Stationary moments for logistic growth with random catastrophes

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A variety of organisms, from arctic reindeer to gastrointestinal bacteria, face stochastic environmental fluctuations that result in population catastrophes. Understanding the statistics of growth-catastrophe processes is a particularly relevant problem at present, due for example to expected increases in environmental volatility as a consequence of climate change and to growing interest in applying ecological theory to the human microbiome. Progress has proven challenging, as the abrupt nature of real catastrophes fails to be captured by traditional Gaussian noise models and is better described by coupling growth to explicitly discontinuous stochastic processes. Statistical properties of these stochastic jump differential equations remain poorly characterized, in part due to a lack of analytically tractable approaches that enable generally applicable insights. To address this, I revisit a minimal model of logistic growth coupled to density-independent catastrophes and derive exact expressions for its stationary moments, neglecting the possibility of extinction. I then use these results to address two outstanding problems concerning random catastrophes and also to show how they are related: (1) the unexplained existence of an effective catastrophe parameter that largely controls low-order statistics, and (2) the quantitative comparison of extinction risks in random catastrophe models with their Gaussian noise counterparts. With regards to the latter, two distinct methods are proposed that both show significantly higher risk of extinction under random catastrophe dynamics over a wide range of parameters, a particularly important conclusion for species conservation efforts. Together, these findings enable succinct and predicative characterizations of an important class of stochastic dynamical systems.

I. INTRODUCTION

Stochastic environmental fluctuations are important drivers of ecological and evolutionary processes [1, 12]. In particular, large fluctuations can result in population catastrophes [8, 12]. Understanding environmentally driven catastrophes is an increasingly important problem at a variety of scales. Globally, increased environmental variability is a likely consequence of anthropogenic climate change [13]. At the opposite extreme, changes in the composition of multi-species gastrointestinal microbiomes of humans and other animals are increasingly realized to be abrupt, driven by external perturbations [11, 12, 14, 15]. Traditional examples of environmental stimuli of sudden population collapses include harsh winters [8], fires [10], and epidemics [17], but the concept of catastrophes has also been extended to the physical displacement of organisms from their local environment. In this light, “catastrophes” describe fast dispersal dynamics in a metapopulation. A classic example is a rocky shore ecosystem [10], where organisms in the intertidal zone are displaced by crashing waves. More recently, the population dynamics of a zebrafish intestinal microbiota was shown to exhibit similar collapses due to the sudden displacement of bacterial aggregates from the intestine during peristalsis [11].

The drops in population observed in these systems happen rapidly compared to the timescale of growth. As such, they fail to be described by traditional Gaussian noise models, also called Environmental Stochasticity models, in which growth is coupled to Brownian motion processes [18]. Instead, catastrophes are typically modeled by an explicitly discontinuous stochastic process, usually the Poisson process [18]. While mathematical models of growth coupled to random catastrophes have existed for decades, their statistical properties remain poorly characterized, in part due to a lack of analytically tractable models that illuminate the essential dynamics, limiting our ability to understand and predict ecological outcomes.

In 1981 Hanson and Tuckwell [19] introduced an ideal minimal model: single-species logistic growth coupled to Poisson catastrophes of constant fraction, referred to here as the Logistic Random Catastrophe (LRC) model. The LRC model can be written analytically as an Itô Stochastic Differential Equation (SDE):

\[ dX_t = rX_t \left( 1 - \frac{X_t}{K} \right) dt - (1 - f)X_t \, dN_t. \]  

The first term on the right hand side, of order \( dt \), encodes deterministic logistic growth with growth rate \( r \) and carrying capacity \( K \). The second term encodes random catastrophes with the use of a differential Poisson process, \( dN_t \), which is equal to one if a catastrophe happens at time \( t \) and zero otherwise. Poisson catastrophes arrive with a constant probability...
per unit time, $\lambda$, and have a size set by $f$, the fraction of the population remaining after catastrophe. The notation $X_t - dN_t$ indicates the It\'o integration convention \cite{18,20}. By including logistic growth, the LRC model captures realistic density-dependent regulation; by including catastrophes of constant fraction, it captures the realistic feature that larger populations can experience larger losses, assuming that all individuals are equally susceptible to the disturbance. However, the discontinuities of the Poisson processes, combined with the non-linearity of logistic growth, complicate traditional analytic methods for stochastic differential equations, such as those based on the Kolmogorov operators \cite{2,4,18}.

Since \cite{19} there have been a number of studies on the LRC and related models \cite{21,25}, but most focus solely on extinction risk \cite{21,22,25}. Missing from the literature are direct estimates of ensemble statistics, such as the variance, which aid forecasting and analysis of real systems. Furthermore, analytic expressions give direct insight into the role of each model parameter, leading to more general conclusions and exposing connections between models. To this end, I used the method of moment equations \cite{27} to derive exact expressions for the stationary moments of the LRC model, neglecting the possibility of extinction. The derivation is sketched out in section II, with details found in the Appendix. I then used these results to address two previously identified, unsolved problems related to the LRC model, and also to demonstrate how they are fundamentally related.

The first problem was raised recently \cite{11} and concerns the unexplained appearance of an effective catastrophe parameter: A single combination of the average catastrophe rate, $\lambda$, and magnitude, $f$, namely $\lambda \ln f$, was observed in numerical simulations to completely determine the long-term population mean, and approximately determine the variance. That is, the average population in the long time limit was invariant under simultaneous changes of $\lambda$ and $f$ (and the variance approximately invariant), as long as the product $\lambda \ln f$ remained unchanged, implying that small, frequent catastrophes have the same effect on mean as large, infrequent ones. The use of this effective parameter aided the analysis of experimental data in \cite{11}, reducing the number of parameters that needed to be estimated. However, there was no theoretical basis for its existence. This effective parameter is discussed in section IIIA. It is shown how the analytic results of section II affirm its existence and delineate the range of its validity.

The second problem is older \cite{21} and concerns how to quantitatively compare the risk of extinction in random catastrophe models with their Gaussian noise analogs. The natural Gaussian noise analog to the LRC model, referred to here as the Logistic Environmental Stochasticity (LES) Model, is

$$dX_t = rX_t \left(1 - \frac{X_t}{K}\right) + \sigma X_t - dB_t,$$

with $B_t$ the standard Brownian motion process, whose intervals are independent, Gaussian distributed variables with $\mathbb{E}[B_t] = 0$ and $\text{Var}[B_t] = t$, and $\sigma$ setting the strength of the noise. The mean times to extinction for both the LRC and LES models, defined as the first passage time to a low population threshold (i.e., a single remaining organism),

FIG. 1. Sample paths of LRC and LES models. A: A sample path from the LRC model. Simulation parameters: $r = 1$, $K = 10^4$, $\lambda = 0.07$, $f = 10^{-2}$, $dt = 0.01$. B: A sample path from the LES model. Simulation parameters: $r = 1$, $K = 10^4$, $\sigma = 0.53$, $dt = 0.01$. 

per unit time, $\lambda$, and have a size set by $f$, the fraction of the population remaining after catastrophe. The notation $X_t - dN_t$ indicates the It\'o integration convention \cite{18,20}. By including logistic growth, the LRC model captures realistic density-dependent regulation; by including catastrophes of constant fraction, it captures the realistic feature that larger populations can experience larger losses, assuming that all individuals are equally susceptible to the disturbance. However, the discontinuities of the Poisson processes, combined with the non-linearity of logistic growth, complicate traditional analytic methods for stochastic differential equations, such as those based on the Kolmogorov operators \cite{2,4,18}.

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can be computed numerically or approximated analytically and have been reported in the literature. However, which model contains a higher risk of extinction remains an open question, despite its relevance to conservation efforts. For a given growth rate and carrying capacity, the answer depends on the values of the noise parameters, \((\lambda, f)\) for the LRC model and \(\sigma\) for the LES model. The problem of comparing extinction risk in the two models therefore comes down to finding a meaningful way to map their noise parameters onto one another. In this work, two methods are proposed, derived from the analytic results of section II, that both show a mean time to extinction orders of magnitude lower for random catastrophes than for environmental stochasticity in a wide range of parameter space. Section IIIB describes the first method, which is based on equating the stationary means of the two models in the absence of extinction. Section IIIC describes the second, which is based on constructing the LES model as a special case of the LRC model in the limit of infinitely frequent, infinitesimal catastrophes, and computing the mean time to extinction at various points along this limit. Interestingly, both methods are fundamentally related to the effective catastrophe parameter of section IIIA.

Taken together, these results highlight the power of analytically tractable models of stochastic population dynamics. The expressions derived here aid the analysis of experimental and observational data, inform the design of computer simulations, and reveal deep connections between distinct stochastic processes relevant for a wide range of dynamical systems.

II. COMPUTING STATIONARY MOMENTS

A. Analytic Results

In this section the derivation of the stationary moments for the LRC and LES models is sketched out, with details in Appendix A. The approach taken is the method of moment equations [27, 28], in which deterministic Ordinary Differential Equations (ODEs) for the moments are derived by averaging all terms in the SDE. Non-linearities in the SDE result in a hierarchy of moment equations, in which the \(n\)th moment is coupled to the \((n+1)\)th moment. This hierarchy cannot be solved exactly. However, in the absence of an absorbing state, the presence of a carrying capacity results in a non-trivial steady state, in which the hierarchy of ODEs reduces to an algebraic recursion relation. The first moment (mean) is obtained via separate computation, thereby obtaining all moments. The approach outlined is applicable to both LRC and LES models, though the results for the LES model are already well known; standard methods [2, 20] can be used to derive the full stationary distribution, a Gamma distribution.

For simplicity, only the stationary mean and variance of the LRC model are derived here, with the generalization to all moments given in Appendix A. To begin, a relation between the first and second moment is obtained by taking an ensemble average of each term in SDE (1). The expectation of \(X_t\)– \(dN_t\) can be factored, since the two processes are mutually independent and \(X_t\) is nicely bounded. An informal proof is given in the Appendix. Taking the average and looking at the steady state produces the relation

\[
E[X^2] = K \left(1 - \frac{\lambda(1 - f)}{r} \right) E[X].
\]

The mean must now be computed independently. To do this, a change of variables is made to \(\ln X_t\), using the chain rule for jump processes [18]. The resulting equation for \(dE[\ln X_t]/dt\) depends only on \(E[X]\) and constants, just as it would in the deterministic model. In the steady state, this equation produces an explicit expression for the mean, which can be combined with the previous mean-variance relation to compute the variance. The results are

\[
E[X]_{LRC} = K \left(1 + \frac{\lambda}{r} \ln f \right),
\]

\[
Var[X]_{LRC} = K^2 \frac{\lambda}{r} (-\ln f - (1 - f)) \left(1 + \frac{\lambda}{r} \ln f \right)
\]

(recall that \(f \in (0, 1)\), so \(\ln f\) is negative for \(f < 1\)). Repeating the procedure using the chain rule for diffusion process [18, 20] results in

\[
E[X]_{LES} = K \left(1 - \frac{\sigma^2}{2r} \right),
\]

\[
Var[X]_{LES} = K^2 \frac{\sigma^2}{2r} \left(1 - \frac{\sigma^2}{2r} \right)
\]

reproducing the known results.

In the generalization of this method to compute all stationary moments, one first changes variables to \(X^n\), the \(n\)th power of \(X_t\). Averaging the SDE for \(X^n\) and looking at the steady state produces a relation between \(E[X^n]\) and \(E[X^{n+1}]\), which can be recursively iterated to express \(E[X^n]\) in terms of the mean, \(E[X]\). The results are

\[
E[X^n]_{LRC} = K^n \left(1 + \frac{\lambda}{r} \ln f \right) \prod_{m=1}^{n-1} \left(1 - \frac{\lambda(1 - f^m)}{mr} \right),
\]

\[
E[X^n]_{LES} = K^n \left(1 - \frac{\sigma^2}{2r} \right) \prod_{m=1}^{n-1} \left(1 - \frac{\sigma^2}{2r} \right).
\]
Analytic results reveal statistical structure of LRC model. A: Analytic results for stationary cumulants agree with numerical simulations. Time evolution of the first 4 cumulants, $C_n$, of the LRC model, computed numerically (solid lines). Dashed lines indicate the asymptotic values predicted by the analytic results, with the cumulants computed from the moments given by equation (8). Parameters: $r = 1$, $K = 10^4$, $\lambda = 0.1$, $f = 0.0012$, $dt = 0.01$, $N_{trial} = 5 \times 10^3$. B: Range of validity of $\ln f$ as an effective catastrophe parameter. Parameters were scaled according to $\lambda' = \beta \lambda$ and $\ln f' = \beta^{-1} \ln f$ by dimensionless scale factor $\beta$. Dashed lines are analytic results for first 4 stationary cumulants as a function of $\beta$. Parameters same as in A.

$$E[X^n]_{LES} = K^n \left(1 - \frac{\sigma^2}{2r} \right) \prod_{m=1}^{n-1} \left(1 + \frac{(m-1)\sigma^2}{2r}\right),$$

with the complete derivation given in Appendix A.

These results agree well with simulations, as shown in Figure 2A in the form of cumulants, which generally provide more intuitive information than moments. The solid lines show the time evolution of the first 4 cumulants, $C_n$, of the LRC model, computed via stochastic simulation of the Poisson process with no absorbing state representing extinction (see the section on Numerical Methods below). The dashed lines are the analytic results, computed from the expressions for the moments in equation (8). Each cumulant asymptotes to the analytic value.

B. Numerical Methods

The following simulation method was used in all LRC model calculations. First, sample paths of the differential Poisson process were generated in a Bernoulli fashion. For each time point, a random number was drawn from a uniform distribution on $(0,1)$. If this number was less than $\lambda \Delta t$, a jump occurred at time $t$ and $\Delta N = 1$; if it was greater than $\lambda \Delta t$, no jump occurred and $\Delta N = 0$. These sample paths of the differential Poisson process were then used in the numerical integration of the LRC model. For most calculations, the logistic growth equation was integrated with the Euler method between jump times, at which the population was reduced by a factor of $f$. This integration method is referred to here as the Piecewise-Deterministic Markov Process (PDMP) method. However, in section III, this work considers the limit of frequent, small collapses that approach $O(\Delta t)$ in size, from which the LES model emerges. In the LES model, drift and noise are balanced at the infinitesimal scale, so for those calculations, the deterministic contribution of order $\Delta t$ must be retained, resulting in a more straightforward Euler-type integration scheme, referred to here as the direct Euler (DE) integration method. The LES model was integrated with a straightforward application of the Milstein method [29]. All code is available at [https://github.com/bschloma/lrc](https://github.com/bschloma/lrc).

III. APPLICATIONS: EFFECTIVE PARAMETERS AND EXTINCTION TIMES

In this section the analytic expressions for the stationary moments derived above are used to address two outstanding problems related to the LRC and LES models.
A. An effective catastrophe parameter

The analytic results for the LRC model reveal its statistical structure and provide a theoretical basis for a recent empirical observation [11]: an effective catastrophe parameter in the LRC model. In computer simulations [11], the population mean and variance were observed to be largely controlled by a single combination of the average catastrophe rate ($\lambda$) and size (fraction remaining $f$). Parameter estimation analysis suggested that this parameter had the form $\lambda \ln f$ [11], but there was no theoretical basis for the observation.

This phenomenon is demonstrated in Figure 2B, which shows the response of the first four stationary cumulants of the LRC model to simultaneous, reciprocal scaling of $\lambda$ and $\ln f$ via a dimensionless scale factor, $\beta$. Specifically, for $\beta$ ranging from $10^{-2} - 10^3$, catastrophe parameters were scaled as $\lambda' = \beta \lambda$ and $\ln f' = \beta^{-1} \ln f$. Stationary moments were computed for each value of $\beta$ using the analytic results derived above and converted to cumulants. The stationary mean is invariant under this scaling, as is clear from equation (4). Higher order cumulants are approximately invariant for low values of $\beta$, corresponding to rare, large catastrophes, but decay to zero for large values of $\beta$, corresponding to frequent, small catastrophes.

The large $\beta$ limit is a dynamic analog to the law of large numbers, in which the Poisson process that drives the LRC model tends to its average value. Recall that for a Poisson process, all cumulants are equal to the mean, $\lambda t$, just as all cumulants of a Poisson distribution are equal to the mean. The $n^{th}$ cumulant of the scaled process $(1 - f) N_t$ is therefore $(1 - f)^n \lambda t$. As $\beta \to \infty$, $\lambda' \to \infty$ and $f' \to 1$, such that $\lambda' \ln f'$ is constant. In this limit, $-(1 - f) \ln f$, so, higher cumulants of the Poisson process decay as $\beta^{-(n-1)}$ and mean field behavior is recovered. The mean field limit of the LRC model is therefore equivalent to Levins’ original metapopulation model [20], which highlights its relevance to dispersal dynamics.

In addition to emerging naturally from the statistics of the LRC model, the effective parameter $\lambda \ln f$ has an intuitive interpretation: It is the correction to the long-run growth rate due to catastrophes. This has been previously identified as an important quantity in a variety of related models. It appears in the strong solutions to both the LRC model [24] and the corresponding model with purely exponential growth [15], controls the asymptotics for a related exponential model [22], and determines the mean time to extinction for an exponential model with a hard wall carrying capacity [21]. From the expression for the mean equation (4), it also acts as a correction to the carrying capacity.

The existence of this effective catastrophe parameter has important consequences for analyzing experimental data. As was done in [11], fitting ensemble statistics with the effective catastrophe parameter reduces the number of parameters that needs to be estimated from data. In fact, attempting to fit both the rate ($\lambda$) and size ($f$) independently results in highly unconstrained parameter estimates [11] and should be avoided. The analytic results derived here put the use of this effective parameter on firmer ground and delineate the range of its validity. Qualitatively speaking, the effective parameter approximation is more valid in the case of rare, large catastrophes, than frequent, small ones.

B. Comparing extinction risk, method I: Mapping stationary means

A long standing question in population ecology [21, 25] concerns relative risks of extinction in the LRC and LES models: Which population is at a higher risk of extinction, one that experiences continuous but small environmental fluctuations, or an identical population whose environment is stable save for occasional, large disturbances that result in catastrophe? From the perspective of conservation this is an important question. To answer it mathematically, one needs a sensible way to map parameters between the two models and facilitate fair comparison.

The expressions for the stationary moments derived above reveal similar structure between LRC and LES models: Which population is at a higher risk of extinction, one that experiences continuous but small environmental fluctuations, or an identical population whose environment is stable save for occasional, large disturbances that result in catastrophe? From the perspective of conservation this is an important question. To answer it mathematically, one needs a sensible way to map parameters between the two models and facilitate fair comparison.

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essence compares the decay rates of the means for the two models given that they would have reached the same stationary value. The LRC curve decays faster than the LES curve in Figure 3A, suggesting that extinction happens faster in the LRC model.

The mean time to extinction in the two models was also compared directly by stochastic simulation for a range of noise parameters, with $\sigma^2 = -2\lambda \ln f$ as prescribed above. Extinction was defined as an absorbing state at a low-lying population threshold, $x^*$. Each realization of the model was integrated in time (using the PDMP method for the LRC model), starting from an initial population $x_0$, until the population dropped below the threshold. Figure 3B shows the mean time to extinction, $\tau$, plotted in units of inverse growth rate, for a range of $\sigma$ values, with $x^* = 1$ and $x_0 = 10$. The LES model exhibits longer extinction times for the relevant ranges of noise strengths than the LRC model, implying that the risk of extinction is higher for random catastrophes than for environmental stochasticity. The inset in Figure 3B shows the mean time to extinction plotted against carrying capacity for both models, which both appear to exhibit the asymptotic power law behavior described by [21] for simpler models of exponential growth up to a hard wall carrying capacity. While the two curves do appear to follow power laws, the power is greater for the LES model when parameters are mapped to achieve equal stationary means. This is another indicator of less risk of extinction in the LES model than the LRC model.

C. Comparing extinction risk, method II: The diffusion limit

The mapping presented above allowed quantitative comparison between LRC and LES models by normalizing the effect of fluctuations on their respective stationary means. While well motivated, this comparison isn’t perfect, as other reasonable mappings between the two models could be constructed. In this section a new method is presented that circumvents this issue by treating the LES model not as its own, distinct model, but as an extreme version of the LRC model in the limit of infinitely frequent, infinitesimal catastrophes. In this way, extinction risk was assessed as a function of LRC model parameters, which are scaled according to a transformation derived analytically below that smoothly morphs the LRC model into the LES model. The results recapitulate those of the previous mapping of station-
ary means, demonstrating higher risk of extinction with random catastrophes than with environmental stochasticity in the case of logistic growth.

The method is based on the functional generalization of the Central Limit Theorem (CLT), or Donsker’s Theorem \cite{31}, which says that fluctuations of the Poisson process about its mean converge in distribution to the Brownian motion process in the limit of infinite jump rate and infinitesimal jump size. In Appendix B it is shown that the relevant limits are

\[
\ln f(N_t - \alpha t) \xrightarrow{\lambda \to \infty, f \to 1} \sqrt{\lambda} \ln f B_t. \tag{10}
\]

Crucially, these dual limits are taken such that \(\sqrt{\lambda} \ln f\) is constant. Consequently, the mean drift of the scaled Poisson process diverges as \(\sqrt{\lambda}\), the variance remains finite and all higher cumulants go to zero. These are functional analogs to what happens when a Poisson distribution limits to a Gaussian in the classic CLT. To obtain a non-trivial limiting process, the diverging drift -which is proportional to effective catastrophe parameter \(\lambda \ln f\) discussed above - must be subtracted off manually before taking limits. This subtraction can be absorbed into a rescaling of the growth rate and carrying capacity, such that the final transformation from the LRC model to the LES model involves rescaling all four LRC model parameters.

To see the subtleties of taking these limits, it is useful to consider in more detail what happens to the LRC model variance in the limits \(\lambda \to \infty, f \to 1, \sqrt{\lambda} \ln f \to \text{constant}\), using the analytic results obtained in section IIA. There is no question that the variance diverges towards negative infinity, but it turns out that only part of it does, leaving another part finite:

\[
\text{Var}[X] \to K^2 \frac{\lambda}{r} \left( \ln f - (1 - f) \right) \left( 1 + \frac{\lambda}{r} \ln f \right)
\]

\[
\xrightarrow{\text{limits}} K^2 \frac{\lambda}{r} \frac{\ln f}{2r} \left( 1 + \frac{\lambda}{r} \ln f \right)
\]

\[
= K^2 \frac{c^2}{2r} - K^2 \frac{c^3}{r^2} \sqrt{\lambda}. \tag{11}
\]

with \(c = \text{const} = -\sqrt{\lambda} \ln f\). In taking the limit \(f \to 1\), the relation \((- \ln f - (1 - f)) \to 2^{-1} \ln^2 f\) was used, based on a 2\textsuperscript{nd} order Taylor expansion.

The finite piece of the variance in this limit is exactly the variance of an LES model with \(\sigma^2 = \lambda \ln^2 f\) and increased growth parameters \(K_{ES} = K(1 + (2r)^{-1} \sigma^2)\), and \(r_{ES} = r(1 + (2r)^{-1} \sigma^2)\). Looking at the behavior of the mean in this limit leads to the same conclusion. This suggests that this limit does take the LRC model into an LES model, but one that is accompanied by a noise-induced drift that diverges as \(\sqrt{\lambda}\). To obtain a non-trivial limiting process, this drift needs to be subtracted off, for example, by adding a term \(-\lambda \ln f dt\) to the LRC model SDE (1). This is equivalent to rescaling the growth rate and carrying capacity each by a factor of \((1 - r^{-1} \ln f)\).

The complete transformation from the LRC to LES model will now be specified formally. The parameters \(\lambda\) and \(f\) will be kept fixed at reference values and the limit will be taken with the use of a dimensionless scale parameter, \(\alpha\). The prescription is as follows. Start from an LRC model together with a target LES noise strength \(\sigma\) and fix \(\lambda \ln^2 f = \sigma^2\). Then transform the LRC parameters according to

\[
\lambda' = \alpha \lambda, \quad \ln f' = -\sigma / \sqrt{\lambda'},
\]

\[
r' = r \left( 1 - \frac{\lambda' \ln f'}{r} \right), \quad K' = K \left( 1 - \frac{\lambda' \ln f'}{r} \right).
\]

The claim is that in taking the limit \(\alpha \to \infty\), the LRC model \(LRC(r', K', \lambda', f')\) gets mapped to an LES model \(LES(r_{ES}, K_{ES}, \sigma)\), with \(\sigma = \lambda \ln^2 f\), \(r_{ES} = r(1 + (2r)^{-1} \sigma^2)\), and \(K_{ES} = K(1 + (2r)^{-1} \sigma^2)\). Importantly, the stationary mean of the process remains constant throughout this transformation, fixed at \(K\), making it well suited to study extinction risk.

This transformation is shown visually in Figure 4A, which depicts numerical results for the stationary distribution of the LRC model (in log variables for visual reasons) being transformed with \(\alpha\) increasing on the interval \((1, 75)\). The distribution approaches that of the target LES model, shown in green in panel (vi). As discussed in section IIB on numerical methods, the direct Euler (DE) integration method was used in simulations since catastrophes shrink to a size on the order of the numerical timestep. To minimize numerical artifacts, an adaptive timestep was used, scaling \(r \Delta t\) identically to \(\ln f\) in equation (12) with increasing \(\alpha\), such that the relative sizes of growth and catastrophe were preserved. To complement these numerical calculations, this transformation was applied directly to the LRC model SDE and was shown analytically to result in the correct LES model (Appendix B).

With this transformation the question of relative risks of extinction under the LRC model and the LES model was revisited. The mean time to extinction, \(\tau\), was computed via stochastic simulation of the LRC model for various values of \(\alpha\), rescaling LRC model parameters according to equation (11) for each \(\alpha\). The same DE integration method and numerical timestep was used as in the distribution transformation of figure 4A. The results are shown in the bottom panel of Figure 4B. The LRC
FIG. 4. Method II, the diffusion limit, also shows higher extinction risk under LRC dynamics. A: Smoothly transforming the stationary distribution of LRC model to that of LES model in the diffusion limit. LRC model (no extinction) was simulated for $T_{\text{max}} = 300$ units of inverse growth rate for 5 values of the scale parameter $\alpha$, rescaling parameters according to equation (12). Frames i-v depict the stationary distribution of log $X$ (for visual clarity) for $\alpha = 1, 2.94, 8.66, 25.49, 75.00$ respectively, estimated from $10^6$ paths. Frame vi depicts the stationary distribution of log $X$ for the target LES model. Parameters: $r = .68, K = 6800, \lambda = .1, \sigma = .8, \ln f = -\sigma/\sqrt{\lambda}$, $dt = .01$. B: Mean time to extinction increases as the LRC model is morphed into the LES model (bottom), despite the stationary mean remaining constant throughout the transformation (top). Parameters: Same as in A but $\alpha$ ranges logarithmically from 1 to 500 and $\sigma = 1$.

model (purple circles) extinction time increases with increasing $\alpha$ and asymptotes to the LES model extinction time (green square) with appropriate parameters. The top panel of figure 4B shows that, in the absence of extinction, the stationary population mean does indeed remain constant throughout the transformation.

IV. DISCUSSION

This work presented new results for the Logistic Random Catastrophe (LRC) model, a minimal model of single species logistic growth coupled to random, density-independent catastrophes. The LRC model was originally introduced to model large, unpredictable losses of population due to death by natural disaster, epidemic, or extreme environmental fluctuations. However, it also is relevant for populations that exhibit fast, concerted dispersal dynamics, such as aggregates of bacteria that get physically displaced from their local environment.

With the aim of providing a direct look at the statistical structure of the LRC model, the method of moment equations was used to derive exact expressions for its stationary moments. These expressions can be used to estimate the expected long-term variance of a population subject to random catastrophes and inform conservation efforts. In addition, from these analytic results spawned applications to two outstanding problems in population ecology.

First, the analytic results provided a theoretical basis for an approximation useful for analyzing experimental data [11]: Low-order statistics of the LRC model depend approximately just on a single combination of the average catastrophe rate ($\lambda$) and size ($f$), $\lambda \ln f$. Using this single effective parameter reduces the number of parameters that needs to be estimated from data. Analytic results demonstrated that this approximation is most valid in the limit of rare, large catastrophes.

Second, the analytic results presented here illuminated the correspondence between the LRC model and its Gaussian noise counterpart, the Logistic Environmental Stochasticity (LES) model. Traditionally, it has been difficult to quantitatively compare the risk of extinction under the two models as their parameters describe different aspects of noise: Random catastrophes in the LRC model are characterized by an average rate ($\lambda$) and size ($f$), while the LES model has a single noise-strength parameter ($\sigma$). The analytic results derived above informed the development of two methods for mapping these parameters, facilitating quantitative comparison of
the two models.

The first method was based on equating the stationary means of the two models as a way to normalize the effect of noise. For models with equal growth rates and carrying capacities, this is achieved by equating $\sigma^2$ with the effective catastrophe parameter $-2\lambda \ln f$. Using this mapping the mean times to extinction for the two models were computed over a wide range of noise strengths. The mean time to extinction for the LES model was larger than for the LRC model across noise strengths, by orders of magnitude in the low noise limit, implying significantly higher risk of extinction under random catastrophes than under environmental stochasticity.

The second method for comparing extinction risk in the two models was based on constructing the LES model from the LRC model in the limit of infinitely frequent, infinitesimal catastrophes. In this light, the LES model can be considered a special case of the LRC model, existing in a sub-space of the LRC parameter space. The transformation derived here is a prescription, in the form of a curve through parameter space, for traveling from an LRC model to an LES model. As the catastrophe rate $\lambda$ diverges in this limit, the LES sub-space exists as a limit along the $\lambda$ axis. This is analogous to how exponential growth can be considered a special case of logistic growth with infinite carrying capacity. Computed at various points along this limit, the mean time to extinction monotonically increased and asymptoted to the corresponding LES model value.

This smooth transformation from the LRC model to the LES model is not limited to the study of extinction risk, nor is it limited to the these particular models, but is generally applicable to the quantitative comparison of a broad class of stochastic differential equations. It is based only on the ubiquitous Central Limit Theorem (CLT). The CLT is most often thought of as a statement about statistics in the large sample limit, but in its functional generalization to stochastic processes, the CLT can also be viewed as a statement about iterative temporal coarse graining: Any stochastic process with increments that are independent, have zero mean, and finite variance will tend to the Brownian motion process when view on large timescales, with appropriate rescaling. In this way, method II is related to Renormalization Group methods of theoretical physics [32].

Beginning with the work of Paine on intertidal zones, random catastrophes continue to permeate metapopulation frameworks, where they describe abrupt dispersal dynamics. The LRC model and its body of analytic results form a sound foundation from which to study such processes. It would be interesting to study spatial metapopulation models subject to catastrophe-type hopping dynamics and the resulting large scale dispersal patterns, which may be relevant to rocky shore and gastrointestinal ecosystems alike. Additionally, adaptation of species under conditions of catastrophic dynamics [33] provides further topics for study, again of practical relevance. In both of these cases, the correspondence between random catastrophes and environmental stochasticity presented here would be useful in illuminating how they fundamentally differ in their ecological and evolutionary consequences.

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Appendix A: Detailed calculation of stationary moments

In this section an expression for the $n^{th}$ stationary moment for the LRC model is derived. The approach is analogous for the LES model and since the results are already known, a derivation isn’t given, though one remark is made on the application of this method to diffusion processes.

1. LRC model

Before beginning, the chain rule for jump processes [18] is stated without proof, for reference. Let $X_t$ by a general process given by

$$dX_t = f(X_t, t)dt + h(X_t, t^-)dN_t$$

with $f$ and $h$ deterministic functions, $N_t$ a Poisson process with rate $\lambda$, and $t^-$ denoting the Itô convention...
as in the main text. Further let $Y_t \equiv F(X_t, t)$ be a transformed process. Then $Y_t$ is governed by

$$
dY_t = (\partial_t F(X_t, t) + f(X_t, t)\partial_X F(X_t, t)) \, dt + \Delta Y_t^{jump} \, dN_t \tag{A2}
$$

with $\Delta Y_t^{jump} \equiv F(X_{t-} + h(X_{t-}, t^-)) - F(X_{t-}, t^-)$.

Now recall the LRC model,

$$
dX_t = rX_t \left(1 - \frac{X_t}{K}\right) \, dt - (1 - f)X_t \, dN_t. \tag{A3}
$$

The first step is to change variables to $X^n_t$ using the stochastic chain rule for jump SDEs. The result is

$$
dX^n_t = nrX^n_t \left(1 - \frac{X_t}{K}\right) \, dt - (1 - f^n)X^n_t \, dN_t. \tag{A4}
$$

Then, each term in this SDE is averaged. The expectation of $X^n_t \, dN_t$ can be factored: $\mathbb{E}[X^n_t \, dN_t] = \mathbb{E}[X^n_{t^-}] \mathbb{E}[dN_t] = \mathbb{E}[X^n_{t^-}] \lambda \, dt$. Intuitively, this is because the two processes appear mutually independent. The Poisson process has independent increments, and since the Itô convention was used, $X^n_{t-}$ is independent of $N_t$, which occurs in the future. This is certainly true for a discrete time model, but care must be taken in the continuous limit.

A more rigorous argument can be made using the Dominated Convergence Theorem. The case $n = 1$ is considered without loss of generality. Consider $X_j$, a discrete partition of the continuous time process $X_t$, such that $X_j \to X_t$ in probability. Then, sums of $X_j$ converge in probability to integrals, in particular,

$$
\sum_j X_{j-1} \Delta N_j \to \int_T X_t \, dN_t, \tag{A5}
$$

where $\Delta N_j$ is a partition of the Poisson process. The Dominated Convergence Theorem says that if $X_t$ is dominated by an integrable function on the interval $T$,

$$
\mathbb{E} \left[ \sum_j X_{j-1} \Delta N_j \right] \to \mathbb{E} \left[ \int_T X_t \, dN_t \right] \tag{A6}
$$

in probability. Since populations in the LRC model are bounded by the carrying capacity for all time, this is always valid. The expectation of the sum is straightforward, leading to the result,

$$
\mathbb{E} \left[ \int_T X_t \, dN_t \right] = \int_T \mathbb{E}[X_{t^-}] (\lambda \, dt), \tag{A7}
$$

from which the infinitesimal version follows as a special case.

Factoring the expectation results in an ODE for the $n^{th}$ moment. In the steady state, this becomes the recursion relation

$$
\mathbb{E}[X^{n+1}] = K \left(1 - \frac{\lambda(1 - f^n)}{nr}\right) \mathbb{E}[X^n]. \tag{A8}
$$

Defining

$$
c_n \equiv \left(1 - \frac{\lambda(1 - f^n)}{nr}\right), \tag{A9}
$$

the $n^{th}$ moment can be expressed in terms of the mean as

$$
\mathbb{E}[X^n] = K^{n-1} \left(\prod_{m=1}^{n-1} c_m\right) \mathbb{E}[X]. \tag{A10}
$$
To complete the recursion relation, the mean must be computed independently. This is accomplished by changing variables to $\ln X_t$ using the chain rule for jump processes:

$$d \ln X_t = r \left(1 - \frac{X_t}{K}\right) dt + \ln f \, dN_t,$$

which in the steady state gives an expression for the stationary mean,

$$\mathbb{E}[X] = K \left(1 + \frac{\lambda}{r} \ln f\right).$$

Plugging this back into equation (A10) gives the final result

$$\mathbb{E}[X^n] = K^n \left(1 + \frac{\lambda}{r} \ln f\right)^{n-1} \prod_{m=1}^{n-1} \left(1 - \frac{\lambda(1-f^m)}{m r}\right).$$

Evaluating this equation for $n = 2$ leads to the expression for the variance in the main text:

$$\text{Var}[X]_{LRC} = K^2 \frac{\lambda}{r} (-\ln f - (1-f)) \left(1 + \frac{\lambda}{r} \ln f\right).$$

2. LES model

The derivation is analogous for the LES model, except that Itô’s chain rule for diffusion processes is used. Since the results are already known, derived with traditional methods, the computation will not be given. However, one remark worth making concerns the expectation of $X_t - dB_t$. The intuitive argument outlined for the LRC model - that since the Itô convention was employed the expectation of the product can be factored - gives the correct answer in this case, but is in fact not generally valid. Essentially, for processes governed by equations of the form

$$dX_t = f(X_t, t) dt + g(X_t, t)dB_t,$$

the integral $\int g(X_t, t^-) dB_t$ can acquire non-zero expectation if the function $g$ grows too quickly. A classic example is the CEV model of quantitative finance [34], which is of the form $f(X_t, t) = X_t$ and $g(X_t, t) = X_t^\gamma$ for $\gamma > 1$. However, one can use the fact that the exponential version of the LES model, i.e. $K \to \infty$, is a well known SDE for which $\mathbb{E} \left[ \int X_t^- dB_t \right] = 0$. This model is known as Geometric Brownian Motion and describes asset prices in the Black-Scholes model of quantitative finance [34]. Since paths of the exponential model almost surely dominate paths of the LES model, $\int X_t^- dB_t$ for the LES model inherits the martingale property from the exponential case, which implies zero expectation.

Appendix B: Derivation of the mapping from the LRC model to the LES model

In the main text a transformation of parameters was given that takes the LRC model into the LES model, along with numerical results that showed the transformation of its probability distribution. Here the transformation is performed analytically on the LRC model SDE, resulting in the appropriate LES model.

The proposed transformation was as follows. Let $\alpha$ be a scale parameter, $LRC(r, K, \lambda, f)$ an LRC model, and $\sigma$ be the target noise-strength parameter of the limiting LES model. Fix $\lambda \ln f = \sigma^2$, and scale

$$X' = \alpha X, \quad \ln f' = -\sigma / \sqrt{X'}$$

and

$$r' = r \left(1 - \frac{\lambda' \ln f'}{r}\right) = r \left(1 + \frac{\sigma \sqrt{X}}{r} \sqrt{\alpha}\right),$$
The claim is that in taking the limit $\alpha \to \infty$, the LRC model $LRC(r', K', \lambda', f')$ gets mapped to an LES model $LES(r_{ES}, K_{ES}, \sigma)$, with $\sigma^2 = \lambda \ln^2 f$, $r_{ES} = r(1 + (2r)^{-1} \sigma^2)$, and $K_{ES} = K(1 + (2r)^{-1} \sigma^2)$, such that the stationary means of both models are equal.

To begin the derivation, recall the LRC model, 
\begin{equation}
        dX_t = r X_t \left( 1 - \frac{X_t}{K} \right) dt - (1 - f) X_t \cdot dN_t. \tag{B2}
\end{equation}

First, the transformation (B1) is applied with $\alpha$ finite. The notation $N_t'$ is used for a Poisson process with rate $\lambda'$. Evaluating $r'$ and $K'$, the LRC model becomes 
\begin{equation}
        dX_t = r' X_t \left( 1 - \frac{X_t}{K'} \right) dt - (1 - f') X_t \cdot dN_t'. \tag{B3}
\end{equation}

The multiplicative coupling $X_t \cdot dN_t'$ complicates taking the diffusion limit, so the noise will be turned into additive before taking limits by transforming to $\ln X_t$ using the chain rule for jump processes given above. The result is
\begin{equation}
        d \ln X_t = r \left( 1 - \frac{\lambda'}{r'} \ln f' \right) \left( 1 - \frac{X_t}{K'} \right) dt + \ln f' dN_t'. \tag{B4}
\end{equation}

The average drift of the differential Poisson process, $\lambda' dt$ will now be separated from the fluctuations and be cancelled, by design, by the scale factors of the growth rate and carrying capacity. In terms of the compensated Poisson process, $\tilde{N}_t = N_t - E[N_t] = N_t - \lambda t$, the model becomes
\begin{equation}
        d \ln X_t = r \left( 1 - \frac{X_t}{K} \right) dt + \ln f' d\tilde{N}_t. \tag{B5}
\end{equation}

Now the compensated Poisson process can be transformed into the Brownian motion process by the functional CLT, equation (10) in the main text, corresponding to $\alpha \to \infty$. The limiting population process is denoted by $X_t^*$. 
\begin{equation}
        d \ln X_t \to d \ln X_t^* = r \left( 1 - \frac{X_t^*}{K} \right) dt + \sqrt{\lambda} \ln f dB_t. \tag{B6}
\end{equation}

Finally, Itô’s chain rule \[18\] is used to transform back to linear variables, by which a new noise induced drift appears:
\begin{equation}
        dX_t^* = r X_t^* \left( 1 - \frac{X_t^*}{K} \right) dt + \frac{1}{2} \lambda \ln^2 f X_t^* dt + \sqrt{\lambda} \ln f X_t^* dB_t 
        = r \left( 1 + \frac{\sigma^2}{2r} \right) X_t^* \left( 1 - \frac{X_t^*}{K \left( 1 + \frac{\sigma^2}{2r} \right)} \right) dt - \sigma X_t^* dB_t, \tag{B7}
\end{equation}

where $-\sqrt{\lambda} \ln f$ has been identified as $\sigma$. Following equation (10) in the main text as written results in a negative sign in front of $dB_t$ that is not present in the definition of the LES model, but convergence in the functional CLT is in distribution, and $-B_t$ follows the same distribution as $B_t$, so the two are, in the present context, equivalent. The limiting process is an LES model with increased growth parameters as specified above. Comparing this model to the transformed LRC model of (B3) using the analytic results for the stationary mean equations (4) and (6) in the main text reveals that the two models do indeed have the same stationary mean.

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