \frac{2D \sin(\pi t) A' - \pi \sigma^2 E'}{2D \sin(\pi t) B' - \pi \sigma^2 F'}, \quad (\text{D5})$$

where

$$\begin{aligned} 1A' &= -te^q q^t \Gamma(-t) \Gamma(t) + e^q q^t \Gamma(-t) \Gamma(1+t) \\ &\quad + te^q q^t \Gamma(t) \Gamma(-t, q), \end{aligned} \quad (\text{D6})$$

$$\begin{aligned} B' &= te^q \gamma_E \Gamma(t) q^t \Gamma(-t) - te^q \gamma q^t \Gamma(t) \Gamma(-t, q) \\ &\quad + \Gamma(t) {}_1\mathcal{F}_1^R(1, 1-t, q) \\ &\quad + e^q q^t \Gamma_P(0, 1+t) \Gamma(-t) \Gamma(1+t) \\ &\quad + q^t \Gamma(-t) \Gamma(1+t) {}_1\mathcal{F}_1^R(1+t, 1+t, q), \end{aligned} \quad (\text{D7})$$

$$E' = -1/\Gamma(-t), \quad (\text{D8})$$

This suggests that  $\bar{y}$  converges to zero whenever  $\mu < a/c'_D$ , which retrieves the equation for  $\mu_c$  (C6).

So for small noise, the critical fitness scales as  $\sigma_d^2$ , but for large noise it scales as  $\sigma_d \sqrt{\ln(\sigma_d)}$ , as described in the main body of the paper.

#### APPENDIX D: MOMENTS FOR MIXED NOISE

Here, we look at the case with mixed seascape and demographic noise, that is,

$$dy = [\mu y - ay^2 + D(\bar{y} - y)]dt + \sqrt{\sigma^2 y^2 + \sigma_d^2 y} dW, \quad (\text{D1})$$

where  $\sigma$  and  $\sigma_d$  are the respective amplitudes of seascape and demographic noises. As always, we assume uniform initial conditions and the existence of a stationary distribution  $\rho$  with a self-consistent mean  $\langle y \rangle = \bar{y}$ . By transforming the above into a Fokker-Planck equation, we find the unnormalized stationary distribution

$$\hat{\rho}(y) = e^{-c_a y} y^{-1+z'} (y+s)^{-1-t-z'}, \quad (\text{D2})$$

where  $c_a = 2a/\sigma^2$ ,  $s = \sigma_D^2/\sigma^2$ ,  $z' = 2D\bar{y}/\sigma_d^2$ ,  $q = 2a\sigma_d^2/\sigma^4$ , and  $t = 2(D-\mu)/\sigma^2 - q$ .

To get the self-consistent mean, we need to use the following equation:

$$F' = \gamma/\Gamma(-t) + \int_0^q u^t e^u du - {}_1\mathcal{F}_1^R(1,0,0)(0, -t, q), \quad (\text{D9})$$

where  $\gamma_E \approx 0.577$  is the Euler-Mascheroni constant,  $\Gamma_P$  is the polygamma, and  $\Gamma(x, y)$  is the incomplete gamma function  $\int_y^\infty u^{x-1} e^{-u} du$ .

We can then assert that there is some  $\mu_c$  (with corresponding  $t_c$ ) where the mean transitions from zero to nonzero. Given this, and assuming  $\mu = \mu_c + \delta\mu$ , with  $c_{\delta\mu} = 2\delta\mu/\sigma^2$ , we find for small  $\delta\mu$  that

$$\bar{y} \simeq \frac{\pi \delta E' + \pi c_D \cos(t_c \pi) A' - c_D \sin(\pi t_c) \delta A'}{c'_D \sin(\pi t) B' - \pi c'_D F'} c_{\delta\mu}, \quad (\text{D10})$$

where  $c_D = 2D/\sigma^2$ ,  $c'_D = 2D/\sigma_d^2$ ,

$$\begin{aligned} 1\delta A' &= -e^q q^{t_c} \{ \Gamma(t_c) \Gamma(-t_c, q) \\ &\quad + \Gamma(t_c) \Gamma(-t_c, q) [t_c \ln(q) + t_c \Gamma_P(0, t_c)] \\ &\quad - \Gamma(-t_c) \Gamma(t_c) [1 + t_c \Gamma_P(0, t_c)] \\ &\quad + \Gamma(-t_c) \Gamma(t_c) t_c \Gamma_P(0, 1+t_c) \\ &\quad - t_c \Gamma(t_c) \Gamma^{(1,0)}(-t_c, q) \}, \end{aligned} \quad (\text{D11})$$

and

$$\delta E' = \Gamma_P(0, -t_c)/\Gamma(-t_c). \quad (\text{D12})$$

In particular, this means that near extinction, the mean scales as  $\bar{y} \propto \mu - \mu_c$ , with the scaling slope known from the above.

As in the previous seascape and demographic noise cases, we can attain the second moment simply by taking the

expectation of both sides of the dynamics to get  $\langle y^2 \rangle = (\mu/a)\langle y \rangle$ . From here it is easy to see that

$$\frac{\langle y^2 \rangle}{\langle y \rangle^2} \propto \frac{1}{\bar{y}} \propto \frac{1}{\delta\mu}. \quad (\text{D13})$$

So despite the presence of seascape noise, the scaling of the moment ratio near extinction is identical to the purely demographic noise case.

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