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EXTINCTION AND GROWTH IN EVOLUTIONARY AND BIOLOGICAL SYSTEMS

William C. Troy
Department of Mathematics
University of Pittsburgh
Thack 503, Pittsburgh, PA 15260, USA
e-mail: troy@pitt.edu

Abstract: The consequences of global warming include predictions of 300,000 deaths per year, as well as the extinction of 100-500 species of birds per degree centigrade warming. Warming effects are also thought to play a role in runaway growth, e.g. the quagga mussel invasion of Lake Mead. At the same time the global financial community is suffering the effects of runaway growth (e.g. the housing market bubble), and the collapse of financial markets. The mechanisms underlying growth or extinction are poorly understood. We investigate these mechanisms in a scalar, continuous time equation which models the effects of environmental fluctuations. In addition to modeling biological populations, the model is the first component of Black Scholes stock price theory. In both settings the model predicts extinction of realizations when volatility exceeds a critical value. A major challenge is to estimate realizations at specific times during growth or extinction events. Thus, we derive dynamic bounds which estimate realizations during such events. These estimates give new insights into stock price collapse. We extend our results to a two-species system where the first is dominant, yet the second is less vulnerable to environmental fluctuations. When variation exceeds criticality the first species goes extinct, and the second emerges into a new state. We derive an estimate for the time lag between extinction and emergence. This estimate provides a step towards explaining the 2000 Kirchner-Weil discovery of a significant time lag between mass extinctions and repopulation.

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1. Background and Goals

It is becoming increasingly clear that the nations of planet earth cannot agree on global carbon emission policies which are sufficient to stem the effects of global warming. Thus, there is a substantial probability of a 4-6 degree (centigrade) global rise in temperature 2100, and a tipping point may be reached where the existence of the human race, as well as a multitude of other species, is at peril. The 2009 Global Humanitarian Forum report on the human impact of climate change and global warming estimates that, already, 300,000 lives are lost each year due to climate change and environmental degradation, see [7]. A 2008 study [20] predicts that "worldwide, every degree centigrade of warming projects a nonlinear increase of bird extinctions of 100-500 species." Warming effects may also be a factor in the *runaway growth* of other species. At the 2009 Lake Mead Symposium it was reported that: "In one part of Lake Mead as many as 55,000 quagga mussels per square meter were found where none had been in 2007. Warmer conditions, together with the right mix of food, calcium and dissolved oxygen form an ideal habitat which allows the mussels to reproduce six times per year", see [18]. The exponential increase of mussels in Lake Mead is a classic example of runaway Malthusian growth, see [15]. In addition to climate change, the financial community is facing the consequences of the global economic meltdown. In 2006, in advance of the current crisis, the U.S. National Academies/National Research Council and the Federal Reserve Bank of New York held a conference whose goal was to determine conditions disposing an ecological or financial systems to suddenly switch from a stable state of existence into collapse [12]. However, it clear that none of the experts has understood the mechanisms responsible for the present market disaster, see [6], [21].

In this paper we pursue a general modeling approach to investigate the effects of uncertainty during the course of extinction and runaway growth events in stochastic models which incorporate the effects of environmental fluctuations: a continuous time scalar equation, and its extension to a multi-species system. As we show below, the scalar model describes diverse settings: (i) it models a biological population in a fluctuating environemnt, and (ii) it is the fundamental component of classical Black-Scholes stock price theory [2]. Our goals are the following:

(I) Show how easily fluctuations can trigger extinction or runaway growth (Section 1).

(II) Derive formulas which reflect the effects of uncertainty, and accurately estimate realizations at specific times during the entire course of such events (Section 2).

(III) Extend our results to multi-species systems. Our estimates give insights into the Kirchner and Weil [9] discovery of a significant time lag between mass extinctions and repopulation (Section 3).

The Scalar Model. The equation we study is derived from the Malthusian (see [15]) population model

$$dX = \mu X dt, \quad X(0) = X_0 > 0. \tag{1.1}$$

The solution of (1.1) is $X(t) = X_0 e^{\mu t}$, where $t \geq 0$, $X(t)$ is a population, and $\mu > 0$ is its growth rate. It is biologically reasonable to assume that the growth rate μ is time dependent, and that it undergoes variations due to environmental fluctuations. Thus, following May [16], we set $\mu = \lambda(t) + \sigma(t)\zeta(t)$, where $\lambda(t)$ is a time dependent mean value, $\zeta(t)$ is white noise, $\sigma(t)$ is volatility, and obtain the stochastic model

$$dX(t) = \lambda(t)X(t)dt + \sigma(t)X(t)dW(t), \ X(0) = X_0, \tag{1.2}$$

where $W(t)$ denotes the Wiener process. One can envision settings in which $\lambda(t)$, or $\sigma(t)$, increases (e.g. the Lake Mead mussel invasion), decreases, or changes signs multiple times. Environmental fluctuations may be induced by drought, volcanic activity, or fossil fuel burning. When $\lambda(t)$ and $\sigma(t)$ are identically constant, we set $\lambda(t) \equiv \bar{\lambda}$ and $\sigma(t) \equiv \bar{\sigma} > 0$, and (1.2) reduces to the geometric Brownian motion equation

$$dX(t) = \bar{\lambda}X(t)dt + \bar{\sigma}X(t)dW(t), \ X(0) = X_0. \tag{1.3}$$

Equation (1.3) is a key component of Black-Scholes theory [2], which posits that $X(t)$ represents A main focus of Black-Scholes theory is the time t when $X(t) = K$, an options striking price. We do not analyze stock options in this paper. Instead, our goal is to understand the complete time course of realizations independent of any constraints (see [17] for an overview).

We demonstrate how easily realizations $X(t)$ of (1.3) can go extinct (Figure 1, right panel). First, since the mean satisfies $\mathrm{E}\left(X(t)\right) = X_0 e^{\bar{\lambda} t} \to \infty$ as $t \to \infty$, then one might predict that all realizations of (1.3) must become unbounded

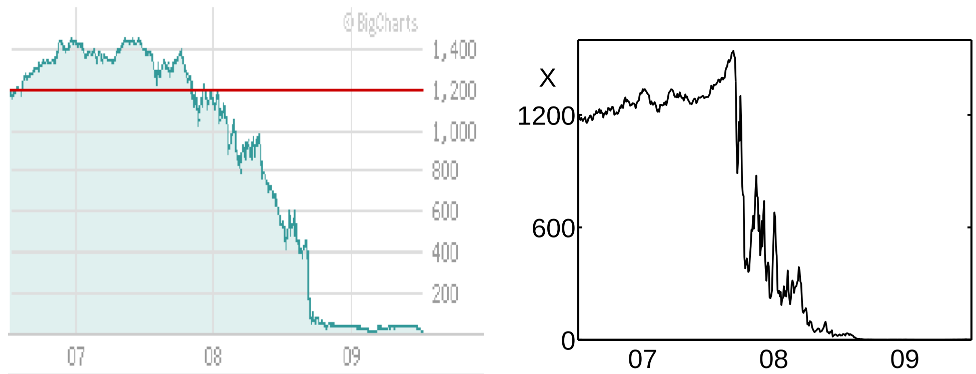

Figure 1: Left: AIG stock profile from July, 06 to July, 09 (data from CNN.com). Bailouts prevent the price from reaching zero. Right: Realization of (1.3). $X_0 = 1200$ matches the initial AIG stock value, $\bar{\lambda} = .03$ gives moderate growth rate. Horizontal axis denotes time, starting with July, 06 at left endpoint; $\bar{\sigma} = .13 < \sigma_{crit} = \sqrt{2\bar{\lambda}} = .245$, and growth occurs for $0 \leq t < 1.25$ At time $t^* = 1.25$ (approximately Sept. 07 on this scale) $\bar{\sigma}$ is reset to $\bar{\sigma} = .6 > \sigma_{crit}$, and $X(t)$ goes extinct.

as $t \rightarrow \infty$. This is not the case. Lamperti [14] showed that:

$$\begin{aligned} &\text{if } \tfrac{\bar{\sigma}^2}{2} - \bar{\lambda} < 0 \ \text{ then } \ X(t) \rightarrow \infty \ \text{ a.s. } \ \text{as } \ t \rightarrow \infty, \\ &\text{if } \tfrac{\bar{\sigma}^2}{2} - \bar{\lambda} = 0 \ \text{ then } \ X(t) \text{ fluctuates between large and small positive values} \\ &\text{as } \ t \rightarrow \infty, \\ &\text{if } \tfrac{\bar{\sigma}^2}{2} - \bar{\lambda} > 0 \ \text{ then } \ X(t) \rightarrow 0 \ \text{ a.s. } \ \text{as } \ t \rightarrow \infty. \end{aligned} \tag{1.4}$$

Thus, a tipping point phenomenon occurs as $\frac{\bar{\sigma}^2}{2} - \bar{\lambda}$ increases through the critical value $\frac{\bar{\sigma}^2}{2} - \bar{\lambda} = 0$. This phenomenon is not predicted by evaluation of the mean $E(X(t))$, which does not reflect the uncertainty in $X(t)$ caused by volatility. Furthermore, the prediction of (1.4), that a species or stock price must collapse (with probability one) when $\frac{\bar{\sigma}^2}{2} - \bar{\lambda} > 0$, is counterintuitive to the current econophysicist view that classic theory cannot explain the propensity of a stock to crash. The econophysicist view is that classic theory based on gaussian noise does not have sufficiently fat tails to easily cause large price swings, see [3]. Hence, it is thought that the Black-Scholes model has low probability of causing a stock to crash. However, as (1.4) shows, every realization *must* collapse to zero (with probability one) when $\bar{\sigma} > \sigma_{crit}$, and σ_{crit} can be a fairly low value, depending on the growth rate $\bar{\lambda}$. This theoretical result suggests that both stocks and biological species may crash more easily than previously thought. Figure 1 shows the collapse of AIG stock, and a qualitatively similar realization of (1.3).

2. Theoretical Predictions

In this section we investigate (1.2), and develop methods to predict how long an extinction (or growth) event takes to be completed. We address the following issues:

(i) Once an extinction event has been initiated, say at $t = 0$, can we accurately estimate, for any prescribed level of certainty, the values of realizations at each time $t > 0$?

(ii) Similarly, once a runaway growth event is initiated, can we predict how fast realizations will grow?

(iii) Can we extend our techgniques and answer (i) and (ii) for logistic models?

In Theorem 2.1 we develop estimates which provide an approach to answering these questions. We show how our methods generalize to the stochastic logistic equation. In the next section we use Theorem 2.1, and also our logistic equation results, and extend our results to a two-species model. The first step in the analysis is to determine general conditions on the $\lambda(t)$ and $\sigma(t)$ which guarantee that extinction (or runaway growth) takes place. For this we note that the function $\frac{\sigma^2(t)}{2} - \lambda(t), \quad t \geq 0$, gives a dynamic measure of the trade off between the stabilizing effect of growth rate and the destabilizing effects of uncertainty due to volatility. For example, suppose that $\frac{\sigma^2(0)}{2} - \lambda(0) < 0$ so that, according to (1.4), the system is initially in a state of fluctuation where realizations are expected to undergo exponential growth. As t increases we also suppose that the growth rate decreases in the face of increasing volatility, and that $\frac{\sigma^2(t)}{2} - \lambda(t)$ becomes positive at a critical time $t_{crit} > 0$. If the net effect of growth rate and uncertainty causes $\frac{\sigma^2(t)}{2} - \lambda(t)$ to continue its increase unabated, then we predict that realiations must go extinct. To prove this claim we first note that Lamperti's proof of (1.4) is based on the iterated logarithm property

$$\limsup_{t\to\infty} \frac{W(t)}{\sqrt{2t\ln(\ln(t))}} = 1 \quad \text{a.s.}, \tag{2.1}$$

A straightforward modification of Lamperti's proof leads to the following 'limiting' (i.e. as $t \to \infty$) results for realizations of (1.2):

Extinction. If there is a value $\delta > 0$ such that

$$\frac{\sigma^2(t)}{2} - \lambda(t) \geq \delta > 0 \quad \forall t \geq 0 \quad \text{then} \quad X(t) \to 0 \quad \text{as} \quad t \to \infty \quad \text{a.s.} \tag{2.2}$$

Runaway Growth. If there is a value $\nu > 0$ such that

$$\frac{\sigma^2(t)}{2} - \lambda(t) \leq -\nu < 0 \quad \forall t \geq 0 \quad \text{then} \quad X(t) \to \infty \quad \text{as} \quad t \to \infty \quad \text{a.s.} \tag{2.3}$$

Properties (2.2) and (2.3) allow for a wide range of behavior of $\lambda(t)$ and $\sigma(t)$, yet at the same time extinction or runaway growth still must take place. In the special case of equation (1.3), where $\lambda(t) \equiv \bar{\lambda}$ and $\sigma(t) \equiv \bar{\sigma}$, property (2.2) reduces to

$$\frac{\sigma^2(t)}{2} - \lambda(t) = \frac{\bar{\sigma}^2}{2} - \bar{\lambda} \geq \delta > 0 \quad \forall t \geq 0, \tag{2.4}$$

and (2.3) reduces to

$$\frac{\sigma^2(t)}{2} - \lambda(t)t = \frac{\bar{\sigma}^2}{2} - \bar{\lambda} \leq -\nu < 0 \quad \forall t \geq 0, \tag{2.5}$$

and the original Lamperti result (1.4) holds.

We now turn to the primary goal of this section, which is to develop techniques to dynamically estimate realizations of (1.2) at each time $t \geq 0$ during the entire course of an extinction (or runaway growth) event. For this we *cannot* use Lamperti's iterated logarithm method because (i) the iterated logarithm property (2.1) is a limiting result which holds only 'in the limit as $t \to \infty$,' and (ii) it *cannot* be modified to give estimates on realizations at small t values. To understand our approach, which is completely different and more straightforward than Lamperti's, we first note that a standard criterion for proving extinction is to show that, for arbitrarily chosen $L > 0$, realizations satisfy

$$\text{Prob}\,\{X(t) \leq L\} \to 1 \quad \text{as} \quad t \to \infty \quad \text{a.s.} \tag{2.6}$$

A similar criterion holds for runaway growth. Our technique is to replace L in (2.6) with a sutiably chosen function of the form $X_0 e^{-K(t)t}$, and make use of the SDE satisfied by $Y = \ln(X(t))$ in order to derive an expression for

$$\text{Prob}\left\{X(t) \leq X_0 e^{-K(t)t}\right\}, \quad t \geq 0. \tag{2.7}$$

The role of $X_0 e^{-K(t)t}$ is to provide a measure of certainty to the value of a realization during an extinction event. In Theorem 2.1 we assume that condition (2.2) holds so that extinction occurs, and derive an expression for the bound (2.7). We also derive an analogous exact expression which allows us to dynamically estimate runaway growth events when (2.3) holds. In Example 1 we demonstrate how to design the function $K(t)$ to give optimal estimates.

Theorem 2.1. *$X(t)$ denote a realization of (1.2). Then the following upper and lower bound dynamic estimates for $X(t)$ hold:*

(i) Extinction. *If $\lambda(t)$ and $\sigma(t)$ satisfy condition (2.2) then $X(t) \to 0$ as $t \to \infty$ a.s. In addition, if $K(t)$ is a function which satsifies*

$$\left(\frac{1}{t}\int_0^t \left(\frac{\sigma^2(\eta)}{2} - \lambda(\eta)\right) d\eta - K(t)\right)\sqrt{t} \to \infty \quad \text{as} \quad t \to \infty, \tag{2.8}$$

then

$$\text{Prob}\left\{X(t) \le X_0 e^{-K(t)t}\right\} = \int_{-\infty}^{\left(\frac{1}{t}\int_0^t \left(\frac{\sigma^2(\eta)}{2} - \lambda(\eta)\right) d\eta - K(t)\right)\frac{\sqrt{t}}{\sigma(t)}} \frac{1}{\sqrt{2\pi}} \times \exp\left(-\frac{x^2}{2}\right) dx \to 1 \quad \text{as} \quad t \to \infty. \tag{2.9}$$

(ii) Growth. *If $\lambda(t)$ and $\sigma(t)$ satisfy condition (2.3) then $X(t) \to \infty$ as $t \to \infty$ a.s. In addition, if $B(t)$ is a function which satisfies*

$$\left(\frac{1}{t}\int_0^t \left(\frac{\sigma^2(\eta)}{2} - \lambda(\eta)\right) d\eta - B(t)\right)\sqrt{t} \to -\infty \quad \text{as} \quad t \to \infty, \tag{2.10}$$

then

$$\text{Prob}\left\{X(t) \ge X_0 e^{B(t)t}\right\} = \int_{\left(\frac{1}{t}\int_0^t \left(\frac{\sigma^2(\eta)}{2} - \lambda(\eta)\right) d\eta + B(t)\right)\frac{\sqrt{t}}{\sigma(t)}}^{\infty} \frac{1}{\sqrt{2\pi}} \times \exp\left(-\frac{x^2}{2}\right) dx \to 1 \quad \text{as} \quad t \to \infty. \tag{2.11}$$

Remarks. (i) At each $t \ge 0$, estimates (2.9) and (2.11) are *uniform* with respect to realizations since their right sides do not involve $X(t)$.

(ii) The equality in (2.9) and (2.11) hold independent of (2.8) and (2.10). The role of (2.8) and (2.10) is to guarantee that the integrals in (2.9) and (2.11) approach one as $t \to \infty$. An algorithm for optimally choosing $K(t)$ or $B(t)$ is given in the example following the proof of the theoerm.

Proof of Theorem 2.1. We prove (2.9). The details for the proof of (2.11) are similar, and are omitted for brevity. Applying Ito's Lemma [10] to $Y(t) = \ln(X(t))$ gives

$$d\ln(X(t)) = \left(\lambda(t) - \frac{\sigma^2(t)}{2}\right) dt + \sigma(t) dW(t), \quad t \ge 0. \tag{2.12}$$

An integration of (2.12) shows that

$$\ln\left(X(t)\right) = \ln\left(X_0\right) + \int_0^t \left(\lambda(\eta) - \frac{\sigma^2(\eta)}{2}\right) d\eta + \sigma W(t), \quad t \geq 0. \tag{2.13}$$

Since $\ln(x)$ is an increasing function, then

$$\text{Prob}\left\{X(t) \leq X_0 e^{-K(t)t}\right\} = \text{Prob}\left\{\ln\left(X(t)\right) \leq \ln\left(X_0\right) - K(t)t\right\}. \tag{2.14}$$

Substituting (2.13) into (2.14) leads to

$$\begin{aligned}\text{Prob}&\left\{X(t) \leq X_0 e^{-K(t)t}\right\} \\ &= \text{Prob}\left\{\int_0^t \left(\lambda(\eta) - \frac{\sigma^2(\eta)}{2}\right) d\eta + \sigma(t)W(t) \leq -K(t)t\right\}.\end{aligned} \tag{2.15}$$

Setting $W(t) = \sqrt{t}\mathrm{N}(0,1)$ reduces (2.15) to

$$\begin{aligned}\text{Prob}&\left\{X(t) \leq X_0 e^{-K(t)t}\right\} \\ &= \text{Prob}\left\{\mathrm{N}(0,1) \leq \left(\frac{1}{t}\int_0^t \left(\frac{\sigma^2(\eta)}{2} - \lambda(\eta)\right) d\eta - K(t)\right)\frac{\sqrt{t}}{\sigma(t)}\right\}.\end{aligned} \tag{2.16}$$

Combining (2.16) with the definition of $N(0,1)$ gives

$$\begin{aligned}\text{Prob}&\left\{X(t) \leq X_0 e^{-K(t)t}\right\} \\ &= \int_{-\infty}^{\left(\frac{1}{t}\int_0^t\left(\frac{\sigma^2(\eta)}{2} - \lambda(\eta)\right)d\eta - K(t)\right)\frac{\sqrt{t}}{\sigma(t)}} \frac{1}{\sqrt{2\pi}}\exp\left(-\frac{x^2}{2}\right) dx \quad \forall t \geq 0.\end{aligned} \tag{2.17}$$

This completes the proof of equality in (2.9). Assumption (2.8) shows that the upper bound in the integral term in (2.17) tends to ∞ as $t \to \infty$. Thus, the right side of (2.17) approaches one as $t \to \infty$, and the proof of (2.9) is complete. □

Example 1. This example illustrates the effectiveness of estimates (2.9) and (2.11) in Theorem 2.1. We demonstrate two methods to choose $K(t)$ in (2.9). Similar techniques apply to choosing $B(t)$ in (2.11).

Method 1. We design $K(t)$ to give a uniform level of confidence over the entire interval $0 < t < \infty$. Here we choose 85 percent accuracy (other percent choices work equally well). To obtain 85 percent uniform accuracy, we design $K(t)$ so that

$$\text{Prob}\left\{X(t) \leq X_0 e^{-K(t)t}\right\} = .85 \quad \forall t \geq 0. \tag{2.18}$$

The first step is to note that $\int_{-\infty}^{1.037} \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{x^2}{2}\right) dx = .85$ Combining this and (2.18) with the upper limit in the integral term in (2.9) shows that $K(t)$

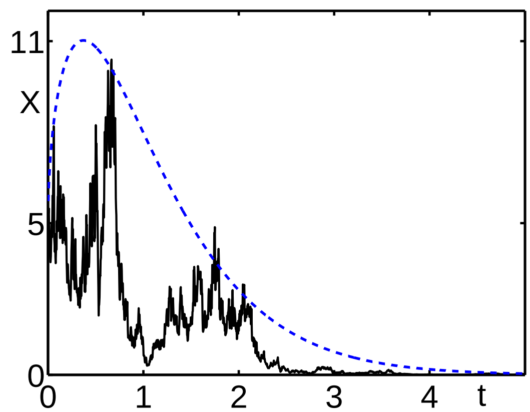

Figure 2: Illustration of Example 1. Solid curve shows the extinction of a realization of (1.3) when $(\bar{\sigma}, \bar{\lambda}, X_0) = (2.5, 1, 5)$. Dashed curve is the 85 percent uniformly accurate dynamic bound $X_0 \exp(-tK(t)) = 5 \exp\left(-t\left(2.125 - \frac{2.59}{\sqrt{t}}\right)\right)$ which appears in the prediction $\text{Prob}\left\{X(t) \leq 5 \exp\left(-t\left(2.125 - \frac{2.59}{\sqrt{t}}\right)\right)\right\} = .85\ \forall t \geq 0.$

must satisfy

$$\left(\frac{1}{t}\int_0^t \left(\frac{\sigma^2(\eta)}{2} - \lambda(\eta)\right) d\eta - K(t)\right) \frac{\sqrt{t}}{\sigma(t)} = 1.037 \quad \forall t \geq 0. \tag{2.19}$$

For simplicity we assume that $\lambda(t)$ and $\sigma(t)$ are constants, with values

$$\lambda \equiv 1 \quad \text{and} \quad \sigma(t) \equiv 2.5 \quad \forall t \geq 0. \tag{2.20}$$

Substituting (2.20) into (2.19), and solving for $K(t)$, gives the formula

$$K(t) = 2.125 - \frac{2.5925}{\sqrt{t}} \quad \forall t \geq 0. \tag{2.21}$$

By way of example, we let $X_0 = 5$, substitute (2.19)-(2.20)-(2.21) into (2.9), and obtain the 85 percent uniforml;y accurate estimate

$$\text{Prob}\left\{X(t) \leq 5 \exp\left(-t\left(2.125 - \frac{2.5925}{\sqrt{t}}\right)\right)\right\} = .85 \quad \forall t > 0. \tag{2.22}$$

We test (2.22) at sample times $t = 3,\ t = 4$ and $t = 5$, and obtain

$$\text{Prob}\{X(3) \leq .76\} = .85, \quad \text{Prob}\{X(4) \leq .18\} = .85 \quad \text{and} \quad \text{Prob}\{X(5) \leq .09\} = .85. \tag{2.23}$$

Figure 2 illustrates our extinction estimate.

Method 2. Let $K(t) \equiv \bar{K}$, a constant. To compare the results of this method with those in Method 1, we evaluate (2.21) at $t = 3$, and set $\bar{K} = K(3) = .63$. As t increases from $t = 3$ the upper bound $X_0 \exp(-.63t)$ gives an increasing level of accuracy. For example, the parameter choice $(\sigma, \lambda, \bar{K}, X_0) = (2.5, 1, .63, 5)$ gives

$$\text{Prob}\left\{X(t) \leq 5e^{-.63t}\right\} = \int_{-\infty}^{.5987\sqrt{t}} \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{x^2}{2}\right) dx \quad \forall t \geq 0. \tag{2.24}$$

From this we get

$$\text{Prob}\{X(3) \leq .76\} = .85, \quad \text{Prob}\{X(4) \leq .41\} = .88 \quad \text{and} \quad \text{Prob}\{X(5) \leq .22\} = .91. \tag{2.25}$$

When $K(t)$ is a constant, the accuracy of (2.25) improves as t increases from $t = 3$.

The Logistic Model. We now turn our attention to extinction properties of more biologically reasonable extensions of (1.3) and (1.2), the stochastic logistic equation

$$dX(t) = \left(\bar{\lambda}X(t) - X^2(t)\right) dt + \bar{\sigma}X(t)dW(t), \; X(0) = X_0, \; t > 0, \tag{2.26}$$

and the 'generalized stochastic logistic equation'

$$dX(t) = \left(\lambda(t)X(t) - X^2(t)\right) dt + \sigma(t)X(t)dW(t), \; X(0) = X_0, \; t > 0. \tag{2.27}$$

A useful approach to determine the behavior of realizations of (2.27) is to make use of the associated Fokker-Plank equation

$$\frac{\partial \rho}{\partial t} = -\frac{\partial}{\partial X}\left((\lambda(t)X - X^2)\rho\right) + \frac{\sigma^2(t)}{2}\frac{\partial^2}{\partial X^2}\left(X^2\rho\right), \quad X > 0, \; t > 0. \tag{2.28}$$

When $\lambda(t) \equiv \bar{\lambda}$ and $\sigma(t) \equiv \bar{\sigma}$ this equation reduces to the FPE for (2.26), namely

$$\frac{\partial \rho}{\partial t} = -\frac{\partial}{\partial X}\left((\bar{\lambda}X - X^2)\rho\right) + \frac{\bar{\sigma}^2}{2}\frac{\partial^2}{\partial X^2}\left(X^2\rho\right), \quad X > 0, \; t > 0. \tag{2.29}$$

The relevant solution of both (2.28) and (2.29) is denoted by $\rho\left(X, t|X_0, 0\right)$, and satisfies

$$\rho(X, 0|X_0, 0) = \delta(X - X_0) \;\text{ and }\; \int_0^\infty \rho(\eta, t|X_0, 0)d\eta = 1 \;\; \forall X > 0, \; t \geq 0. \tag{2.30}$$

We focus on (2.29)-(2.30). A standard first step is to determine whether, as $t \to \infty$, $\rho\left(X, t|X_0, 0\right)$ approaches a time dependent stationary solution, $\rho_s(X)$, which satisfies

$$-\frac{d}{dX}\left((\bar{\lambda}X - X^2)\rho_s\right) + \frac{\bar{\sigma}^2}{2}\frac{d^2}{dX^2}\left(X^2\rho_s\right) = 0, \; X > 0, \tag{2.31}$$

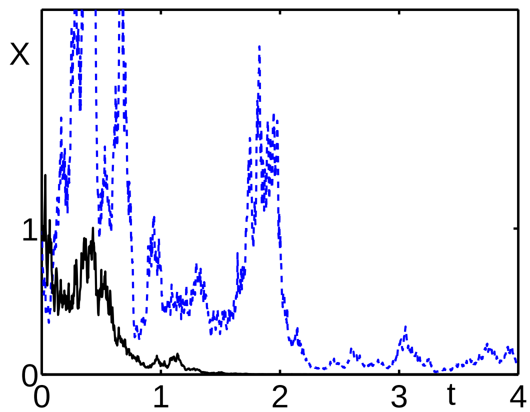

Figure 3: Two realizations of the stochastic logistic equation (2.26) showing variation in behavior of solutions. One realization (solid, black curve) quickly collapses to zero by time $t \approx 1.5$, while the second (dashed, blue curve) continues to exist without decreasing to zero, on the entire interval $0 \leq t \leq 4$. Parameters are $(\bar{\lambda}, \bar{\sigma}) = (1, 2)$ and $X(0) = 1$. See text.

$$\int_0^\infty \rho_s(X) = 1 \quad \text{and} \quad \lim_{X \to \infty} \big(\rho_s(X), \rho_S'(X)\big) = (0, 0). \tag{2.32}$$

Problem (2.31)-(2.32) has a solution if and only if $\frac{\bar{\sigma}^2}{2} - \bar{\lambda} < 0$, and this solution is given by

$$\rho_s(X) = N X^{2(\bar{\lambda}/\bar{\sigma}^2 - 1)} \exp\left(\frac{-2X}{\bar{\sigma}^2}\right), \quad X > 0, \tag{2.33}$$

where N is the normalizing constant

$$N = \left(\int_0^\infty x^{2(\bar{\lambda}/\bar{\sigma}^2 - 1)} \exp\left(\frac{-2x}{\bar{\sigma}^2}\right) dx\right)^{-1} \tag{2.34}$$

When $\frac{\bar{\sigma}^2}{2} - \bar{\lambda} \geq 0$ it is clear that $N = \infty$, hence a stationary solution does not exist.

In 1973 May ([16], p. 121) claimed that:

If the FPE has no stationary solution then realizations are doomed to speedy extinction. (2.35)

This claim is mathematically illegitimate in two fundamental ways. First, it is *not* true in general that realizations of an SDE must decay to zero as $t \to \infty$

when a stationary solution of the FPE does not exist. Instead, one must do a deeper study of the FPE in order to give full details of a proof that the extinction criterion (2.6) holds, i.e. that for abitrarily chosen $L > 0$, realizations satisfy

$$\text{Prob}\,\{X(t) \leq L\} \to 1 \quad \text{as} \quad t \to \infty \quad \text{a.s.} \tag{2.36}$$

This criterion can be proved for equation (2.26) by making use of its solution

$$X(t) = \frac{X_0 e^{-(\bar{\sigma}^2/2-\bar{\lambda})t+\sigma W(t)}}{1 + X_0 \int_0^t e^{-(\bar{\sigma}^2/2-\bar{\lambda})s+\sigma W(s)} ds}, \; t \geq 0. \tag{2.37}$$

To complete the proof substitute (2.37) into (2.36), and use the iterated logarithm property (Doering, private communication). The second way in which (2.35) is illegitimate is May's ambiguous claim that extinction is 'speedy.' Figure 3 illustrates two different realizations of (2.26) for the parameter set $(\bar{\lambda}, \bar{\sigma}) = (1, 2)$, which lies in the parameter regime where $\frac{\bar{\sigma}^2}{2} - \bar{\lambda} > 0$ so that extinction must occur. One of the realizations quickly collapses to zero by time $t \approx 1.5$. The second realization in Figure 3 continues to exist on the much larger interval $0 \leq t \leq 4$. Thus, although extinction occurs (as $t \to \infty$), it is clear from these numerical computations that it is not necessarily 'speedy.' These insights demonstrate the need for the development of practical, accurate methods which can determine the rate of collapse of realizations in the parameter regime where extinction of realizations occurs.

3. Extension to Systems

Our predictions of the time course of growth or extinction events are applicable to widely diverse systems. Here we show how our approach leads to a switching mechanism in which an event at time t^* causes an increase in volatility which triggers a system to switch from one stable configuration to another. We study this mechanism in a two-species system $(X(t), Y(t))$ which satisfies:

(A1) $X(t)$ inhibits the rate of change of $Y(t)$, but the rate of change of $X(t)$ is unaffected by $Y(t)$.

(A2) $Y(t)$ is less susceptible to environmental variations than $X(t)$.

(A3) An event at time $t^* > 0$ produces a large variation in environmental fluctuations which cause $X(t)$ to go extinct, but not $Y(t)$.

In 1980 Alvarez et al [1] gave evidence which led to the hypothesis that an asteroid impact caused environmental fluctuations sufficient to wipe out the dinosaurs. In 2000 Kirchner and Weil [9] (also, see [5], [8], [11], [13]) analyzed fossil record data from multiple mass extinctions, and found that "independent

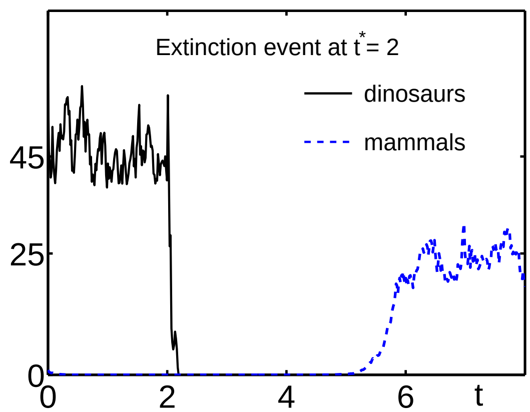

Figure 4: A realization of (3.1) showing the dinosaur population (black curve) when $0 \leq t < t^*$, and the onset of extinction at $t^* = 2$ in response to an event (e.g. asteroid impact). After a delay, the mammal population (dashed curve) emerges at $t \approx 5.1$. Parameters: $(\lambda, \mu, \alpha, \sigma_2) = (45, 25, 25, 1)$, $\sigma_1 = 1$ on $[0, t^*)$, and $\sigma_1 = 10$ when $t \geq t^*$. $(X(0), Y(0)) = (45, 1)$ represents a large ratio of dinosaurs to mammals.

of the severity of extinction, the recovery of biodiversity seems to lag behind the peak of an extinction by about ten million years." This result was a surprise since it was previously thought that niches left open by a mass extinction would be immediately repopulated by surviving species. In light of the threat to the human race by climate change, an analysis of the 'repopulation problem' becomes increasingly important. Holmes [8] recently addressed the following question: "If our civilzation collapses in an orgy of runaway warming, could the planet recover?" As a first step towards a theoretical analysis of the repopulation problem, we investigate a model system and show how assumptions A1-A3 can lead to the extinction of a dominant species, which we refer to as a dinosaur population, followed by the emergence of a second species, which we refer to as a mammal population, see [13]. We demonstrate how the results in Theorem 2.1 provide an accurate estimate of the lag time τ between extinction of the first species and the emergence of the second. Our system is

$$\begin{aligned} dX(t) &= \big(\lambda X(t) - X^2(t)\big)\, dt + \sigma_1 X(t) dW(t), \\ dY(t) &= \big(\mu Y(t) - Y^2(t) - \alpha X(t) Y(t)\big)\, dt + \sigma_2 Y(t) dW(t), \end{aligned} \tag{3.1}$$

where $X(t)$ and $Y(t)$ are dimensionless variables representing dinosaur and mammal populations, and t is dimensionless time. For simplicity, we have assumed that the average growth rates λ and μ are constant. We assume that $X(t)$ and $Y(t)$ experience the same environmental fluctuations, but with different intensities σ_1 and σ_2. Our results are not altered if we assume independent sources of fluctuations. We assume that the rate of change of $X(t)$ is unaffected by $Y(t)$, hence the $X(t)$ equation is independent of $Y(t)$. The term $-X^2(t)$ reflects competition between dinosaurs for resources, and $-Y^2(t)$ reflects competition between mammals; $-\alpha X(t)Y(t)$ represents the inhibitory affect of $X(t)$ on $Y(t)$, and $\alpha > 0$ gives the strength of this effect. We focus on the regime $\alpha > \frac{\mu}{\lambda}$. In the previous section we showed that $X(t)$ goes extinct (i.e. $X(t)$ dips below a threshold of sustainability) when $\sigma_1 > \sqrt{2\lambda}$. Figure 4 shows the effects of an extinction level event when $(\lambda, \mu, \alpha) = (45, 25, 1.25)$. $(X(0), Y(0)) = (45, 1)$ supposes a large initial ratio of dinosaurs to mammals. Evidence for the exact initial ratio is scant, see [13], and simulations show that a large range of combinations of $X(0)$ and $Y(0)$ give results similar to those shown here. When $0 \leq t < 2$ we let $(\sigma_1, \sigma_2) = (1, 1)$ and see that $X(t)$ fluctuates around the mean $X = 45$, hence the term $-\alpha X(t)Y(t)$ causes $Y(t)$ to decrease. At time $t^* = 2$ an event causes large environmental fluctuations which have greater impact on $X(t)$ than $Y(t)$. Thus, at $t^* = 2$ we reset $\sigma_1 = 10$ and assume that the change in σ_2 is much smaller. For simplicity we leave σ_2 unchanged. Since $\sigma_1 = 10 > \sqrt{2\lambda} = \sqrt{90}$, this causes the onset of extinction of $X(t)$, and by $\bar{t} = 2.25$ the dinosaur population dips below the level of sustainability, and is essentially extinct. When $t > \bar{t}$ the mammal population remains low until it emerges and reaches $Y = 1$ at $\hat{t} \approx 5.1$ where $Y(t)$ quicky reaches a stable state of fluctuation around the mean $Y = 25$. We now estimate the size of the delay $\tau = \hat{t} - \bar{t}$, i.e. the time to repopulation, between dinosaur extinction and mammal emergence. First, when $0 \leq t \leq \bar{t}$ we set $X = \lambda$ (its mean value) in the Y equation, and solve to obtain $Y(\bar{t}) \approx \exp((\mu - \alpha\lambda)\bar{t}) < 1$. When $t > \bar{t}$ the terms $X(t)Y(t)$ and $Y^2(t)$ are negligible as long as $Y(t)$ remains small, hence $Y(t)$ satisfies

$$dY(t) = \mu Y(t)dt + \sigma_2 Y(t)dW(t), \quad Y(\bar{t}) = \exp((\mu - \alpha\lambda)\bar{t}). \tag{3.2}$$

To determine τ within a reasonable level of confidence, we apply the samed method in part (i) of Example 1 to (3.2), and obtain the 90% uniformly accurate estimate

$$\text{Prob}\left\{Y(t) \geq \exp\left((\mu - \alpha\lambda)\bar{t} + (t - \bar{t})\left(\mu - \frac{\sigma_2^2}{2} - \frac{1.28\sigma_2}{\sqrt{t - \bar{t}}}\right)\right)\right\} = .9 \quad \forall t \geq \bar{t}.$$

From this estimate we get Prob $\{Y(\bar{t}+\tau) \geq 1\} = .9$ if

$$(\mu - \alpha\lambda)\bar{t} + \tau\left(\mu - \frac{\sigma_2^2}{2} - \frac{1.28\sigma_2}{\sqrt{\tau}}\right) = 0.$$

Thus,

$$\sqrt{\tau} = \frac{1.28\sigma_2 + \sqrt{(1.28\sigma_2)^2 - 4(\mu - .5\sigma_2^2)(\mu - \alpha\lambda)\bar{t}}}{2\mu - \sigma_2^2}.$$

Setting $(\lambda, \mu, \alpha, \bar{t}) = (45, 25, 1.25, 2.25)$ gives $\tau = 2.96$, hence the mammal specie 'switches on' and its emergence is predicted at $\hat{t} = \bar{t} + \tau = 5.21$, which is within 2.3% of the value 5.1 for the realization in Figure 4.

4. Discussion

We examined the dynamics of extinction and runaway growth in stochastic, population based models. These include both scalar equations and two-species systems specifically designed to reflect the effects of environmental fluctuations. For scalar models our theoretical studies focused on two issues:

(i) We identified ranges of growth rate and voltaility, both of which are allowed to vary with time, where realizations go extinct, or exhibit runaway growth, as $t \to \infty$.

(ii) We developed rigorous estimates which predict, within any given level of certainty, the range of values of realizations during the entire course of extinction or runaway growth events.

The Switching Mechanism. We extended our results to two-species systems, and identifed a simple, fluctuation driven mechanism which causes the dominant specie to switch from a stable state of fluctuation around a mean value, to a state of extinction, hence freeing the second specie from its influence. Subsequently, after a time delay, the second specie 'switches on' and emerges to quickly attain a new, stable state of fluctuation around a mean value. We derived a technique to estimate the length of the time delay for repopulation to be initiated once the extinction of the dominant specie is completed.

Future Studies. A generalization of the two-species model (3.1) consists of the system

$$\begin{aligned} dX(t) &= \big(\lambda(t)X(t) - X^2(t)\big)\,dt + \sigma_1(t)X(t)dW_1(t), \\ dY(t) &= \big(\mu(t)Y(t) - Y^2(t) - \alpha X(t)Y(t)\big)\,dt + \sigma_2(t)Y(t)dW_2(t), \end{aligned} \tag{4.1}$$

where the growth rates $\lambda(t)$ and $\mu(t)$, and volatilities $\sigma_1(t)$ and $\sigma_2(t)$, are now time dependent functions, and the noise terms $dW_i(t)$ may be independent or dependent. An alternative mechanism of intiating extinction of the X species is the setting in which the growth rate $\lambda(t)$ *decreases* in response to gradually increasing environmental volatility $\sigma_1(t)$, e.g. as global warming becomes more pronounced. In this case, as mentioned earlier, the critical quantity $\frac{{\sigma_1}^2}{2} - \lambda(t)$ is time dependent and decreasing, and when it dips to a level which is sufficiently negative, we again expect extinction to be initiated. The derivation of estimates to accurately predict realizations during such extinction events, and also the eventual emegence of the surviving population, remain a challenging open problem.

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