Extinction in population dynamics

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We study a generic reaction-diffusion model for single-species population dynamics that includes reproduction, death, and competition. The population is assumed to be confined in a refuge beyond which conditions are so harsh that they lead to certain extinction. Standard continuum mean field models in one dimension yield a critical refuge length $L_c$ such that a population in a refuge larger than this is assured survival. Herein we extend the model to take into account the discreteness and finiteness of the population, which leads us to a stochastic description. We present a particular critical criterion for likely extinction, namely, that the standard deviation of the population be equal to the mean. According to this criterion, we find that while survival can no longer be guaranteed for any refuge size, for sufficiently weak competition one can make the refuge large enough (certainly larger than $L_c$) to cause extinction to be unlikely. However, beyond a certain value of the competition rate parameter it is no longer possible to escape a likelihood of extinction even in an infinite refuge. These unavoidable fluctuations therefore have a severe impact on refuge design issues.

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I. INTRODUCTION

Population dynamics is a venerable and important subject that has been studied thoroughly for decades [1]. Understanding ecological systems is interesting in itself, as are applications of this understanding to a large variety of important practical problems such as, for example, the spread of a virus or other disease over a host population [2], and strategies for the elimination of pests or for the protection of endangered species [3]. These examples point to the importance of the study of the extinction of populations and of the conditions that lead to extinction as well as those that protect against it.

The oldest population models pose relatively simple rate equations for a total population, e.g., those of the logistic variety, and typically take basic events such as births and deaths into account through appropriate rate processes. A generic example is the logistic form [4, 5]

$$\frac{dX}{dt} = \mu X - X^2,$$

where $X$ is a measure of the size of a population and is therefore nonnegative. The parameter $\mu$ is the difference between birth and death rates of the population, and $X = 0, \mu$ are its steady states. All that is required for survival is that $\mu > 0$. Fairly early on, the possible role of fluctuations in these models was recognized and included by way of additional fluctuating terms. The sources of the fluctuations included in this way in the earliest models were associated with variations in the external environment in which the population evolves, and appeared as a fluctuation in the parameters of the equations. For example, a fluctuating birth and/or death rate in the logistic form might lead to the description [4]

$$\frac{dX}{dt} = \mu X - X^2 + \xi(t) X,$$

where $\xi(t)$ is a zero-centered Gaussian white noise. The role of “internal fluctuations” arising from the fact that the populations are finite and discrete was also recognized, and the stochastic contributions to the population equations were obtained from an appropriate expansion of a master equation [5]. Writing the logistic equation in appropriately rescaled form, one would have with $Y = X/\mu$ and $\tau = \mu t$,

$$\frac{dY}{d\tau} = Y(1 - Y) + \sigma \sqrt{Y(1 - Y)} \xi(t).$$

The parameter $\sigma$ is also determined by the rates that determine $\mu$. Other sources of stochasticity have also been recognized, namely, those arising from natural catastrophes and from changes in gene frequencies [6].

The per capita growth rate of the population according to the deterministic logistic model [1] is

$$\frac{1}{X} \frac{dX}{dt} = \mu - X$$

which clearly decreases to zero as $X$ approaches the steady state value $\mu$ but that has a maximum as $X \to 0$. A point that was observed early on in the biological ecology literature is that this latter behavior is not descriptive of real populations in many cases, and that in fact the per capita growth rate also tends to decrease when the population becomes very small. Various possible mechanisms have been discussed for this in the literature, but many of them are based on the recognition that not only the total population but also its density may play a crucial role in population dynamics, particularly in questions related to extinction.

More recent population models have recognized the importance of describing not only the total populations but also its spatial distribution, thereby getting a handle on density-related issues. Perhaps the easiest way of dealing with a spatial distribution is by way of reaction-diffusion equations, and indeed such studies in the biological/ecological context have a long history. Reaction-diffusion equations describe deterministic continuous densities. Therefore, whereas they do deal with some of the density-dependence issues of great importance in the assessment of extinction probabilities, they do not in general include the other feature discussed above that is also of great consequence in these problems, namely, the effect of fluctuations. These fluctuations can again arise from a variety of internal and external sources. Herein we address the problem of internal fluctuations.

Populations are composed of discrete numbers of individuals. That populations are not continuous is particularly relevant at low densities and at low total populations. The importance of these effects have been recognized and analyzed in various ways in recent years, most prominently in works that deal with a master equation description of the population instead of a reaction-diffusion model. These master equations are typically solved numerically and provide important information on various measures for extinction.

We take a different approach to the problem, our interest lying in an analytic formulation of the problem of internal fluctuations and their consequences. On the one hand, an analytic approach necessarily requires a more narrow focus on a particular question, and therefore requires some restriction as to the range of issues that we can address. On the other hand, analytic results may provide insights that are difficult to obtain in purely numerical work.

Our specific question arises from the following situation. Suppose that a population lives in a one-dimensional bounded refuge with favorable conditions for life, while outside of the refuge the conditions are extremely harsh. A question that has been considered prominently in the mathematical literature is that of the critical size $L_c$ of such a refuge that will guarantee the survival of the population, $P_{\text{ext}} = 0$. This problem, and many generalizations of it, have been solved, but to our knowledge existing analytic solutions are based on the assumption of a continuous population. We show that accounting for the discreteness and finiteness of the population profoundly modifies the known results and may reopen an array of questions for reconsideration.

Our starting point is a master equation to describe the following scenario. In a refuge of volume $V$ we have a population composed of a single stream of individuals called $A$ that diffuse with constant diffusion coefficient $D$ on a $d$-dimensional lattice (later $d$ is set to unity) with lattice spacing $\Delta x$. We further suppose that the individuals reproduce by fission ($A \rightarrow A + A$, as may be the case with bacteria) with rate constant $\sigma_1$, they die ($A \rightarrow \emptyset$) with rate coefficient $\sigma_2$, and they compete according to the reaction $A + A \rightarrow A$ with rate coefficient $\lambda$. We suppose that $\sigma_1 > \sigma_2$, because otherwise the population eventually becomes extinct with certainty. We also assume that the nutrients are homogeneously distributed so that the coefficients do not depend on the lattice site. The microscopic description of the system within the refuge is given by the master equation

$$\frac{dP(n_i; t)}{dt} = \sum_i \left\{ \frac{D}{(\Delta x)^2} \sum_m \left[ (n_m + 1)P(\ldots, n_i - 1, n_m + 1, \ldots; t) - n_iP(\ldots, n_i, n_m, \ldots; t) \right] 
+ \lambda \left[ (n_i + 1)n_iP(\ldots, n_i + 1, \ldots; t) - n_i(n_i - 1)P(\ldots, n_i, \ldots; t) \right] 
+ \sigma_1 \left[ (n_i - 1)P(\ldots, n_i - 1, \ldots; t) - n_iP(\ldots, n_i, \ldots; t) \right] 
+ \sigma_2 \left[ (n_i + 1)P(\ldots, n_i + 1, \ldots; t) - n_iP(\ldots, n_i, \ldots; t) \right] \right\}. \quad (5)$$

Here the occupation number $n_j$ is the number of bacteria at site $j$ and $\{n_j\} \equiv \{(\ldots, n_{j-1}, n_j, n_{j+1}, \ldots)\}$ is the set of all occupation numbers. The index $i$ in the sum ranges over all lattice sites and $m$ denotes the set of nearest neighbors of $i$. We choose a homogeneous initial condition given by an uncorrelated Poisson distribution with average population $\bar{n}$ at each site:

$$P(\{n_i\}; 0) = e^{-\bar{n}} \prod_i \frac{n_i^{n_i}}{n_i!}. \quad (6)$$

Outside of the refuge living conditions are assumed to be extremely harsh, represented by the addition of the process $A \rightarrow \emptyset$ with a large rate coefficient $\gamma$. In the limit $\gamma \to \infty$ (certain death outside of the refuge), we can implement this
contribution by requiring that \( P(\{n_k\}; t) \) vanish whenever \( n_k \neq 0 \), where \( k \) denotes any site just beyond the refuge boundary. Thus, “harshness” is implemented as a set of boundary conditions.

In Sec. IV we discuss the derivation of a stochastic Langevin equation whose moments can be related to those of the fluctuating population described by the master equation. In Sec. III we present criteria for survival or extinction. In this section we discuss whether a refuge can be made sufficiently large to make extinction unlikely. A summary of our results and some directions for future research are presented in Sec. V.

II. THE MODEL

It is well known that the continuum (mean field) description of the local concentration \( \rho(x, t) \) is the Fisher-Kolmogorov-Petrovsky-Piscunov (FKPP) equation [18]

\[
\frac{\partial \rho(x, t)}{\partial t} = D \nabla^2 \rho(x, t) + (\sigma_1 - \sigma_2)\rho(x, t) - \lambda \rho(x, t)^2,
\]

which has been the phenomenological starting point in a huge number of problems in physics, chemistry, and biology. In one dimension and with the refuge extending inside the interval \([-\frac{L}{2}, \frac{L}{2}]\), the equation is to be solved subject to the boundary conditions

\[
\rho\left(-\frac{L}{2}, t\right) = \rho\left(\frac{L}{2}, t\right) = 0.
\]

For small \( L \) the only solution to this problem as \( t \to \infty \) is \( \rho(x, t) \to 0 \), that is, the population becomes extinct. There is a critical refuge size \( L_c \) beyond which extinction does not occur and the population will be nonzero (albeit small). Since \( \rho(x, t) \) is small near \( L_c \), to find this critical value it is appropriate to linearize Eq. (7) around zero population density and solve the simpler equation [14]

\[
\frac{\partial \rho(x, t)}{\partial t} = D \frac{\partial^2 \rho(x, t)}{\partial x^2} + (\sigma_1 - \sigma_2)\rho(x, t),
\]

subject to the boundary conditions [8]. The Fourier decomposition of the solution is given by

\[
\rho(x, t) = \sum_n a_n \rho_n(x, t),
\]

\[
\rho_n(x, t) = \exp\left[(\sigma - \frac{n^2 \pi^2}{L^2} D) t\right] \sin\left[\frac{n \pi}{L} \left(x + \frac{L}{2}\right)\right],
\]

where \( \sigma = \sigma_1 - \sigma_2 \), \( n = 1, 2, ..., \) and the \( a_n \) depend on the initial condition. Thus, all Fourier modes decrease to zero in time if and only if \( L < \pi \sqrt{\frac{D}{\sigma}} \), leading to the conclusion that for these values of \( L \), \( \rho_n(x, t) \to 0 \) when \( t \to \infty \) for any \( n \). We can therefore conclude that the critical length of the refuge is

\[
L_c = \pi \sqrt{\frac{D}{\sigma}}.
\]

That is, the population becomes extinct with certainty if \( L < L_c \) and it certainly does not become extinct if \( L > L_c \) (in fact, the Fourier components grow without bound in this case, but the linearized equation is then no longer valid). This result, and extensions of it, have been known for more than fifty years [9], and has served as a background for the design and analysis of refuges. Note that the linearization argument that leads to Eq. (9) is valid for any nonlinearity that can be neglected near extinction in Eq. (7), and that therefore the resulting \( L_c \) is obtained not only for this specific model [14].

The above mean field analysis does not take into account the effect of the fluctuations associated with the fact that the population is really discrete and finite. To do this short of solving the full master equation, one must formulate a generalization of the FKPP model that takes the resulting fluctuations into account. Such generalizations exist in the literature in other contexts. In particular, on the basis of a theory first proposed by Doi [13], further elucidated by Peliti [20], used for the study of critical phenomena associated with bulk transitions in reaction dynamics [21], explicitly applied to a reaction-diffusion front problem by Pechkin and Levine [22], and subsequently used in a number of other contexts related to Fisher waves (see e.g. [23]), one arrives at a stochastic differential equation for a field whose moments can be related to those of the population in the original master equation. The connection
comes about as follows. The master equation Eq. (5) can be projected onto a problem in quantum field theory by the construction of an adequate Fock space. Since this calculation has been performed many times in the literature we only indicate some of the main steps. A detailed review of the procedure can be found in [21]. Consider the following operator algebra:

$$[a_i, a_j^+] = \delta_{ij}, \quad [a_i, a_j] = 0, \quad [a_i^+, a_j^+] = 0,$$

(12)

where $a_i, a_i^+$ are destruction and creation operators and the square brackets denote the commutator [20]. A state vector can be defined as

$$|\psi(t)\rangle = \sum_{\{n_i\}} P(n_1, n_2, \ldots; t) a_1^{+n_1} a_2^{+n_2} \cdots |0\rangle,$$

(13)

where $P(n_1, n_2, \ldots; t) = P(\{n_i\}, t)$ is the solution of the master equation, and the sum is performed over all possible configurations of the $\{n_i\}$. The state vector obeys the imaginary time Schrödinger equation

$$\frac{d|\psi(t)\rangle}{dt} = -\hat{H} |\psi(t)\rangle,$$

(14)

whose formal solution is

$$|\psi(t)\rangle = e^{-\hat{H}t} |\psi(0)\rangle.$$

(15)

In our case the (non-hermitian) Hamiltonian is

$$\hat{H} = \sum_i \left[ -\frac{D}{(\Delta x)^2} \sum_{\{n_i\}} a_i^+(a_m - a_i) - \lambda(1 - a_i^+)a_i^+a_i^2 + \sigma_1[1 - a_i^+]a_i^+a_i - \sigma_2(1 - a_i^+)a_i \right].$$

(16)

Note that we recover Eq. (5) by substituting Eqs. (13) and (16) into Eq. (14).

One introduces the Glauber state as the projection state

$$\langle S | = \langle 0 | \prod_i e^{a_i^+ a_i}.$$

(17)

The expected values of observables $A(\{n_i\})$ can then be written as

$$\langle A(t) \rangle = \sum_{\{n_i\}} A(\{n_i\}) P(\{n_i\}; t) = \langle S | \hat{A} e^{-\hat{H}t} |\psi(0)\rangle,$$

(18)

where $\hat{A}$ is the operator obtained by replacing every $n_i$ in the function $A(\{n_i\})$ by the number operator $\hat{n}_i = a_i^+ a_i$.

The steps that we do not repeat [21, 22] show that this second-quantized theory can be expressed in terms of a path integral. Furthermore, from this path integral one can derive a “classical” action from which one can in turn derive the mean field continuum equation Eq. (7). If one concentrates on the path integral itself instead of moving on to the classical action, one can show an equivalence between the master equation and the following Langevin equation [21, 22]:

$$\frac{\partial \psi(r, t)}{\partial t} = D \nabla^2 \psi(r, t) + (\sigma_1 - \sigma_2)\psi(r, t) - \lambda \psi^2(r, t)$$

$$+ \sqrt{2[\sigma_1 \psi(r, t) - \lambda \psi^2(r, t)]} \xi(r, t),$$

(19)

where $\xi(r, t)$ is Gaussian white noise with mean and correlation given by [24]:

$$\langle \xi(r, t) \rangle = 0,$$

(20)

$$\langle \xi(r, t) \xi(r', t') \rangle = \delta(t - t') \delta(r - r').$$

(21)

The multiplicative noise in Eq. (15) must be interpreted according to Itô.
It is important to note that the noise in Eq. (19) can be imaginary, so the value of \( \psi \) is in general complex. This makes it clear that the field is not to be interpreted as the population density. The field \( \psi \) is the complex eigenvalue of the destruction operator, so one can relate its moments to the moments of the population density using the commutation relations Eq. (12) and the property of the Glauber state \( \langle S|a^+ = \langle S \rangle a^+ \). For the first two moments we have:

\[
\langle \rho(r, t) \rangle = \langle a_i \rangle = \langle a_i^+ a_i \rangle = \langle S|a_i^+ a_i |\psi(t)\rangle = \langle S|a_i |\psi(t)\rangle = \langle a_i \rangle = \langle \psi(r, t) \rangle,
\]

\[
\langle \rho^2(r, t) \rangle = \langle n,n_i \rangle = \langle a_i^+ a_i^+ a_i a_i \rangle = \langle a_i^+ a_i^+ a_i a_i + a_i^+ a_i \rangle = \langle S|a_i^+ 2a_i^2 + a_i^+ a_i |\psi(t)\rangle
\]

\[
= \langle S|a_i^+ |\psi(t)\rangle + \langle S|a_i |\psi(t)\rangle = \langle a_i^+ \rangle + \langle a_i \rangle = \langle \psi^2(r, t) \rangle + \langle \psi(r, t) \rangle.
\]

(22)

Higher moments can also be calculated following this procedure. Here the lattice site \( i \) is associated with the volume \((\Delta x)^d\) around point \( r \) and we have set \( \Delta x \equiv 1 \) for economy of notation.

As a side note we point out that the so-called stochastic FKPP equation of the form

\[
\frac{\partial \rho(x, t)}{\partial t} = D \frac{\partial^2 \rho(x, t)}{\partial x^2} + \sigma_1 \rho(x, t) - \lambda \rho^2(x, t) + \sqrt{2 \sigma_1 \rho(x, t) - \lambda \rho^2(x, t)} \xi(x, t)
\]

(23)

can not represent the population density either since it does not allow fluctuations around the equilibrium population density \( \rho = \sigma_1/\lambda \) because the population is real, while these fluctuations do not vanish in the original discrete system. However, a connection between Eq. (23) and the original master equation Eq. (5) without the death process has recently been elaborated. This connection is different from the one presented above involving the stochastic equation (19).

III. EXTINCTION PROBABILITY

The mean field model for the refuge population predicts certain extinction if the refuge size \( L < L_c \) and certain survival if \( L > L_c \). In this section we show that the fluctuations destroy this certainty of survival, that is, that survival is in fact never guaranteed.

In the biological literature one encounters the concept of a minimum viable population \([1, 10]\). There are some variations in its definition, but one that seems to be widely accepted is that a minimum viable population is the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the presence of foreseeable fluctuations. Clearly one can vary the two numbers that appear in this criterion, but, in any case, it involves a probability of survival in a finite period of time. We wish to make clear at the outset that our analytic theory is not yet developed to the point of being able to handle finite times, and we are therefore not able to implement a criterion of this sort. Instead, the theory (like the mean field prediction stated above) deals only with steady state probabilities.

Near extinction one can show directly from the master equation (5) that the competition term (the term proportional to \( \lambda \)) can be neglected. As a result, in this limit the contributions \( \lambda \psi^2 \) in the stochastic equation (19) can also be neglected, and to find the critical refuge size one only needs to deal with the simpler Langevin equation

\[
\frac{\partial \psi(x, t)}{\partial t} = D \nabla^2 \psi(x, t) + \sigma \psi(x, t) + \sqrt{2 \sigma \psi(x, t)} \xi(x, t).
\]

(24)

The mean value of \( \psi \) obeys the equation

\[
\frac{\partial \langle \psi(x, t) \rangle}{\partial t} = D \frac{\partial^2 \langle \psi(x, t) \rangle}{\partial x^2} + \sigma \langle \psi(x, t) \rangle,
\]

(25)

which is the same equation, Eq. (4), that we solved for the deterministic case. Since \( \langle \psi(x, t) \rangle = \langle \rho(x, t) \rangle \), we have the same boundary conditions as in Eq. (4), which implies that the mean value of the population density is zero, that is, that extinction is certain, for \( L < L_c \). Since \( \langle \psi(x, t) \rangle = \langle \rho(x, t) \rangle > 0 \) for \( L > L_c \), this in turn implies that extinction is certain if and only if \( L < L_c \). This, however, does not tell us whether or not the extinction probability is zero for \( L > L_c \) (as predicted in mean field theory). Indeed, we now show that the extinction probability is greater than zero for any finite length of the refuge.

It is fairly obvious that \( P_{ext} \) does not vanish if one has a finite population and thus a nonzero probability (albeit perhaps small) of a total extinction event. We will place this statement on a more formal footing. However, an arbitrarily small extinction probability is not necessarily very important since in most design problems one deals with at least some uncertainties. It is therefore useful to establish a criterion as to what constitutes a non-negligible extinction probability and what the minimal size \( L^* \) of the refuge must be to insure a probability smaller than this.
Clearly, $L^* \geq L_c$. We will establish such a criterion and show that (depending on parameter values) the size $L^*$ may be much larger than $L_c$ and even infinite.

First, to establish the obvious fact that fluctuations lead to a nonzero extinction probability even for $L > L_c$, let us suppose that we begin with an infinite refuge and exclude death events $A \to \emptyset$ altogether. The population inside an interval of length $L$ of this infinite refuge is then greater than or equal to the population inside our actual finite refuge of length $L$. The population density inside the finite interval of the infinite refuge in the steady state is given by the Poisson distribution

$$P(\{n_i\}) = e^{-2\sigma_i/\lambda} \prod_i \frac{(2\sigma_i/\lambda)^{n_i}}{n_i!},$$  \hspace{1cm} (26)

so that the probability of an unbounded realization of the process is zero. Since the integral of a bounded function over a bounded interval is bounded, we can conclude that the total population inside the interval is finite. Therefore so is the total population inside the finite refuge. Furthermore, with $\delta$-correlated Gaussian fluctuations \cite{24, 26}, even the most rare fluctuations occur in a finite mean time and therefore a rare fluctuation caused by the reaction $A \to \emptyset$ could kill the entire population in a finite time. We thus conclude that the probability of extinction is greater than zero whenever $L < \infty$. In the case of an unbounded refuge the mean value of the population density is $\sigma/\lambda$ and is homogeneously distributed, so a local fluctuation cannot kill the population. We can summarize these conclusions as follows:

$$P_{\text{ext}} = 1 \quad \text{if} \quad L < L_c$$

$$0 < P_{\text{ext}} < 1 \quad \text{if} \quad L_c < L < \infty$$

$$P_{\text{ext}} \to 0 \quad \text{when} \quad L \to \infty.$$  \hspace{1cm} (27)

We can furthermore state that since the number of individuals in the population increases as the length of the refuge increases, the probability of extinction decreases monotonically and continuously as $L$ increases continuously. Thus, consideration of the internal fluctuations drastically changes the picture; now there is no finite size of the refuge that can be considered absolutely safe for the population. However, we have not been able to derive the explicit functional dependence of $P_{\text{ext}}$ on the size of the refuge.

As an alternative to such an explicit full solution, we propose a criterion for deciding when a population is under substantial risk of extinction, and calculate the critical size $L^*$ of the refuge associated with this criterion. Suppose that a population density $\rho(x)$ in a refuge of length $L$ described according to mean field Eq. (4) has a maximum steady state density $M > 0$. Clearly, $L \geq L_c$. The maximum occurs at $x = 0$, in the middle of the refuge, that is, $\rho(x = 0) = M$ \cite{14, 24}. Now consider the description of this population that includes the fluctuations, and compare the average population density $\langle \psi(x) \rangle = \langle \rho(x) \rangle$ with the deterministic result $\rho(x)$. This average distribution also has a maximum at $x = 0$ (see below), $\langle \psi(x = 0) \rangle = M'$. We define the critical size $L^*$ as the refuge length associated with two conditions:

1. The deterministic and stochastically obtained maxima are equal, $M = M'$;

2. The standard deviation of the stochastic population density is equal to its mean at each $x$.

Clearly, our idea is that a population density whose standard deviation everywhere equals its mean is in danger of extinction, and we call this a “critical population.” It is not clear \textit{a priori} that these conditions can be simultaneously satisfied, but in fact it turns out that they can. The second condition above says that for the critical population

$$\langle \rho(x,t) \rangle^2 = \langle \rho^2(x,t) \rangle - \langle \rho(x,t) \rangle^2,$$  \hspace{1cm} (28)

or, equivalently, in terms of the field $\psi$, one for which

$$\langle \psi(x,t) \rangle^2 = \langle \psi^2(x,t) \rangle + \langle \psi(x,t) \rangle - \langle \psi(x,t) \rangle^2.$$  \hspace{1cm} (29)

From Eq. (10) we obtain the following equation linking the first and second moments of $\psi$:

$$\frac{\partial \langle \psi(x,t) \rangle}{\partial t} = D \nabla^2 \langle \psi(x,t) \rangle + \sigma \langle \psi(x,t) \rangle - \lambda \langle \psi(x,t) \rangle^2.$$  \hspace{1cm} (30)

Inserting Eq. (29) for the critical field then results in a closed equation for the first moment,

$$\frac{\partial \langle \psi(x,t) \rangle}{\partial t} = D \nabla^2 \langle \psi(x,t) \rangle + (\sigma + \lambda) \langle \psi(x,t) \rangle - 2\lambda \langle \psi(x,t) \rangle^2.$$  \hspace{1cm} (31)
Note that the apparent irrelevance of the fluctuations in Eq. (19) other than their mean value in arriving at Eq. (31) is illusory since the relation (22) and consequently Eq. (29) are intimately connected to the precise form of the fluctuations.

In the steady state Eq. (31) reduces to the boundary value problem

$$D \frac{d^2 \langle \psi(x) \rangle}{dx^2} + (\sigma + \lambda) \langle \psi(x) \rangle - 2\lambda \langle \psi(x) \rangle^2 = 0,$$  \hspace{1cm} (32)

with boundary conditions as in Eq. (30). To find $L^*$ we multiply Eq. (22) by $d\langle \psi(x) \rangle/dx$ and rewrite the result as

$$\frac{d}{dx} \left( \frac{D}{2} \left( \frac{d\langle \psi(x) \rangle}{dx} \right)^2 + \frac{(\sigma + \lambda)}{2} \langle \psi(x) \rangle^2 - \frac{2\lambda}{3} \langle \psi(x) \rangle^3 \right) = 0,$$  \hspace{1cm} (33)

from which it follows that

$$\frac{D}{2} \left( \frac{d\langle \psi(x) \rangle}{dx} \right)^2 + \frac{(\sigma + \lambda)}{2} \langle \psi(x) \rangle^2 - \frac{2\lambda}{3} \langle \psi(x) \rangle^3 = \text{constant}.$$  \hspace{1cm} (34)

Symmetry considerations show that the solution of this problem has only one maximum at $x = 0$, and since the first derivative of the solution should vanish at any maximum, we can explicitly write the constant as

$$\frac{D}{2} \left( \frac{d\langle \psi(x) \rangle}{dx} \right)^2 + \frac{(\sigma + \lambda)}{2} \langle \psi(x) \rangle^2 - \frac{2\lambda}{3} \langle \psi(x) \rangle^3 = \frac{\sigma + \lambda}{2} M^2 - \frac{2\lambda}{3} M^3,$$  \hspace{1cm} (35)

where $M$ is the maximum introduced earlier. Since this maximum occurs at $x = 0$, we can integrate Eq. (35) for $x > 0$ to obtain

$$x = \sqrt{\frac{D}{2}} \int_{\langle \psi(x) \rangle}^{M} \frac{dz}{\sqrt{\frac{\sigma + \lambda}{2} M^2 - \frac{2\lambda}{3} M^3 - \frac{\sigma + \lambda}{2} z^2 + \frac{2\lambda}{3} z^3}}.$$  \hspace{1cm} (36)

Taking into account that the population vanishes at the edge of the refuge we can obtain the value of the length $L$ of the refuge as a function of the maximum of the average population density:

$$L = \sqrt{2D} \int_{0}^{M} \frac{dz}{\sqrt{\frac{\sigma + \lambda}{2} M^2 - \frac{2\lambda}{3} M^3 - \frac{\sigma + \lambda}{2} z^2 + \frac{2\lambda}{3} z^3}}.$$  \hspace{1cm} (37)

With the change of variables $w = z/M$ and setting $\varepsilon \equiv \lambda/\sigma$ we can rewrite this relation as

$$\sqrt{\frac{\sigma}{D}} L = 2 \sqrt{1 + \varepsilon} \int_{0}^{1} \frac{dw}{\sqrt{1 - w^2 - \frac{4}{3}(1 + \varepsilon)(1 - w^3)M}}.$$  \hspace{1cm} (38)

The steady state deterministic equation obtained by setting the left hand side of Eq. (7) equal to zero is formally identical to the critical field equation Eq. (32) with modified parameters. Since we are choosing $L^*$ as the value where the maximum of the critical average population density is equal to the maximum of the mean field population density, the mean field model provides us with a second relation between $M$ and $L$:

$$\sqrt{\frac{\sigma}{D}} L = 2 \frac{1}{\varepsilon} \int_{0}^{1} \frac{dw}{\sqrt{1 - w^2 - \frac{4}{3}\varepsilon(1 - w^3)M}}.$$  \hspace{1cm} (39)

The simultaneous solution of Eqs. (38) and (39) then leads to the value of $L^*$ (and incidentally also of $M$).

The two equations reduce to the same equation if $\lambda = 0$ ($\varepsilon = 0$), and in this case $L^* = L_c$ and $M$ diverges. The reason for the equality is that when the nonlinearity is not present, the total steady state population is unbounded (thermodynamic limit) and there are no fluctuations. In general, the two simultaneous equations can only be solved numerically, and the results are shown in Fig 14.

A number of important points should be noted about our results. First, $L^*$ is indeed greater than $L_c$ except for the single trivially coincident point when $\lambda = 0$, that is, when there is no competition. Thus, according to our criterion whereby the risk of extinction is substantial when the mean and standard deviation of the population density are...
equal, one must increase the size of the refuge considerably beyond the deterministic refuge size to avoid this risk. Indeed, when $\lambda/\sigma = 1$ the size $L^*$ diverges logarithmically and the population density becomes uniform at density $\sigma/\lambda$. As $\lambda$ grows beyond $\sigma$ it is no longer possible to avoid considerable risk of extinction for any finite size of the refuge. The increase in $M$ with decreasing $L^*$ can be understood by moving from right to left in the figure: decreasing critical refuge size is associated with the requirement of a larger population (and hence a larger maximum population density) to insures against extinction. At $L_c$ the maximum $M$ diverges because no population, no matter how large, can be protected against extinction below this length. We can obtain an analytic expression for $L^*$ for small values of $\lambda/\sigma$:

$$\sqrt{\frac{\sigma}{D}}L^* = \pi \left[ 1 + \frac{\lambda}{2\sigma} + o \left( \left( \frac{\lambda}{\sigma} \right)^2 \right) \right].$$

(40)

We can also see analytically that $L^*$ must diverge when $\lambda/\sigma = 1$: at this point the two integrals for $L$ can only be equal if they both vanish (which they do not) or if they both diverge (which they do when $M = 1$).

IV. CONCLUSIONS

The main point of this paper has been to assess the effects of the inevitable internal fluctuations on the prediction of the risk of extinction of a population in a refuge as a function of the size of the refuge. In the usual mean field deterministic model in one dimension, the population is treated as a continuum and one obtains a critical refuge length $L_c$ such that the population becomes extinct with certainty if the length of the refuge is below this critical value, $L < L_c$, whereas survival is certain if $L > L_c$. It is well known that, as predicted by the mean field approach, the smaller the area occupied by a population, the lower are its chances for survival \[28\]. However, it is also known that a small size or low density of a population may also increase its chances of extinction, a feature that mean field theories do not capture \[3\]. Our approach deals with both of these features simultaneously through the interplay of discreteness and nonlinearity in a spatially distributed model. We have argued that the discreteness of the population and its finite size make fluctuations unavoidable, and have shown that whereas $L < L_c$ still guarantees extinction, $L > L_c$ by no means guarantees survival. While we have not been able to find an analytic expression for the survival probability as a function of $L$, we have focused on a sensible risk criterion for which we have found explicit results up to quadrature. Comparing deterministic and average stochastic population densities with a given maximum $M$, we
have chosen to define a new critical length \( L^* \) as one for which the mean of the population density and its standard deviation are equal, reasoning that this variability implies considerable susceptibility of the population to extinction. We have shown that \( L^* \geq L_c \) and, most importantly, that \( L^* \) diverges when the competition rate coefficient grows beyond that of the net growth rate of the population. For some parameter values it is possible to protect (albeit not with certainty) a population from extinction by placing it in a sufficiently large refuge, one that is certainly larger than that predicted by the standard mean field model. For other parameter values (in particular, when competition is too strong), it is not possible to evade the risk of extinction (at least according to our criterion) by enlarging the size of the refuge. Clearly, these results have serious implications for the expectations in the design of refuges.

Many questions still remain to be answered. For instance, an exact result for the extinction probability would clarify many issues. So would the ability to obtain time dependent solutions so as to deal with a more realistic criterion of survival over a long but finite time interval. Also, we have only considered the simplest most generic situation, whereas real systems (particularly ones not designed in the laboratory) are likely to be seriously affected by many complicating factors, some connected with the necessary extension to higher dimensions. Examples include the presence of convection, different boundary conditions, and spatial inhomogeneities inside the refuge. Similar questions can and should be posed when multiple species are present. In any case, in light of our results it would seem prudent to reconsider other critical size population problems to assess the effects of discreteness. As we have shown in the simple model considered here, the consequences can indeed be profound.

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