Critical Thresholds for Eventual Extinction in Randomly Disturbed Population Growth Models

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Abstract

This paper considers several single species growth models featuring a carrying capacity, which are subject to random disturbances that lead to instantaneous population reduction at the disturbance times. This is motivated in part by growing concerns about the impacts of climate change. Our main goal is to understand whether or not the species can persist in the long run. We consider the discrete-time stochastic process obtained by sampling the system immediately after the disturbances, and find various thresholds for several modes of convergence of this discrete process, including thresholds for the absence or existence of a positively supported invariant distribution. These thresholds are given explicitly in terms of the intensity and frequency of the disturbances on the one hand, and the population's growth characteristics on the other. We also perform a similar threshold analysis for the original continuous-time stochastic process, and obtain a formula that allows us to express the invariant distribution for this continuous-time process in terms of the invariant distribution of the discrete-time process, and vice versa. Examples illustrate that these distributions can differ, and this sends a cautionary message to practitioners who wish to parameterize these and related models using field data. Our analysis relies heavily on a particular feature shared by all the deterministic growth models considered here, namely that their solutions exhibit an exponentially weighted averaging property between a function of the initial condition, and the same function applied to the carrying capacity. This property is due to the fact that these systems can be transformed into affine systems.

1 Introduction

Much of the present work was motivated by general discussions with ecologists on *critical thresholds* in natural systems and the desire to construct tractable models that illustrated how such thresholds could emerge from population dynamics and for which critical thresholds could be understood and expressed as functions of other key system parameters. This is a critical research problem that was identified in a 2010 NSF Conference Report *Toward a Science of Sustainability*, organized by William C. Clark and Simon Levin at the Airlie Center, in Warrenton, VA, November 29, 2009 – December 2, 2009.

This paper is organized as follows. We first provide a brief overview of prior work on both deterministic and stochastic population growth models. We then define a general, random catastrophe model for which the discrete-time process (population sizes just after catastrophes) and continuous-time process can be analyzed separately. This is followed by results for various special cases that correspond to specific choices of the deterministic growth model that is followed between disturbances. Results for the exponential, logistic, Richards and Gompertz growth models are presented, and different critical thresholds are identified for convergence of expected values (L^1 convergence), for almost sure convergence toward extinction (sample path by sample path), and/or convergence in distribution to non-trivial invariant distributions. These sections include several examples where results (e.g., non-trivial invariant distributions) can be given in closed form, most often for the case where the disturbance factors have a uniform distribution. We then present theorems that establish the relationship between the invariant distributions for the discrete-time and continuous-time process, utilizing the general theory of Davis (1984) and Costa (1990) for piecewise deterministic Markov processes. We also present a few simulation results from an open-source implementation of the random catastrophe model in the Python programming language. One might argue that the theory should also permit *nonstationarities* in the evolutions, and/or *correlations* between disturbance times that are not present in Poisson models. While outside the scope of the present paper, the distinction between *trends* and *statistical dependence* is itself a non-trivial problem for data analysis that might better be addressed first in this regard; e.g., see (Bhattacharya, Gupta, Waymire, 1983) for illustration of this point in a hydrologic context. Having a general framework for stationary and uncorrelated disturbances has the advantage of being more self-contained, while providing a benchmark to (theoretically and/or computationally) test the impact of such relaxations.

2 Background

2.1 Deterministic Population Growth Models

There is a long and fascinating history of deterministic, sigmoidal growth laws being used to model the size of single-species populations over time, starting with the classic paper on the logistic growth model by Verhulst (1838). Kingsland (1982) provides a very nice summary of this history with extensive references. The simplest growth laws are predicated on several simplifying assumptions (some of which are simple facts), that can be summarily stated as follows:

(H1) The growth rate of population size at time t, $N'(t)$, is a smooth function, G of the population size, $N(t)$, at time t. That is, $N'(t) = G(N(t))$.

($H1'$) It is also generally assumed that G depends on t only through $N(t)$, that is, that the resulting ODE is *autonomous*. Moreover, one assumes that there is a unique evolution of the population $N(t)$ defined for all $t \geq 0$ for any initial size $N(0) = N_0 > 0$.
(H2) Reproduction is not possible with a population size of zero, i.e., $G(0) = 0$.
(H3) There is an upper limit to the size of the population based on availability of required resources (e.g., food, water, space, etc.) called the *carrying capacity* and denoted by K. It follows that $G(N)$ must decrease to 0 as $N \uparrow K$. That is, one assumes that there is a maximal interval $(0, K)$ over which G is positive, and $G(0) = G(K) = 0$.
(H4) If the environment is stable, then K is not a function of time, t.
(H5) The per capita growth rate $G(N)/N$ is a decreasing function of N, reflecting negative density dependence. This represents increasing competition for available resources.
(H6) As population size N becomes small, the per capita growth rate $G(N)/N$ approaches a positive constant r (which may be even be infinite), known as the *maximal per capita growth rate*: $r = \lim_{N \searrow 0} G(N)/N$. Constancy of r expresses that population demographics are stable, and do not fluctuate in time.

Under such conditions, the unique solution $N(t), t \geq 0$, to the growth equation

$$\frac{dN(t)}{dt} = G(N(t)), \quad N(0) = N_0, \text{ with } N_0 < K \tag{1}$$

will increase from the specified initial population size N_0 toward K.

Information about how a given species reproduces can be used to further restrict the functional form of G. Notice that the list of model assumptions does not explicitly account for the *age structure* of the population; that is, the fact that fertility of individuals is a function of their age, with no reproduction until they reach maturity. Similarly, they do not account for a gestation period during which an individual cannot reproduce, nor for seasonal variation of reproductive rates, which is well-documented for many species. For a sufficiently large population and period of observation, however, these effects can be accommodated by the choice of G. Some of these effects can also be accommodated by using discrete-time approximations to (1) in the form of *difference equations*, so that a fixed amount of time is allowed to pass before the population size can increase. Difference equations also accommodate integer-valued population sizes, although it is generally accepted that differential equations with real-valued population sizes can provide reasonable approximations (idealizations) when population size is sufficiently large.

As pointed out by Lotka (1925), taking only the first two terms of a Taylor series expansion for $G(N)$ provides the simplest choice for $G(N)$ having the required properties: $G(N) = rN(1 - N/K)$. This provides the well-known *logistic growth model*, first introduced by Verhulst (1838). Retaining only the linear term results in unchecked exponential growth, which is not limited by a carrying capacity, i.e., $K = \infty$. Any model with a linear lowest order term will exhibit exponential growth at early times. The *Richards growth model* (Richards, 1959) is a more general model with this feature, generalizing the logistic and exponential models as special cases. The Richards growth model is defined by $G(N) = rN\,[1 - (N/K)^\alpha]$, with $\alpha > 0$, and is also known as the *theta-logistic* model (Lande et al., 2003; Gilpin and Ayala, 1973). By contrast, the *Gompertz growth model*, defined by $G(N) = -rN \ln(N/K)$, does not possess a Taylor expansion at $N = 0$; the derivative at $N = 0$ is infinite. So growth at early times is therefore *faster* than exponential. Moreover, the parameter r is not the limit as $N \to 0$ for $G(N)/N$. In fact this limit is infinite. We will see that results for stochastic extensions of the Gompertz model differ from these other growth models in important ways due to such differences.

While the various classical models presented above differ in details, the solutions share a common *averaging dynamic* that is noteworthy. Namely, we will show that *a suitably transformed measure of the population size evolves as a temporally weighted average between the (transformed) initial population size and the (transformed) carrying capacity.* The proof rests on a more basic fact that every increasing, continuously differentiable function $x(t)$, $0 \le t < \infty$ can be represented as a weighted average by time-varying weights of its initial data x_0, and its limit asymptotic limit x_∞ (assumed finite for simplicity) as follows:

Lemma 2.1 *Suppose that* $x : [0,\infty) \to [x_0, x_\infty)$ *is continuously differentiable and monotonically increasing with* $x_\infty = \lim_{t\to\infty} x(t)$*, and let* $\nu > 0$ *be arbitrary. Then there exists a monotone (increasing or decreasing) function* $h : [x_0, x_\infty] \to \mathbb{R}$ *such that*

$$h(x(t)) = h(x_\infty)(1 - \mathrm{e}^{-\nu t}) + h(x_0)\,\mathrm{e}^{-\nu t},\ t \ge 0.$$

Proof. Since $x(t)$ is continuously differentiable and increasing, it is invertible with continuously differentiable inverse $\tau(x)$, where $\tau : [x_0, x_\infty) \to [0, +\infty)$, such that $\tau(x_0) = 0$, $\lim_{x\to x_\infty} \tau(x) = +\infty$, and $d\tau/dx > 0$. Let c_1 and c_2 be arbitrary real numbers such that $c_1 \neq c_2$. Define $h : [x_0, x_\infty] \to \mathbb{R}$ as follows:

$$h(x) := c_1(1 - \mathrm{e}^{-\nu\tau(x)}) + c_2\,\mathrm{e}^{-\nu\tau(x)} \tag{2}$$

Then h is continuously differentiable, with derivative

$$\frac{dh}{dx} = (c_1 - c_2)\nu\frac{d\tau}{dx}.$$

Since $c_1 \neq c_2$, $\nu > 0$, and $d\tau/dx > 0$, it follows that h is increasing (if $c_1 > c_2$) or decreasing (if $c_1 < c_2$). In either case, h is invertible, and by taking the inverse in the definition (2), and setting $x = x(t)$, we obtain the claimed result by noting that $c_1 = h(x_\infty)$ and $c_2 = h(x_0)$ (recall that $\tau(x_0) = 0$ and $\lim_{x\to x_\infty} \tau(x) = +\infty$).■

Of course the transformation h depends on the parameter $\nu > 0$. The latter sets a time scale for the averaging dynamic and may be normalized to one, or otherwise adapted to other natural time scale parameters of the model, e.g., the maximal per capita growth rate when it exists. Such averaging dynamics explicitly reveal the (non-transformed) solution to be given by

$$x(t) = h^{-1}\left(h(x_\infty)(1 - \mathrm{e}^{-\nu t}) + h(x_0)\,\mathrm{e}^{-\nu t}\right),\ t \geq 0. \tag{3}$$

One-to-one transformations, e.g., logarithms, exponentials, reciprocals, centering and scalings, are often found to be convenient and natural when graphing and analyzing biological data. Generally, it is an apparently adhoc choice through a single transformation, which turns out to be *independent* of initial data. This and Lemma 2.1 naturally beg the question of characterizing the class of equations (1) for which *all* solutions can be represented as above with the common one-to-one transformation h, independent of the initial condition, and can be answered as follows:

Lemma 2.2 *Consider equation* (1)*, and assume that (H1)-(H6) hold. Fix an arbitrary* $\nu > 0$*. Suppose that there exists a monotone (increasing or decreasing) continuously differentiable transformation* $h : (0, K] \to \mathbb{R}$*, such that:*

$$h(N(t)) = h(K)\left(1 - \mathrm{e}^{-\nu t}\right) + h(N_0)\,\mathrm{e}^{-\nu t},\ \forall N_0 \in (0, K] \text{ and } \forall t \geq 0, \tag{4}$$

where $N(t)$*,* $t \geq 0$*, denotes the unique solution of* (1) *with initial condition* $N(0) = N_0$*. Then* $x(t) := h(N(t))$ *must satisfy the following affine equation:*

$$\frac{dx(t)}{dt} = -\nu x(t) + \nu h(K), \tag{5}$$

for all $t \geq 0$ *and all* $N_0 \in (0, K]$*.*
Conversely, if there exists a monotone (increasing or decreasing) continuously differentiable transformation $h : (0, K] \to \mathbb{R}$ *such that* $x(t) := h(N(t))$ *(here again,* $N(t)$*,* $t \geq 0$*, is the unique solution of* (1) *with* $N(0) = N_0$*) satisfies the affine equation* (5) *for all* $t \geq 0$ *and all* $N_0 \in (0, K]$*, then the solution* $N(t)$ *of system* (1) *with* $N(0) = N_0$*, can be represented by* (4)*, for all* $t \geq 0$*, and for all* $N_0 \in (0, K]$*.*

Proof. By direct calculation, and applying the invertible map h to (4):

$$\begin{aligned}
\frac{dx(t)}{dt} &= \frac{d}{dt}\left(h(N(t))\right) \\
&= \frac{d}{dt}\left(h(K)\left(1 - \mathrm{e}^{-\nu t}\right) + h(N_0)\,\mathrm{e}^{-\nu t}\right) \\
&= -\nu\left(-h(K)\,\mathrm{e}^{-\nu t} + h(N_0)\,\mathrm{e}^{-\nu t}\right) \\
&= -\nu\left(h(K)\left(1 - \mathrm{e}^{-\nu t}\right) + h(N_0)\,\mathrm{e}^{-\nu t} - h(K)\right) \\
&= -\nu h(N(t)) + \nu h(K) \\
&= -\nu x(t) + \nu h(K).
\end{aligned}$$

For the converse, we first solve the affine equation by the variation of parameters formula:

$$\begin{aligned} x(t) &= x_0 \,\mathrm{e}^{-\nu t} + h(K)\left(1-\mathrm{e}^{-\nu t}\right) \\ &= h(N_0)\,\mathrm{e}^{-\nu t} + h(K)\left(1-\mathrm{e}^{-\nu t}\right), \end{aligned}$$

and then using the definition $x(t) = h(N(t))$, and the fact that h is invertible (because it is monotone), we obtain (4) by applying the inverse h^{-1}.■

So the class of systems (1) for which there exists a rescaling function $h(N)$ such that all solutions can be represented as in (4), are precisely those systems which can be transformed to an affine system. It is revealing to re-examine the previously discussed population models from this perspective. In particular, we will see that each is an *affinely transformable* model. Moreover, as we will see in our subsequent analysis, this property is key to analyzing the behavior of these models under certain stochastic disturbance scenarios.

Example 2.1 *For logistic growth,* $G(N) = rN(1 - N/K)$*, the choice* $h(N) = 1/N$ *transforms system* (1) *into* (5) *with* $\nu = r$*. Consequently, the (transformed) solution of* (1) *may be expressed as*

$$\frac{1}{N(t)} = \frac{1}{K}(1-\mathrm{e}^{-rt}) + \frac{1}{N_0}\,\mathrm{e}^{-rt}. \tag{6}$$

Figure 1 is a plot of the logistic (Verhulst) growth curve, and exhibits how it is distinct from exponential (Malthusian) growth.

Example 2.2 *For Richards growth,* $G(N) = rN(1 - (N/K)^{\alpha})$*, the choice* $h(N) = 1/N^{\alpha}$ *transforms system* (1) *into* (5) *with* $\nu = \alpha r$*. Consequently, the solution of* (1) *is*

$$\frac{1}{N^{\alpha}(t)} = \frac{1}{K^{\alpha}}(1-\mathrm{e}^{-\alpha rt}) + \frac{1}{N_0^{\alpha}}\,\mathrm{e}^{-\alpha rt}. \tag{7}$$

Example 2.3 *For Gompertz growth,* $G(N) = -rN\ln(N/K)$*, the choice* $h(N) = \ln(N)$ *transforms system* (1) *into* (5) *with* $\nu = r$*. Consequently, the solution of* (1) *is*

$$\ln N(t) = \ln K(1-\mathrm{e}^{-rt}) + \ln N_0\,\mathrm{e}^{-rt} \tag{8}$$

The standard forms of the non-transformed solutions are readily obtained using (3).

Deterministic growth laws provide an important foundation or starting point for analyzing more complex population dynamics and have been generalized in many different ways, resulting in a vast literature. Driven by observations, many extensions of these models have been proposed, analyzed and compared to observations. These extensions can be grouped into the following broad categories.

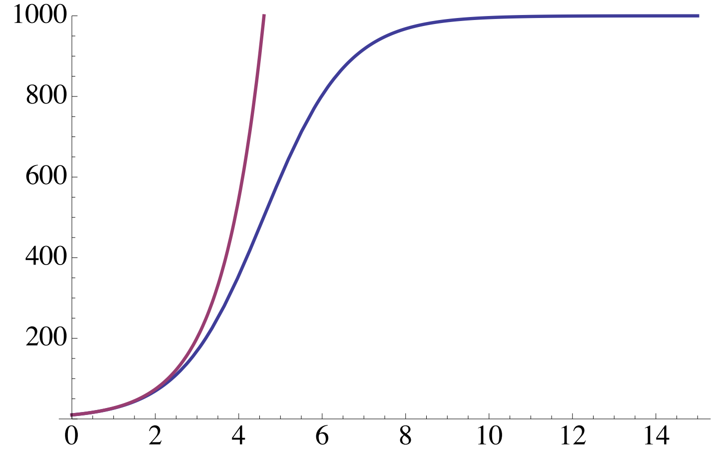

Figure 1: Population growth curves, $N(t)$ vs. t, with $r = 1$ and $N_0 = 10$, for (a) simple exponential growth ($K = \infty$ in (6)) and (b) the logistic growth model ($K = 1000$ in (6)).

(1) Extensions based on a different growth laws, with different assumptions and ODEs. (e.g. Richards, Birch, Gompertz, Bi-logistic, etc.)
(2) Extensions based on difference equations (with a lag effect) vs. differential equations. (e.g. Beverton-Holt, Hassell and Ricker models, etc.)
(3) Extensions that allow model parameters such as maximal per capita growth rate, r, and carrying capacity, K, to vary with time, e.g., see (Meyer, 1994).
(4) Diffusion-type models that result from a deterministic growth model that is subject to *additive* perturbations.
(5) Piecewise continuous models that result from a deterministic growth model that is subject to *multiplicative* perturbations, but only during disturbance events. The frequency of disturbances is often modeled as a Poisson event process, while their magnitude is modeled as a random fraction of the population that survives a disturbance.

We now turn to a brief review of stochastic model extensions of types (4) and (5).

2.2 Stochastic Population Growth Models

A stochastic population growth model is generally constructed by introducing stochastic effects into a deterministic, sigmoidal growth model. Recall that deterministic models have two main control parameters: the maximal, per capita reproductive rate, r, and the carrying capacity of the environment, K. While r is a characteristic of a single-species population, K is a characteristic of the environment that supports the population. Models that allow r to vary in time as a stochastic process are said to exhibit *demographic stochasticity.* This type of randomness, for example, may result from natural, genetic variation in reproductive success or issues associated with finding mates, especially for smaller populations. Similarly, models that treat K as a stochastic process in time are said to exhibit *environmental stochasticity.* For example, natural variation in rainfall rates affects the lushness of vegetation which therefore affects carrying capacity for herbivores. For both types of stochasticity, it is natural to model them as additive, stochastic fluctuations around nominal, mean values. As pointed out by Engen et al. (1998), for a sufficiently large population, such effects often lead to fluctuations that are small relative to the total size of the population, so that the population's growth curve may still appear to be essentially deterministic, closely following a sigmoidal growth curve over time. While a stochastic model may introduce just one type of stochasticity, it is more common to combine them into an additive, diffusion-type model of the form

$$dN(t) = G(N(t))dt + \sigma(N(t))dB(t), \quad N(0) = N_0, \tag{9}$$

where $G(x)$ is deterministic growth growth and $\sigma(x)$ is a generally ad hoc prescription of the mean square fluctuations. For example, if one assumes that $G(x) = rx, \sigma(x) = \sigma x$ are both linear, then $N(t)$ evolves as a (positive) *geometric Brownian motion*; A *geometric Ornstein-Uhlenbeck process* is obtained by taking $\sigma(x) = \sigma x$ linear with $G(x) = \frac{1}{2}\sigma^2 x - cx \log x$; e.g., see (Bhattacharya and Waymire (1992, 2009), p. 384–385). In both cases the process $\{N(t)\}$ remains positive for all $t > 0$ if $N(0) > 0$.

If one discretizes via a standard numerical scheme, $t_0 = 0, t_{n+1} = t_n + \Delta$, then writing $N_n = N(t_n)$,

$$N_{n+1} = [N_n + G(N_n)\Delta] + \sigma(N_n)\sqrt{\Delta}\epsilon_{n+1}. \tag{10}$$

where $\epsilon_1, \epsilon_2, \ldots$ are i.i.d. standard normally distributed, i.e., a discrete time white noise.

Another important type of stochasticity that can affect a population is due to relatively rare, episodic disturbances or *random catastrophes.* Examples of catastrophes include severe storms, meteor impacts, epidemics, forest fires, floods, droughts, infestations, volcanic eruptions and so on. The episodic nature of such disturbances means that it is natural to model their occurrence times as a Poisson event process in time, where the parameter λ determines their mean frequency of occurrence. One can model the resulting mortality by either subtracting a random number from the population, or by assuming that only a random fraction of the population survives the disturbance. However, the latter, multiplicative model seems more natural in this case because it scales with the population size. That is, the mortality in an additive model can be larger than the total size of the population. Note that whether the mortality due to a catastrophe is additive or multiplicative, the resulting stochastic process for the population size, $N(t)$, is no longer continuous, but rather piecewise continuous, with jump discontinuities occurring at the times of catastrophes.

Hanson and Tuckwell (1978, 1981, 1997) appear to be among the earliest to consider population dynamics models that included random catastrophes. In each of their papers, these authors modeled the disturbance times with a Poisson event process and modeled the growth between disturbances with deterministic, logistic growth. Their focus in each paper was on solving for the expected time to extinction (also known as the *persistence time*) for a given initial population size x, which they denoted as $T(x)$. Their approach was to employ *first-passage time* methods for stochastic processes with discontinuous sample paths. This involves using the Markov process semi-group theory (e.g., see Gihman and Skorokhod 1972), which leads to the differential-difference equation

$$r\,x\left(1-\frac{x}{K}\right)T'(x)+\lambda\,[T(x-\epsilon)-T(x)]=-1,\quad 0<x<K. \tag{11}$$

with the boundary conditions $T(1)=0$, and the observation that K is an inaccessible boundary. In their 1978 paper, for each disturbance the population size was *additively* reduced by a constant amount $\epsilon>0$. In their 1981 paper, they obtained results for disasters with multiplicative reductions so that the population size after a disaster was given by $\epsilon\,N(t)$, where $N(t)$ was the population size before the disaster and ϵ was a constant in $(0,1)$. They referred to these as *density-independent* disasters. In this context they introduced a nonzero, *effective extinction level*, Δ, and solved for the first passage time to Δ. Finally, Hanson and Tuckwell (1997) extended their results on mean extinction times via numerical simulations and asymptotic approximations for both of these prior models by allowing additive reductions to have an exponential distribution and multiplicative reductions to have a uniform distribution. They also examined a related model with exponential decay subject to *bonanzas* vs. disasters. Many of their results were presented in terms of the ratio $p=\lambda/r$, which they called the *bio-disaster ratio*, q. For their 1997 Model B, with multiplicative disturbance factors drawn from a uniform distribution, they were able to give asymptotic approximations for $T(x)$, showing that as $K/\Delta\to\infty$,

$$\begin{aligned}&T(x)\to\infty \text{ algebraically for } p\in(0,1),\\&T(x)\to\infty \text{ logarithmically for } p=1 \text{ and}\\&T(x)\sim[p/(p-1)]\ln(e\,x/\Delta) \text{ for } p>1.\end{aligned}$$

Lande (1993) reviewed and extended prior work on the relative importance of demographic and environmental stochasticity as well as random catastrophes; see also Lande et al. (2003). In the analysis of the multiplicative model from Hanson and Tuckwell (1981), a threshold parameter called the *long run growth rate* emerges, given by $\tilde{r}=r+\lambda\ln(\epsilon)$, where $\epsilon\in(0,1)$ is the constant fraction of the population that survives each disturbance. The sign of $\tilde{r}$ was seen to distinguish between two distinct types of long-term dynamics. We will see that a very closely related parameter arises in the more general context of the current paper, where the *disturbance factors* are allowed to be i.i.d. randomly varying fractions with any distribution on $(0,1)$. In the present paper the focus is on general long-term stochastic dynamics and *critical thresholds* rather than expected extinction times, but these two sets of results are naturally complementary. In fact, the more general description of the long-term dynamics helps to explain the asymptotic mean extinction behavior obtained by Hanson and Tuckwell (1997) for their Model B.

3 Definition of the Model

When treating disturbance models the blanket assumption that the disturbance factors are positive with positive probability is made throughout. Obviously if disturbances are permitted to destroy the entire population with probability one, i.e., $P(\mathcal{D} = 0) = 1$, then there is no recovery under the given model assumptions.

3.1 Continuous-time Model

The stochastic model of interest here falls within a general class of piecewise deterministic Markov models singled out by Davis (1984), in which a single-species population undergoes deterministic growth determined by an ordinary differential equation (1), but which also experiences random, episodic disturbances that remove a random fraction of the population. In this model, net growth is deterministic while the frequency and magnitude of disturbances that lead to mortality are treated as stochastic. The competition between the population's net reproductive rate and its mortality rate due to disturbances sets up a situation where critical thresholds can be computed in terms of model parameters that determine what will happen to the size of the population in the long term. This model can be expressed as

$$\begin{aligned} &\frac{dN}{dt}(t) = G(N(t)), \quad \tau_i \le t < \tau_{i+1}, \quad i = 0, 1, 2, \ldots, \\ &N(\tau_i) = \mathcal{D}_i\, N(\tau_i^-), \quad N(0) = N_0 > 0, \text{ with } N_0 < K, \end{aligned} \tag{12}$$

where $0 = \tau_0 < \tau_1 < \tau_2 < \cdots$ is the sequence of arrival times of a Poisson renewal process $\{\Lambda(t) : t \ge 0\}$ with intensity $\lambda > 0$, and $\mathcal{D}_1, \mathcal{D}_2, \ldots$ is a sequence of independent and identically distributed (i.i.d.) disturbance factors on the interval $[0, 1]$, and independent of the arrival time process. These disturbance factors determine the fraction of the population that survives a given disturbance. The function G is assumed to satisfy the hypotheses (H1)-(H6). Our goal is to understand the dynamics of the resulting discrete-time stochastic process $N(\tau_i)$, $i = 1 = 0, 1, 2, \ldots$, as well as of the continuous-time stochastic process $N(t)$, $t \ge 0$. We will present a number of results for the exponential, logistic, Richards and Gompertz growth models subject to various scenarios of the random disturbances.

One may note that $G(0) = 0$ implies that $N = 0$ is an absorbing state for (12). In particular the Dirac (point mass) probability distribution δ_0 is always an invariant (equilibrium) distribution for the population in accordance with assumption (H2). We are interested in conditions under which this is the only invariant distribution, as well as conditions in which another invariant distribution also exists on the interval $(0, K)$.

Note that (12) defines a *reducible* Markov process since the state $N = 0$ is inaccessible from states in $(0, \infty)$. The present paper takes advantage of some special techniques and observations to exploit this reducibility to the benefit of a rather complete theory for the model (12). In particular, it will be possible to apply existing theory to understand the long term stability of the stochastic process $N(t)$ using a theorem of Brandt (1986) for affine linear maps, together with a theory of "contraction maps on average" introduced by Diaconis and Freedman (1999). Interestingly, owing to a technical condition on topological completeness of the phase space in this latter reference and affine linearity in the former, neither of these is sufficient for the full set of results given here, but in combination they lead to a rather complete picture of the long time behavior.

3.2 Discrete-time Post-disturbance Model

In addition to the continuous time model (12), a natural discrete time model is obtained by considering the population sizes at the sequence of times at which disturbances occur. That is,

$$N_n = \mathcal{D}_n \, N(\tau_n^-), \quad n = 0, 1, 2, \ldots, \quad \tau_0^- = 0, \quad \mathcal{D}_0 = 1, \tag{13}$$

where N_n is the random size of the population immediately *after* the nth episodic disturbance. Here the left-hand limit notation $N(\tau_n-) = \lim_{t \uparrow \tau_n} N(t)$ is used to capture the population size just *before* the nth disturbance.

3.3 Relationship between Invariant Distributions of the Continuous and Discrete-time models

For the continuous time growth models we will take advantage of the existence of a one-to-one correspondence between the invariant distributions of the (discrete-time) post-jump Markov chain and the continuous time piecewise deterministic Markov process originally obtained by Costa (1990) in more generality than required here. In order to keep the present paper self-contained we provide a derivation for the special disturbance models of interest here.

Let's first recall the overall structure in which we consider a class of deterministic population models interrupted by i.i.d. random multiplicative disturbances (factors) $\mathcal{D}_1, \mathcal{D}_2, \ldots$ at arrival times $\tau_1 = T_1, \tau_2 = T_1 + T_2, \ldots$ of a Poisson process with i.i.d. exponentially distributed inter-arrival times $T_1, T_2, \ldots$ with mean $\frac{1}{\lambda}$. Between disturbances, the deterministic law of evolution of the population continuously in time is given by an equation of the general form

$$\frac{dN(t)}{dt} = G(N(t)), \quad N(0) = x, \tag{14}$$

where G satisfies assumptions (H1)-(H6), and whose solution may be expressed as

$$N(t) = g(t,x), t \geq 0, x > 0,$$

where the population flows $x \to g(t,x)$ are continuous, one-to-one maps with a continuous inverse, such that $g(0,x) = x$, and $g(s+t,x) = g(t, g(s,x)), s,t \geq 0, x > 0$. In particular, the uninterrupted evolutions considered here have unique solutions at all times for a given initial value.

By (H2), a common feature of these models is that $x = 0$ is a *steady state*, i.e., $g(t,0) = 0$. This trivial equilibrium persists in the disturbed evolutions as well. Thus we focus on initial states $x > 0$ in what follows.

On the other hand, the discrete-time disturbed population model is given by

$$N_0 = x, \quad N_n = \mathcal{D}_n g(T_n, N_{n-1}),\ n = 1, 2, \ldots. \tag{15}$$

The following theorem describes the relationship between steady state distributions of the continuous and discrete time evolutions. The result follows as a special case of a much more general theory for piecewise deterministic Markov processes due to Davis (1984) and Costa (1990); however, as remarked earlier, we sketch a proof (in the Appendix) that takes advantage of the specific nature of the disturbance model of interest here.

Theorem 3.1 (Continuous and discrete time invariant distributions) *Let $g(t,x)$ be the flow of the deterministic system* (14)*, which satsifies (H1)-(H6). Then*

(i) Given an invariant distribution π for the discrete time post-disturbance population model (15)*, let Y be a random variable with distribution π, and let T be an exponentially distributed random variable with parameter λ, independent of Y. Then the distribution*

$$\mu(C) = P(g(T,Y) \in C), \quad C \subset (0,\infty),$$

is an invariant distribution for the corresponding continuous time disturbance model (12)*.*

(ii) Given an invariant distribution μ, for the continuous time disturbance model (12)*, let Y be a random variable with distribution μ, and let $\mathcal{D}$ be distributed as the random disturbance factor distributed in* $(0,1)$*, independent of Y. Then*

$$\pi(C) = P(\mathcal{D}Y \in C), \quad C \subset (0,\infty),$$

is an invariant distribution for the corresponding discrete time post-disturbance model (15)*.*

Proof. See Appendix A.

4 Exponential Growth with Episodic Disturbances

As a warm-up to the more complex, sigmoidal growth models, it is instructive to first consider random disturbances of purely exponential growth, for which $G(x) = rx$. Results for the discrete-time model are followed by results for the continuous-time model.

4.1 Disturbance of Exponential Growth: Discrete-time Model

For simple exponential growth, we have $N(\tau_n^-) = N_{n-1}\, e^{r\,T_n}$ so that $N_n = N_{n-1}\, e^{r\,T_n}\mathcal{D}_n$ for the discrete-time model. This can be iterated to obtain

$$N_n = N_0 \prod_{k=1}^{n} \left[e^{r\,T_k}\mathcal{D}_k\right], \tag{16}$$

where N_0 is a given initial condition in $(0, K)$, $T_n \equiv \tau_n - \tau_{n-1}\,(n > 1)$ is the random time interval between disturbances, and $\mathcal{D}_n$ is the fraction of the population that survives the nth disturbance. Since we have assumed that disturbances occur according to a Poisson process, the random variables $T_n, n \geq 1$, are mutually independent and exponentially distributed with parameter $\lambda > 0$; e.g., see Bhattacharya and Waymire (1992, 2009). The random variable $S_n = \exp(r\,T_n)$ takes values in $[1, \infty)$ and has a Pareto distribution with cumulative distribution function $F_{S_n}(s) = 1 - s^{-p}, s > 0$, where $p := \lambda/r > 0$. Here, $E(S_n) = p/(p-1) = (\lambda/r)/((\lambda/r) - 1)$ if $\lambda/r > 1$ and is infinite otherwise. The disturbance factors $\mathcal{D}_n$ are also assumed to be independent and identically distributed (i.i.d.), and independent of the disturbance times.

Theorem 4.1 (Threshold for almost sure convergence) *Let τ_n be a sequence of arrival times of a Poisson process with intensity $\lambda > 0$, and $\mathcal{D}_n$ be a sequence of i.i.d. random disturbance variables on $[0, 1]$ which is independent of the Poisson process. Suppose that $G(N) = rN$ for some $r > 0$. Then*
(i) If $0 < E\left[\ln \mathcal{D}_1\right] + \frac{r}{\lambda} < \infty$, then $N_n \to \infty$ a.s. as $n \to \infty$.
(ii) If $-\infty < E\left[\ln \mathcal{D}_1\right] + \frac{r}{\lambda} < 0$, then $N_n \to 0$ a.s. as $n \to \infty$.

Proof. Taking logarithms in (16) we have

$$\ln(N_n) = \ln(N_0) + \sum_{k=1}^{n} \ln(\mathcal{D}_k) + r \sum_{k=1}^{n} T_k. \tag{17}$$

Now apply the strong law of large numbers to get

$$\frac{\ln(N_n)}{n} \to E\left[\ln \mathcal{D}_1\right] + \frac{r}{\lambda} \text{ as } n \to \infty, \text{ a.s.}$$

If the limit is positive then $\ln(N_n)$, and therefore N_n is unbounded as $n \to \infty$. If the limit is negative then $\ln(N_n) \to -\infty$ and therefore $N_n \to 0$, almost surely. ■

The threshold behavior defined by this result is in terms of behavior of sample paths that occurs with probability one (i.e., almost surely). This implies convergence in distribution, but is generally stronger than convergence in mean. In view of the following calculation, this threshold would not be observed in the (weaker) behavior of the averages.

Theorem 4.2 (Threshold for convergence in mean) *Assume that the conditions of Theorem* 4.1 *hold. Then, as $n \to \infty$,*

$$E\left(N_n\right) \to \begin{cases} 0, & \text{if } E(\mathcal{D}_1) + \frac{r}{\lambda} < 1 \\ N_0, & \text{if } E(\mathcal{D}_1) + \frac{r}{\lambda} = 1 \\ \infty, & \text{if } E(\mathcal{D}_1) + \frac{r}{\lambda} > 1 \end{cases} \tag{18}$$

Proof. Observe that

$$E\left(N_n\right) = \begin{cases} N_0 \left(E\left(\mathcal{D}_1\right) E\left(e^{r\,T_1}\right)\right)^n = N_0 \left(E\left(\mathcal{D}_1\right) \frac{(\lambda/r)}{(\lambda/r)-1}\right)^n, & \text{if } \lambda/r > 1 \\ \infty, & \text{if } \lambda/r \le 1. \end{cases}$$

Thus, $E(N_n)$ approaches zero if $\lambda/r > 1$ and $E(\mathcal{D}_1)\frac{(\lambda/r)}{(\lambda/r)-1} < 1$, $E(N_n)$ approaches N_0 if $\lambda/r > 1$ and $E(\mathcal{D}_1)\frac{(\lambda/r)}{(\lambda/r)-1} = 1$, and $E(N_n)$ approaches infinity otherwise. These three distinct cases can be re-phrased as in (18). ■

Remark. If $E(\mathcal{D}_1)+r/\lambda < 1$, then $E\left[\ln(\mathcal{D}_1)\right]+r/\lambda < 0$. This follows from $\ln(x) \le (x-1)$ for $x > 0$ and taking expectations. Theorems 4.1 and 4.2 therefore imply that for the disturbed exponential growth model, if $N_n \to 0$ in L^1, then $N_n \to 0$ almost surely, but not conversely. In more general settings to follow in which the limit is a not an almost sure constant, e.g., zero or infinity in the present cases, the primary threshold will be that of convergence in distribution.

Theorems 4.1 and 4.2 distinguish between convergence with probability one and convergence in expectation and they identify two distinct thresholds. In the context of our model, it makes sense to express these thresholds as a comparison of the intrinsic per capita growth rate, r, to the other (environmental) model parameters that characterize the magnitude and frequency of episodic disturbances that lead to mortality. An evolution toward eventual extinction results when the mortality rate due to disturbances overpowers the undisturbed net growth rate, r. The threshold conditions in Theorems 4.1 and 4.2 are then $r < \lambda\, E[-\ln(\mathcal{D}_1)] =: r_2$ and $r < \lambda[1 - E(\mathcal{D}_1)] =: r_1$, respectively, and since $r_1 \le r_2$, the second inequality implies the first. In analogy with their common use in Markov-Monte Carlo simulation theory, and in statistical physics, we refer to these two parameter regimes as *quenched* (Theorem 4.1) threshold for almost sure convergence) and *annealed* (Theorem 4.2) threshold for convergence in expectation). In the case where $r_1 < r < r_2$ (quenched but not annealed), we have $N_n \to 0$ almost surely but $E(N_n) \to \infty$.

Example 4.1 (Uniformly distributed disturbance) *Suppose that* $\mathcal{D}_1 \overset{d}{\sim}$ *Uniform*$(0,1)$. *Then* $E(\mathcal{D}_1) = 1/2$, $E[\ln(\mathcal{D}_1)] = -1$ *and the two regimes are given by* $r/\lambda < 1/2$ *and* $r/\lambda < 1$, *respectively. Compare this to Example 5.1.*

Example 4.2 (Two-valued distributed disturbance) *Suppose that* $\mathcal{D}_1 = 1$ *(no disturbance) or* δ *with equal probabilities, where* $0 < \delta < 1$ *is fixed. Then* $E(\mathcal{D}_1) = (1+\delta)/2$, $E[\ln(\mathcal{D}_1)] = \ln(\delta)/2$ *and the two regimes are given by*

$$\frac{r}{\lambda} < \frac{1-\delta}{2} \quad \text{and} \quad \frac{r}{\lambda} < \frac{-\ln\delta}{2},$$

respectively. So with $\delta = 1/4$, *the annealed regime is* $r/\lambda < 3/8 \approx 0.375$, *while the quenched regime is* $r/\lambda < \ln 2 \approx 0.693$.

Example 4.3 (Disturbance with Beta$(a,1)$ **distribution)** *This example provides a case in which the distribution of* N_n *can be given in closed form for all* n. *We begin with equation (17). Since the* T_k *are i.i.d. exponential random variables with parameter,* λ, *the second sum of random variables has a Gamma(*$n, \lambda/r$*) distribution. Now suppose that the* $\mathcal{D}_k$ *have the distribution given by* $F_{\mathcal{D}_k}(x) = x^a$, $a > 0$, $x \in (0,1)$ *(i.e.* $\mathcal{D}_k \sim$ *Beta(a,1)). Then* $B = -\ln(\mathcal{D}_k)$ *will have have an exponential distribution with parameter* a. *As a result, the first sum in (17) has a Gamma(*n,a*) distribution, with a leading minus sign. The distribution of (17) is then given by the difference of two independent random variables having a Gamma distributions. The pdf for the resulting distribution can be computed as*

$$f_{Z_n}(z) = \frac{(p\,a)^n e^{\frac{(a-p)}{2}z} \left(\frac{p+a}{|z|}\right)^{1/2-n} K_{n-\frac{1}{2}}\left[(p+a)|z|/2\right]}{\sqrt{\pi}\,(n-1)!}, \tag{19}$$

where $Z_n = \ln(N_n/N_0)$, $z \in (-\infty, \infty)$, $p = \lambda/r$ *and* $K_\nu(x)$ *is the modified Bessel function of the second kind. However, for integer* $n > 1$, $K(n-\frac{1}{2}, x)$ *can be written as*

$$K_{n-\frac{1}{2}}(x) = \sqrt{\frac{\pi}{2x}}\,\frac{e^{-x}}{\Gamma(n)} \int_0^\infty e^{-t}\, t^{n-1} \left(1 + \frac{t}{2x}\right)^{n-1} dt \tag{20}$$

$$= \sqrt{\frac{\pi}{2x}}\, e^{-x} \sum_{k=0}^{n-1} \frac{1}{(2x)^k} \binom{n-1}{k} \frac{\Gamma(n+k)}{\Gamma(n)} \tag{21}$$

$$\equiv \sqrt{\frac{\pi}{2x}}\, e^{-x}\, Q_n(x), \tag{22}$$

where the binomial theorem is used to get the second equality (Pope, 2003). The function $Q_n(x) > 1$ *for all* x *and* n, *diverges for* $x = 0$, *and decreases to* 1 *as* $x \to \infty$ *for all* n. *Using (22), (19) can be written in terms of simple functions as*

$$f_{Z_n}(z) = \begin{cases} \frac{1}{(n-1)!} \left(\frac{p\,a}{p+a}\right)^n |z|^{n-1} e^{az}\, Q_n\left[\left(\frac{p+a}{2}\right)|z|\right], & z < 0 \\ \frac{1}{(n-1)!} \left(\frac{p\,a}{p+a}\right)^n |z|^{n-1} e^{-pz}\, Q_n\left[\left(\frac{p+a}{2}\right)|z|\right], & z \geq 0 \end{cases} \tag{23}$$

If $a = p$, this distribution is symmetric about $z = 0$ (so N_n is log-symmetric), while for $a < p$ and $\alpha > p$ it is skewed to the left or right, respectively. Now the pdf for N_n can be computed in closed form as

$$f_{N_n}(x) = \tfrac{1}{x} f_{Z_n}\left[\ln\left(\tfrac{x}{N_0}\right)\right], \qquad x \in (0, \infty). \tag{24}$$

It is also easily shown that $E(Z_n) = n\,(1/p - 1/a)$. Note that $E(\mathcal{D}_1) = a/(1+a)$ and $E\left[\ln(\mathcal{D}_1)\right] = -1/a$, so the two threshold regimes are given by

$$\frac{r}{\lambda} < \frac{1}{1+a} \quad \textit{and} \quad \frac{r}{\lambda} < \frac{1}{a},$$

These are equivalent to $p > 1 + a$ and $p > a$, respectively.

4.2 Disturbance of Exponential Growth: Continuous-time Model

Theorem 4.3 *Assume that the conditions of Theorem* 4.1 *hold. Then the solution $N(t)$ of* (12) *satsifies:*

(i) $E[N(t)] = N_0\, e^{t[r-\lambda(1-E(\mathcal{D}_1))]}$.
(ii) $E\left[N^2(t)\right] = N_0^2\, e^{2\,r\,t-\lambda\, t\left[1-E(\mathcal{D}_1^2)\right]}$.
(iii) $E\left[N(t)\right] \to 0$ *if, and only if,* $E(\mathcal{D}_1) < 1 - r/\lambda$.

Proof. Let $M(t)$ be the random number of disturbances that occur before time t and let τ be the time of the last (most recent) disturbance before time t, given by

$$\tau = \sum_{k=1}^{M(t)} T_k. \tag{25}$$

We can then write the population size at an arbitrary time, t, in terms of the deterministic growth that has occurred since the last disturbance event as

$$N(t) = N_{M(t)}\, e^{r(t-\tau)}. \tag{26}$$

Here, $N_{M(t)}$ denotes the value of the discrete-time process immediately after the last disturbance event. Since disturbances follow a Poisson event process, $M(t)$ has a Poisson distribution with parameter λt. Between time τ and t, the population again experiences deterministic, exponential growth. Interestingly, the product of the exponential (deterministic) growth terms contained in $N_{M(t)}$ combine with the one in (26) to give simply $e^{r\,t}$. This allows (26) to be written as a product of a random number of i.i.d. random variables

$$N(t) = N_0\, e^{r\,t} \prod_{k=1}^{M(t)} \mathcal{D}_k. \tag{27}$$

Using conditional probabilities and noting the probability generating function for the Poisson distribution, one has that

$$
\begin{aligned}
E\left[\prod_{k=1}^{M(t)} \mathcal{D}_k\right] &= E\{\prod_{k=1}^{M(t)} E[\mathcal{D}_k|M(t)]\} \\
&= E\{(\mathcal{D}_1))^{M(t)}\} \\
&= e^{-\lambda\, t(1-E(\mathcal{D}_1))}. \qquad (28)
\end{aligned}
$$

Inserting this into (27), we obtain assertion (i). In the long-time limit, the expected size of the population therefore diverges or converges to 0 depending on whether the argument of the exponential function is positive or negative, respectively. This is the same threshold condition that was found for the discrete-time model in Theorem (4.2). Result (ii) is obtained by the same method after squaring (27). Together, (i) and (ii) also allow the variance to be computed. ■

5 Logistic Growth with Episodic Disturbances

While the exponential growth model allowed us to compute threshold criteria in terms of model parameters and nicely illustrates the distinction between the *quenched* and *annealed* parameter regimes, it is an unrealistic long-term model because it puts no upper bound on the population size. We now turn to the case of *logistic growth*, where $G(x) = rx(1 - \frac{x}{K})$ in our general model, (12). It turns out that the *reciprocal transform* $h(N) = 1/N$ established in Example 2.1 provides the key to analyzing the discrete-time model in this case.

5.1 Disturbance of Logistic Growth: Discrete-time Model

Recall that N_n denotes the random size of the population immediately after the nth episodic disturbance. As a result of Example 2.1 and (13), since N_{n-1} becomes the (new) initial condition for the next disturbance interval, we have

$$
N_n = \mathcal{D}_n \frac{1}{\frac{1}{K}\,(1 - e^{-r\,T_n}) + \frac{1}{N_{n-1}} e^{-r\,T_n}}, \qquad (n \geq 1)\,, \tag{29}
$$

where N_0 is given, T_1 is the random time until the first disturbance, $T_n \equiv \tau_n - \tau_{n-1}\,(n > 1)$ is the random time interval between successive disturbances and $\mathcal{D}_n$ is the fraction of the population that survives the nth disturbance. The case $r > 0, K = \infty$ is that of exponential growth, treated in the previous section. As in that section, we assume that disturbances occur according to a Poisson process, so the random variables $T_n, n \geq 1$, are mutually independent and exponentially distributed with parameter $\lambda > 0$. The random variable $S_n = \exp(-r\,T_n)$ has the distribution function $F_{S_n}(s) = s^p$, where $p = \lambda/r$. That is,

$S_n \overset{d}{\sim} \text{Beta}(p, 1)$, for $s \in (0, 1)$. (Note that in the disturbed exponential growth model we had $S_n = \exp(r\,T_n)$.) The disturbance factors $\mathcal{D}_n$ are again assumed to be independent and identically distributed, and independent of the disturbance times.

The recursion (29) can also be written as an iterated random function dynamics (see Bhattacharya and Majumdar (2007), Schreiber (2012)) for extensive theory of such dynamics),

$$N_n = \gamma_{\Theta^{(n)}} \circ \gamma_{\Theta^{(n-1)}} \circ \cdots \circ \gamma_{\Theta^{(1)}}, \tag{30}$$

where $\Theta^{(i)} = \left(\theta_1^{(i)}, \theta_2^{(i)}\right)$, $i \geq 1$, are i.i.d with independent components $\theta_1 \in (0, 1)$ and $\theta_2 \overset{d}{\sim} Exp(\lambda)$, and

$$\gamma_\Theta(x) \equiv \gamma_{(\theta_1, \theta_2)}(x) = \theta_1 \frac{1}{\frac{1}{K}\left(1 - e^{-r\theta_2}\right) + \frac{1}{x}e^{-r\theta_2}}. \tag{31}$$

While it is difficult to analyze the logistic growth model in terms of N_n directly, significant progress can be made by instead examining its reciprocal, N_n^{-1}. Specifically, letting $J_n = 1/N_n \in (1, \infty)$, one has for all $n = 1, 2, \ldots$

$$J_n = A_n\, J_{n-1} + B_n, \quad J_0 = 1/N_0, \tag{32}$$

where $A_n = S_n/\mathcal{D}_n$, $B_n = (1 - S_n)/K\mathcal{D}_n$ and (A_1, B_1), (A_2, B_2), ... are i.i.d. The general solution to this linear recurrence relation is given by

$$J_n = J_0 \left(\prod_{k=1}^{n} A_k\right) + \left(\sum_{j=1}^{n-1} B_j \prod_{i=j+1}^{n} A_i\right) + B_n. \tag{33}$$

We can now establish convergence of the distribution of the stochastic process N_n to steady state.

Theorem 5.1 (Threshold for convergence in distribution) *Let τ_n be a sequence of arrival times of a Poisson process with intensity $\lambda > 0$, and $\mathcal{D}_n$ be a sequence of i.i.d. random disturbance variables on $[0, 1]$ which is independent of the Poisson process. Suppose that $G(N) = rN(1 - N/K)$ for some $r > 0$ and $K > 0$.*

(i) If $E\left[\ln(\mathcal{D}_1)\right] + \frac{r}{\lambda} > 0$, then $\{N_n\}_{n=0}^{\infty}$ converges in distribution to a unique invariant distribution with support on $(0, K)$.

(ii) If $E\left[\ln(\mathcal{D}_1)\right] + \frac{r}{\lambda} < 0$, then $\{N_n\}_{n=0}^{\infty}$ converges in distribution to zero. Moreover, in this latter case, the convergence to $\delta_{\{0\}}$ is exponentially fast in the (Prokhorov) metric of convergence in distribution.

Proof. To prove (i), consider the reciprocal dynamics given by (32). According to Theorem 1 in Brandt (1986), a sufficient condition for the existence of a unique invariant distribution on the state space $(1, \infty)$ is negativity of the parameter

$$E \ln |A_1| < 0,$$

or equivalently,

$$-E\left[\ln\left(\mathcal{D}_1\right)\right] - \frac{r}{\lambda} < 0,$$

and the negativity of the parameter

$$E[\ln |B_1|]^+ < 0, \text{ where } [x]^+ = \max(x, 0),$$

but this follows automatically from the condition in (i). This establishes assertion (i), since the map $x \to x^{-1}$ of $(0, K)$ onto $(\frac{1}{K}, \infty)$ is continuous with a continuous inverse.

To prove (ii), we need to obtain uniqueness of the invariant distribution on $[0, K)$ for $\{N_n\}$. For this we apply the Diaconis and Freedman (1999) condition of "contraction on average" on the complete metric space $[0, K]$. Specifically, in the representation as i.i.d. iterated random maps (30), one also has

$$\gamma_\Theta'(x) = \theta_1 x^{-2} \frac{e^{-r\theta_2}}{\left(\frac{1}{K_1}\left(1 - e^{-r\theta_2}\right) + \frac{1}{x} e^{-r\theta_2}\right)^2} \leq \theta_1 \, e^{r\,\theta_2}. \tag{34}$$

Thus,

$$|\gamma_\Theta(x) - \gamma_\Theta(y)| \leq M_\Theta \, |x - y|$$

for all $0 \leq x, y \leq K$, where

$$M_\Theta = \theta_1 \, e^{r\,\theta_2}.$$

Now, $\delta_{\{0\}}$ is the unique invariant probability on $[0, K]$ provided that

$$E\left[\ln\left(\mathcal{D}_1\right)\right] + \frac{r}{\lambda} \equiv E\left[\ln\left(M_\Theta\right)\right] < 0.$$

Moreover, a direct application of the theorem of Diaconis-Freedman (1999) yields the asserted exponential rate of convergence to steady-state distribution. ■

Next we show that there is a different threshold to assure that the reciprocal of the population converges in mean. This can be significant when parametrizing this model based on data analysis of averages.

Theorem 5.2 (Convergence in mean of the reciprocal) *Assume that the conditions of Theorem* 5.1 *holds. Then, as* $n \to \infty$,

$$E\left(\frac{1}{N_n}\right) \to \begin{cases} \frac{E(\mathcal{D}_1^{-1})}{K\left(1 - \frac{\lambda}{r}\left(E(\mathcal{D}_1^{-1}) - 1\right)\right)}, & \textit{if } \frac{r}{\lambda} > E(\mathcal{D}_1^{-1}) - 1, \\ \infty, & \textit{if } \frac{r}{\lambda} \leq E(\mathcal{D}_1^{-1}) - 1. \end{cases} \tag{35}$$

Proof. First, since the T_n are independent and exponentially distributed, there follows that $E(S_n) = E(\mathrm{e}^{-rT_1}) = \lambda/(\lambda + r)$. Taking expectations in (32), and using the independence of J_{n-1} and A_n, yields:

$$E(J_n) = E(A_1)\, E(J_{n-1}) + E(B_1), \quad n \geq 1, \tag{36}$$

because the A_n and B_n are identically distributed. Hence, as $n \to \infty$

$$E(J_n) \to \begin{cases} \frac{E(B_1)}{1-E(A_1)}, \text{ if } E(A_1) < 1 \\ \infty, \text{ otherwise} \end{cases}$$

Recalling that $A_1 = S_1\mathcal{D}_1^{-1}$, and $B_1 = (1 - S_1)K^{-1}\mathcal{D}_1^{-1}$, and exploiting independence of S_1 and $\mathcal{D}_1^{-1}$, a calculation shows that the above limit is finite if $r/\lambda > E(\mathcal{D}_1^{-1}) - 1$ with the limit given in (35), and infinite otherwise. ■

Theorem 5.2 establishes a new threshold for the growth rate r, namely $r_3 := \lambda \left(E(\mathcal{D}_1^{-1}) - 1\right)$ guaranteeing convergence or divergence of the mean of the reciprocal of the population. For future reference, we note that $r_2 \leq r_3$, where $r_2 = \lambda E(-\ln(\mathcal{D}_1))$ was defined before. This follows from Jensen's inequality and the fact that $\ln(x) \leq x - 1$ for all $x > 0$.

Example 5.1 (Uniformly distributed disturbance) *This example provides a case where the invariant distribution of the reciprocal of the population, and of the population can be given in closed form. For the evolution of the population sizes at successive disturbances, consider $J_n \equiv K/N_n \in (1, \infty)$ satisfies the recurrence (32) scaled by K. An invariant distribution for reciprocal recurrence must be such that J_{n+1} and J_n have the same distribution, so let J denote a random variable having this distribution. Then J must satisfy*

$$J \stackrel{d}{=} A_1\, J + B_1 = \frac{S_1\,(J-1) + 1}{\mathcal{D}_1}. \tag{37}$$

It follows that

$$F_J(z) = P\left[J \leq z\right] = P\left[J \leq \left(\frac{z\,\mathcal{D}_1 - 1}{S_1}\right) + 1\right]. \tag{38}$$

Since the random variables $\mathcal{D}_1$ and S_1 are independent, their joint pdf is $f_{S_1}(s)\, f_{\mathcal{D}_1}(x)$ and

$$F_J(z) = \int_0^1 \int_0^1 F_J\left(1 + \frac{z\,x - 1}{s}\right) f_{S_1}(s) f_{\mathcal{D}_1}(x)\, ds\, dx. \tag{39}$$

Thus (39) provides an integral equation that $F_J(z)$ must satisfy. Since $S_1 = \exp(-r\,T)$, $f_{S_1}(s) = p\, s^{p-1}$ (or $S_1 \stackrel{d}{\sim} Beta(p, 1)$), where $p = \lambda/r$ and $s \in (0, 1)$. Also, since J takes values on $(1, \infty)$, $F_J[1 + (z\,x - 1)/s] = 0$ for $x < 1/z$. Given a solution for $F_J(z)$, we *can easily compute the corresponding invariant distribution for N since $P[N \leq Ku] = P[K/N \geq 1/u]$ and therefore*

$$F_N(Ku) = 1 - F_J(1/u)\,. \tag{40}$$

Changing variables to $u = z\,x$ in (39), and noting that the first integral is zero from $x = 0$ to $x = 1/z$, we have

$$F_J(z) = \int_{u=1}^{z} \left(\frac{1}{z}\right) f_{\mathcal{D}_1}\left(\frac{u}{z}\right) \int_{s=0}^{1} F_J\left(1 + \frac{u-1}{s}\right) f_{S_1}(s)\, ds\, du. \tag{41}$$

Changing variables again to $v = 1 + (u-1)/s$, and using the fact that $f_{S_1}(s) = p\,s^{p-1}$, where $p = \lambda/r$, we find after simplifying that

$$z\,F_J(z) = \int_{u=1}^{z} f_{\mathcal{D}_1}\left(\frac{u}{z}\right)(u-1)^p \left[\int_{v=u}^{\infty} \frac{p\,F_J(v)\,dv}{(v-1)^{p+1}}\right] du. \tag{42}$$

Now assume that $\mathcal{D}_1 \overset{d}{\sim}$ Uniform$(0,1)$. Then all z-dependence, except from the upper limit of integration, is removed from the right-hand side. Taking the derivative of both sides with respect to z twice, we obtain

$$\left[\frac{[z\,F_J(z)]'}{(z-1)^p}\right]' = \frac{-p\,F_J(z)}{(z-1)^{p+1}}. \tag{43}$$

Solving this ODE for $F_J(z)$ with the constraints $z \geq 1$, $F_J(1) = 0$ and $F_J(\infty) = 1$, we find that if $0 < p < 1$ (or $\lambda < r$), the cdf for the invariant distribution simplifies to

$$F_J(z) = \frac{B(1, 1-p, 1+p) - B(\frac{1}{z}, 1-p, 1+p)}{B(1, 1-p, 1+p) - B(0, 1-p, 1+p)}, \quad z \geq 1 \tag{44}$$

where $B(z, a, b)$ is the incomplete Beta function. However, $B(0, 1-p, 1+p) = 0$ for $0 < p < 1$. One may check that $E(J) = \infty$, which is consistent with (35), since $E(\mathcal{D}_1^{-1}) = \infty$ for $\mathcal{D}_1 \overset{d}{\sim}$ Uniform$(0,1)$. Finally, since the limiting population size is given by $N = KJ^{-1}$, we can use (40) to compute the cdf for N as

$$F_N(Ku) = \frac{B(u, 1-p, 1+p)}{B(1, 1-p, 1+p)}, \quad 0 \leq u \leq 1, \tag{45}$$

and therefore the pdf of N is given by

$$f_N(v) = C(p, K)\left(1 - \frac{v}{K}\right)^p \left(\frac{v}{K}\right)^{-p}, \quad 0 \leq v \leq K, \tag{46}$$

where $C(p, K)$ is the normalization constant. In particular the rescaled population $\frac{N}{K}$ has a Beta distribution on $[0,1]$ with parameters $1-p$ and $1+p$, and we previously required that

$0 < p \leq 1$. *Recall from Theorem* 5.1 *that there is a unique, nontrivial invariant distribution when* $E[\ln(\mathcal{D}_1)] + 1/p > 0$ *and otherwise* $N \to 0$ *almost surely. Since* $\mathcal{D}_1 \overset{d}{\sim}$ *Uniform*$(0, 1)$, $E[\ln(\mathcal{D}_1)] = -1$ *and the first condition is equivalent to* $p < 1$. *Note also that the pdf given by (46) diverges at* $u = 0$ *for all* $p > 0$. *In addition,*

$$E(N) = (1-p)K/2, \tag{47}$$

$$Var(N) = (1-p^2)K^2/12. \tag{48}$$

5.2 Disturbance of Logistic Growth: Continuous-Time Model

Since the logistic growth model is a special case ($\alpha = 1$) of the Richards growth model, we postpone analysis of the continuous time logistic growth to the latter analysis where the general form of the continuous time invariant distribution function for general disturbance distributions will be given in terms of the corresponding discrete time invariant distribution. In anticipation of those results, it will follow from Theorem 6.2, see Example 6.1 for details, that in the case of uniformly distributed disturbances, i.e., $\mathcal{D}_1 \overset{d}{\sim} U(0, 1)$ as in Example 5.1, and if $\frac{r}{\lambda} > 1 = -E \ln \mathcal{D}_1$, then the invariant distribution of the rescaled population, N/K associated to the continuous-time model (12), will have the Beta distribution supported on $(0, 1]$ with parameters $(1 - p, 1)$ given by

$$\mu_K(x) = \frac{d}{dx}\mu[0, x] = C_2(p)x^{-p}, \qquad x \in (0, 1]. \tag{49}$$

where $p = \lambda/r < 1$, $C_2(p) = 1/B(1-p, 1)$ and $B(a, b) = \int_0^1 x^{a-1}(1-x)^{b-1}$ denotes the Beta normalization constant. In particular,

$$E(N) = \frac{1-p}{2-p}K \tag{50}$$

$$Var(N) = \frac{(1-p)}{(2-p)^2(3-p)}K^2 \tag{51}$$

Notice that, although both the discrete-time invariant distribution π and μ are Beta distributions, the pdf μ differs from that of its discrete-time counterpart (46) in Example 5.1. This has significant consequences for statistical parameter estimation and calibration of these models, as can be seen by comparing the moments in (47), (48) to (50) and (51) respectively. For instance, the mean of the invariant distribution for the discrete time model is a factor of $\frac{2-p}{2} < 1$ of the mean of the continuous time model, and thus always smaller. As will be shown in Theorem 6.2 in connection with the continuous time post-disturbance Richard's model, a general result is possible that displays the invariant distribution for the continuous time disturbance model as an integral with respect to the invariant distribution of the discrete-time post disturbance model.

6 Richards Growth with Episodic Disturbances

The Richards growth model is a generalization of the logistic growth model with an additional parameter, $\alpha > 0$. In terms of our general model (12) this model is given by $G(N) = r\,N\,[1-(N/K)^{\alpha}]$. The logistic model is the special case of $\alpha = 1$. In particular, as an application of Lemma 2.2, we showed in Example 2.2 that the transformation $h(N) = 1/N^{\alpha}$, and the assignment $\nu = \alpha r$, transforms the system into an affine equation, from which follows that the solution $N(t)$ of the Richards growth model with initial condition N_0 can be written as:

$$N(t) = \frac{1}{\left(\frac{1}{K^{\alpha}}\left(1-e^{-\alpha r\,t}\right)+\frac{1}{N_0^{\alpha}}e^{-\alpha r\,t}\right)^{\frac{1}{\alpha}}}. \tag{52}$$

This curve has an inflection point where $N(t)/K = \left[1/\left(1+\alpha\right)\right]^{1/\alpha}$.

6.1 Disturbed Richards Growth: Discrete-time Model

The discrete-time disturbance model associated with (52) is

$$N_n = \mathcal{D}_n \frac{1}{\left(\frac{1}{K^{\alpha}}(1-e^{-r\alpha T_n})+\frac{1}{N_{n-1}^{\alpha}}e^{-r\alpha T_n}\right)^{1/\alpha}}, \qquad (n \geq 1)\,. \tag{53}$$

The reciprocal transform for the analysis of the Richards growth model is given by $J_n = 1/N_n^{\alpha} \in (K^{1-\alpha}, \infty)$. Define $S_n = \exp\left(-r\alpha\, T_n\right)$, $A_n = S_n \mathcal{D}_n^{-\alpha}$ and $B_n = \left(1-S_n\right) K^{-\alpha}\mathcal{D}_n^{-\alpha}$. One then has

$$J_n = A_n\, J_{n-1} + B_n, \qquad J_0 = 1/N_0^{\alpha}. \tag{54}$$

The following result covers the disturbed logistic growth model as noted earlier by taking $\alpha = 1$.

Theorem 6.1 (Threshold for convergence in distribution) *Let τ_n be a sequence of arrival times of a Poisson process with intensity $\lambda > 0$, and $\mathcal{D}_n$ be a sequence of i.i.d. random disturbance variables on $[0,1]$ which is independent of the Poisson process. Suppose that $G(N) = rN(1-(N/K)^{\alpha})$ for some $r > 0$, $\alpha > 0$ and $K > 0$.*

(i) If $E\left[\ln(\mathcal{D}_1)\right] + \frac{r}{\lambda} > 0$, then $\{N_n\}_{n=0}^{\infty}$ converges in distribution to a unique invariant distribution with support on $(0, K)$.

(ii) If $E\left[\ln(\mathcal{D}_1)\right] + \frac{r}{\lambda} < 0$, then $\{N_n\}_{n=0}^{\infty}$ converges in distribution to 0. Moreover, in this case, the convergence to $\delta_{\{0\}}$ is exponentially fast in the (Prokhorov) metric of convergence in distribution.

Proof. The proof of (i) is similar to the proof of Theorem 5.1: Apply Theorem 1 from Brandt (1986) to the process (54) to show that $J_n = 1/N_n^\alpha$, evolves to a unique, invariant distribution on $(K^{-\alpha}, \infty)$. Then (i) follows because the map $x \to 1/x^\alpha$ of $(0, K)$ onto $(K^{-\alpha}, \infty)$ is continuous with a continuous inverse. To prove (ii) we also proceed as in the proof of Theorem 5.1, and apply the result of Diaconis-Freedman (1999). ■

Remark. It is noteworthy that the threshold condition for the Richards growth model does *not* depend on the parameter α. That said, of course the details of the asymptotic invariant distribution, when it exists, will depend on α.

6.2 Disturbed Richards Growth: Continuous-time Model

The following theorem demonstrates the relationship between invariant distributions associated to the discrete-time and continuous time stochastic processes as stated in general in Theorem 3.1, for the Richards growth model.

Theorem 6.2 *Assume that the conditions of Theorem* 6.1 *hold, and that* $1/p := r/\lambda > -E \ln \mathcal{D}_1$. *Then the rescaled continuous time disturbed Richards model* $\frac{N}{K}$ *has the invariant cumulative distribution function*

$$\mu_K(0, x] = \int_0^x \left(\frac{y^{-\alpha} - x^{-\alpha}}{y^{-\alpha} - 1} \right)^{\frac{\lambda}{\alpha r}} \pi_K(dy) \quad 0 \le x \le 1, \tag{55}$$

where π_K *is the rescaled invariant distribution for the discrete-time distributed Richards model from (i) in Theorem* 6.1.

Proof. Assume $r/\lambda > -E(\ln \mathcal{D}_1)$. Let $\pi_K(dx)$ denote the invariant distribution for the discrete-time post-disturbance Richards model, rescaled by K to a distribution on $[0, 1]$. That is if Y denotes a random variable with distribution $\pi(dx)$ on $[0, K]$ then let $Y_K = K^{-1}Y$, and denote its distribution by $\pi_K(dx)$ on $[0, 1]$. Scaling the post-disturbance evolution accordingly, one has

$$\frac{N_n}{K} = \mathcal{D} \left[e^{-r\alpha t} + \left(\frac{N_{n-1}}{K} \right)^{-\alpha} (1 - e^{-r\alpha T}) \right]^{-\frac{1}{\alpha}}.$$

Thus, letting

$$g_\alpha(T, Y) = [e^{-r\alpha T} + Y_K^{-\alpha}(1 - e^{-r\alpha T})]^{-\frac{1}{\alpha}},$$

where T is exponentially distributed with parameter $\lambda > 0$ and independent of Y_K, by Theorem 3.1 the invariant distribution of the population size rescaled by $\frac{1}{K}$ can be computed as follows.

$$
\begin{aligned}
P\left(g_\alpha(T,Y_K)\le x\right) &= P\left(T \ge -\frac{1}{\alpha r}\ln\left(\frac{x^{-\alpha}-Y_K^{-\alpha}}{1-Y_K^{-\alpha}}\right), Y_K \le x\right)\\
&= E\left[\mathbb{1}_{[Y_K\le x]}\left(\frac{x^{-\alpha}-Y_K^{-\alpha}}{1-Y_K^{-\alpha}}\right)^{\frac{\lambda}{\alpha r}}\right]\\
&= \int_0^x \left(\frac{y^{-\alpha}-x^{-\alpha}}{y^{-\alpha}-1}\right)^{\frac{\lambda}{\alpha r}} \pi_K(dy) \quad 0\le x\le 1. \qquad (56)
\end{aligned}
$$

■

Example 6.1 (Continuous-time disturbed logistic model revisited) *If one assumes a uniformly distributed disturbances on* $[0,1]$*, hence* $1/p = r/\lambda > 1 = -E\ln\mathcal{D}_1$*, and* $\alpha = 1$ *yielding logistic growth, then, according to (46),* Y_K *has the pdf* $C_p\,(1-y)^p\,y^{-p}, 0\le y\le 1$*. Thus, the invariant distribution function for the (rescaled) population in the continuous time Richards growth model is given by*

$$
\begin{aligned}
\mu_K[0,x] &= \int_0^x \left(\frac{y^{-1}-x^{-1}}{y^{-1}-1}\right)^p C_p(1-y)^p y^{-p}\,dy\\
&= C_p'\,x^{1-p}, \quad 0\le x\le 1,\, p=\frac{\lambda}{r}. \qquad (57)
\end{aligned}
$$

The corresponding pdf, i.e., Beta density with parameters $(1-p,1)$ *was displayed earlier at (49).*

7 Gompertz Growth with Episodic Disturbances

The Gompertz growth model is another growth model that can be viewed as the limiting case, $\alpha\to 0+$, of the Richards growth model. To see this, let $r(\alpha)$ be a function such that $\lim_{\alpha\to 0+}\alpha r(\alpha) = r$, where $r>0$ is a constant, and then for all $N>0$:

$$
\lim_{\alpha\to 0+} r(\alpha)N\left[1-\left(\frac{N}{K}\right)^\alpha\right] = \lim_{\alpha\to 0+}\alpha\, r(\alpha)N\frac{1-\mathrm{e}^{\alpha\ln\left(\frac{N}{K}\right)}}{\alpha} = -rN\ln\left(\frac{N}{K}\right),
$$

which is the right-hand side in the Gompertz model. The solution obtained in Example 2.3 may be expressed as

$$
N(t) = K\left(\frac{N_0}{K}\right)^{e^{-rt}} \qquad (58)
$$

In particular, this growth curve has faster growth at early times than the exponential, logistic or Richards model, with an inflection point when $N(t)/K = e^{-1}\approx 0.368$.

7.1 Disturbed Gompertz Growth: Discrete-time Model

The discrete-time disturbance model associated with (58) is

$$N_n = K\left(\frac{N_{n-1}}{K}\right)^{e^{-rT_n}} \mathcal{D}_n \qquad (n \geq 1)\,. \tag{59}$$

Recall that the appropriate transformation for the (rescaled) Gompertz model is $J_n = \ln(N_n/K) \in (-\infty, 0)$, and defining $A_n = e^{-rT_n}$ and $B_n = \ln(\mathcal{D}_n)$. Accordingly one has

$$J_n = A_n\, J_{n-1} + B_n, \qquad J_0 = \ln(N_0/K)\,,\ n = 1, 2, \ldots \tag{60}$$

Theorem 7.1 (Absence of steady state threshold for Gompertz model) *Suppose that $G(N) = -rN\ln(N/K)$ for some $r > 0$ and $K > 0$. Let τ_n be a sequence of arrival times of a Poisson process with intensity $\lambda > 0$, and $\mathcal{D}_n$ be a sequence of i.i.d. random disturbance variables on $[0, 1]$ which is independent of the Poisson process, and such that $E[\ln(-\ln(\mathcal{D}_n))]^+ < \infty$, where $[x]^+ = \max(0, x)$.*

Then $\{N_n\}_{n=0}^{\infty}$ converges in distribution to a unique invariant distribution supported on $(0, K)$.

Proof. Applying Theorem 1 in Brandt (1986) with $A_n = e^{-r\,T_n}$, $B_n = \ln(\mathcal{D}_n)$, one can verify that condition (0.4) in that Theorem 1 holds; namely, $-\infty \leq E\ln|A_1| < 0$ (since $-r/\lambda < 0$) and $E[\ln|B_1|]^+ < \infty$ (since $E[\ln(-\ln(\mathcal{D}_1))]^+ < \infty$ by assumption). Therefore, $J_n = \ln(N_n/K)$ evolves to a unique, nontrivial invariant distribution. The result follows because the map $x \to \ln(x/K)$ of $(0, K)$ onto $(0, 1)$ is continuous with a continuous inverse.

Remark. This result is remarkable compared to the results for disturbed logistic growth or, more generally, disturbed Richards growth in Theorem 6.1 because here there is no threshold, and convergence to extinction cannot occur unless one begins with $N(0) = 0$. The cause of this phenomenon is that in case of Gompertz growth at small population levels, the population grows at a super-exponential rate, and the disturbances occur too infrequently, no matter how strong they are, to counter this.

Example 7.1 (Uniformly distributed disturbance of Gompertz growth) *Let $\tilde{N} = \lim_{n\to\infty}(N_n/K)$ be the normalized population size associated with the invariant distribution. We can derive an integral equation for the cdf of $\tilde{N}$ using the same approach as was used to obtain (39), which yields*

$$F_{\tilde{N}}(z) = \int_{x=z}^{1}\int_{w=1}^{\infty} F_{\tilde{N}}\left(\left(\frac{z}{x}\right)^{w}\right) f_W(w)\, f_{\mathcal{D}}(x)\, dw\, dx. \tag{61}$$

Here, $W = e^{rT}$ has a Pareto distribution with $F_W(w) = 1 - w^{-p}$, $w \geq 1$ and $p = \lambda/r > 0$. As in the example for the logistic growth model, we can change variables twice ($u = z/x$

and $v = u^w$), to get

$$\frac{F_{\tilde{N}}(z)}{z} = \int_{u=1}^{z} f_{\mathcal{D}}\Big(\frac{z}{u}\Big) \frac{\ln^p(u)}{u^2} \left[\int_{v=0}^{u} \frac{p\, F_{\tilde{N}}(v)\, dv}{v\, [\ln(v)]^{p+1}} \right] du. \tag{62}$$

If we assume that $\mathcal{D}_1 \overset{d}{\sim}$ Uniform$(0,1)$, then the only z-dependence on the right-hand side is from the upper limit of integration. Taking derivatives of both sizes with respect to z twice and simplifying, we get the ODE

$$\left[\frac{z^2}{\ln^p(z)} \left(\frac{F_{\tilde{N}}(z)}{z} \right)' \right]' = \frac{p\, F_{\tilde{N}}(z)}{z\, [\ln(z)]^{p+1}}. \tag{63}$$

Solving this with the constraints, $0 \le z \le 1$, $F_{\tilde{N}}(0) = 0$ and $F_{\tilde{N}}(1) = 1$, we find that

$$F_{\tilde{N}}(z) = \frac{\Gamma(1+p, -\ln(z))}{\Gamma(1+p)}, \quad z \in (0,1), \tag{64}$$

where the incomplete Gamma function is used in the numerator. The corresponding pdf is given by

$$f_{\tilde{N}}(z) = \frac{[-\ln(z)]^p}{\Gamma(1+p)}, \quad z \in (0,1). \tag{65}$$

Note that this diverges at $z = 0$ for all $p > 0$. Unlike Example (5.1) (logistic growth, with uniform disturbances), where the existence of the invariant distribution was subject to the threshold condition $p < 1$, this pdf is defined for all $p > 0$. The moments are given by $E(\tilde{N}^a) = (1+a)^{-(1+p)}$, for $a > -1$.

8 Simulation Results

In order to explore the dynamics of the randomly disturbed logistic growth model in greater detail, the model was coded in the Python programming language and is available as open-source code on GitHub at: github.com/peckhams/disturbed_logistic. The code uses the Python packages *numpy* (for numerics and random number generators), *matplotlib* (for plotting sample paths) and *scipy* (for the digamma function, to compute η for the Beta distribution). Note that for the Beta distribution with parameters α and β,

$$\eta = E\left[-\ln(\mathcal{D}_1)\right] = \psi(\alpha+\beta) - \psi(\alpha), \tag{66}$$

where $\psi(x) = \Gamma'(x)/\Gamma(x)$ is the *digamma function*. The model simulates the Poisson event process for the disturbance times and determines the magnitude of multiplicative disturbance events by drawing from a Beta distribution on $[0,1]$. Depending on the choice of parameters, α and β, the Beta distribution can take on a rich variety of forms which makes it a flexible choice to use for the distribution of $\mathcal{D}_1$. When $\alpha = \beta$ the pdf is symmetric, while for $\alpha < \beta$ and $\alpha > \beta$ it is skewed toward $x = 0$ and $x = 1$, respectively. The Uniform distribution is given by $\alpha = \beta = 1$, and the pdf is U-shaped when α and β are both less than one. For other parameter settings, the pdf can diverge at either $x = 0$ or $x = 1$.

The three panels on the left side of Figure 3 show sample paths for parameter settings where the model is in the subcritical regime, and shows the population often close to the carrying capacity between disturbances. The three panels on the right side of Figure 3 show sample paths for parameter settings that are well within the supercritical regime, and show that despite partially recovering from disturbances a number of times, the population size drops to zero fairly rapidly for every realization (or sample path). The six panels in Figure 4 all show sample paths for the model when the parameter settings are at the critical threshold.

9 Conclusions and Open Problems

In this paper we have presented the foundations of a general theory for the dynamics of populations that are episodically disturbed by random catastrophes. We provided a relatively extensive literature review and showed how our results unify and extend a number of results that have been obtained previously for these types of models. A key feature of these models is that many of them exhibit critical thresholds that can be understood as a condition for which mortality rate due to the frequency and magnitude of episodic disturbances exceeds the natural, net growth rate of a population. These critical thresholds can be computed directly in terms of three key model parameters and they mark a boundary between two distinctly different regimes: one where populations persist with a fluctuating size that is described by an invariant distribution, and another where populations become extinct at an exponentially fast rate. However, there is an important difference between real populations and our "model populations", and that is that real populations cannot recover from arbitrarily small sizes or biomass. It can be shown in our models that the population size, $N(t)$, will reach values arbitrarily close to zero repeatedly, even when the model is on the "good side" of the critical threshold, although this occurs with a very small probability. While such events would result in extinction for a real population, the model population can recover from an arbitrarily small, positive size. Despite this fact, even real populations will experience distinctly different dynamics on either side of the critical threshold, and this was a key point in the work of Hanson and Tuckwell. Their model included an *effective extinction level*, $\Delta > 0$, to capture this aspect of real populations, and they gave asymptotic results for the limit of $K/\Delta \to \infty$. They also showed that the distribution of *persistence time* on either side of the threshold is completely different, with very long expected persistence times (e.g. measured in millions of years) on one side and exponentially fast extinction on the other side. Although our results do not specifically address the distribution of persistence time, we obtain exponentially fast convergence to

Table 1: Convergence results for the disturbed growth models. The word *invar* indicates convergence in distribution to an invariant distribution with support on $(0, K)$.

$0 < r < r_1$	$r_1 < r < r_2$	$r_2 < r < r_3$	$r_3 < r$
Exponential			
$E(N_n) \to 0$ $N_n \to 0$, a.s.	$E(N_n) \to \infty$ $N_n \to 0$, a.s.	$E(N_n) \to \infty$ $N_n \to \infty$, a.s.	$E(N_n) \to \infty$ $N_n \to \infty$, a.s.
Logistic			
$N_n \to 0$ (a.s.) $E(N_n^{-1}) \to \infty$	$N_n \to 0$ (a.s.) $E(N_n^{-1}) \to \infty$	$N_n \to$ invar (dist.) $E(N_n^{-1}) \to \infty$	$N_n \to$ invar (dist.) $E(N_n^{-1}) \to c > 0$
Gompertz			
$N_n \to$ invar (dist.)	$N_n \to$ invar (dist.)	$N_n \to$ invar (dist.)	$N_n \to$ invar (dist.)

extinction beyond the critical threshold for the general class of models analyzed in the paper.

Besides providing several specific examples for the exponential, logistic, Richards and Gompertz growth laws — for which critical thresholds as well as invariant distributions were computed in closed form — our results extend existing theory in various directions. We offered a new perspective on deterministic growth laws that shows how they can be represented as a continuous-time weighted average of an appropriately transformed (or measured) initial population size and a similarly transformed carrying capacity. We also distinguished between continuous-time and discrete-time versions of these models and showed how their invariant distributions are different but related; this result has important, practical implications for statistical inference and estimation of parameters. In addition, we illustrated how different types of convergence are characterized by different critical thresholds, including convergence of sample realizations (probability one convergence), convergence in distribution and convergence of means (L^1 convergence).

A summary of threshold regimes are displayed in Table 1, where the thresholds are expressed in terms of critical values of the intrinsic growth rate, r. In Table 1, $r_1 \le r_2 \le r_3$, where

$$r_1 = \lambda \left[1 - E(\mathcal{D}_1)\right], \tag{67}$$

$$r_2 = \lambda \, E\left[-\ln(\mathcal{D}_1)\right], \tag{68}$$

$$r_3 = \lambda \left[E(\mathcal{D}_1^{-1}) - 1\right]. \tag{69}$$

The constant c equals $E(\mathcal{D}_1^{-1})/K\left(1 - \frac{\lambda}{r}(E(\mathcal{D}_1^{-1}) - 1)\right)$, and appeared in Theorem 4.2. Recall that for disturbed Gompertz growth, there is no critical threshold.

Our results also demonstrate the potential for populations to move closer to critical thresholds if key parameters change over time, thereby putting populations at risk of extinction that were not previously at risk. For example, climate change is expected to lead to an increase in the frequency and severity of disturbances (e.g. storms, fires, floods, droughts, infestations) and could also lead to a decrease in the net reproductive rate of various populations (e.g. due to water, food or habitat shortages or difficulty in finding mates). Effects that increase the *disturbance frequency*, λ, or *severity*, as measured by $E[-\ln(\mathcal{D})]$, or that decrease the per capita growth rate, r, can all be seen to move populations closer to the threshold for extinction. In fact, one could potentially estimate these parameters from population and climate data and then use the difference, $I = r - \lambda E[-\ln(\mathcal{D})]$ to measure or monitor the "distance" of a given population from the threshold. This could be used to help identify the most endangered populations, and perhaps suggest actions that would modify the values of the key parameters enough to reduce the risk of extinction.

A natural extension of the disturbances introduced here would allow for climatic effects that could produce a gradual increase in the average frequency of disturbances in the Poisson process. That is, $\Lambda(t), t \geq 0$, would be replaced by a time-inhomogeneous Poisson process with a non-decreasing intensity function $\lambda(t), t \geq 0$, e.g., $\lambda(t) = t^{\theta}$, or $\lambda(t) = \log(1+t), t \geq 0$. However, as is well-known, if $\int_0^\infty \lambda(t)dt = \infty$, then it is possible to homogenize the Poisson process by an appropriate (nonlinear) change in time scale. Under such a time change, the general form of the model remains the same, but the parameters of the logistic curve then become time dependent.

Finally, while the constancy of K and r in the respective assumptions (H3) and (H6) may be reasonable for many species, it is clearly violated for humans. Humans are exceptional in that they have access to contraception and other technologies that affect their intrinsic rates of reproduction and mortality. Individuals and governments also make conscious decisions about reproduction based on economic and societal conditions. In addition, human technology has the potential to significantly increase or decrease the carrying capacity of the planet. Extensions to deterministic growth laws that are intended to apply to human population growth and other trends that are influenced by technology include the *bi-logistic growth* model (Meyer, 1994) which allows the carrying capacity to increase over time and leads to an additional inflection point in the growth curve, compared to simple logistic growth which has at most one inflection point. Marchetti et al. (1996) showed good fits of the bi-logistic model to the populations of several industrialized countries, including England and Japan. Meyer and Ausubel (1999) showed how bi-logistic growth can result from allowing a dynamic carrying capacity, $K(t)$, which itself follows a logistic growth curve. These models offer additional directions for future work.

10 Appendix A: Proof of Theorem 7

The continuous time evolution can be expressed in terms of the semigroup of linear contraction operators defined by

$$T(t)f(x) = E_x f(N(t)), \quad t \geq 0, x > 0,$$

via its infinitesimal generator given by

$$Lf(x) = T'(0)f(x) = \frac{d}{dt} f(g(t,x))|_{t=0} + \lambda\{Ef(\mathcal{D}x) - f(x)\}.$$

To derive this simply observe that up to $o(t)$ error as $t \downarrow 0$, either one or no disturbance will occur in the time interval $[0,t)$. Thus

$$\frac{T(t)f(x) - f(x)}{t} = \frac{f(g(t,x))e^{-\lambda t} - f(x)}{t} + \frac{1}{t}\int_0^t E\left(f(\mathcal{D}g(s,x))\right)\lambda e^{-\lambda s} ds + o(t).$$

The first term is, by the product differentiation rule,

$$\frac{f(g(t,x))e^{-\lambda t} - f(g(0,x))e^{-\lambda 0}}{t} \to \frac{d}{dt} f(g(t,x))e^{-\lambda t}|_{t=0} = \frac{d}{dt} f(g(t,x))|_{t=0} - \lambda f(x).$$

The second term is $\lambda Ef(\mathcal{D}x)$ in the limit as $t \downarrow 0$.
If μ is an invariant probability distribution for this continuous time evolution then one has essentially from the Fokker-Planck equation $L^*\mu = \frac{d}{dt}\mu = 0$ for the adjoint operator, e.g., see Bhattacharya and Waymire (1990). In particular, for f belonging to the domain of L as an (unbounded) operator on $L^2(\mu)$,

$$0 =< f, L^*\mu >=< Lf, \mu >= \int_0^\infty Lf(x)\mu(dx), f \in L^2(\mu).$$

In the case of the discrete time evolution, the one-step transition operator is defined by

$$Mf(x) = Ef(\mathcal{D}g(T_1, x)), \; x > 0.$$

The condition for π to be an invariant probability distribution for the discrete time evolution is that for integrable functions f,

$$\int_0^\infty Mf(x)\pi(dx) = \int_0^\infty f(x)\pi(dx).$$

In particular, it suffices to consider indicator functions $f = 1_C, C \subset (0,\infty)$, in which case one has

$$\int_0^\infty P(\mathcal{D}g(T,x) \in C)\,\pi(dx) = \pi(C).$$

These are the essential calculations required for the proof.
Let's begin with part (i). First note from the definition of μ that

$$\int_0^\infty Lf(x)\mu(dx) = \int_0^\infty \int_0^\infty Lf(g(t,y))\lambda e^{-\lambda t}\, dt\, \pi(dy).$$

Now, in view of the above calculation of L, one has

$$\int_0^\infty Lf(g(t,y))\lambda e^{-\lambda t}\, dt = \int_0^\infty \left(\frac{\partial f(g(t,x))}{\partial t} + \lambda \left[Ef(\mathcal{D}g(t,x)) - f(g(t,x)) \right] \right) \lambda e^{-\lambda t} dt.$$

After an integration by parts this yields

$$\int_0^\infty Lf(g(t,y))\lambda e^{-\lambda t} dt = \lambda\{Ef(\mathcal{D}g(T,x)) - f(x)\}$$

Thus, using this and the invariance of π for the discrete process, one has

$$\int_0^\infty Lf(x)\mu(dx) = \lambda \int_0^\infty \{Ef(\mathcal{D}g(T,x)) - f(x)\}\pi(dx) = 0.$$

This proves part (i).
To prove part (ii), first apply L to the function $x \to P(\mathcal{D}g(T,x) \in C)$. First note from the composition property and an indicated change of variable,

$$P(\mathcal{D}g(T,x) \in C) = P(\mathcal{D}g(T+t,x) \in C) = e^{\lambda t} \int_t^\infty P(\mathcal{D}g(s,x) \in C)\lambda e^{-\lambda s} ds.$$

In particular the first term of $LP(\mathcal{D}g(T,x) \in C)$ is

$$\frac{d}{dt} P(\mathcal{D}g(T,x) \in C)|_{t=0} = \lambda\{P(\mathcal{D}g(T+t,x) \in C) - P(\mathcal{D}x \in C)\}.$$

Adding this to the second term yields,

$$LP(\mathcal{D}g(T,x) \in C) = \lambda\{\int_0^\infty P(\mathcal{D}g(T,y) \in C)P(\mathcal{D}x \in dy) - P(\mathcal{D}x \in C)\}.$$

Integrating with respect to the continuous time invariant distribution μ yields

$$0 = \lambda \int_0^\infty \{\int_0^\infty P(\mathcal{D}g(T_1,y) \in C)P(\mathcal{D}x \in dy) - P(\mathcal{D}x \in C)\}\mu(dx),$$

or equivalently,

$$\int_0^\infty \int_0^\infty P(\mathcal{D}g(T,y) \in C)P(\mathcal{D}x \in dy)\mu(dx) = \int_0^\infty P(\mathcal{D}x \in C)\mu(dx).$$

But since by definition $\pi(dy) = \int_0^\infty P(\mathcal{D}x \in dy)\mu(dx)$, this is precisely the condition

$$\int_0^\infty P(\mathcal{D}g(T,y) \in C)\pi(dy) = \pi(C),$$

i.e., that π is an invariant probability for the discrete time distribution. ■

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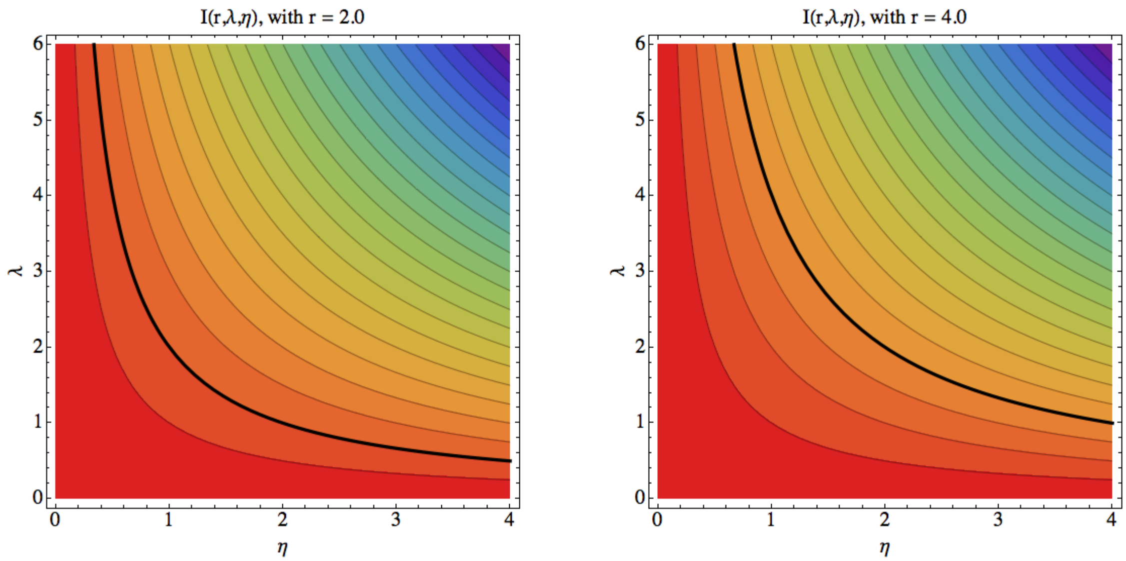

Figure 2: Filled contour plot for the indicator function $I(r, \lambda, \eta) = r - \lambda\,\eta$ for the special cases (a) $r = 2.0$ and (b) $r = 4.0$. The threshold condition, $I = 0$, is shown in each plot as a black curve, with $I < 0$ above the curve and $I > 0$ below the curve. Eventual extinction occurs almost surely where $I < 0$. The black curves in (a) and (b) should be viewed as slices through a black, hyperbolic surface that divides the three-parameter state space into two regions where $I < 0$ and $I > 0$.

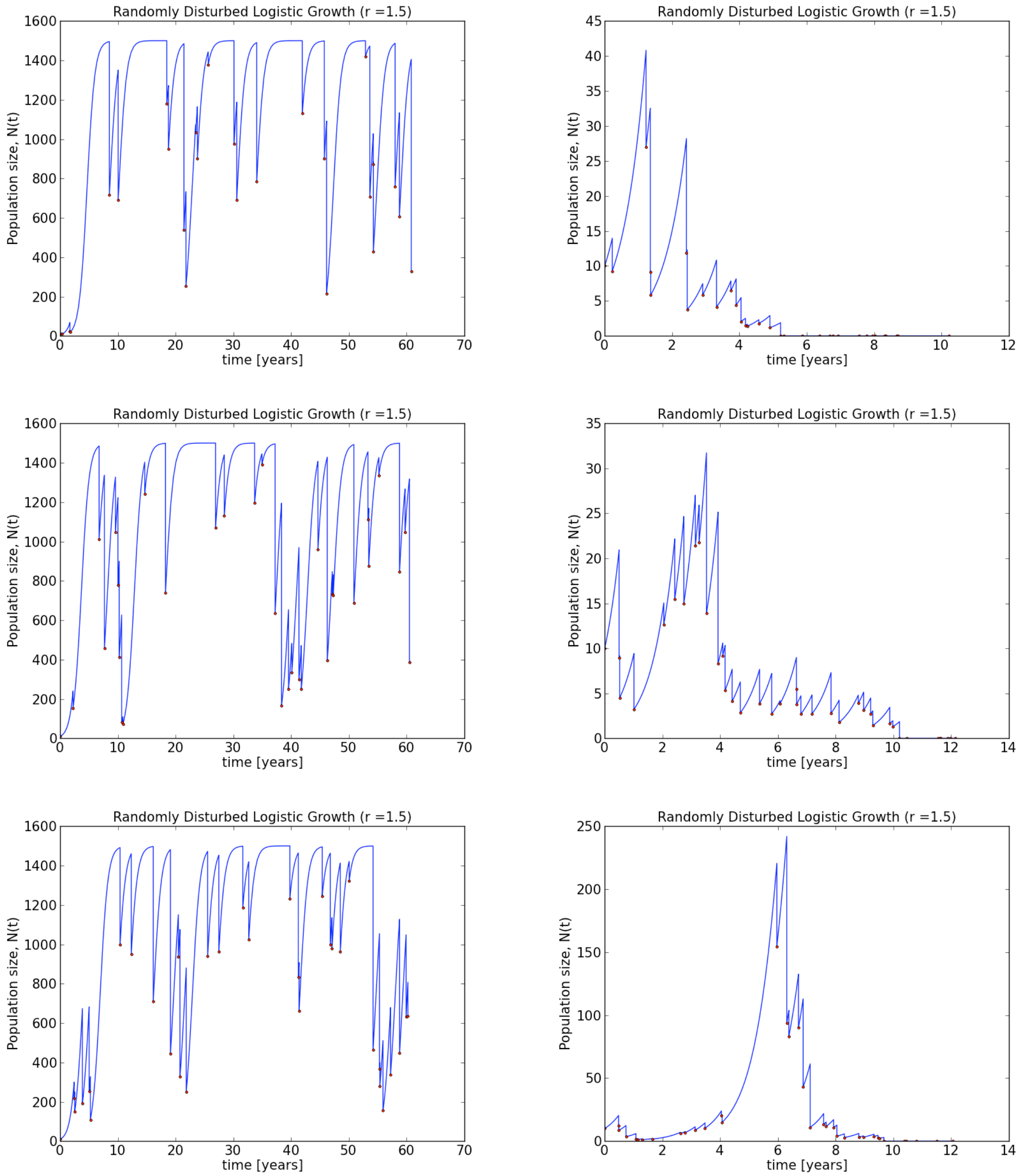

Figure 3: Simulations of the randomly disturbed logistic model, all with $N_0 = 10$, $r = 1.5$, $b = 0.001$ and $m = 2$. The figures on the left show subcritical cases ($I = 1$) with $\lambda = 0.5$, while those on the right show supercritical cases ($I = -1$) with $\lambda = 2.5$. A beta distribution with $a = 3$ and $b = 2$ was used for the random fractions $\mathcal{D}_n$.

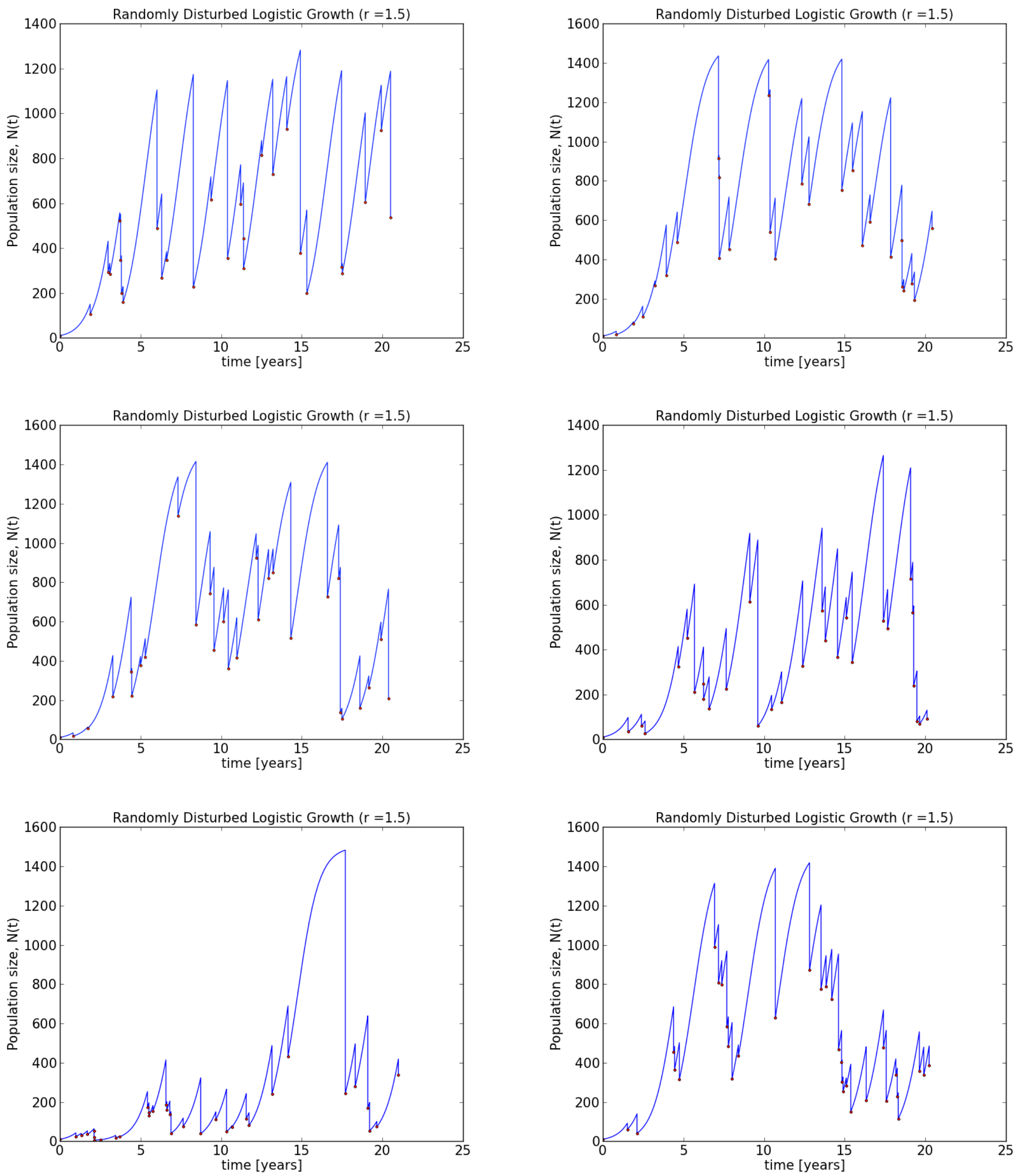

Figure 4: Simulations of the randomly disturbed logistic model, all with $N_0 = 10$, $r = 1.5$, $b = 0.001$, $m = 2$ and $\lambda = 1.5$. This represents the critical threshold value of $I(r, \lambda, m) = 0$. A beta distribution with $a = 3$ and $b = 2$ was used for the random fractions $\mathcal{D}_n$.

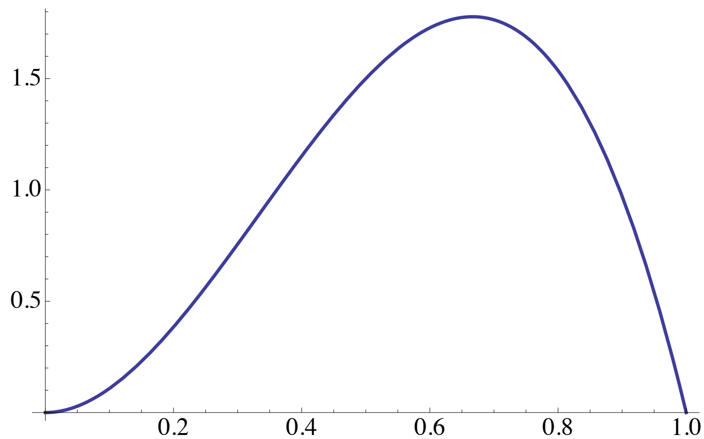

Figure 5: Density function for the Beta distribution with $a = 3$ and $b = 2$. For these parameters, the distribution has $\mu = E(\mathcal{D}) = 3/5$, $m = E(1/\mathcal{D}) = 2$ and $\eta = MISSING$.