Extinction in a self-regulating population with
demographic and environmental noise

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1 Introduction

Models of population dynamics have been the subject of much study in biology. The essay of Malthus [1798] first suggested exponential growth. The idea of quantitative limits on growth is usually attributed to Verhulst [1838], who pioneered the use of the logistic equation (LE), and to Lotka [1920] and Volterra [1926], who considered models of predators and prey. Typically these early studies of population dynamics regards the units of interest as the number of individuals in populations of one or more species, without regard to genetic diversity within a population.

Given an initial focus on large population sizes, this early work focused on deterministic equations with continuous rather than discrete variables. A related approach is the logistic map (LM) which is also deterministic and continuous, but treats time as a series of discrete generations [May, 1976]. Continuous population equations like this can be extended to include external environmental fluctuations. For continuous time, this results in a continuous stochastic logistic equation (SLE) used to model populations: typically for ecological studies. While it is possible to extend continuous state models to incorporate genetics, they are limited by the fact that reproduction and mutation have an intrinsically random nature, requiring a statistical treatment of a discrete jump process.

The discrete logistic equation (DLE) was introduced by Feller [1939]. This is a continuous time Markov process with discrete states. It describes the
probabilistic time-evolution of a discrete rather than continuous population, in which the rates of birth or death are linear or quadratic in the total population number. This model and variations of it have been the subject of study by a number of researchers, mostly in the context of calculating extinction times (Nasell 2001; Matis et al. 2003; Matis and Kiffe 2004; Newman et al. 2004; Doering et al. 2005). One of the principle virtues of the model is that it can treat demographic noise: the inevitable stochasticity intrinsic to discrete random events such as birth and death.

A particular special case of stochastic logistic growth is obtained when density dependence occurs only through asymptotically decreasing birth rates, such that a hard upper limit in population size (known as the maximum carrying capacity) can never be exceeded (Dushoff 2000). This model originally arose in mathematical epidemiology as the closed stochastic SIS model (Weiss and Dishon 1971; Nasell 1996); a simple model of endemic disease in which the maximum carrying capacity is the (constant) size of the host population. It is also possible to construct a discrete logistic equation that has density dependent death rates, which is the approach we use here.

Any continuous-time discrete-state Markov process of this type can be canonically described by a birth-death master equation and such equations are widely used in chemistry and physics (Gardiner 2004). An approximate way to treat Master equations - introduced by Kramers and Moyal - is to replace the discrete variables (like population size) by continuous variables undergoing a diffusion process (Kramers 1940; Moyal 1949). With truncation, this results in a Fokker-Planck equation. After transforming to a continuous variable stochastic equation, this is simply equivalent to the SLE (Feller 1951).

This approximation results in a form of the SLE which can describe the effects of demographic noise in the limit of large population numbers. Thus, the Kramers-Moyal approximation to the discrete logistic equation is similar to the stochastic logistic equation for environmental noise, but with a different interpretation of the noise source. It has the drawback that it is not accurate for small populations. This leads to exponentially large errors (Gaveau et al. 1996) for important problems like extinction times, which necessarily involve a small population. Nevertheless, many published works in mathematical ecology and epidemiology that address demographic stochasticity have used the Kramers-Moyal or even more serious types of approximation.

At the same time, quantitative statistical models of the genetic evolution of populations are based on the pioneering work of population geneticists Fisher (Fisher 1918, 1930; Wright 1930) and Haldane (1932), whose combined work has laid the foundation for subsequent research in this area. However, many important questions are inaccessible by current techniques, because most population genetic theory is based on the idealized Wright-Fisher
model of population and the coalescent (Kingman, 1982), neither of which handle small randomly fluctuating populations. Thus, the fields of mathematical ecology and epidemiology, where questions about extinction, population viability (Boyce, 1992; Lande, 1993; Foley, 1994; Engen and Saether, 2000; Hakoyama and Iwasa, 2000; Drake, 2006; Cairns et al., 2007) and short-term population dynamics are important, have developed quite independently from theoretical population genetics.

Recently there has been renewed interest in unifying these fields from two different directions. Firstly researchers interested in the study of viral evolutionary dynamics have long realized that epidemiological dynamics and population genetics have overlapping time scales in viruses (Pybus et al., 2001, 2003; Kelly et al., 2003; Grenfell et al., 2004). Secondly and more recently there have been a number of attempts to develop general theoretical results aimed at extending classical population genetics concepts and results to the analysis of self-regulating stochastic population models. Notable examples include calculation of the effective population size of fluctuating populations that have both environmental and demographic stochasticity (Engen et al., 2007); development of a branching-process analogue of the stochastic logistic model with linear birth rates and density-dependent death rates (Lambert, 2005) and its application to the analysis of fixation probabilities in statistically varying populations (Lambert, 2006; Champagnat and Lambert, 2007); and analysis of the one-locus two-allele fixation probability in closed stochastic SIS model (Parsons and Quince, 2007).

Similar underlying mathematical issues to those faced by biologists have been known in the physical sciences for some time. Efficient techniques for solving master equations directly by simulation were introduced by Gillespie (1977). An exact transformation of master equations to a continuous Fokker-Planck equation and hence a stochastic form was introduced by Gardiner (2004), and is known as the Poisson representation. This approach differs from the commonly used Kramers-Moyal approximation in that it is exact for small numbers, provided boundary terms vanish, and hence can be used to reliably calculate extinction times (among other things). The more recently developed stochastic-gauge Poisson representation (Deuar and Drummond, 2002; Drummond and Deuar, 2003; Drummond, 2004) eliminates boundary term errors that can occur in the Poisson method, thus making the technique more generally useful.

In this paper, we apply these theoretical techniques to the problem of calculating and simulating extinction times in the discrete logistic equation with environmental noise added. We consider a logistic model that includes demographic noise due to birth, death, density-dependent intraspecific competition and a simple model of environmental noise. We obtain exact analytic results in this equation which unifies the DLE and SLE models. For pure demographic
noise, we have verified that our exact results agree precisely with a Monte-Carlo simulation of the master equation, showing that the discrete jump and continuous noise approaches are exactly equivalent with these techniques. We also compare our results with direct simulations of stochastic equations and with steepest-descent approximations. These provide useful analytic expressions, valid in the limit of large populations.

We present asymptotic results demonstrating that while large carrying capacity increases extinction times exponentially, it is not the only factor involved. There is also an exponential dependence on the reproductive ratio. For a given growth rate and carrying capacity, populations are exponentially shorter-lived at small reproductive ratio, as $R \to 1$.

In a following paper, we will extend these results to show that spatial connectedness provides a robustness against global extinction of a population. We do this by describing the relationship between the rate of extinction and the size and connectedness of the metapopulation. This is analysed quantitatively using a combination of analytic and numerical techniques. Extensions to include genetics will be treated elsewhere.

2 Methods

In this paper we will revisit and extend the logistic model of population dynamics. In its original form this model simply assumed that while small populations may grow exponentially, this growth saturates due to nonlinear effects such as density-dependent competition for resources. Thus, for a time-dependent population $N(t)$ of a given species,

$$\frac{\partial N}{\partial t} = N(g - cN), \quad (1)$$

where $g$ is the initial growth rate, $c$ describes competition, and $N_c = g/c$ is the deterministic carrying capacity. This is known as the logistic equation [Verhulst 1838]. If the initial population values are small, it has the simple property of an initial growth followed by a gradual approach to the steady-state, in which $N \to N_c$. Without the competition term there is an unrealistic exponential growth that fails to account for the inevitable competition for limited resources that occurs in all natural populations.
2.1 Environmental and demographic stochasticity

Nothing is more certain than uncertainty. All populations experience random fluctuations in numbers. These fluctuations are intrinsic to the random timing of population changing events, together with the granularity of populations that are made up of a finite number of individuals. To describe this reality, it is necessary to use master equations that deal with discrete outcomes, rather than continuous rate equations. We wish to analyse this demographic stochasticity, as a measure of minimum, irreducible randomness which cannot be eliminated from real population dynamics. In nature, there is also randomness in the birth and death rates, caused by the chaotic fluctuations in any real environment. Obviously, this environmental stochasticity represents a large part of observed stochasticity, and should not be ignored.

Traditional deterministic population equations may include environmental noise. However, they frequently ignore demographic stochasticity, even though this is essential to the analysis of extinction rates, where the discrete difference between zero and one is important. Conversely, previous treatments of the discrete stochastic logistic model have generally ignored external fluctuations. An environmental fluctuation may change the death rate in a population, but at close to zero population the demographic statistical fluctuations become more important. These determine the minimum survivable population, before extinction becomes a near certainty.

The standard treatment of genetic drift also includes stochastic fluctuations in the frequencies of different genotypes, but ignores such fluctuations in the overall number of individuals in the population. Our model can be extended to include both effects and thus provides a platform for further development in this new area [Parsons and Quince 2007].

2.2 Master Equations

One can show that there is a stochastic, or random equation that corresponds exactly - both in terms of averages and fluctuations - to the types of process we are considering here. Such equations were first considered in the context of the logistic model, by Feller. Generically, they are known as birth-death master equations. We first note that all of the number fluctuations we are interested in can be understood by combining the genotype and location labels together into one abstract species \( X_z \).

Here, the combined label \( z = \{ j, x \} \) indicates genotype \( j \) at location \( x \). Thus, there are a set of discrete position labels \( x \), each indicating a cell or lattice site within which there is relatively strong mixing. For convenience, we label
these abstract combinations of location and species in this section simply as $X_1$, $X_2$, and so on.

To derive the stochastic equations, first consider the most general kinetic equation we are interested in. As a simple model for stochastic birth/death events, we consider a binary reaction

$$
\varepsilon_1 X_1 + \varepsilon_2 X_2 \xrightarrow{k(t)} \varepsilon_3 X_3 + \varepsilon_4 X_4,
$$

which describes $\varepsilon_1$ individuals of type $X_1$ combining with $\varepsilon_2$ individuals of type $X_2$, to give $\varepsilon_3$ individuals of type $X_3$ and $\varepsilon_4$ individuals of type $X_4$. The rate for the process is $R(t)$, which may be time-dependent or stochastic. There is a birth-death master equation whose solution gives the time-evolution of probabilities $P(N)$, for finding the total number of individuals of each type equal to $N = (N_1,..,N_D)$. Here $D$ is the genetic/spatial dimension, equal to the number of distinct genotypes multiplied by the number of lattice sites under consideration.

This master equation is obtained by summing over all processes, where each binary reaction generates a term of the form:

$$
\frac{d}{dt} P(N) = -k(t)N_1^{\varepsilon_1}N_2^{\varepsilon_2} P(N) + k(t)(N_1')^{\varepsilon_1}(N_2')^{\varepsilon_2} P(N')
$$

Here, $N' = (N_1 + \varepsilon_1, N_2 + \varepsilon_2, N_3 - \varepsilon_3, N_4 - \varepsilon_4,..,N_D)$, with obvious modifications in cases of identical labels. This is difficult to solve as it stands, due to the large dimensionality of the space of distributions over integer populations. This complexity increases exponentially with the dimensionality $D$, which means that both the vector $P(N)$ and the matrix that describe its microscopic changes, rapidly become too large to be stored or numerically analysed in the memory of any computer.

However, there are several techniques for solving these equations which make use of mappings into probabilistic Markov processes or stochastic equations. These do not have exponential complexity, but rather trade off extremely large matrices in favour of sampling over a probabilistic distribution. While this introduces sampling errors, the amount of error can be controlled and reduced by increasing the number of samples. In some cases, exact or approximate analytic solutions can be obtained without requiring simulations.

Two methods we will use here are the direct method of Gillespie and the
2.3 Direct Gillespie Simulation

The direct method of simulating stochastic rate equations was originally applied to the problem of simulating chemical kinetics by Gillespie (1977). Applied to population dynamics this technique is essentially an in-silico direct model of the population. In this method a single event is one reaction process, each event adding or subtracting an individual after a random time interval whose mean is the inverse of the reaction rate.

The Gillespie algorithm produces a single forward-time realization of the stochastic process of interest. In order to obtain statistics on the average time-evolution of the process, many replicates are simulated, each starting with a different random number seed so that a sample of realisations is obtained that represent the range of outcomes. An individual Gillespie simulation proceeds one event at a time. The events considered in this paper are birth, death, and death by density-dependent competition, although extensions to more general models are easily made.

The Gillespie method is straightforward to implement and provides a useful base-line for comparisons, especially when demographic noise is the main source of fluctuations. Its main limitations are that it cannot be used to model large populations due to its computationally intensive approach, and the addition of environmental noise is nontrivial.

2.4 Poisson Representation

While direct simulations are extremely useful computational tool, they are not directly amenable to analytic solutions, nor are they immediately suitable for describing a unified theory that combines demographic and environmental noise. An efficient alternative technique for this purpose is to use the Poisson representation (Chaturvedi et al., 1977; Gardiner and Chaturvedi, 1977; Chaturvedi and Gardiner, 1978; Gardiner, 2004) - an exact expansion over Poisson distributions - to map these equations into a stochastic differential equation for a continuous Poisson amplitude.

This proceeds by expanding $P(N)$ in a basis of elementary multivariate Poisson distributions, so that:

$$P(N) = \int d[\bar{x}] f(\bar{x}) P(N; \bar{x}) ,$$

(4)
where \( P(\mathbf{N} | \bar{x}) \) is the Poisson distribution, with:

\[
P(\mathbf{N}; \bar{x}) = \prod_i e^{-x_i} \frac{(x_i)^{N_i}}{N_i!}.
\]  (5)

Each elementary process generates an equivalent Fokker-Planck equation (where \( \partial_i = \partial/\partial x_i \)):

\[
\frac{d}{dt} f(t, \mathbf{x}) = k(t) [(1 - \partial_3)^{\varepsilon_3} (1 - \partial_4)^{\varepsilon_4} - (1 - \partial_1)^{\varepsilon_1} (1 - \partial_2)^{\varepsilon_2}] \\
\times x_1^{\varepsilon_1} x_2^{\varepsilon_2} f(t, \mathbf{x}).
\]  (6)

After summing over all elementary processes, one obtains the total Fokker-Planck equation:

\[
\frac{d}{dt} f(t, \mathbf{x}) = \sum_i \partial_i \left[ -A_i(t, \mathbf{x}) + \frac{1}{2} \sum_j \partial_j D_{ij}(t, \mathbf{x}) \right] f(t, \mathbf{x}).
\]  (7)

The utility of the Poisson representation is that it can be used to directly calculate the factorial moments and correlations, through the equivalences:

\[
\langle x^n \rangle = \langle N(N-1)\ldots(N-n+1) \rangle.
\]  (8)

2.5 Stochastic realizations

The Fokker-Planck equation can also be readily converted into an Ito stochastic differential equation for direct numerical simulation, where:

\[
dx_i^t = A_i(t, \mathbf{x}) \, dt + \sum_j B_{ij}(t, \mathbf{x}) \, dW_j(t)
\]  (9)

Here, \( D_{ij} = \sum_k B_{ik} B_{jk} \), and the terms \( dW_i \) are independent real Gaussian noise terms with

\[
\langle dW_i dW_j \rangle = \delta_{ij} dt.
\]  (10)

It is necessary that \( D_{ij} \) is positive-definite. This may require introducing a complex Poisson variable \( x_i \), together with additional stochastic gauge terms to ensure stability. Relevant technical details are presented elsewhere (Drummond, 2004). The Ito form of stochastic equation corresponds most directly to a...
standard Fokker-Planck equation form, which is generated directly from the Poisson representation of demographic noise. This describes a forward step in which the multiplicative noise term is evaluated at the current time.

There is another commonly used form of stochastic equation. The Stratonovich equation describes a time-symmetric step, which is the broad-band limit of a finite band-width physical noise. This is the correct form in which to introduce environmental noise sources originating from time-dependent rate fluctuations $R(t)$. The two forms can be converted from one to the other, since the equivalent Stratonovich equation has the form:

$$dx^S_i = \tilde{A}_i(t, x) \, dt + \sum_j B_{ij}(t, x) \, dW_j(t) \quad (11)$$

where

$$\tilde{A}_i(t, x) = A_i(t, x) - \frac{1}{2} \sum_j B_{kj}(t, x) \partial_k B_{ij}(t, x). \quad (12)$$

These become formally identical if the noise term is independent of the phase-space variable $x$. This case is termed additive noise or constant diffusion. We will make use of a variable change to achieve constant diffusion behaviour in the analytic calculations.

2.6 Population processes on individuals

We can categorize biologically relevant kinetic processes into the following list, in which we give the simplest stochastic equation in each case.

2.6.1 Transformation

A transformation is a unary reaction in which one species changes to another at a constant rate, either through mutation or spatial motion (recall that the subscripts describe both physical and genetic space). In practise, this may be catalysed by other organisms or molecules, or involve additional precursor molecules. As long as these additional species have a constant concentration, they can be neglected, leading to the reaction:

$$X_1 \xrightarrow{a} X_2 \quad (13)$$
• Fokker-Planck equation:
\[
\frac{d}{dt} f(t, x) = a \left[ \partial_1 - \partial_2 \right] x f(t, x). \tag{14}
\]

• Stochastic equation (noise-free):
\[
dx_1 = -a x_1 dt \\
dx_2 = a x_1 dt. \tag{15}
\]

As an example, the death of an organism will be treated in a simplified way, where the final product is neglected:
\[
X \rightarrow 0 \tag{16}
\]

• Fokker-Planck equation:
\[
\frac{d}{dt} f(t, x) = a \partial_x f(t, x). \tag{17}
\]

• Stochastic equation (noise-free):
\[
dx = -a x dt. \tag{18}
\]

None of these processes involve stochastic terms, unless the rates themselves fluctuate. This implies that, at constant rates, transformation processes map one Poisson distribution into another Poisson distribution.

2.6.2 Birth

Consider birth: a process in which a pre-existing organism \(X_1\) generates two further organisms \(X_2\) and \(X_3\). A special case of this occurs when all of the species involved are identical.

\[
X \rightarrow 2X \tag{19}
\]

• Fokker-Planck equation:
\[
\frac{d}{dt} f(t, x) = b \left[ -\partial_x + \partial_x^2 \right] x f(t, x). \tag{20}
\]

• Ito stochastic equation:
\[
dx = b x dt + \sqrt{2b} x dW(t) \tag{21}
\]
The fact that there is noise in these equations simply implies that birth is intrinsically noisy, in the sense that it increases local fluctuations above the Poisson level.

2.6.3 Competition

Next, consider competition: a process in which two pre-existing organisms $X_1$ and $X_2$ compete (usually for resources), reducing the total number to just one, $X_3$. As in birth, a special cases of this occurs when all of the species involved are identical:

$$2X \xrightarrow{c} X$$

(22)

- Fokker-Planck equation:

$$\frac{d}{dt}f(t, x) = c \left[ \partial_x - \partial_x^2 \right] x^2 f(t, x).$$

(23)

- Ito stochastic equation:

$$dx = -cx^2dt + ix\sqrt{2cd}dW(t)$$

(24)

Competition tends to reduce fluctuations below the Poisson level. This results in complex Poisson amplitudes in general, unless the fluctuations of another process keep the overall variance real. This equation in its present form is unstable, and would require additional stochastic gauges to be treated correctly (Drummond, 2004). This issue does not arise in the stochastic logistic model, due to the additional positive diffusion from the birth term.

3 Discrete logistic model

Consider the discrete logistic model of a birth process $X \rightarrow 2X$, together with competition $2X \rightarrow X$, and a death process $X \rightarrow 0$. This type of random process can be represented kinetically as:

$$X \xrightarrow{a} 0.$$  

$$X \xrightarrow{b} 2X,$$  

(25)
For small populations the resulting net growth rate is \( g = b - a \), which corresponds to the Malthusian fitness of type \( X \). However, we have a model of fitness which is also density dependent and stochastic [Feller, 1939]. In this model the density-dependence come from the death by competition. It is also possible to have density-dependent birth-rates, which gives an extra parameter at the expense of more complicated stochastic behaviour.

Apart from the growth rate \( g \) which sets the relevant time-scales, this process is described by two dimensionless parameters; \( N_c = g/c \) is the carrying capacity, and \( R = b/a \) is the birth-death ratio, also called the reproductive ratio.

### 3.1 Master Equation

The master equation corresponding to the dynamical behaviour in Eq (25) is:

\[
\frac{d}{dt} P(N) = -(a + b + cN) NP(N) \\
+ b(N-1) P(N-1) \\
+ c(N+1)^2 P(N+1) \\
+ a(N+1) P(N+1)
\]

(26)

This is a set of coupled differential equations which can be treated directly in a single-species case, provided the total population is not too large. However, such techniques are difficult to extend to multiple species problems, due to exponentially increased complexity. Therefore, in this paper we focus on techniques which can be readily scaled to treat more complex multi-species cases.

As an example, we show a graph in Figure 1 of a single Gillespie-type realization of this jump process, leading to an extinction, together with the average over many realizations. Note that in this picture the population \( N \) is always discrete, with integer jumps at random times.
Figure 1. Direct simulation results using Gillespie algorithm with parameters $b = 2$, $a = 1$, $c = 0.2$. This corresponds to $N_c = 5$, $R = 2$, $g = 1$. The initial condition of $N_0 = 8$ was sampled from a Poissonian with mean of $x_0 = 5$. The solid line is a single stochastic realization, showing integer jump behaviour. The dotted line is an average of 10000 realizations, showing the exponential decline in average population leading to extinction.

3.2 Poisson Equation

The master equation (26) corresponds exactly to the following Fokker-Planck equation in the Poisson representation for $f(x)$:

\[
\frac{d}{dt}f(x) = \frac{\partial}{\partial x} \left[ -gx + cx^2 + \frac{\partial}{\partial x} (bx - cx^2) \right] f(x). \tag{27}
\]

In terms of the abstract notation of Eq (9),

\[
A(x) = gx - cx^2
\]

\[
D(x) = 2(bx - cx^2) \tag{28}
\]

which implies there is a corresponding Ito stochastic differential equation:

\[
dx^I = (gx - cx^2)\, dt + \sqrt{2(bx - cx^2)}\, dW, \tag{29}
\]
where:
\[
\langle dW^2 \rangle = dt.
\]

(30)

This transforms the discrete master equation given above to a completely equivalent Ito stochastic differential equation. The equation is valid in the domain \(0 \leq x \leq c/b\), in which region the noise terms are all real. As the noise term vanishes at the boundaries, it is appropriate to use reflecting boundary conditions. The boundary at \(x = 0\) is absorbing; once it is reached, the variable \(x\) remains at zero. This corresponds to extinction of the population on this trajectory.

3.3 Numerical Solutions

In Figure 2, we show a single stochastic realization of this equation, together with a time average. Note that here the stochastic variable \(x\) is continuous; it is the mean of one of the Poisson distributions used in the expansion. Even though there is no direct correspondence between each realization in Figures 1 and 2, they have identical means. More general observables can be transformed between these stochastic methods using the factorial moment equivalences, [8].

In these computer simulations, we use an implicit central difference method with the time-symmetric Stratonovich form of Eq (11), including the transformed drift term of Eq (12), again supplemented by absorbing boundary conditions at \(x = 0\):

\[
dx^S = \left( [g + c] x - b/2 - cx^2 \right) dt + \sqrt{2} \left( bx - cx^2 \right) dW,
\]

(31)

Points to notice about this approach are:

- The stochastic equation is for the mean of an 'equivalent' Poisson distribution
- \(P(N)\) must be reconstructed from an average over these Poisson distributions
- Even if \(g = 0\) there is noise if \(b \neq 0\); births cannot cancel deaths exactly.
- This intrinsic random noise occurs in addition to any environmental fluctuations
- The relative noise size scales as \(1/\sqrt{N}\) of the deterministic terms in the equation
- There is no noise if \(x = 0\); this means extinction, as shown by the Ito form.
Figure 2. Poisson simulation results using Stratonovich equations with parameters $b = 2$, $a = 1$, $c = 0.2$ or $R = 2$, $N_c = 5$ as in Figure 1. The initial condition was a Poissonian with mean of $x_0 = 5$. The solid line is a single stochastic realization, showing continuous stochastic behaviour. The dotted line is an average of 10000 realizations, showing the exponential decline in average population leading to extinction, just as in the Gillespie result. Integration step-size utilized was $dt = 0.04$, RK4 Runge-Kutta algorithm. Average extinction time $T = 10.04 \pm 0.27$ using Eq.(39).

3.4 Population statistics

In order to demonstrate an important property of the model, consider the time-evolution of moments, without competition so that $c = 0$. In the stochastic case, moments can be calculated, using standard Ito variable change (Gardiner, 2004) rules:

$$
\langle dx^n \rangle = \langle (x + dx)^n \rangle - \langle x^n \rangle \\
= n \langle dx x^{n-1} \rangle + \frac{n(n-1)}{2} \langle dx^2 x^{n-2} \rangle \\
= n g \langle x^n \rangle dt + n (n-1) b \langle x^{n-1} \rangle .
$$

This means that, even if $g = 0$, the population distribution does change statistically. In classical population dynamics, one would have a stable equilibrium with a constant population. However, demographic noise modifies this substantially. If we start from a Poissonian with amplitude $x_0$, then the factorial
moments *increase* with time even though the mean is constant:

\[
\begin{align*}
\langle x^1 \rangle &= x_0 \\
\langle x^2 \rangle &= x_0^2 + 2bt x_0 \\
\langle x^3 \rangle &= x_0^3 + 6 (bt)^2 x_0 \\
\langle x^4 \rangle &= x_0^4 + 24 (bt)^3 x_0 .
\end{align*}
\]  

(33)

Thus, for example, the standard deviation \( \sigma = \sqrt{\langle N^2 - \bar{N}^2 \rangle} \) can now be calculated to give:

\[
\sigma = \sqrt{\bar{N} \left( 1 + 2bt \right)} ,
\]  

(34)

This shows that the initial Poissonian variance (equal to the population mean) increases linearly with time. Some populations become large, others become extinct even if \( g \), the growth rate, is zero.

### 4 Demographic extinction times

We wish to analyse the extinction rate of a single isolated population undergoing discrete logistic population dynamics with competition included. We will assume an initial Poissonian distribution with mean \( x_0 \), as this allows us to include some of the effects of initial population fluctuations in biologically relevant cases.

There are several equivalent methods to carry out this calculation. One method is a direct calculation from the master equation, which gives a result without any environmental noise effects. A direct Gillespie simulation is also feasible. We will use this as a reference calculation, since the technique has the advantage that it can be readily extended to more complex cases. Because the simulations are relatively time-consuming for large populations and long extinction times, alternative approaches are desirable.

To obtain analytic results, we will use the Poisson equation. This has both exact and asymptotic approximate solutions for extinction times. In the next section we show that the approach can be readily extended to include environmental noise.
4.1 Exact extinction times

Calculating first-passage times for diffusion or Fokker-Planck processes is a well known problem in physics, and there is an extensive literature. Here there is an interesting subtlety. Even when the Poisson variable is non-vanishing so that \( x > 0 \), there is a fraction of size \( e^{-x} \) in the corresponding sample of real populations that is already extinct. To take account of this, the standard first-passage time calculation needs modifications.

We start by defining the rate of extinction at time \( t \) given an initial Gaussian with mean \( x_0 \) as \( \mathcal{R}(t|x_0) \). This is given by the rate of change of the probability for extinction \( \mathcal{E}(t|x_0) \) given an initial Poisson distribution at \( x_0 \):

\[
\mathcal{R}(t|x_0) = \frac{d}{dt} \mathcal{E}(t|x_0) = \frac{d}{dt} \int f(t,x|x_0) e^{-x} dx.
\]  

(35)

The average time to extinction \( T \) given an initial Poisson distribution at \( x_0 \) involves a time-integral over the extinction rate:

\[
T(x_0) = \int_0^\infty t \mathcal{R}(t|x_0) dt
= \int_0^\infty t \frac{d}{dt} \mathcal{E}(t|x_0) dt
= -\int_0^\infty t \frac{d}{dt} \mathcal{A}(t|x_0) dt.
\]  

(36)

Here we have introduced an alive probability defined as

\[
\mathcal{A}(t|x_0) = 1 - \mathcal{E}(t|x_0)
= \int_0^{x_m} f(t,x|x_0) \left[ 1 - e^{-x} \right] dx.
\]  

(37)

The absorbing state at \( x = 0 \) means that the distribution decays to a delta function at long times: \( f(\infty,x|x_0) = \delta(x) \), so that:

\[ \lim_{t \to \infty} t \mathcal{A}(t|x_0) = 0. \]
This last result allows a further simplification from integration by parts, so that:

\[ T(x_0) = \int_{0}^{\infty} A(t, |x_0|) \, dt . \] (38)

Since \( f(t, x|x_0) \) is a normalized, probabilistic propagator function in the Poisson representation, this leads to a simple prescription for calculating extinction times in a numerical simulation:

\[ T(x_0) = \int_{0}^{\infty} \langle 1 - e^{-x} \rangle \, dt . \] (39)

Analytically, however, we can do better, and even find an exact solution just requiring numerical integration. \( A \) is a linear functional of the Poisson distribution \( f(t, x|x_0) \), and as such must satisfy the well known 'backward' Kolmogorov equation (Gardiner, 2004) in terms of its initial condition:

\[ \frac{d}{dt} A(t|x_0) = \left[ A(x_0) \partial_{x_0} + \frac{1}{2} D(x_0) \partial^2_{x_0} \right] A(t|x_0) . \] (40)

We can now integrate the above equation over all times to obtain an ordinary differential equation for \( T(x_0) \). Initially, \( A(0|x_0) = 1 - e^{-x_0} \) so that:

\[ A(\infty|x_0) - A(0|x_0) = e^{-x_0} - 1 = \left[ A(x_0) \partial_{x_0} + \frac{1}{2} D(x_0) \partial^2_{x_0} \right] T(x_0) . \] (41)

We note the following boundary condition on the extinction time: \( T(0) = 0 \). This simply means that a population starting with a zero Poisson mean is extinct immediately, as can also be verified from the absorbing boundary condition on \( A \). This condition can be utilized to solve the extinction time differential equation, Eq (41).

We first introduce an auxiliary function,

\[ \psi(x_0) = \frac{2}{D(x_0)} \exp \left[ \frac{\int_{x_0}^{\infty} 2 A(x) \, dx}{D(x)} \right] , \]
\[ = \frac{1}{x_0 (b - cx_0)} \exp \left[ \int_{x_0}^{\infty} \left( 1 - \frac{a}{b - cx} \right) \, dx \right] \]
\[ = \frac{e^{x_0}}{x_0 (b - cx_0)^2} , \] (42)
where $\nu \equiv a/c - 1$. In terms of $\psi$, Eq. (41) has the particular solution:

$$T(x_0) = 2 \int_0^{x_0} \frac{dx}{D(x)\psi(x)} \int_x^{x_m} \psi(z) \left(1 - e^{-z}\right) dz. \quad (43)$$

This satisfies the backward Kolmogorov equation, and the boundary condition at $x = 0$. In principle, another solution is possible, as the differential equation is of second order. However, Eq. (41) has a regular singular point at $x = x_m$, whose indicial equation indicates that any other independent solution of the homogeneous equation would be singular at $x = x_m$, and hence inadmissible.

This result is remarkably similar to the standard expression for a first-passage time of a diffusion process (Gardiner, 2004) except for the factor of $(1 - e^{-z})$ in the integrand. This has the simple intuitive interpretation that it projects out the fraction of the population in a given Poisson ensemble that is still ‘alive’, i.e., has not yet reached extinction. While this term is essential if an exact result is required, it is typically a small correction in an expression dominated by the exponential factors in $\psi$.

Extinction time results for typical parameter values are given in Table ( ), compared to results for direct Gillespie simulations. There is agreement within two standard deviations of the computational sampling error in all cases. This provides numerical evidence for the equivalence between the discrete and continuous variable techniques for calculating extinction times. Numerical integrations of Eq. (43) were checked for accuracy to at least four significant figures, using an adaptive routine (tolerance of $0.5 \times 10^{-6}$) for the outer integral, and a fixed step integration with $4 \times 10^3$ steps of the $\sqrt{z}$ variable to ensure good accuracy at small $z$ values.

This set of calculations and simulations investigates the mean time to extinction for a variety of parameter combinations. The first two sets of population sizes are relatively small to facilitate direct comparison between the Gillespie method and exact approach. The Gillespie results were obtained by simulation of $10^6$ realizations for each of the first twelve parameter combinations. Computational limitations necessitated reduction of the number of Gillespie simulations for the last three parameter combinations, although the numerical integration of the exact result is straightforward. Each simulated realization started with a population size drawn from a Poisson distribution with mean of $N_c = g/c$. This is also the initial condition for the exact computations. The extinction time results versus carrying capacity at different $R$ values are also graphed in Figure 3. Nearly identical results (within sampling error) were found in a number of stochastic simulations, using the Stratonovich form to give increased numerical accuracy.
Table 1
Time to extinction in stochastic logistic population dynamics, relative to $g = 1$.

| $R$ | $N_c$ | Exact $T_e$ | Gillespie $gT_e$ | Asymptotic $T_e$ | # Gillespie simulations |
|-----|-------|-------------|------------------|------------------|-------------------------|
| 1.2 | 5     | 1.820       | 1.821 ± 0.002    | 5.031            | $10^6$                  |
| 1.5 | 5     | 4.587       | 4.583 ± 0.004    | 6.580            | $10^6$                  |
| 2.0 | 5     | 10.126      | 10.13 ± 0.01     | 11.18            | $10^6$                  |
| 3.5 | 5     | 32.91       | 32.97 ± 0.03     | 32.32            | $10^6$                  |
| 6   | 5     | 83.92       | 83.95 ± 0.08     | 79.99            | $10^6$                  |
| 1.2 | 10    | 3.996       | 3.990 ± 0.004    | 5.534            | $10^6$                  |
| 1.5 | 10    | 12.86       | 12.84 ± 0.01     | 11.97            | $10^6$                  |
| 2.0 | 10    | 41.22       | 41.27 ± 0.04     | 36.66            | $10^6$                  |
| 3.5 | 10    | 291.3       | 291.5 ± 0.3      | 276.9            | $10^6$                  |
| 6   | 10    | 1430        | 1431 ± 1.4       | 1399             | $10^6$                  |
| 1.2 | 20    | 10.60       | 10.60 ± 0.01     | 9.472            | $10^6$                  |
| 1.5 | 20    | 66.03       | 66.06 ± 0.06     | 56.09            | $10^6$                  |
| 2.0 | 20    | 593.9       | 589.7 ± 1.9      | 557.6            | $10^5$                  |
| 3.5 | 20    | $2.835 \times 10^4$ | $2.825 \times 10^4 \pm 89$ | $2.874 \times 10^4$ | $10^5$                  |
| 6   | 20    | $5.884 \times 10^5$ | $5.936 \times 10^5 \pm 6.0 \times 10^3$ | $6.053 \times 10^5$ | $10^4$                  |

A clear feature of the results is the exponential increase of extinction times with total population number. In addition, the results show that there can be changes of just as large a magnitude when the reproductive ratio $R$ of birth to death rates change. This is graphed directly in Figure 4.

These effects will be analyzed in more detail in the remainder of this section, where we derive the approximate analytic result found in the last column of the table.

4.2 Quasi steady-state

In order to understand these results as a diffusion process, consider the effect of an artificial reflecting boundary at $x = \varepsilon$. One can imagine this as being caused by the external intervention of a benevolent ecologist, wishing to prevent extinction by adding further individuals when the population becomes too small to be viable.

With this new boundary there is a steady-state equilibrium, which allows us
Figure 3. Dimensionless time to extinction versus carrying capacity (population) $N$, for the same range of $R$ values as in the table. Starting from the lower lines, $R = 1.2, 1.5, 2, 3.5, 6$. Solid lines are exact from Eq (43), dashed line are the steepest descent result from Eq (51), dotted lines are asymptotic (large $N$) expressions from Eq (53).

to derive an effective potential for the Fokker-Planck equation. The solution is then:

$$f_\infty(x) = \frac{2N}{D(x)} \exp \left[ \int \frac{2A(z)}{D(z)} dz \right]$$

$$= N \psi(x)$$

$$= N \frac{e^x}{x} (b - cx)'.$$

Apart from the normalization factor $N$, the steady-state distribution is just the auxiliary function used to calculate extinction times given above. This distribution is not normalizable in the limit of $\varepsilon \to 0$, which indicates it is not a true steady-state. With this isolated population model, the steady-state probability of having $x < \epsilon$ becomes infinite, for arbitrarily small values of $\varepsilon$. Thus, while a local equilibrium can be reached over short times which has a quasi-steady-state behaviour, the only true steady-state has population zero.

While we already have a result for the extinction time, we can use the concept
Figure 4. Dimensionless time to extinction versus reproductive ratio $R$, for $N = 10, 20$ (lower and upper curves respectively). Solid line is the exact result, dashed line is the asymptotic expression \[53\] of a quasi-steady-state to develop approximate expressions which give a better intuitive understanding.

### 4.3 Approximate extinction times

This quasi-steady-state distribution is typically double-peaked. Some populations are near the deterministic steady-state, while some populations are zero. This may be thought of as due to a potential barrier. There is a finite probability that a population which is locally stable will penetrate the potential barrier and reach the irreversible state of $x = 0$, which means that an extinction has occurred. We can calculate the extinction time approximately as an escape probability, from the deterministic or locally stable value through to extinction at $x = 0$. This is equivalent to a steepest descent approximation \cite{Gardiner2004} to the exact integral expression given in Eq \[43\].

To simplify this calculation, we first change to a new variable $y$, with constant diffusion rate. The variable change is defined so that:

\[
\frac{dx}{dy} = \Delta = \sqrt{x (b - cx)} .\] \[45\]
The Fokker-Planck equation for the corresponding probability distribution 
\( g(y) = \Delta f(x) \) is:

\[
\frac{\partial}{\partial t} g(y) = \left[ \frac{\partial}{\partial y} V'(y) + \frac{\partial}{\partial y} \right] g(y), \tag{46}
\]

where \( V'(y) = dV/dy \), and \( V(y) \) is the potential for the new distribution. This is obtained from the quasi-steady-state distribution - since

\[
V(y) = -\ln(\Delta f_{\infty}) = -x + \frac{1}{2} \ln \left[ x (b - cx)^{1-2d/c} \right]. \tag{47}
\]

The potential derivative, which defines the turning points, is:

\[
V'(y) = \frac{1}{\Delta} \left[ cx^2 - (g + c)x + \frac{b}{2} \right]. \tag{48}
\]

The potential has turning points at \( V'(y^\pm) = 0 \), that are given by solving the corresponding quadratic in the Poisson variable \( x \), so that:

\[
x^\pm = \frac{g + c \pm \gamma}{2c}, \tag{49}
\]

where \( \gamma \equiv \sqrt{(g + c)^2 - 2bc} \). We now follow standard techniques to calculate first-passage times, and neglect the small Poisson correction of \( (1 - e^{-x}) \) in the integrand. It is also necessary to calculate the curvature of the potential, which is:

\[
V''(y^\pm) = \Delta \frac{d}{dx} V'(y^\pm) = \pm \gamma. \tag{50}
\]

The average extinction time is governed by the potential difference and curvature. Provided \( g \gg \sqrt{2bc} \), it is given approximately by:

\[
T = \frac{2\pi}{\gamma} \exp \left[ V(x^-) - V(x^+) \right]. \tag{51}
\]

### 4.4 Limiting behavior

The table and graphs show an exponential increase in extinction times with carrying capacity \( N_c \), as well as a further marked dependence on the ratio of
gain to death rate. Here $R = b/a$ is the birth-death ratio, also called the reproductive ratio, which we introduce to obtain a dimensionless expression. We can make a further simplification by calculating the limit of the approximate exponential term at large carrying capacity, or $c \to 0$. This gives the limiting result for the turning points that:

$$
x^+ = N_c = \frac{g}{c} + 1 - \frac{b}{2g} \quad \text{and} \quad x^- = b/2g.
$$

Next, using these asymptotic values, and evaluating the potentials at the turning points, we find to leading order that:

$$
T = T_0 \exp \{N_c [1 - \ln (R) / (R - 1)]\} + O (1/N_c)
= T_0 \exp \{N_{\text{eff}}\}.
$$

Here we define a fundamental time-scale of $T_0$, and an effective carrying capacity $N_{\text{eff}}$ which determines the exponent:

$$
T_0 = \frac{2\pi R}{ge} \sqrt{\frac{1}{2N(R - 1)}} \quad \text{and} \quad N_{\text{eff}} = N_c [1 - \ln (R) / (R - 1)].
$$

This expression is obtained assuming that $R \ll N_c$, since we are interested here in the limit of large carrying capacity. It is instructive to consider what happens at large and small relative death rates, which gives a leading order asymptotic results of:

$$
\lim_{R - 1 \ll 1} \ln T = N_{\text{eff}} \to \frac{1}{2} N_c (R - 1) + O (\ln N_c)
\lim_{R \gg 1} \ln T = N_{\text{eff}} \to N_c + O (\ln N_c).
$$

A comparison of the approximate method with exact results is given in Table (I). The method performs worst for the first set of population parameters, which exhibit very rapid extinction rates. This is due to the fact that many populations in this regime are below the critical threshold immediately, so don’t have a quasi-steady-state. However the approximation behaves very well for larger population sizes where a genuine quasi-steady-state exists as demonstrated by the $N_c = 20$ simulations, where the approximation is generally within 10% of the exact results.
Figure 5. Relative error in time to extinction, $(T_{approx} - T)/T$ versus carrying capacity (population) $N$, for $R=1.5$ (black line), $R=2.0$ (blue line) and $R=3.5$ (green line). Small $R$ values are the least accurate (uppermost) lines at the $N = 5$ intercepts.

This approximate result is also compared to the exact calculation in Figure 5, where the relative error is graphed for three different $R$ values. Agreement is excellent for large populations, provided that growth is larger than critical, i.e., $g \gg g_c = \sqrt{2bc}$, which means that $N_c \gg 2R/(R-1)$. If the growth rate is less than this critical value, the potential has no local minimum, and extinction will occur on time-scales of the order of the inverse growth-rate for any initial population. We found no advantage in using the full steepest descent result of Eq (51) over the simpler equation (53), with the asymptotic result actually giving smaller errors at low $N$ values.

In summary, the asymptotic results from the steepest-descent method are accurate to within a few percent at large carrying capacity, but are not reliable below the critical carrying capacity, where exact results or direct simulations can be used.

These asymptotic results dramatically show that while large carrying capacity increases extinction times exponentially, it is not the only factor involved. There is also an exponential dependence on the reproductive ratio. For a given growth rate and carrying capacity, populations are exponentially shorter-lived at small reproductive ratio, as $R \rightarrow 1$.

In summary, with carrying capacity above the critical value, there is a quasi-
stable population at \( x^+ \approx g/c \). A population of this size can last an exponentially long time, although it is not globally stable. There is a saddle-point, or local maximum in the potential at a minimum critical population of \( x = x^- \).

If fluctuations occur below this minimum critical population of \( x^- \approx b/2g \), the population is too low to be sustainable. This means that extinction becomes likely over a short time-scale. Extinction is exponentially much more rapid with small carrying capacity \( N_c \), and also with a small reproductive ratio \( R \), which leads to large demographic fluctuations.

5 Stochastic discrete logistic model

So far we have only included demographic noise, due to the intrinsic random behavior of discrete jump events. In addition to this, there are external fluctuations, due to variations in environmental parameters like temperature that affect food supply or other factors relevant to survival. In our approach, these are represented as random, i.e., stochastic, time-dependent rate constants \( k(t) \).

In general, knowledge of these rate constants and their statistical fluctuations would allow more accurate predictions of average extinction times. We know that the rates have a finite correlation time; no changes are instantaneous. Despite this, it is useful to treat the limit of a short correlation time relative to the average growth rate \( g \). It is this limit that we consider here due to its analytic simplicity. More general results are possible that include the effects of finite correlation times, but will not be included here.

Effects of this type are sometimes treated by including fluctuating terms at the rate equation level, without demographic noise due to discrete events. This has the drawback that the logistic model with time-varying rates cannot lead to extinction. It simply has no absorbing state.

This problem may be circumvented approximately by assuming that a small population - say \( x = 1 \) - is equivalent to extinction. However, as we have shown in the previous section, demographic noise itself plays a role in causing fluctuations leading to extinctions, even in a static environment. Further, the critical population leading to a high likelihood of demographic extinction is not necessarily at \( x = 1 \), but instead is at \( x^- \approx b/2g \). This depends critically on the ratio of birth to growth rates. Assuming that \( x = 1 \) is equivalent to extinction can therefore lead to a serious over-estimation of extinction times if death and birth rates nearly cancel.

In the following section we develop a unified theory that includes both environmental and demographic fluctuation effects in calculating the extinction rate.
5.1 Environmental noise

We now include a specific model for the environmental noise. Environmental parameters are the time-dependant rates in the logistic equation, which are positive, and physically have finite bandwidth fluctuations. These can be modeled by writing the environmental rate parameters as \( k_i(t) = k_0^i \exp(\phi_i(t)) \). Here \( \phi_i \) describes the fluctuations, and is modeled using a stochastic differential equation of form:

\[
d\phi = -\gamma_i \left[ \phi \, dt + \sigma_i \, dW_i^{\text{env}} \right],
\]

where \( dW_i \) is an external environmental noise-source such that \( \langle dW_i dW_j \rangle = \delta_{ij} dt \), and \( \gamma_i, \sigma_i \) describe the rate of change and the relative noise variance of the \( i \)-th rate parameter. The resulting master equation with time-dependent rates can be termed the stochastic discrete logistic equation, or SDLE.

For analysis, the time-varying rates can simply be inserted directly into the demographic Stratonovich equation, \([31]\). This can be numerically integrated with any model of environmental stochasticity.

If the environmental fluctuation time-scales \( \gamma_i^{-1} \) are much smaller than the demographic time-scales \( g^{-1} \), adiabatic elimination will result in an approximate broad-band stochastic noise with variance \( (k_0^i \sigma_i)^2 \delta(t) \). Provided this variance is relatively small compared to the rate, the fluctuations can then be linearized to give additive environmental noise in the rates.

While one can solve the stochastic equations numerically without these simplifications, the result is more readily treated analytically, and will be treated in detail in the remainder of this section. As a simple example of this, we will consider a fluctuating death rate with environmental noise variance in the broad-band limit given by:

\[
\langle \delta a(t) \delta a(t') \rangle \simeq 2\sigma \delta(t - t') .
\]

We emphasize that broad-band external noise of this type must be included in the Stratonovich form of the demographic stochastic equation. Unlike the Ito form, the Stratonovich equation has a well-defined broad-band limit with an external noise source. The relative effect of the environmental noise depends on the competition term \( c \), so we will define \( r = \sigma/c \) as the relative environmental noise.
5.2 Unified Stratonovich equations

Adding a fluctuating death rate to the demographic equation in Stratonovich form, Eq \([31]\), we obtain:

\[
\begin{align*}
    dx^S &= \left( [g + c - \delta a(t)] x - b/2 - cx^2 \right) dt + \sqrt{2} (bx - cx^2)dW ,
\end{align*}
\]

(58)

Because the demographic and environmental fluctuations are assumed to be independent, their variances can be added. As both competition and environmental noise are now broad-band noise sources proportional to \(x\), we introduce \(\tilde{c}\) to describe the combined noise variance, where

\[
    \tilde{c} = c - \sigma = c(1 - r) .
\]

(59)

It would not be correct to make this change in \([29]\), the demographic Ito stochastic equation; this does not correspond to the broad-band limit of a finite bandwidth stochastic process.

Environmental noise has the opposite effect to demographic noise from density-dependent competition. It increases the variance to super-Poissonian levels, while intra-specific competition reduces the variance. The resulting unified Stratonovich equation with demographic and environmental noise is:

\[
\begin{align*}
    dx^S &= \left( [g + c] x - b/2 - cx^2 \right) dt + \sqrt{2} (bx - \tilde{c}x^2)dW ,
\end{align*}
\]

(60)

As previously, we assume absorbing boundary conditions at \(x = 0\). This means that a negative value of \(x\) will not occur. For positive \(\tilde{c}\), there is a reflecting boundary at \(x = b/\tilde{c}\). Since \(x < b/\tilde{c}\), the equation always remains real. If \(\tilde{c}\) is negative, the upper boundary is at infinity.

A typical simulation of these equations is given in Figure 6. The dimensionless parameter values are \(r = 0.75\), \(N_c = 10\), \(R = 2\). These simulations use an RK4 (Runge-Kutta) algorithm, with step-size \(\Delta t = 0.08\). There are 1000 trajectories in the ensemble averages. The mean extinction time, using the method of Eq \([39]\), was calculated to be \(T = 29.18 \pm 0.9\), with time-scales chosen so that \(g = 1\).

5.3 Extinction times

We now wish to analyse the combined effects of demographic and environmental noise on extinction times. This is obtained by transforming the unified
We note from Eq (12), that the transformation introduces an additional term in the drift that originates from the environmental noise term in the Stratonovich equation. The quasi-stationary (steady-state) solution is then:

$$\tilde{\psi}(x) = \frac{1}{x(b - \tilde{c}x)} \exp \left[ \int_0^x \left( \frac{1}{1 - r} - \frac{\tilde{a}}{b - \tilde{c}x} \right) dx \right].$$

(62)

Here we have introduced a new parameter $\tilde{a} \equiv b/(1 - r) - cr - g$. This equation can be integrated to give:

$$\tilde{\psi}(x) = \frac{e^{x/(1-r)}}{x} (b - \tilde{c}x)^{\tilde{a}/\tilde{c}-1}.$$

(63)
As with pure demographic fluctuations, an exact extinction time result is obtainable using:

\[
\tilde{T}(x_0) = 2 \int_{0}^{x_0} \frac{dx}{D(x)\tilde{\psi}(x)} \int_{x}^{x_m} \tilde{\psi}(z) \left(1 - e^{-z}\right) dz. \tag{64}
\]

We note that for \(\sigma > c\), one formally has \(x_m = \infty\) in this treatment. This is an artifact of the use of a Gaussian noise source, in which there is a small probability of an anomalous, negative death rate. However, as the large \(N\) tails of the distribution have little or no effect on the extinction time, we expect this to be relatively unimportant. It should be remarked that the detailed behaviour of the tails of distribution of death rate for large positive values are much more significant, especially if there are appreciable departures from Gaussian statistics. Applying this result to the parameters given in Figure 6, we obtain \(T = 28.2109\), within one standard deviation of the stochastic simulation results.

This excellent agreement between analytic results and simulations demonstrates that one does not have to use this exact theory. In fact it may be better not to in some cases. If the environmental noise has known statistical properties different to those assumed here, it is preferable to use the simulations described above, with appropriate noise sources having the true environmental statistics.

### 5.4 Steepest Descent Approximation

The quasi-steady-state distribution is still double-peaked but with appreciably smaller peak potentials when \(\sigma \geq c\). Approximate results are obtained as before by calculating the extinction time as an escape probability, from the deterministic or locally stable value through to extinction at \(x = 0\). We change to a new variable \(\tilde{y}\), with constant diffusion rate. This variable change is now defined so that:

\[
\frac{dx}{dy} = \tilde{\Delta} = \sqrt{x(b - \tilde{c}x)}. \tag{65}
\]

The Fokker-Planck equation for the corresponding probability distribution \(g(\tilde{y}) = \Delta f(x)\) is:

\[
\frac{\partial}{\partial t} g(\tilde{y}) = \left[ \frac{\partial}{\partial \tilde{y}} V'(\tilde{y}) + \frac{\partial}{\partial \tilde{y}} \right] g(\tilde{y}), \tag{66}
\]

30
where \( V'_\sigma(\tilde{y}) = \frac{dV_\sigma}{d\tilde{y}} \), and \( V_\sigma(\tilde{y}) \) is the potential for the new distribution. This is obtained from the quasi-steady-state distribution - since

\[
V_\sigma(\tilde{y}) = -\ln(\Delta f_\infty)
= -\frac{x}{(1 - r)} + \frac{1}{2} \ln \left[ x (b - \tilde{c}x)^{1 - 2a/c} \right].
\] (67)

Alternatively, we can make a variable change to the Stratonovich form of the drift, which gives the derivative in an equivalent but simpler form as:

\[
V'_\sigma(\tilde{y}) = \frac{1}{\Delta} \left[ cx^2 - (g + c)x + \frac{b}{2} \right].
\] (68)

The potential has turning points at \( V'_\sigma(\tilde{y}^\pm) = 0 \), that are exactly the same as in the pure demographic case. They correspond to the points where the drift vanishes in the Stratonovich form of the equation, which is not changed by environmental noise, so that:

\[
x^\pm = \frac{g + c \pm \gamma}{2c},
\] (69)

where \( \gamma \equiv \sqrt{(g - c)^2 - 2bc} \) as in the purely demographic case.

To obtain the extinction time, it is also necessary to calculate the curvature of the potential, which is, surprisingly, unchanged from the purely demographic case:

\[
V''_\sigma(\tilde{y}^\pm) = \Delta \frac{d}{dx} V'_\sigma(\tilde{y}^\pm)
= \pm \gamma.
\] (70)

The average extinction time is now given by:

\[
T_e = \frac{2\pi}{\gamma} \exp \left[ V_\sigma(x^-) - V_\sigma(x^+) \right].
\] (71)

This result includes both environmental and demographic contributions to the extinction time in a single expression. Just as in the case of pure demographic noise, we can simplify this expression by taking the large \( N \) limit, while fixing the relative level of external noise. To simplify the resulting expressions, it is convenient to define an effective reproductive ratio, defined as \( \tilde{R} = b/(b + (r - 1)g) \). For a stationary environment, \( \tilde{R} = R \). This, of course, is not the actual reproductive ratio, but rather a scaled parameter that reflects the relative size of fluctuations in birth events.
This gives rise to the following simple result, which clearly reduces to the purely demographic result at $r = 1$:

\[
T = T_0 \exp \left\{ \frac{N_c}{1 - r} \left[ 1 - \ln \left( \frac{\tilde{R}}{(\tilde{R} - 1)} \right) \right] \right\} + O \left( \frac{1}{N_c} \right) \\
= T_0 \exp \left\{ N_{\text{eff}} \right\} .
\]  

(72)

As before, we can define a fundamental time-scale of $T_0$, and an effective carrying capacity $N_{\text{eff}}$ which determines the exponent:

\[
T_0 = \frac{2\pi \tilde{R}^{1/(1-r)}}{g} \sqrt{\frac{1 - r}{2Ne(\tilde{R} - 1)}} \\
N_{\text{eff}} = \frac{N_c}{1 - r} \left[ 1 - \ln \left( \frac{\tilde{R}}{(\tilde{R} - 1)} \right) \right].
\]

(73)

Just as in the previous section, one can consider what happens at large and small $\tilde{R}$, which gives a leading order asymptotic result of:

\[
\lim_{\tilde{R} - 1 < 1} \ln T = N_{\text{eff}} \rightarrow \frac{N_c}{2(1 - r)} \left( \tilde{R} - 1 \right) + O \left( \ln N_c \right) \\
\lim_{\tilde{R} \gg 1} \ln T = N_{\text{eff}} \rightarrow \frac{N_c}{(1 - r)} + O \left( \ln N_c \right) .
\]

(74)

Graph showing typical results are given in Figures 7 and 8 for relative environmental fluctuations of $r = 1.5$ and $r = 3$ respectively. We see that extinction rates for carrying capacity of $N = 20$ are now three orders of magnitude more rapid than with demographic effects alone; this relative discrepancy is even larger at higher carrying capacity.

A clear feature of the results is that environmental fluctuations have the greatest relative effect on species with a large reproductive ratio, which otherwise would have an extremely long extinction time in a static environment. These long extinction times are reduced by many orders of magnitude, even with relatively small environmental noise. This is because environmental noise effects can easily be much larger than the low level of population fluctuations purely due to demographic causes with large $R$ values. Since environmental fluctuations are practically unavoidable, we see that the exceptionally long lifetimes found with large reproductive ratios are probably not achievable in real world environments.

The effects of varying environmental noise at fixed carrying capacity $N$ are shown in Figure 9. This shows the strong effects of environmental noise at
Figure 7. Graph of scaled time to extinction versus carrying capacity (population) $N$, for the same range of $R$ values as in the table, but including environmental noise with $r = 1.5$. Starting from the lower lines, $R = 1.2, 1.5, 2, 3.5, 6$. Solid lines are the exact results. Asymptotic results using steepest descent from Eq (73) are shown with dashed lines.

large reproductive ratio. It also demonstrates that the much smaller extinction times found with low reproductive ratios are not as sensitive to these external effects. This is because small $R$ values mean high death and birth rates, so that the fundamental demographic noise is high. In this situation, extinction is always rapid. Hence the faster extinctions due to environmental noise are not so dramatic, although still very significant when the noise is increased further.

Discussion

We have described a simple class of models that can be used to describe an isolated self-regulating population, including both demographic and environmental fluctuations. We believe the stochastic discrete logistic model represents an appropriate basis for a new synthesis of population genetics, mathematical epidemiology and theoretical ecology. We have used three equivalent techniques for analysing population dynamics and extinction times: direct master equation simulations, stochastic equations and exactly soluble Fokker-Planck equations.
Figure 8. Graph of scaled time to extinction versus carrying capacity (population) $N$, for the same range of $R$ values as in the table, but including environmental noise with $r = 3$. Starting from the lower lines, $R = 1.2, 1.5, 2, 3.5, 6$. Solid lines are the exact results. Approximate results using steepest descent from Eq (73) are shown with dashed lines. Parameters are the same as in Fig 3.

We emphasize that in the Poisson representation used here, all three techniques are exact and give identical results. This is to be contrasted with previous work using truncated forms of the Fokker-Planck equation, in which there can be exponentially large errors introduced by the diffusion approximation.

The Fokker-Planck method has the useful feature that it allows precise yet analytically tractable calculations of the asymptotic extinction times for large carrying capacity. At large $N_c$, we find a general dependence of $\log T \propto N_c$, but with a very different constants depending on the reproductive ratio $R$ and the relative environmental noise $r$. A single analytic expression agrees to within a few percent of the exact extinction times over a wide range of parameter values, if the carrying capacity is not too low. Provided these parameter values can be estimated, this provides a useful basis for risk analysis of survival probabilities in small, isolated populations.

Our results show that extinction times have an exponential dependence on carrying capacity above a critical carrying capacity that depends on the reproductive ratio. Surprisingly, the effect of small reproductive ratio is just as serious as small carrying capacity, in that both cause exponential reductions in extinction time to the point of almost total non-viability in the short term.
Figure 9. Graph of scaled time to extinction versus relative environmental noise $r$ for the same range of $R$ values as in the table, at a carrying capacity of $N = 20$. Starting from the lower lines, $R = 1.2, 1.5, 2, 3.5, 6$. Solid lines are the exact results. Approximate results using steepest descent from Eq (73) are shown with dashed lines. Parameters are the same as in Fig 3.

Environmental fluctuations have a similar effect, although these are much more pronounced when extinction rates are low, as occurs with large $R$ values. These results show clearly that carrying capacity or observed population sizes in isolated ecosystems are not by themselves a reliable guide to long-term viability. Instead, the total picture of reproductive ratio and fluctuations in growth rates due to environmental causes needs to be included as well in any risk assessment.

There are many ways in which this work can be extended. The most obvious is to extend this analysis to include genetics so that extinction would represent the loss of an allele from the population. By introducing mutation, a revised neutral theory of evolution could be developed that accommodated demographic fluctuations directly. Similarly natural selection could be modeled either through differential growth rates, differential death rates or inter-genotype competition.

A more challenging direction of enquiry will be to develop a framework for inference under the spatial logistic model analogous to that which Kingman’s coalescent provides for analyzing the idealized Wright-Fisher and Moran population models.
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Figure Captions

Figure 1  Direct simulation results using Gillespie algorithm with parameters $b = 2$, $a = 1$, $c = 0.2$. This corresponds to $N_c = 5$, $R = 2$, $g = 1$. The initial condition of $N_0 = 8$ was sampled from a Poissonian with mean of $x_0 = 5$. The solid line is a single stochastic realization, showing integer jump behaviour. The dotted line is an average of 10000 realizations, showing the exponential decline in average population leading to extinction.

Figure 2  Poisson simulation results using Stratonovich equations with parameters $b = 2$, $a = 1$, $c = 0.2$ or $R = 2$, $N_c = 5$ as in Figure 1. The initial condition was a Poissonian with mean of $x_0 = 5$. The solid line is a single stochastic realization, showing continuous stochastic behaviour. The dotted line is an average of 10000 realizations, showing the exponential decline in average population leading to extinction, just as in the Gillespie result. Integration step-size utilized was $dt = 0.04$, RK4 Runge-Kutta algorithm. Average extinction time $T = 10.04 \pm 0.27$ using Eq(39).

Figure 3  Dimensionless time to extinction versus carrying capacity (population) $N$, for the same range of $R$ values as in the table. Starting from the lower lines, $R = 1.2, 1.5, 2, 3.5, 6$. Solid lines are exact from Eq(43), dashed line are the steepest descent result from Eq (51), dotted lines are asymptotic (large $N$) expressions from Eq (53).

Figure 4  Dimensionless time to extinction versus reproductive ratio $R$, for $N = 10, 20$ (lower and upper curves respectively). Solid line is the exact result, dashed line is the asymptotic expression (53).

Figure 5  Relative error in time to extinction, $(T_{approx} - T)/T$ versus carrying capacity (population) $N$, for $R=1.5$ (black line), $R=2.0$ (blue line) and $R=3.5$ (green line). Small $R$ values are the least accurate (uppermost) lines at the $N = 5$ intercepts.
Figure 6  Graph of Poisson population versus time: mean values given by the dotted line, sample simulation given by the solid line, including environmental noise with $r = 0.75$, $N = 10$, $R = 2$.

Figure 7  Graph of scaled time to extinction versus carrying capacity (population) $N$, for the same range of $R$ values as in the table, but including environmental noise with $r = 1.5$. Starting from the lower lines, $R = 1.2, 1.5, 2, 3.5, 6$. Solid lines are the exact results. Asymptotic results using steepest descent from Eq (73) are shown with dashed lines.

Figure 8  Graph of scaled time to extinction versus carrying capacity (population) $N$, for the same range of $R$ values as in the table, but including environmental noise with $r = 3$. Starting from the lower lines, $R = 1.2, 1.5, 2, 3.5, 6$. Solid lines are the exact results. Approximate results using steepest descent from Eq (73) are shown with dashed lines. Parameters are the same as in Fig 3.

Figure 9  Graph of scaled time to extinction versus relative environmental noise $r$ for the same range of $R$ values as in the table, at a carrying capacity of $N = 20$. Starting from the lower lines, $R = 1.2, 1.5, 2, 3.5, 6$. Solid lines are the exact results. Approximate results using steepest descent from Eq (73) are shown with dashed lines. Parameters are the same as in Fig 3.

References

Boyce, M., 1992. Population viability analysis. Annual Review of Ecology and Systematics 23, 481–497.
Cairns, B. J., Ross, J. V., Taimre, T., 2007. A comparison of models for predicting population persistence. Ecological Modelling 201, 19–26.
Champagnat, N., Lambert, A., 2007. Evolution of discrete populations and the canonical diffusion of adaptive dynamics. Annals of Applied Probability 17, 102–155.
Chaturvedi, S., Gardiner, C. W., 1978. Poisson representation. JOURNAL OF STATISTICAL PHYSICS 18, 501.
Chaturvedi, S., Gardiner, C. W., Matheson, I. S., Walls, D. F., 1977. Stochastic analysis of a chemical-reaction with spatial and temporal structures. JOURNAL OF STATISTICAL PHYSICS 17, 469.
Deuar, P., Drummond, P., 2002. Gauge p representations for quantum-dynamical problems: Removal of boundary terms. Phys. Rev. A 66 (3).
Doering, C., Sargsyan, K., Sanders, L., 2005. Extinction times for birth-death processes: exact results, continuum asymptotics, and the failure of the fokker-planck approximation. SIAM Journal of Multiscale Modeling and simulation 3, 283–299.

Drake, J. M., 2006. Extinction times in experimental populations. Ecology 87 (9), 2215–2220.

Drummond, P., 2004. Gauge poisson representations for birth/death master equations. European Physical Journal B 38 (4), 617–634.

Drummond, P., Deuar, P., 2003. Quantum dynamics with stochastic gauge simulations. Journal of Optics B: Quantum and Semiclassical Optics 5, S281–S289.

Dushoff, J., 2000. Carrying capacity and demographic stochasticity: scaling behavior of the stochastic logistic model. Theor Popul Biol 57 (1), 59–65.

Engen, S., Ringsby, T. H., Saether, B.-E., Lande, R., Jensen, H., Lillegard, M., Ellegren, H., 2007. Effective size of fluctuating populations with two sexes and overlapping generations. Evolution Int J Org Evolution 61 (8), 1873–1885.

Engen, S., Saether, B. E., 2000. Predicting the time to quasi-extinction for populations far below their carrying capacity. J Theor Biol 205 (4), 649–658.

Feller, W., 1939. Die grundlagen der volterrasc hen theorie des kampfes ums dasein in wahrscheinlichkeitstheoretischer behandlung. Acta Biotheor. 5, 11–40.

Feller, W., 1951. Diffusion processes in genetics. In: Proc. Second Berkeley Symp. Math. Statist. Probab. Univ. California Press, Berkeley, pp. 227–246.

Fisher, R., 1918. The correlation between relatives on the supposition of mendelian inheritance. Trans. Roy. Soc. Edinb. 52, 399–433.

Fisher, R., 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Foley, P., 1994. Predicting extinction times from environmental stochasticity and carrying capacity. Conservation Biology 8, 124–137.

Gardiner, C. W., 2004. Handbook of stochastic methods for physics, chemistry, and the natural sciences, 3rd Edition. Springer-Verlag, Berlin. URL http://www.loc.gov/catdir/enhancements/fy0818/2004043676-d.html

Gardiner, C. W., Chaturvedi, S., 1977. Poisson representation .1. new technique for chemical master equations. JOURNAL OF STATISTICAL PHYSICS 17, 429.

Gaveau, B., Moreau, M., Tóth, J., 1996. Decay of the metastable state: different predictions between discrete and continuous models. Lett. Math. Phys. 37, 285–292.

Gillespie, D., 1977. Exact stochastic simulation of coupled chemical reactions. The Journal of Physical Chemistry 81 (25), 2340–2361.

Grenfell, B. T., Pybus, O. G., Gog, J. R., Wood, J. L. N., Daly, J. M., Mum-
ford, J. A., Holmes, E. C., 2004. Unifying the epidemiological and evolutionary dynamics of pathogens. Science 303 (5656), 327–332.
Hakoyama, H., Iwasa, Y., 2000. Extinction risk of a density-dependent population estimated from a time series of population size. J Theor Biol 204 (3), 337–359.
Haldane, J. B. S., 1932. The causes of evolution. Longmans, Green and co., London.
Kelly, J. K., Williamson, S., Orive, M. E., Smith, M. S., Holt, R. D., 2003. Linking dynamical and population genetic models of persistent viral infection. Am Nat 162 (1), 14–28.
Kingman, J., 1982. The coalescent. Stochastic Processes and their Applications 13, 235–248.
Kramers, H., 1940. Brownian motion in a field of force and the diffusion model of chemical reactions. Physica 7 (4), 284–304.
Lambert, A., 2005. The branching process with logistic growth. Annals of Applied Probability 15, 1506–1535.
Lambert, A., 2006. Probability of fixation under weak selection: A branching process unifying approach. Theoretical Population Biology 69, 419–441.
Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142, 911–927.
Lotka, A., 1920. Undamped oscillations derived from the law of mass action. J. Am. Chem. Soc. 42, 1595–1599.
Malthus, T., 1798. An Essay on the Principle of Population. J. Johnson, London.
Matis, J. H., Kiffe, T. R., 2004. On stochastic logistic population growth models with immigration and multiple births. Theor Popul Biol 65 (1), 89–104.
Matis, J. H., Kiffe, T. R., Renshaw, E., Hassan, J., 2003. A simple saddle-point approximation for the equilibrium distribution of the stochastic logistic model of population growth. Ecological Modelling 161, 239–248.
May, R., 1976. Simple mathematical models with very complicated dynamics. Nature.
Moyal, J., 1949. Stochastic processes and statistical physics. Journal of the Royal Statistical Society, Series B 11, 150–210.
Nasell, I., 1996. The quasi-stationary distribution of the closed endemic sis model. Advances In Applied Probability 28, 895–932.
Nasell, I., 2001. Extinction and quasi-stationarity in the verhulst logistic model. Journal of Theoretical Biology 211, 11–27.
Newman, T. J., Ferdy, J.-B., Quince, C., 2004. Extinction times and moment closure in the stochastic logistic process. Theor Popul Biol 65 (2), 115–126.
Parsons, T. L., Quince, C., 2007. Fixation in haploid populations exhibiting density dependence i: The non-neutral case. Theor Popul Biol 72 (1), 121–135.
Pybus, O. G., Charleston, M. A., Gupta, S., Rambaut, A., Holmes, E. C., Harvey, P. H., 2001. The epidemic behavior of the hepatitis c virus. Science
Pybus, O. G., Drummond, A. J., Nakano, T., Robertson, B. H., Rambaut, A., 2003. The epidemiology and iatrogenic transmission of hepatitis c virus in egypt: a bayesian coalescent approach. Mol Biol Evol 20 (3), 381–387.

Verhulst, P., 1838. Notice sur la loi que la population suit dans son accroissement. Corresp. Math. Phys. 10 (113-121).

Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118, 558–560.

Weiss, G., Dishon, M., 1971. On the asymptotic behavior of the stochastic and deterministic models of an epidemic. Mathematical Biosciences 11 (261-265).

Wright, S., 1930. The genetical theory of natural selection. Journal of Heredity 21, 349–356.