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Journal of Mathematical Biology

ISSN 0303-6812

J. Math. Biol.
DOI 10.1007/s00285-018-1217-y

Springer

J. Math. Biol.
https://doi.org/10.1007/s00285-018-1217-y

Mathematical Biology

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Received: 24 August 2016 / Revised: 28 January 2018

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.

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Published online: 16 February 2018

Keywords Population growth models · Random perturbations · Thresholds for persistence

Mathematics Subject Classification 92D25 · 60J05

1 Introduction

Many populations are subject to disturbance events that lead to high mortality, yet also provide future growth opportunities because the disturbances often improve the population's habitat. In McMullen et al. (2017) for instance, the effect of river floodings on 3 types of insects, mayflies, dragonflies and ostracods was examined, and the impact of savanna fires on perennial grasses was assessed using a logistic growth model with time-varying parameters that captured both the disturbances as well as improvements to the habitats following a disturbance event. The main question addressed was to determine via simulations when the population was resilient enough to withstand these disturbances, and when it was not. An important feature of disturbances that was neglected in the analysis of this model, is the random nature, both in time as well as in intensity, with which they occur. One goal of this paper is to address this very issue by considering a class of population growth models which are disturbed randomly. This class of models is larger than the one in McMullen et al. (2017), but it does not incorporate habitat improvements following disturbance events; in other words, a worst-case scenario is considered here. Our main goal is to analyze when these models predict population extinction or persistence. Our analysis leads to certain parameter combinations between ecological parameters on the one hand, and disturbance parameters on the other, for which threshold values can be determined such that when these thresholds are crossed, the system's extinction or persistence behavior changes fundamentally.

The model considered here takes the form of a deterministic continuous-time growth model which is interrupted by discrete, stochastic events that reduce the population to a stochastically determined fraction of the current population size. Let $N(t)$ denote the population's size at time $t \geq 0$, set $\tau_0 = 0$, and assume that the disturbances occur at the random times $\tau_1, \tau_2, \ldots$:

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

Here $G(N)$ represents the deterministic growth rate in between consecutive disturbances (e.g. of logistic form, although our proposed theory can handle other commonly used growth rates), and $\mathcal{D}_i$ are the random variables for the fraction to which the population $N(\tau_i^-)$ at the disturbance time τ_i is reduced by the disturbance. Further assumptions regarding the population's growth rate function $G(N)$, the disturbance times τ_i, and the disturbance fractions $\mathcal{D}_i$ will be introduced later in the paper. Our main goal is to understand the dynamics of the resulting discrete-time stochastic process $N(\tau_i)$, $i = 0, 1, 2, \ldots$, as well as of the continuous-time stochastic process $N(t)$,

$t \geq 0$, in particular with respect to population extinction or persistence. These two processes are analyzed separately. For the discrete-time process we take advantage of a rather extensive theory and methods whose development and extensive recent review are available in Bhattacharya and Majumdar (2007) and Schreiber (2012). For the continuous-time process, and its relationship to the discrete-time process, we take advantage of the general theory of Davis (1984) and Costa (1990) for piecewise deterministic Markov processes; also see Löpker and Palmowski (2013) for a recent historic perspective on applications of this class of models. Several modes of convergence are investigated for these models, including convergence of expected values, almost sure convergence to extinction (sample path by sample path), and convergence in distribution to non-trivial invariant distributions. We illustrate our theory on several commonly used undisturbed growth models [exponential, logistic, Richards (1959) and Gompertz 1825], that share an averaging principle that does not seem to be widely known, but is of interest in its own right. We derive thresholds for the various modes of convergence which are stated in terms of the model parameters and the disturbance characteristics, hereby explicitly and quantitatively linking biological and physical features of the processes. We also present simulation results from an open-source implementation of the random catastrophe model in the Python programming language.

2 Background

2.1 Deterministic population growth models and an averaging principle

A generic class of deterministic continuous time models of population growth found in biology can be cast as the unique solution $N(t), t \geq 0$, to the autonomous growth equation

$$\frac{dN(t)}{dt} = G(N(t)), \quad N(0) = N_0, \text{ with } N_0 < K, \tag{2}$$

where the growth function G is assumed to be smooth, zero at $N = 0$ and $N = K$ and positive on $(0, K)$, and where $K > 0$ represents the population's carrying capacity. For given $N(0) = N_0 > 0$, with $N_0 < K$, one has $\lim_{t\to\infty} N(t) = K$. In addition, the existence of a maximal per capita growth rate $r := \lim_{N\searrow 0} G(N)/N$ is generally assumed, although we shall consider an example below where this limit does not exist. Of course there are natural phenomena, such as Allee effects, that are not captured by this class of models. Kingsland (1982) provides a very nice summary of the historical development with extensive references.

As observed by Lotka (1925), taking only the first two terms of a Taylor series expansion for (smooth) $G(N)$ provides $G(N) = rN(1 - N/K)$, one obtains 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., $K = \infty$. On the other hand, 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.

While the various classical models presented above differ in details, their solutions share a common averaging dynamic that may not be widely known. We provide this unifying principle before proceeding to models that include stochastic disturbances:

Averaging Principle *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 main feature of the models discussed above is that their solutions exhibit this averaging principle, and that the transformation is independent of the initial condition:

Theorem 2.1 *Let $N(t)$ be the solution of equation (2) with initial condition $N(0) = N_0$. 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:*

$$h(N(t)) = h(K)\left(1 - \mathrm{e}^{-\nu t}\right) + h(N_0)\,\mathrm{e}^{-\nu t}, \quad \forall N_0 \in (0, K] \text{ and } \forall t \geq 0. \tag{3}$$

Then $x(t) := h(N(t))$ must satisfy the following affine equation:

$$\frac{dx(t)}{dt} = -\nu x(t) + \nu h(K), \tag{4}$$

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 $x(t) := h(N(t))$ satisfies the affine Eq. (4) for all $t \geq 0$ and all $N_0 \in (0, K]$, then the solution $N(t)$ of system (2) with $N(0) = N_0$, can be represented by (3), for all $t \geq 0$, and for all $N_0 \in (0, K]$.

Proof By applying the chain rule to $x(t) = h(N(t))$, (4) is easily verified to follow from (3). 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 (3) by applying the inverse h^{-1}. □

So the class of systems (2) for which there exists a rescaling function $h(N)$ such that all solutions can be represented as in (3), are precisely those systems which can be transformed to an affine system. 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. Before moving on to such models, we determine the appropriate rescaling functions for the logistic, Richards and Gompertz growth models:

Example 2.1 For logistic growth, $G(N) = rN(1 - N/K)$, the choice $h(N) = 1/N$ transforms system (2) into (4) with $\nu = r$. Consequently, the (transformed) solution of (2) may be expressed as

$$\frac{1}{N(t)} = \frac{1}{K}(1 - \mathrm{e}^{-rt}) + \frac{1}{N_0}\,\mathrm{e}^{-rt}\,. \tag{5}$$

Example 2.2 For Richards growth, $G(N) = rN(1 - (N/K)^{\alpha})$, the choice $h(N) = 1/N^{\alpha}$ transforms system (2) into (4) with $\nu = \alpha r$. Consequently, the solution of (2) is

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

Example 2.3 The Gompertz growth model can be viewed as a specific 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. For Gompertz growth, the choice $h(N) = \ln(N)$ transforms system (2) into (4) with $\nu = r$. Consequently, the solution of (2) is

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

which may also be expressed as

$$N(t) = K\left(\frac{N_0}{K}\right)^{e^{-rt}} \tag{8}$$

In particular, this growth curve has faster growth at early times than the exponential, logistic or Richards model.

2.2 Stochastic population growth models

An 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 (McMullen 2012), 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. Whether the mortality due to a catastrophe is additive or multiplicative, the resulting model becomes a stochastic impulsive differential equation. 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 $T(x)$. 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. For their 1997 Model B, with multiplicative disturbance factors drawn from a uniform distribution, they were able to give asymptotic approximations for $T(x)$. 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 stochastic model

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 (2), but which also experiences random, episodic disturbances that remove a random fraction of the population. In this model, net growth is deterministic between consecutive disturbance events, 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

$$\frac{dN}{dt}(t) = G(N(t)), \quad \tau_i \le t < \tau_{i+1}, \quad i = 0, 1, 2, \ldots,$$
$$N(\tau_i) = \mathcal{D}_i\, N(\tau_i^-), \quad N(0) = N_0 > 0, \quad \text{with } N_0 < K, \tag{9}$$

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 $\lambda > 0$, $\mathcal{D}_0 = 1$, 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.

The disturbance factors determine the fraction of the population that survives a given disturbance. The function G is assumed to satisfy the hypotheses made at the beginning of Sect 2.1. Our goal is to understand the dynamics of the resulting discrete-time stochastic process $N(\tau_i)$, $i = 0, 1, 2, \ldots$, 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 unified by the Averaging Principle subject to various scenarios of the random disturbances.

One may note that $G(0) = 0$ implies that $N = 0$ is an absorbing state for (9). In particular the Dirac (point mass) probability distribution δ_0 is always an invariant (equilibrium) distribution for the population. 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 $(0, K)$.

The theory developed here involves various notions of convergence to a stationary, or invariant, distribution for populations $N(t)$ indexed either continuously or discretely by time $t \ge 0$, in the limit as $t \to \infty$. From the perspective of applications these can be viewed as different ways in which to quantify the long time behavior of the population; we allow here the transformed measure of population size without special notation.

To state these types of convergences, suppose that $N(\infty)$ denotes a random variable having the (possibly transformed) stationary distribution, which may be the Dirac distribution δ_0 at zero in the case of extinction. Then

Definitions

- (Convergence in mean) $\lim_{t\to\infty} E|N(t) - EN(\infty)| = 0$
- (Convergence of means) $\lim_{t\to\infty} EN(t) = EN(\infty)$.
- (Convergence in probability) For any $\epsilon > 0$, $\lim_{t\to\infty} P(|N(t) - N(\infty)| > \epsilon) = 0$.
- (Almost Sure convergence) $P(\{\omega \in \Omega : \lim_{t\to\infty} N(t, \omega) = N(\infty, \omega)\}) = 1$.
- (Convergence in distribution) For any bounded continuous function g, $\lim_{t\to\infty} Eg(N(t)) = Eg(N(\infty))$.

The first type of convergence, also referred to as L^1—convergence, implies convergence of the expected values and, by Chebyshev inequality, the third type of convergence in probability as well. The converse is generally not true but, under an added condition of uniform integrability, convergence in mean and in probability are in fact equivalent. That is, if in addition $\lim_{b\to\infty} \sup_t E(N(t)1[N(t) \ge b]) = 0$, then convergence in probability implies convergence in mean. Almost sure convergence implies convergence in probability, but not conversely. Finally, convergence in probability also implies convergence in distribution and, as would be the case for extinction, if $N(\infty)$ is a sure constant then convergence in distribution implies convergence in probability. Accordingly, the quantification of the long time behavior of the populations is a delicate matter. For example, as will be seen, it is possible to have $N(t) \to 0$ almost surely as $t \to \infty$, while $EN(t)$ remains constant, or even grows, as $t \to \infty$. That is the expected population size may remain constant or grow in time, while almost every sample realization of population sizes will go to zero. Such distinctions have obvious importance to management considerations.

3.2 Discrete-time post-disturbance model

In addition to the continuous time model (9), a natural discrete time model is obtained by considering the population sizes at the sequence of times at which disturbances occur. That is,

$$N_n = \mathcal{D}_n\, N(\tau_n^-), \quad n = 0, 1, 2, \ldots, \quad \tau_0^- = 0, \quad \mathcal{D}_0 = 1, \tag{10}$$

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 Davis (1984) and Costa (1990) in more generality than required here. In order to keep the present paper self-contained we provide a more direct derivation in the Appendix for the special disturbance models of interest to the present paper.

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

$$\frac{dN(t)}{dt} = G(N(t)), \quad N(0) = x, \tag{11}$$

where G satisfies assumptions introduced in Sect. 2.1, and whose solution may be expressed as

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

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.

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

$$N_0 = x, \quad N_n = \mathcal{D}_n g(T_n, N_{n-1}), \quad n = 1, 2, \ldots. \tag{12}$$

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 (11). Then

(i) *Given an invariant distribution π for the discrete time post-disturbance population model* (12)*, 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 (9).

(ii) *Given an invariant distribution μ, for the continuous time disturbance model* (9)*, let Y be a random variable with distribution μ, and let $\mathcal{D}_1$ be distributed as the random disturbance factor distributed in* $(0, 1)$*, independent of Y. Then*

$$\pi(C) = P(\mathcal{D}_1 Y \in C), \quad C \subset (0, \infty),$$

is an invariant distribution for the corresponding discrete time post-disturbance model (12).

Proof See Appendix A. □

4 Exponential growth with episodic disturbances

As a warm-up to the more complex 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

$$N_n = N_0 \prod_{k=1}^{n} \left[e^{r\,T_k} \mathcal{D}_k \right], \tag{13}$$

where N_0 is a given initial condition in $(0, K)$, $T_n \equiv \tau_n - \tau_{n-1}$ $(n \geq 1)$ is the random time interval between consecutive 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 (1990). 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. Since many of our convergence statements involve expectations of the natural logarithm of the disturbances, which could be zero, we shall use the convention throughout this paper that $\ln 0 = -\infty$.

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* $0 < r + \lambda E\,[\ln \mathcal{D}_1] < \infty$, *then $N_n \to \infty$ a.s. as $n \to \infty$.*
(ii) *If* $-\infty \leq r + \lambda E\,[\ln \mathcal{D}_1] < 0$, *then $N_n \to 0$ a.s. as $n \to \infty$.*

Proof Taking logarithms in (13) we have

$$\ln(N_n) = \ln(N_0) + \sum_{k=1}^{n} \ln(\mathcal{D}_k) + r \sum_{k=1}^{n} T_k. \tag{14}$$

Now apply the strong law of large numbers to get

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

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. □

Notice that the critical threshold occurs when the quantity $r + \lambda E\,[\ln \mathcal{D}_1]$, which biologically stands for the per capita growth rate + the average (negative) effect of the disturbance, switches sign. Figure 1 helps to visualize the threshold as a surface in the state space of the model that depends on the three parameters r, λ and $\eta = -E[\ln(\mathcal{D}_1)]$. The function $I(r, \lambda, \eta) = r - \lambda\,\eta$ is used to measure distance from the critical threshold.

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, a different threshold is obtained for the (weaker) convergence/divergence behavior of the averages.

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

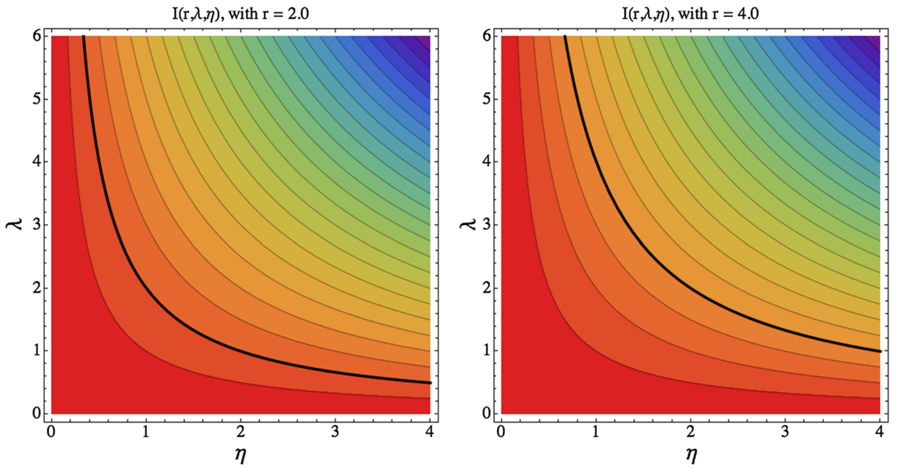

Fig. 1 Filled contour plot for the indicator function $I(r, \lambda, \eta) = r - \lambda\,\eta$, where $\eta = -E[\ln(\mathcal{D}_1)]$, for the special cases **a** $r = 2.0$ and **b** $r = 4.0$. The threshold condition, $I = 0$, is shown in each plot as a black curve, with $I < 0$ above the curve and $I > 0$ 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 $I > 0$

$$E(N_n) \to \begin{cases} 0, & \textit{if } r + \lambda(E(\mathcal{D}_1) - 1) < 0 \\ N_0, & \textit{if } r + \lambda(E(\mathcal{D}_1) - 1) = 0 \\ \infty, & \textit{if } r + \lambda(E(\mathcal{D}_1) - 1) > 0 \end{cases} \tag{15}$$

Proof Observe that

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

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 (15). □

Remark If $r + \lambda(E(\mathcal{D}_1) - 1) < 0$, then $r + \lambda E[\ln(\mathcal{D}_1)] < 0$. 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 $E(N_n) \to 0$, then $N_n \to 0$ almost surely, but not conversely.

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 $r_1 \leq r_2$, the second inequality implies the first. In the case where $r_1 < r < r_2$, we have $N_n \to 0$ almost surely but $E(N_n) \to \infty$. In particular, the sure eventual demise of a population would be misinformed by its mean behavior in such a parameter regime.

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 $r < \lambda/2$ and $r < \lambda$, respectively. Compare this to Example 5.1.

Example 4.2 (Two-valued distributed disturbance) Suppose that $\mathcal{D}_1$ either equals 1 (i.e. no disturbance), or δ for some $0 < \delta < 1$, both with probability 1/2. Then $E(\mathcal{D}_1) = (1+\delta)/2$, $E\,[\ln(\mathcal{D}_1)] = \ln(\delta)/2$ and the two convergence regimes are given by

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

respectively. So with $\delta = 1/4$, one regime is $r < (3/8)\lambda \approx 0.375\lambda$ for convergence of means, while the regime for almost sure convergence is $r < (\ln 2)\lambda \approx 0.693\lambda$.

4.2 Disturbance of exponential growth: continuous-time model

We now highlight some properties for the mean of the disturbed continuous-time exponential growth model.

Theorem 4.3 *Assume that the conditions of Theorem 4.1 hold. Then the solution $N(t)$ of (9) satsifies:*

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

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

$$\tau = \sum_{k=1}^{M(t)} T_k. \tag{16}$$

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

$$N(t) = N_{M(t)}\, e^{r(t-\tau)}. \tag{17}$$

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 (17) to give simply $e^{r\,t}$. This allows (17) to be written as a product of a random number of i.i.d. random variables

$$N(t) = N_0\, e^{r\,t} \prod_{k=1}^{M(t)} \mathcal{D}_k. \tag{18}$$

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

$$\begin{aligned} E\left[\prod_{k=1}^{M(t)} \mathcal{D}_k\right] &= E\left\{\prod_{k=1}^{M(t)} E[\mathcal{D}_k | M(t)]\right\} \\ &= E\{(\mathcal{D}_1))^{M(t)}\} \\ &= e^{-\lambda\, t(1-E(\mathcal{D}_1))}. \end{aligned} \tag{19}$$

Inserting this into (18), 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 (18). Together, (i) and (ii) also allow the variance to be computed. □

5 Logistic growth with episodic disturbances

We now turn to the case of logistic growth, where $G(x) = rx(1 - \frac{x}{K})$ in our general model, (9). 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. In view of the Averaging Principle, we will provide a detailed analysis only for the logistic growth model, and simply state the corresponding theorems for the Richards and Gompertz models.

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 (10), since N_{n-1} becomes the (new) initial condition for the next disturbance interval, we have

$$N_n = \mathcal{D}_n \frac{1}{\frac{1}{K}\left(1 - e^{-r\,T_n}\right) + \frac{1}{N_{n-1}} e^{-r\,T_n}}, \qquad (n \geq 1)\,, \tag{20}$$

where N_0 is given, T_1 is the random time until the first disturbance, $T_n \equiv \tau_n - \tau_{n-1}$ ($n \geq 1$) 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 (20) can also be written as an iterated random function dynamics (see Bhattacharya and Majumdar 2007; Schreiber 2012) for extensive theory of such dynamics),

$$N_n = \gamma_{\Theta^{(n)}} \circ \gamma_{\Theta^{(n-1)}} \circ \cdots \circ \gamma_{\Theta^{(1)}}, \tag{21}$$

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

$$\gamma_\Theta(x) \equiv \gamma_{(\theta_1,\theta_2)}(x) = \theta_1 \frac{1}{\frac{1}{K}\left(1 - e^{-r\theta_2}\right) + \frac{1}{x} e^{-r\theta_2}}. \tag{22}$$

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 $J_n = 1/N_n \in (1, \infty)$,

$$J_n = A_n\, J_{n-1} + B_n, \quad J_0 = 1/N_0, \tag{23}$$

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

$$J_n = J_0 \left(\prod_{k=1}^{n} A_k\right) + \left(\sum_{j=1}^{n-1} B_j \prod_{i=j+1}^{n} A_i\right) + B_n. \tag{24}$$

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 $K > 0$. Then*

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

Proof To prove (i), consider the reciprocal dynamics given by (23). 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,

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

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 (21), one also has

$$\gamma'_\Theta(x) = \theta_1 x^{-2} \frac{e^{-r\theta_2}}{\left(\frac{1}{K_1}\left(1 - e^{-r\theta_2}\right) + \frac{1}{x} e^{-r\theta_2}\right)^2} \leq \theta_1\, e^{r\,\theta_2}. \tag{25}$$

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

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

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

Technical Remarks The model (9) defines a reducible Markov process since states in $(0, \infty)$ are inaccessible from $N = 0$. The proof above takes advantage of some special techniques and observations to exploit this reducibility to the benefit of a rather complete theory for the model (9). Interestingly, owing to a technical condition on topological completeness of the phase space for application of Diaconis and Freedman (1999), and the condition of affine linearity to apply Brandt (1986), 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.

For an alternative approach to the extinction result given here one may apply Theorem 3.1(i) of Schreiber (2012). However the exponential rate obtained by use of Diaconis and Freedman (1999) given here would not follow. In addition, one may also apply Theorem 3.1 of Schreiber (2012) to obtain a stronger form of persistence that, together with boundedness, implies the existence of an invariant probability distribution. This, together with irreducibility on $(0, K]$, would imply uniqueness as well.

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 $n \to \infty$,*

$$E\left(\frac{1}{N_n}\right) \to \begin{cases} \frac{E(\mathcal{D}_1^{-1})}{K\left(1-\frac{\lambda}{r}(E(\mathcal{D}_1^{-1})-1)\right)}, & \text{if } r > \lambda(E(\mathcal{D}_1^{-1}) - 1), \\ \infty, & \text{if } r \le \lambda(E(\mathcal{D}_1^{-1}) - 1). \end{cases} \tag{26}$$

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 (23), and using the independence of J_{n-1} and A_n, yields:

$$E(J_n) = E(A_1)\, E(J_{n-1}) + E(B_1), \quad n \ge 1, \tag{27}$$

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 (26), 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 $r_2 \le r_3$, where $r_2 = -\lambda E(\ln(\mathcal{D}_1))$ was defined before. As before, this follows the fact that $\ln(x) \le x - 1$ for all $x > 0$, and taking expectations.

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 (23) 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

$$J \stackrel{d}{=} A_1\, J + B_1 = \frac{S_1\,(J-1)+1}{\mathcal{D}_1}. \tag{28}$$

It follows that

$$F_J(z) = P\,[J \le z] = P\left[J \le \left(\frac{z\,\mathcal{D}_1 - 1}{S_1}\right) + 1\right]. \tag{29}$$

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

$$F_J(z) = \int_0^1 \int_0^1 F_J\left(1 + \frac{z\,x-1}{s}\right)\, f_{S_1}(s) f_{\mathcal{D}_1}(x)\, ds\, dx. \tag{30}$$

Thus (30) 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 $P\,[N \le K u] = P\,[K/N \ge 1/u]$ and therefore

$$F_N(K u) = 1 - F_J\,(1/u)\,. \tag{31}$$

Changing variables to $u = z\,x$ in (30), and noting that the first integral is zero from $x = 0$ to $x = 1/z$, we have

$$F_J(z) = \int_{u=1}^{z} \left(\frac{1}{z}\right) f_{\mathcal{D}_1}\left(\frac{u}{z}\right) \int_{s=0}^{1} F_J\left(1 + \frac{u-1}{s}\right) f_{S_1}(s)\, ds\, du. \tag{32}$$

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

$$z\,F_J(z) = \int_{u=1}^{z} f_{\mathcal{D}_1}\left(\frac{u}{z}\right)(u-1)^p \left[\int_{v=u}^{\infty} \frac{p\,F_J(v)\,dv}{(v-1)^{p+1}}\right] du. \tag{33}$$

Now assume that $\mathcal{D}_1 \stackrel{d}{\sim}$ 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

$$\left[\frac{[z\,F_J(z)]'}{(z-1)^p}\right]' = \frac{-p\,F_J(z)}{(z-1)^{p+1}}. \tag{34}$$

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

$$F_J(z) = \frac{B(1, 1-p, 1+p) - B(\frac{1}{z}, 1-p, 1+p)}{B(1, 1-p, 1+p) - B(0, 1-p, 1+p)}, \quad z \ge 1 \tag{35}$$

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 (26), 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 (31) to compute the cdf for N as

$$F_N(Ku) = \frac{B(u, 1-p, 1+p)}{B(1, 1-p, 1+p)}, \quad 0 \le u \le 1, \tag{36}$$

and therefore the pdf of N is given by

$$f_N(v) = C(p, K)\left(1 - \frac{v}{K}\right)^p \left(\frac{v}{K}\right)^{-p}, \quad 0 \le v \le K, \tag{37}$$

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 $0 < p \le 1$. 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 (37) diverges at $u = 0$ for all $p > 0$. In addition,

$$E(N) = (1-p)K/2, \tag{38}$$

$$Var(N) = (1-p^2)K^2/12. \tag{39}$$

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 6.1, 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 (9), will have the Beta distribution supported on (0, 1] with parameters $(1-p, 1)$ given by

$$\mu_K(x) = \frac{d}{dx}\mu[0, x] = C_2(p)x^{-p}, \qquad x \in (0, 1]. \tag{40}$$

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

$$E(N) = \frac{1-p}{2-p}K \tag{41}$$

$$Var(N) = \frac{(1-p)}{(2-p)^2(3-p)}K^2 \tag{42}$$

Although in this case, the discrete-time invariant distribution π and μ exist under the same threshold condition ($r/\lambda > 1 = -E \ln \mathcal{D}_1$), and although both are Beta distributions, the pdf μ differs from that of its discrete-time counterpart (37) 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 (38), (39) and (41), (42) 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 6.1 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 and Gompertz growth with episodic disturbances

6.1 Richards growth

The Richards growth model is a generalization of the logistic growth model with an additional parameter, $\alpha > 0$. In terms of our general model (9) 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 2.1, 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 $N(t)$ with initial condition N_0 can be written as:

$$N(t) = \frac{1}{\left(\frac{1}{K^\alpha}\left(1 - e^{-\alpha r\, t}\right) + \frac{1}{N_0^\alpha} e^{-\alpha r\, t}\right)^{\frac{1}{\alpha}}}. \tag{43}$$

The discrete-time disturbance model associated with (43) is

$$N_n = \mathcal{D}_n \frac{1}{\left(\frac{1}{K^\alpha}(1 - e^{-r\alpha T_n}) + \frac{1}{N_{n-1}^\alpha} e^{-r\alpha T_n}\right)^{1/\alpha}}, \qquad (n \geq 1)\,. \tag{44}$$

The following Theorem summarizes the behavior of the discrete and continuous time Richards growth models. Since the proof mirrors the corresponding results for the logistic growth models, it is omitted.

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 $r + \lambda E\,[\ln(\mathcal{D}_1)] > 0$, then $\{N_n\}_{n=0}^\infty$ converges in distribution to a unique invariant distribution with support on* $(0, K)$. *Moreover, the rescaled continuous time disturbed Richards model $\frac{N(t)}{K}$ has the invariant cumulative distribution function*

$$\mu_K(0,x] = \int_0^x \left(\frac{y^{-\alpha} - x^{-\alpha}}{y^{-\alpha} - 1}\right)^{\frac{\lambda}{\alpha r}} \pi_K(dy) \quad 0 \le x \le 1, \tag{45}$$

where π_K is the (rescaled) invariant distribution for N_n.

(ii) *If $r + \lambda E\,[\ln(\mathcal{D}_1)] < 0$, 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 metric of convergence in distribution.*

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.

Example 6.1 (Continuous-time disturbed logistic model revisited) If one assumes a uniformly distributed disturbance on [0, 1], hence $1/p = r/\lambda > 1 = -E \ln \mathcal{D}_1$, and $\alpha = 1$ yielding logistic growth, then, according to (37), 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

$$\begin{aligned} \mu_K[0,x] &= \int_0^x \left(\frac{y^{-1} - x^{-1}}{y^{-1} - 1}\right)^p C_p(1-y)^p y^{-p}\, dy \\ &= C'_p\, x^{1-p}, \quad 0 \le x \le 1,\ p = \frac{\lambda}{r}. \end{aligned} \tag{46}$$

The corresponding pdf, i.e., Beta density with parameters $(1-p, 1)$ was displayed earlier at (40).

6.2 Gompertz growth

Recall the solution of the continuous-time Gompertz model, obtained in Example 2.3:

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

and the solution of the associated discrete-time disturbance model is

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

The behavior of the Gompertz model is as follows; it can be proved in similar fashion to the logistic growth model:

Theorem 6.2 (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* $E[\ln(-\ln(\mathcal{D}_1))]^+ < \infty$, *where* $[x]^+ = \max(0, x)$. *Then* $\{N_n\}_{n=0}^{\infty}$ *converges in distribution to a unique invariant distribution supported on* $(0, K)$.

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 6.2 (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 (30), which yields

$$F_{\tilde{N}}(z) = \int_{x=z}^{1} \int_{w=1}^{\infty} F_{\tilde{N}}\left(\left(\frac{z}{x}\right)^{w}\right) f_W(w)\, f_{\mathcal{D}}(x)\, dw\, dx. \tag{47}$$

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

$$\frac{F_{\tilde{N}}(z)}{z} = \int_{u=1}^{z} f_{\mathcal{D}}\left(\frac{z}{u}\right) \frac{\ln^p(u)}{u^2} \left[\int_{v=0}^{u} \frac{p\, F_{\tilde{N}}(v)\, dv}{v\, [\ln(v)]^{p+1}}\right] du. \tag{48}$$

If we assume that $\mathcal{D}_1 \stackrel{d}{\sim} \text{Uniform}(0, 1)$, 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

$$\left[\frac{z^2}{\ln^p(z)}\left(\frac{F_{\tilde{N}}(z)}{z}\right)'\right]' = \frac{p\, F_{\tilde{N}}(z)}{z\, [\ln(z)]^{p+1}}. \tag{49}$$

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

$$F_{\tilde{N}}(z) = \frac{\Gamma(1 + p, -\ln(z))}{\Gamma(1 + p)}, \quad z \in (0, 1), \tag{50}$$

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

$$f_{\tilde{N}}(z) = \frac{[-\ln(z)]^p}{\Gamma(1 + p)}, \quad z \in (0, 1). \tag{51}$$

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 $a > -1$.

7 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,

$$\eta = E\,[-\ln(\mathcal{D}_1)] = \psi(\alpha+\beta) - \psi(\alpha), \tag{52}$$

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 Fig. 2 show sample paths for parameter settings where the model is in a persistence regime, and shows the population often close to the carrying capacity between disturbances. The three panels on the right side of Figure 2 show sample paths for parameter settings that are well within an extinction 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 Fig. 3 all show sample paths for the model when the parameter settings are at the critical threshold.

Figure 4 shows empirical probability density functions (epdf) for the invariant distribution of the discrete-time model, using a variety of different Beta distributions for the disturbances. Each epdf was constructed from 10 million disturbances and the pdfs of the corresponding Beta distributions are shown as insets. Note that the invariant epdf for the Uniform distribution (a), agrees with the closed-form result from our example for the case $p = 1/2$. When disturbances are drawn from a right triangle distribution with mode at $x = 1$, the invariant epdf appears to be symmetric and is zero at 0 and K. All simulations are in a persistence regime because the epdf would collapse to a delta function at zero if this was not the case.

Figure 5 shows empirical probability density functions (epdf) for the invariant distribution of the discrete-time model, for various values of r in the logistic growth model and a fixed Beta distribution for the disturbances. This figure illustrates the transition through the persistence regime for increasing values of r, and the effect on the skewness of the epdf for increasing r-values. The first epdf is for r slightly larger than r_2 and is concentrated near the origin. For $r_2 < r < r_3 = 0.75$, the mode of the epdf is zero and the slope there is negative. For $r \geq r_3$, the mode of the epdf is positive and the slope at the origin is positive. As r increases, the epdf switches from

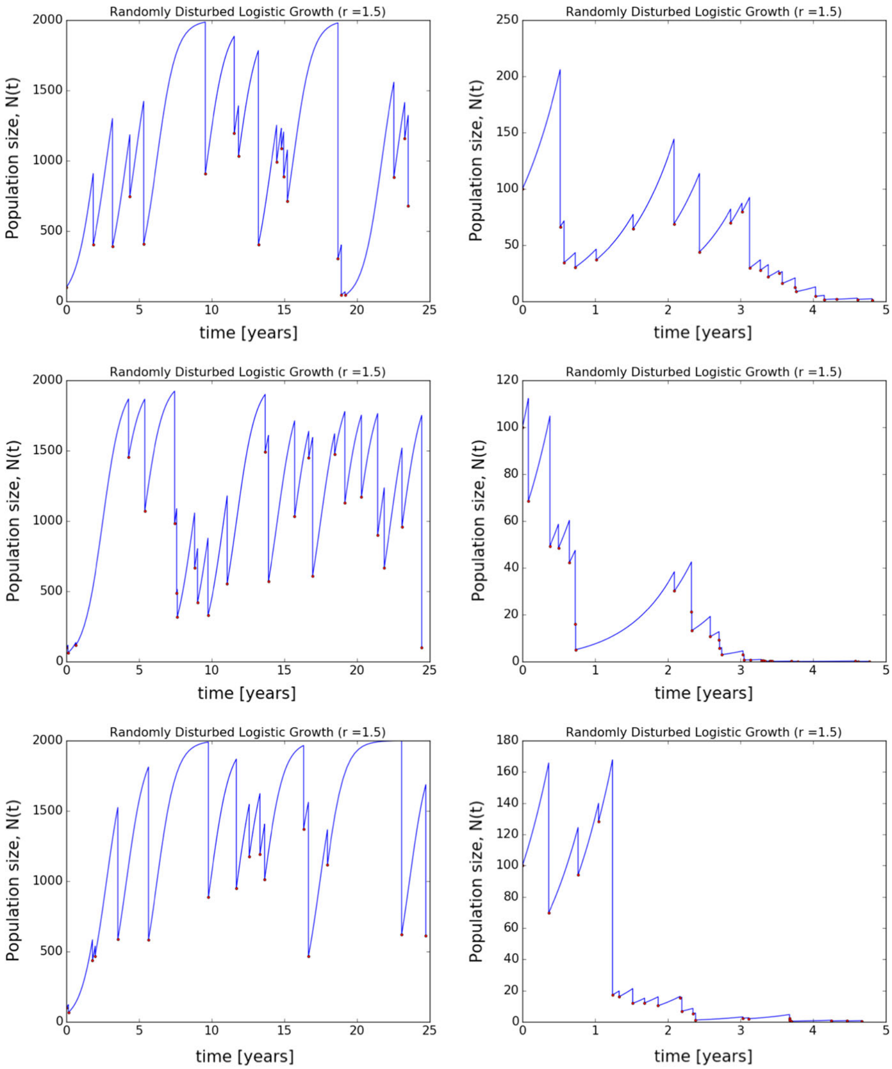

Fig. 2 Simulations of the randomly disturbed logistic model, all with $N_0 = 100$, $r = 1.5$, and $K = 2000$. A beta distribution with $\alpha = 3$ and $\beta = 2$ was used for the random fractions, $\mathcal{D}_n$, with $\eta = 7/12 = 0.5833$. The figures on the left show persistence cases ($I = 1$) with $\lambda = 6/7 = 0.857$, while those on the right show extinction cases ($I = -1$) with $\lambda = 30/7 = 4.285$

left-skewed to right-skewed, being approximately symmetric around $x = K/2 = 50$ for $r = 2.5$. As $r \to \infty$, the sequence of epdfs appears to converge to the most right-skewed curve shown ($r = 1000$).

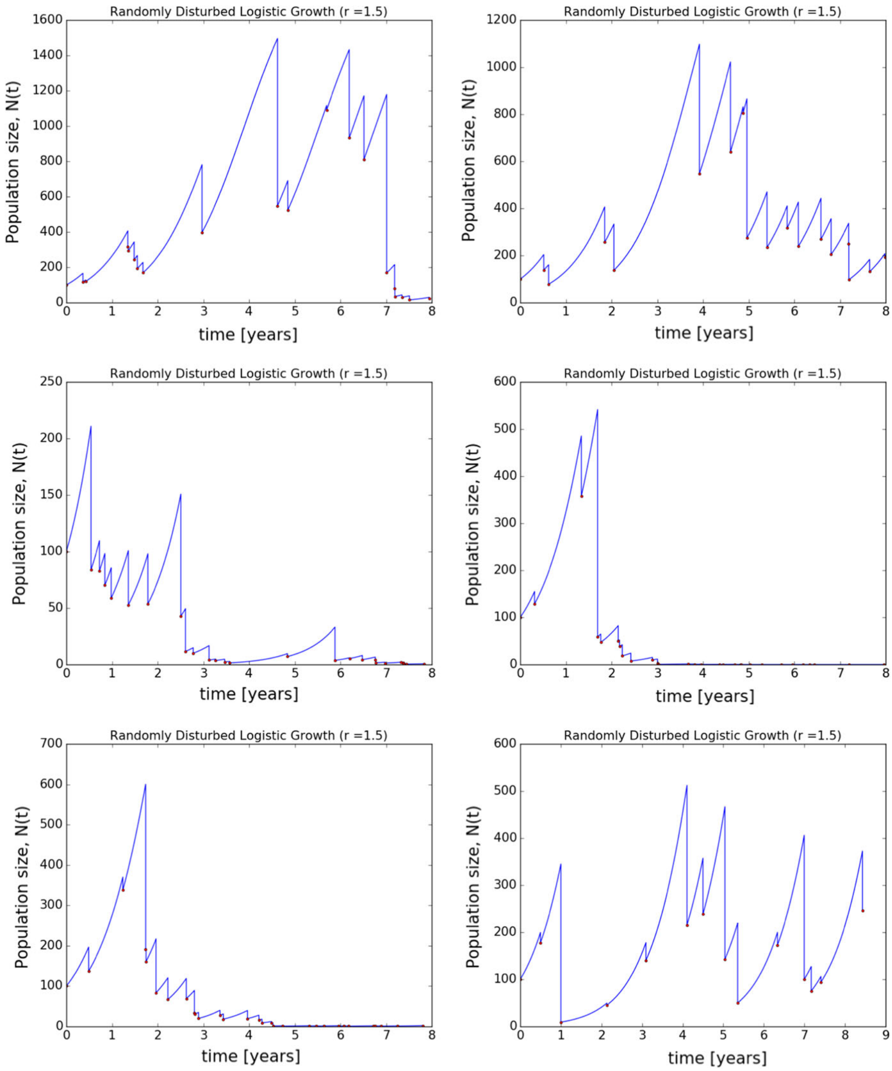

Fig. 3 Simulations of the randomly disturbed logistic model, all with $N_0 = 100$, $r = 1.5$, $K = 2000$ and $\lambda = 18/7 = 2.57$. A beta distribution with $\alpha = 3$ and $\beta = 2$ was used for the random fractions, $\mathcal{D}_n$, with $\eta = 7/12 = 0.5833$. This represents the critical threshold value of $I(r, \lambda, \mu) = 0$

8 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 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

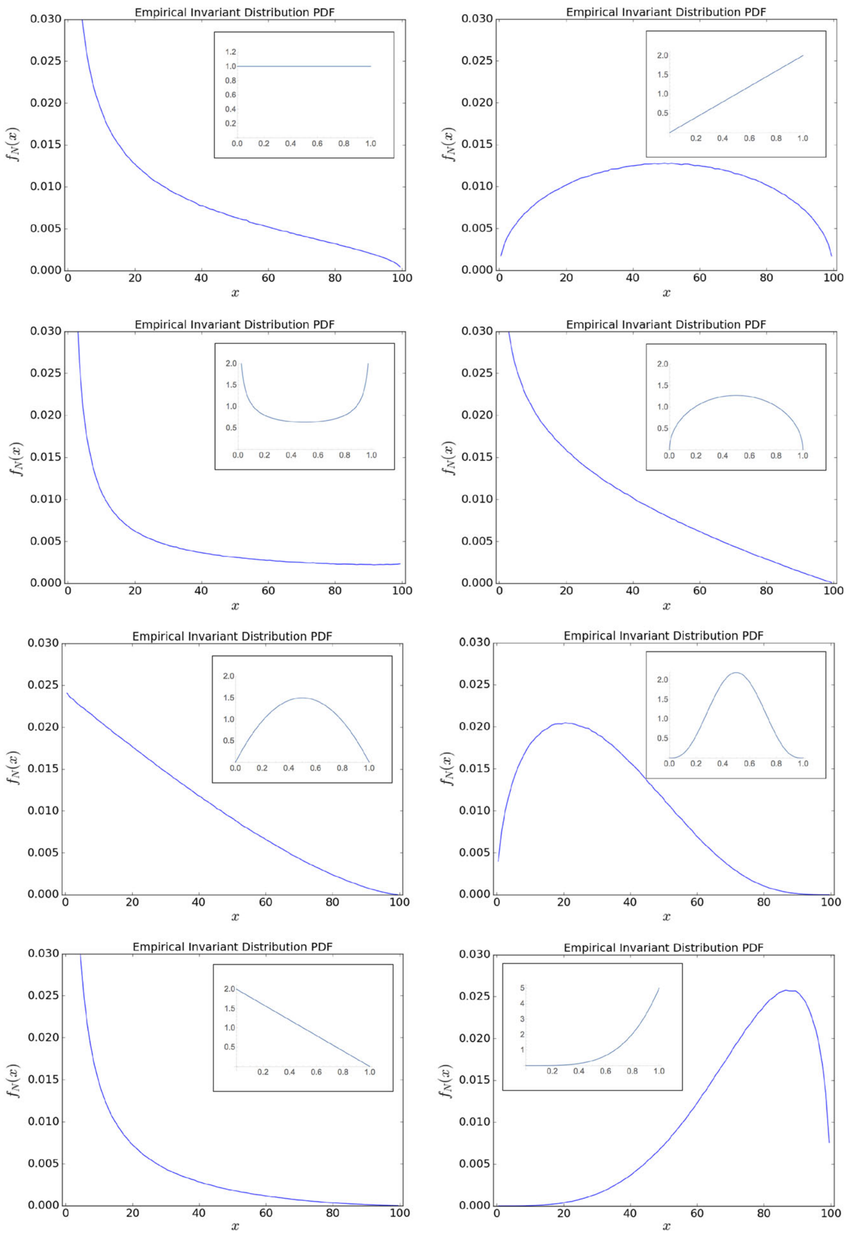

Fig. 4 Empirical probability density functions (epdf) for the invariant distribution with disturbances drawn from a variety of different Beta distributions (plotted as insets). All cases had $r = 1.5$, $\lambda = 0.75$, $K = 100$, $N_0 = 50$ and 10 million disturbances. From left to right, top to bottom: **a** uniform ($a = 1$, $b = 1$, $I = 0.75$, max $= 0.1274$), **b** triangle, right skewed ($a = 2$, $b = 1$, $I = 1.125$, max $= 0.0128$), **c** arcsine ($a = 1/2$, $b = 1/2$, $I = 0.460$, max $= 0.4610$), **d** ellipse ($a = 3/2$, $b = 3/2$, $I = 0.835$, max $= 0.0497$), **e** parabola ($a = 2$, $b = 2$, $I = 0.875$, max $= 0.0241$), **f** bell shape ($a = 4$, $b = 4$, $I = 0.930$, max $= 0.0205$), **g** triangle, left skewed ($a = 1$, $b = 2$, $I = 0.375$, max $= 0.4643$), **h** unnamed ($a = 5$, $b = 1$, $I = 1.35$, max $= 0.0258$). Here, $I = r - \lambda\,\eta$

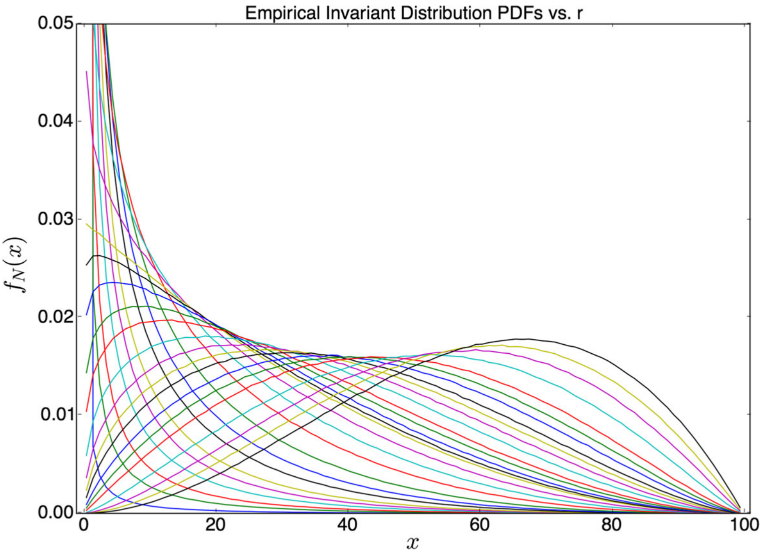

Fig. 5 A set of 28 empirical, steady-state pdfs, each obtained from running the discrete model for 10 million disturbance events with a different value of r. The other model parameters are fixed at $K = 100$, $N_0 = 50$ and $\lambda = 0.75$. Disturbance factors are drawn from a Beta distribution with $\alpha = 3$ and $\beta = 2$. For these parameters, $r_1 = 0.3$, $r_2 = 0.4375$ and $r_3 = 0.75$. The x-axis starts at -1 to better show detail at the origin. For $r < r_2$, the pdf collapses to a delta function at 0, as predicted (not shown). Curves shown are for r-values of 0.44, 0.445, 0.45, 0.46, 0.47, 0.48, 0.5, 0.52, 0.55, 0.6, 0.65, 0.7, 0.75, 0.77, 0.8, 0.85, 0.9, 1.0, 1.1, 1.2, 1.3, 1.5, 1.7, 2.0, 3.0, 5.0, 10.0 and 1000.0

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

Table 1 Convergence results for the disturbed growth models

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

The word invar indicates convergence in distribution to an invariant distribution with support on $(0, K)$

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 (almost sure convergence), convergence in distribution and convergence of means.

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

$$r_1 = \lambda(1 - E(\mathcal{D}_1)), \tag{53}$$

$$r_2 = -\lambda E\left[\ln(\mathcal{D}_1)\right], \tag{54}$$

$$r_3 = \lambda(E(\mathcal{D}_1^{-1}) - 1). \tag{55}$$

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 $\eta = -E[\ln(\mathcal{D}_1)]$, 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, $I = r + \lambda\, E[\ln(\mathcal{D}_1)]$ 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.

Acknowledgements We would like to thank the Associate Editor and one Reviewer for making suggestions that have significantly improved an earlier draft of this paper. Funding was provided by National Science Foundation (Grant Nos. DMS-1411853, DMS-1408947).

9 Appendix A: Proof of Theorem 3.1

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

$$Lf(x) = T'(0)f(x) = \frac{d}{dt} f(g(t,x))|_{t=0} + \lambda\{Ef(\mathcal{D}_1 x) - f(x)\}.$$

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

$$\frac{T(t)f(x) - f(x)}{t} = \frac{f(g(t,x))e^{-\lambda t} - f(x)}{t} + \frac{1}{t}\int_0^t E\left(f(\mathcal{D}_1 g(s,x))\right)\lambda e^{-\lambda s} ds + o(t).$$

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 $\lambda Ef(\mathcal{D}_1 x)$ 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

$$Mf(x) = Ef(\mathcal{D}_1 g(T_1, x)), \quad x > 0.$$

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

$$\int_0^\infty P(\mathcal{D}_1 g(T, x) \in C)\, \pi(dx) = \pi(C).$$

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

$$\int_0^\infty Lf(g(t, y))\lambda e^{-\lambda t}\, dt$$
$$= \int_0^\infty \left(\frac{\partial f(g(t, x))}{\partial t} + \lambda\, [Ef(\mathcal{D}_1 g(t, x)) - f(g(t, x))] \right) \lambda e^{-\lambda t} dt.$$

After an integration by parts this yields

$$\int_0^\infty Lf(g(t, y))\lambda e^{-\lambda t} dt = \lambda\{Ef(\mathcal{D}_1 g(T, x)) - f(x)\}$$

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

$$\int_0^\infty Lf(x)\mu(dx) = \lambda \int_0^\infty \{Ef(\mathcal{D}_1 g(T, x)) - f(x)\}\pi(dx) = 0.$$

This proves part (i).

To prove part (ii), first apply L to the function $x \to P(\mathcal{D}_1 g(T, x) \in C)$. First note from the composition property and an indicated change of variable,

$$P(\mathcal{D}_1 g(T, x) \in C) = P(\mathcal{D}_1 g(T + t, x) \in C) = e^{\lambda t} \int_t^\infty P(\mathcal{D}_1 g(s, x) \in C)\lambda e^{-\lambda s} ds.$$

In particular the first term of $LP(\mathcal{D}_1 g(T,x) \in C)$ is

$$\frac{d}{dt} P(\mathcal{D}_1 g(T,x) \in C)|_{t=0} = \lambda\{P(\mathcal{D}_1 g(T+t,x) \in C) - P(\mathcal{D}_1 x \in C)\}.$$

Adding this to the second term yields,

$$LP(\mathcal{D}_1 g(T,x) \in C) = \lambda \left\{ \int_0^\infty P(\mathcal{D}_1 g(T,y) \in C) P(\mathcal{D}_1 x \in dy) - P(\mathcal{D}_1 x \in C) \right\}.$$

Integrating with respect to the continuous time invariant distribution μ yields

$$0 = \lambda \int_0^\infty \left\{ \int_0^\infty P(\mathcal{D}_1 g(T_1,y) \in C) P(\mathcal{D}_1 x \in dy) - P(\mathcal{D}_1 x \in C) \right\} \mu(dx),$$

or equivalently,

$$\int_0^\infty \int_0^\infty P(\mathcal{D}_1 g(T,y) \in C) P(\mathcal{D}_1 x \in dy) \mu(dx) = \int_0^\infty P(\mathcal{D}_1 x \in C) \mu(dx).$$

But since by definition $\pi(dy) = \int_0^\infty P(\mathcal{D}_1 x \in dy)\mu(dx)$, this is precisely the condition

$$\int_0^\infty P(\mathcal{D}_1 g(T,y) \in C) \pi(dy) = \pi(C),$$

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

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