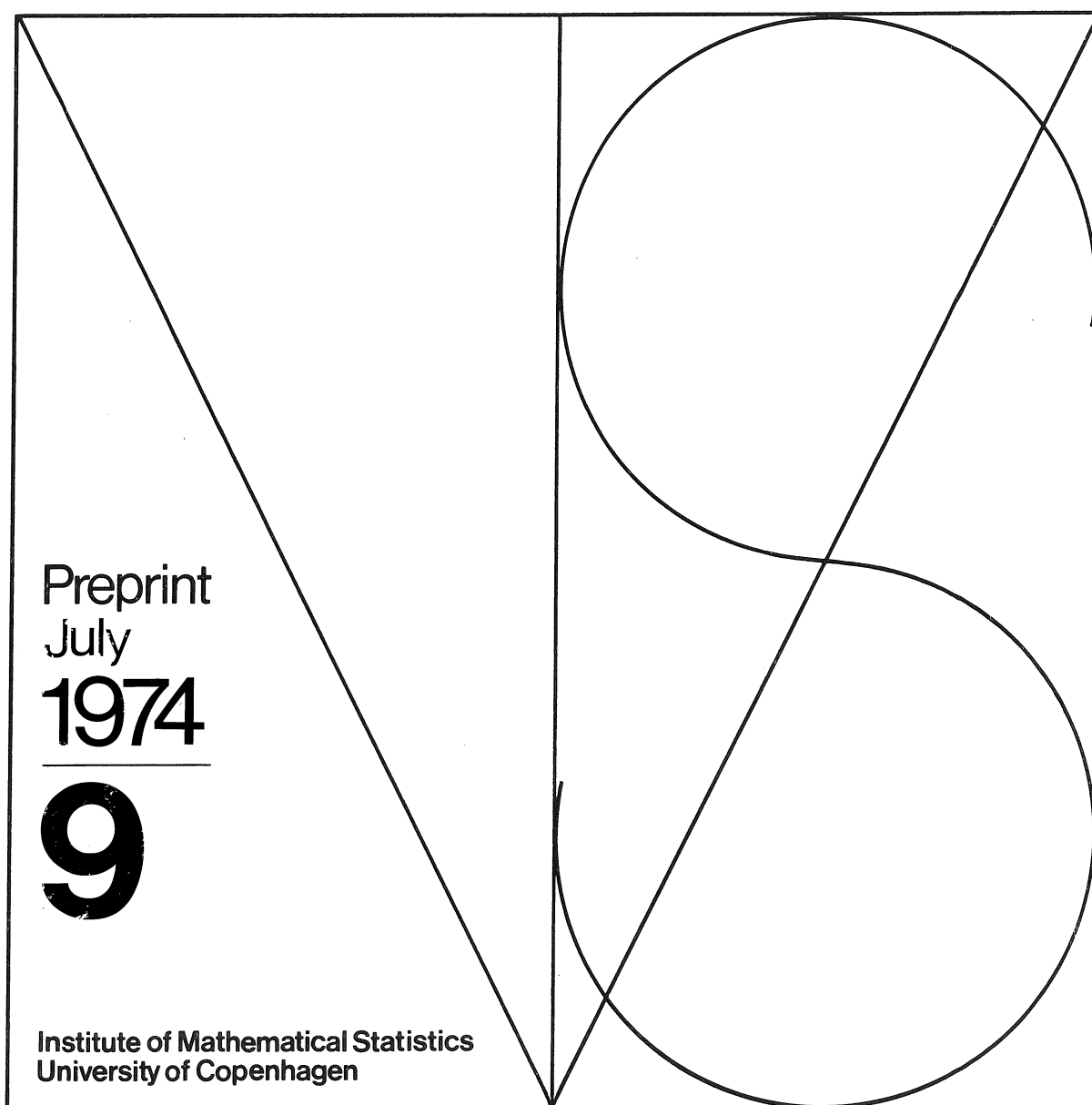


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Extinction and Exponential Growth in Random Environments



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EXTINCTION AND EXPONENTIAL GROWTH
IN RANDOM ENVIRONMENTS

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Summary

The influence of randomly varying environments on unrestricted population growth and extinction is analyzed by means of branching processes with random environments (BPRE). A main theme is the interplay between environmental and sampling (or "demographic") variability. If the two sources of variation are of comparable magnitude, the environmental variation will dominate except as regards the event of extinction.

A diffusion approximation of BPRE is proposed to study the situation of a large population with small environmental variance and mean offspring size little above one.

Comments on the ecological literature as well as on the possible significance of the results in branching process theory are also given.

1. Introduction

Considerable interest has recently been devoted to studies of randomly varying environments in a variety of the familiar models in mathematical ecology as well as population genetics. For the simplest possible case, that of unisexual, unrestricted growth, the literature has developed along two almost independent lines.

In the ecological literature, a basic point was made in the note by Lewontin and Cohen (1969) with the sequel by Levins (1969). These authors remarked that if random environments are imposed on the simple deterministic multiplicative growth model, the condition for ultimate extinction of the population is not that the expected offspring size be less than one, but that the expected log (offspring size) be less than zero. Recent contributions to this literature are diffusion models by Cappocelli and Ricciardi (1974) and Tuckwell (1974), and May (1973) considers diffusion-type arguments for a large class of models for deterministic growth in randomly varying environments. None of these authors incorporate the sampling variation due to the integer-valued size of living populations, and it turns out that accordingly, the possibility of population extinction in finite time is not allowed for in any of these models.

On the other hand, a generalization of the classical branching process models to random environments was given by Smith and Wilkinson (1969) and further developed by Athreya and Karlin (1971 a,b). The condition for certain extinction is equivalent to the condition given by Lewontin and Cohen as discussed above, but in this model,

extinction in finite time is certain in the subcritical case (with negative expected logarithmic offspring mean) and possible in the supercritical case as well.

These results have been applied by Mountford (1971, 1973) but seem otherwise to have had little impact on the ecological literature so far.

Kaplan (1973) defined Markov branching processes (continuous time) in random environments.

It is the purpose of this paper to reconcile these two approaches and to give some further contributions to the theory of the interplay between environmental and sampling variation in the simple model of unrestricted exponential growth.

In Section 2 we briefly review the branching process theory and discuss and generalize a result by Keiding and Nielsen (1973) which roughly states that the environmental variation outweighs the sampling variation except for the event of extinction, and that this latter event is asymptotically independent of the dominant fluctuations around the expected exponential growth. Section 3 contains a similar discussion for continuous time models. In these two Sections, the environmental and sampling variations are assumed to be of comparable size and the results are true for small populations.

Section 4 shows that in a large population, it is possible to obtain a balance between the two sources of variation by letting the environmental variance become small. Specifically, we propose a diffusion approximation of branching processes with random environments generalizing the classical diffusion approximation of Galton-

Watson processes due to Feller (1951). The resulting diffusion process also has as a special case the process recently studied by Cappocelli and Ricciardi (1974) and Tuckwell (1974) and since it is motivated by a discrete approximation rather than by integration of a stochastic differential equation, it may shed some light on the controversy concerning Ito or Stratonovich stochastic integration of white noise, see the remarks and further references by the above-mentioned authors as well as May (1973) and Feldman and Roughgarden (1974), who considered restricted population growth with randomly varying carrying capacity.

We include some remarks on the possible perspective for branching process theory of the proposed diffusion approximation.

The paper is attempted as an expository introduction to the application of some recent developments in branching process theory to some concepts in population dynamics and the subjects included have not always awaited formal mathematical proofs. Two appendices, however, contain some mathematical statements and proofs concerning the material in Sections 2 and 3.

An important omission from the present discussion is the relation of the results to parallel research in population genetics. However, we plan to give this discussion in a future report.

2. Small populations: discrete time

a. Sampling variation in constant environments

The simplest stochastic model of unrestricted growth is the Galton-Watson branching process Z_0, Z_1, \dots given by a common offspring distribution $\{p_i\}$ and independence of reproduction for all individuals. We shall assume throughout that $Z_0 = z$ is fixed. The extinction probability $q = P\{Z_n \rightarrow 0\} = 1 - P\{Z_n \rightarrow \infty\}$ is 1 if and only if the offspring mean $m = \sum i p_i \leq 1$. It is seen that in this case $EZ_n = zm^n \rightarrow \infty$ if and only if $q < 1$. This case is called supercritical, and a further result asserts that under the weak assumption that $E(Z_1 \log Z_1) < \infty$, the growth of the population, if it does not become extinct, is exponential, since in this case $Z_n m^{-n} \rightarrow W$ almost surely, where the random variable W is positive if and only if $Z_n \rightarrow \infty$.

b. Varying environments

We shall consider generalizations of this situation to varying environments, and we shall consider some sort of stationarity throughout. Consider first a periodically varying environment, giving rise to periodically varying offspring distributions with expectations $l_1, l_2, \dots, l_k, l_1, l_2, \dots, l_k, \dots$. Then, it is readily seen that $X_n = Z_{nk}$ is a time-homogeneous Galton-Watson process and thus $P\{Z_n \rightarrow 0\} = 1$ if and only if the offspring expectation $l_1 \dots l_k$ of the X -process is less than or equal to one, or equivalently, if and only if

$$\frac{1}{k} \sum_{i=1}^k \log l_i \leq 0.$$

It is still true that $E(Z_n) \rightarrow \infty$ if and only if $P\{Z_n \rightarrow 0\} < 1$, and in this case (the supercritical case), the random growth is

described by $Z_{nk} \sim (\ell_1 \dots \ell_k)^n W$, where $W > 0$ if and only if

$Z_n \rightarrow \infty$.

c. Random environments

The idea of introducing random environments into branching process theory is due to Smith and Wilkinson (1969), and later Athreya and Karlin (1971 a,b) gave a detailed account of the extinction problem and limiting behavior of branching processes in random environments (BPRES). In this model it is assumed that there is given a sequence $\xi = (\xi_0, \xi_1, \dots)$ of random variables, representing the environments, and that the offspring distributions are parametrized by the values of these random variables. For each given realization of the sequence of environments, all individuals in a given generation n reproduce independently and according to the particular offspring distribution $\{p_i(\xi_n)\}$. Marginally, however, the reproduction of different individuals is no longer independent, being correlated through the common environment. Assuming that the environmental sequence ξ is stationary and ergodic, and under a weak regularity condition, it may be shown first that for almost all environments ξ ,

$$q(\xi) = P\{Z_n \rightarrow 0 \mid \xi\} = 1 - P\{Z_n \rightarrow \infty \mid \xi\}$$

and then that $P\{q(\xi) = 1\} = 0$ or 1 according as $E\{\log \ell(\xi)\} > 0$ or ≤ 0 , where $\ell(\xi_0) = E(Z_1 \mid Z_0 = 1, \xi_0)$ is the conditional offspring mean given that the 0'th environmental variable has the value ξ_0 .

(Notice the analogy with the periodic case.) Therefore, a BPRES with $E\{\log \ell(\xi_0)\} > 0$ is called supercritical.

In the particular case of independent identically distributed environmental variables we clearly get the expectation $E(Z_n) = z m^n$,

$m = E\{\ell(\xi_0)\}$. Since $E\{\log \ell(\xi_0)\} > 0$ implies $E\{\ell(\xi_0)\} > 1$ by Jensen's inequality, it is seen that a supercritical BPRE with independent environments has an exponentially growing mean. However, it is also seen that in the cases where $E\{\ell(\xi_0)\} > 1$ but $E\{\log \ell(\xi_0)\} < 0$ we encounter the apparent paradox that $P\{Z_n \rightarrow 0\} = 1$ but $E(Z_n) \rightarrow \infty$.

The asymptotic growth of supercritical BPREs was studied by Keiding and Nielsen (1973) who showed that provided that

$$0 < \text{Var}\{\ell(\xi_0)\} < \infty,$$

$$\left[Z_n e^{-nE\{\log \ell(\xi_0)\}} \right] n^{-\frac{1}{2}n} \Rightarrow Ue^V \quad (2.1)$$

in distribution, where U and V are independent, $P\{U = 0\} = 1 - P\{U = 1\} = P\{Z_n \rightarrow 0\}$ and V is normal $(0, \text{Var}\{\ell(\xi)\})$. The intuitive meaning of this result might be gathered from the heuristic relation

$$Z_n \sim Ue^{nE\{\log \ell(\xi)\} + n^{\frac{1}{2}} V + o(n^{\frac{1}{2}})}. \quad (2.2)$$

It is seen that the event of extinction is governed by the indicator random variable U which is, in turn, determined by the sampling variation given the environment, as is seen from Keiding and Nielsen's proof. The event of extinction and the long term environmental fluctuations of the offspring mean are independent, and the latter determine, by an order of magnitude, completely the asymptotic size distribution of the population given that it does not become extinct. Finally, this asymptotic distribution is logarithmically normal with median at $e^{nE\{\log \ell(\xi_0)\}}$.

It is important to realize the difference between the growth rate $[E\{\ell(\xi_0)\}]^n$ of the expected population size (the deterministic growth rate) and the median $\exp[nE\{\log \ell(\xi_0)\}]$ of the asymptotic population size given non-extinction.

It is not hard to show that an analogue of (2.1) will hold if instead of independent environmental variables we assume a stationary weakly dependent sequence of environments with some condition which ensures that the central limit theorem is applicable on the sequence $\log \ell(\xi_1) + \dots + \log \ell(\xi_n)$. We give one such generalization in Appendix 1.

d. Deterministic growth in random environments

A contribution independent of the theory of BPRE is due to Lewontin and Cohen (1969) who studied deterministic reproduction in a randomly varying environment. These authors derived the asymptotic logarithmic normality of the population size and noticed the apparent paradox concerning the growth of the expectation and the random growth referred to above. We notice that the independence between U and V in (2.1) and (2.2) and the behavior of V confirm Lewontin and Cohen's results within the present more general model as far as exponential growth is concerned. Although Lewontin and Cohen's condition for extinction also holds true, we want to point out that their study, excluding the sampling variation, will not yield complete inferences on extinction of populations of integer size. The random population size in their model corresponds to the conditional expected population size given the environment in the branching process model, which is positive for all finite times n , so that their statement that "the probability of extinction may approach unity" would be more correctly formulated as "the population size may converge to zero almost surely".

3. Small populations: continuous time

Deterministic unrestricted growth in continuous time may in the simplest situation be represented by the differential equation

$$\frac{dN}{dt} = rN \quad (3.1)$$

where N is the population size.

The solution of (3.1) is

$$N_t = N_0 e^{rt} \quad (3.2)$$

so that this model corresponds to exponential growth with exponent proportional to r , the intrinsic rate of natural increase or the Malthusian parameter, which may be positive, zero, or negative.

a. Sampling variation in constant environments.

A simple stochastic model for the growth of an integer-sized population under similar assumptions is the simple (linear) birth-and-death Markov process X_t given by the birth and death intensities $\lambda \geq 0$ and $\mu \geq 0$ and infinitesimal transition probabilities

$$P \{X_{t+h} = j | X_t = i\} = \left. \begin{array}{ll} i\lambda h + o(h) & j = i + 1 \\ 1 - i(\lambda + \mu)h + o(h) & j = i \\ i\mu h + o(h) & j = i - 1 \\ o(h) & \text{otherwise.} \end{array} \right\}$$

In this model, $E(X_t) = X_0 e^{(\lambda - \mu)t}$ and

$$P\{X_t \rightarrow 0\} = 1 - P\{X_t \rightarrow \infty\} = \begin{cases} (\mu/\lambda)^{X_0} & \lambda > \mu \\ 1 & \lambda \leq \mu \end{cases}$$

By the obvious analogy, $\lambda - \mu$ is called the Malthusian parameter of the birth-and-death process. The growth of the random population

size is described in a much similar manner as for the discrete time branching process studied in Section 2 above, since when $\lambda > \mu$ (the supercritical case)

$$X_t/E(X_t) = X_0 \exp\{(\lambda - \mu)t\} \rightarrow W$$

almost surely, where $W > 0$ if and only if $X_t \rightarrow \infty$. Thus, if the population does not become extinct, it grows at an exponential rate with the Malthusian parameter as its exponent.

Levins (1969), in a sequel to the above-mentioned paper by Lewontin and Cohen, described the sampling variation "in deaths only" by changing the differential equation (3.1) into

$$\frac{dN}{dt} = rN + \{v(1-v)\}^{\frac{1}{2}} \varepsilon(t) \sqrt{N} \quad (3.3)$$

where v is "the mean viability" and $\varepsilon(t)$ is white noise. Apart from the ambiguities in integrating stochastic differential equations with white noise terms (cf. Feldman and Roughgarden (1974)), it is not clear to the present author how (3.3) was derived in the first place. Levins goes on to discuss solutions of the equation, and the model has been adopted without further discussion by later authors, see e.g. Tuckwell (1974). Levins' main conclusion is that

$$E(N) = N_0 e^{rt} + \frac{1}{4r} v(1-v)(e^{rt} - 1)$$

which is quite a different result from that of the birth-and-death process approach above.

b. Birth-and-death processes in random environments

A generalization of Markov branching processes to random environ-

ments was given by Kaplan (1973). In the situation of the birth-and-death process, this amounts to assuming that the birth and death intensities $\lambda(t)$ and $\mu(t)$ are stationary ergodic stochastic processes with almost surely continuous sample functions. (Kaplan's assumption of independence of $\lambda(t) + \mu(t)$ and $\lambda(t)/\{\lambda(t) + \mu(t)\}$ is unimportant, as a careful inspection of his paper shows.)

Kaplan shows that $P\{X_t \rightarrow 0\} + P\{X_t \rightarrow \infty\} = 1$ and his result concerning certain extinction may be reformulated by stating that $P\{X_t \rightarrow 0\} = 1$ if and only if the expected Malthusian parameter $\rho = E\{\lambda(t) - \mu(t)\}$ is non-positive.

In the supercritical case $\rho > 0$, an analogue of the result by Keiding and Nielsen (1973) may again be derived, provided the stochastic process $r(t) = \lambda(t) - \mu(t)$ satisfies mixing conditions sufficient for the central limit theorem to hold. We give in Appendix 2 one possible set of conditions and also an example of a positive, strongly mixing, stationary process with continuous sample functions, thus assuring the existence of such situations. The formal result is that, given the mixing conditions, as $t \rightarrow \infty$

$$(X_t e^{-\rho t}) t^{-\frac{1}{2}} \longrightarrow U e^V$$

in distribution, where U and V are independent, $P\{U=0\} = 1 - P\{U=1\} = P\{Z_n \rightarrow 0\}$ and V is normal with zero mean and variance

$$\sigma^2 = \lim_{T \rightarrow \infty} \frac{1}{T} \text{Var} \left(\int_0^T r(t) dt \right).$$

Heuristically, this may be written as

$$X_t \sim Ue^{tq} + t^{\frac{1}{2}} V + o(t^{\frac{1}{2}})$$

and exactly the same conclusions may be drawn as in Section 2 above.

c. Deterministic growth in random environments

The analysis in the present Section illustrates the continuous time remarks by Lewontin and Cohen (1969) and Levins (1969, Section 1b) in a similar way as in Section 2 above. The condition for certain extinction is now $\bar{\rho} = E\{r(t)\} \leq 0$ (so that "the discrepancy between the arithmetic and logarithmic mean disappears" as Lewontin and Cohen, and independently Kaplan (1973) remark). "But the role of the sampling variation remains the same as in the discrete model: no extinction in finite time is possible without sampling variation.

4. Large populations: a diffusion approximation

In this section we want to present a diffusion process, modeling unrestricted population growth and containing as special cases Feller's (1951) classical diffusion approximation of Galton-Watson processes as well as a model for deterministic growth in random environment discussed recently by Cappocelli and Ricciardi (1974) and Tuckwell (1974). The diffusion process is motivated by a generalization of Feller's approximation scheme to branching processes with random environments. We do not at this time have a rigorous proof of the convergence in distribution (incidentally, this was not published for the Feller scheme until the paper by Jiřina (1969)), but we find the resulting diffusion interesting enough to warrant a discussion.

a. Diffusion approximation of BPRE

Consider a sequence $\{Z_n(k), k = 1, 2, \dots\}$ of branching processes with random environments. We assume the environmental sequences to be independent identically distributed throughout (although the results presumably may be generalized to some sort of weak dependence of the sort discussed in Sections 2 and 3 above). Assume that for the k 'th process $Z_0(k) = k$, $E\{\ell_0(k)\} = 1 + \alpha/k + o(k^{-1})$, $\text{Var}\{\ell_0(k)\} = \omega^2/k + o(k^{-1})$ and $E\{\text{Var}(Z_1(k)|Z_0(k) = 1)\} = \tau^2$.

Define $Y_t(n) = Z_{[nt]}(n)/n$. The infinitesimal mean and variance of $Y_t(n)$ are (strictly speaking, for t an integer multiple of n^{-1}), to the first approximation

$$\begin{aligned} & E(Y_{t+\frac{1}{n}}(n) - Y_t(n) \mid Y_t(n) = y) \\ &= E(Z_{[nt+1]}(n)/n \mid Z_{[nt]}(n) = ny) - y \\ &= ny(1+\frac{\alpha}{n})/n - y = \frac{1}{n} \alpha y \end{aligned}$$

and, ζ_{nt} denoting the nt 'th environmental variable

$$\begin{aligned} & \text{Var}(Y_{t+\frac{1}{n}}(n) - Y_t(n) \mid Y_t(n) = y) \\ &= \text{Var}\{Z_{[nt+1]}(n) \mid Z_{[nt]}(n) = ny\}/n^2 \\ &= \frac{1}{n^2} E[\text{Var}\{Z_{[nt+1]}(n) \mid Z_{[nt]}(n) = ny, \zeta_{nt}\}] \\ &\quad + \frac{1}{n^2} \text{Var}[E\{Z_{[nt+1]}(n) \mid Z_{[nt]}(n) = ny, \zeta_{nt}\}] \\ &= \frac{1}{n^2} ny\tau^2 + \frac{1}{n^2} n^2 y^2 \frac{\omega^2}{n} = \frac{1}{n} (\tau^2 y + \omega^2 y^2). \end{aligned}$$

Drawing the analogy to Feller's diffusion approximation, we, therefore, conjecture that as $n \rightarrow \infty$, $Y_t(n)$ converges in distribution

to a diffusion X_t with state space $[0, \infty)$, $X_0 = 1$ and infinitesimal mean and variance αx and $\tau^2 x + \omega^2 x^2$.

It is clear from the definition that α represents the mean growth, τ^2 the sampling variance (or "demographic stochasticity", cf. May 1973) and ω^2 the environmental variance.

b. The special cases

If in the above scheme the environmental variance $\omega^2 = 0$, the Feller diffusion approximation is recovered. This process has properties very similar to discrete branching processes: if $X_0 = x$, then

$$P\{X_t = 0 \text{ for some } t\} = 1 - P\{X_t \rightarrow \infty \text{ as } t \rightarrow \infty\}$$

$$= \begin{cases} 1 & \text{for } \alpha \leq 0 \\ \exp\left\{-\frac{2\alpha}{\tau^2} x\right\} & \text{for } \alpha > 0 \end{cases}$$

so that either the process becomes extinct in finite time, or it grows indefinitely large, where the latter alternative is possible only in the supercritical case with "mean growth rate" $\alpha > 0$. In that case, the extinction probability is an exponential decreasing function of the initial population size x (and it is increasing in the sampling variance τ^2 .)

If on the other hand, the sampling variance $\tau^2 = 0$, the model is that obtained by Ito integration of the stochastic differential equation

$$\frac{dX_t}{dt} = aX_t,$$

where $a = \alpha +$ white noise with variance ω^2 . This equation was discussed recently by Cappocelli and Ricciardi (1974) who, however, preferred to interpret it in the Stratonovich calculus. We do not

want here to enter into a discussion of which stochastic integral is the more appropriate in this situation, but might point out that the discrete approximation scheme outlined above seems to lead to the Ito solution.

The analysis of this latter diffusion, with infinitesimal mean and variance αx and $\omega^2 x^2$, is facilitated by the remark made by Tuckwell (1974) for the Stratonovich solution, that X_t has the same distribution as $\exp(U_t)$, where U_t is Brownian motion with infinitesimal mean and variance $\alpha - \omega^2/2$ and ω^2 . Thus, if $\alpha = \omega^2/2$, the process is recurrent (although Tuckwell claims that in his corresponding case $P\{X_t \rightarrow \infty\} = P\{X_t = 0\} = \frac{1}{2}$). Otherwise X_t will drift off to either 0 or ∞ , in fact $P\{X_t \rightarrow 0\} = 1$ when $\alpha < \omega^2/2$ and $P\{X_t \rightarrow \infty\} = 1$ when $\alpha > \omega^2/2$. We shall comment further below on the facts that 0 is never attainable ($P\{X_t > 0\} = 1$ in all cases) so that population extinction in finite time will never be possible, and on the perhaps surprising nature of the criticality condition $\alpha = \omega^2/2$ (rather than $\alpha = 0$).

c. Boundary classification

Table 1 summarizes the boundary behavior of the diffusion process.

TABLE 1

BOUNDARY CLASSIFICATION OF THE DIFFUSION PROCESS

		0				∞			
		Attraction		Absorption		Attraction		Absorption	
		Class.	$P\{X_t \rightarrow 0\}$	Class.	$\lim P\{X_t = 0\}$	Class.	$P\{X_t \rightarrow \infty\}$	Class.	$\lim P\{X_t = \infty\}$
$\omega^2 > 0,$	$\alpha > \omega^2/2$	attracting	$(1 + \frac{\omega^2}{2x})^{-1} \frac{2\alpha}{\omega^2}$	exit	$(1 + \frac{\omega^2}{2x})^{-1} \frac{2\alpha}{\omega^2}$	attracting	$1 - (1 + \frac{\omega^2}{2x})^{-1} \frac{2\alpha}{\omega^2}$	natural	0
$\tau^2 > 0$	$\alpha \leq \omega^2/2$	attracting	1	exit	1	repelling	0	natural	0
$\omega^2 > 0,$	$\alpha > \omega^2/2$	repelling	0	natural	0	attracting	1	natural	0
$\tau^2 = 0$	$\alpha = \omega^2/2$	repelling	0	natural	0	repelling	0	natural	0
	$\alpha < \omega^2/2$	attracting	1	natural	0	repelling	0	natural	0
$\omega^2 = 0$	$\alpha > 0$	attracting	$\exp(-\frac{2\alpha}{\tau^2}x)$	exit	$\exp(-\frac{2\alpha}{\tau^2}x)$	attracting	$1 - \exp(-\frac{2\alpha}{\tau^2}x)$	natural	0
$\tau^2 > 0$	$\alpha \leq 0$	attracting	1	exit	1	repelling	0	natural	0

The first question regarding the behavior of a boundary a is whether it is attracting or repelling, that is, whether $P\{X_t \rightarrow a\} > 0$ or $= 0$. The attraction happens (Prohorov and Rozanov (1971, p. 265 ff.)) if and only if the natural scale $S(a) < \infty$, where

$$S(x) = \int^x R(y) dy$$

and

$$R(x) = \exp \left\{ - \int^x \frac{2 \alpha y}{\tau^2 y + \omega^2 y^2} dy \right\}$$

It is seen that 0 is always attracting when the sampling variance $\tau^2 = 0$ and the growth parameter α is less than half the environmental variance ω^2 (including, of course, the case $\alpha \leq 0$). The other boundary, ∞ , is attracting whenever $\alpha > \omega^2/2$, regardless of the value of τ^2 . This is the first and weakest conclusion: we have a "supercritical" case whenever $\alpha > \omega^2/2$, and a subcritical case for $\alpha < \omega^2/2$.

An attracting boundary a may or may not be attainable, that is, $P\{X_t = a \text{ for some } t < \infty\} > 0$ or $= 0$. The boundary a is attainable if and only if the function

$$R_1(x) = R(x) \int^x \frac{2}{(\tau^2 y + \omega^2 y^2) R(y)} dy$$

is integrable in the neighborhood of a . It turns out that for the processes here considered, the attracting boundaries are attainable if and only if the sampling variance $\tau^2 > 0$. This illustrates in a rather conspicuous way the role of the sampling variance in models for population growth: One may shortly say that the positivity of the sampling variation makes the difference between absorption (finite time extinction) or reflecting attraction (asymptotic extinction) of

the boundary 0. Previous authors have recognized the impossibility of absorption in the model without sampling variance, see Cappocelli and Ricciardi (1974, concluding paragraph) or May (1973, Chapter 5). Although they tend to blame this on deficiencies in the model, they recommend identifying extinction with the attainment of some small positive "threshold" value of the population, which clearly will be attainable. It is also interesting that May's (1973, p.121) discrete-time numerical approximations do not retain the feature that $P\{X_t > 0\} = 1$.

To complete the classification of the boundaries, we finally note that the repelling and unattainable boundaries are natural, and the attainable boundaries are exit, all in the sense of Feller (1952). This means that the diffusion processes are uniquely given by the specification of the infinitesimal mean and variance on $(0, \infty)$ (no boundary conditions may be imposed), in particular, when 0 is an exit boundary, it is necessarily absorbing.

Apart from the critical case with no sampling variance ($\tau^2 = 0, \alpha = \omega^2/2$), there is always at least one attracting boundary. When there is only one, its probability of attraction is one, otherwise

$$P\{X_t \rightarrow 0\} = 1 - P\{X_t \rightarrow \infty\} = \frac{\int_0^x R(y) dy}{\int_0^{\infty} R(y) dy}$$

where the denominator is finite since both 0 and ∞ are attracting. The values of this probability are also given in Table 1.

d. The criticality condition

The criticality condition $\alpha = \omega^2/2$ of the diffusion approximation may be compared to the criticality condition $E\{\log \ell(\zeta_0)\} = 0$ of BPRE. Expanding, and omitting the explicit reference to the environmental variable ζ_0 , we get

$$\log \ell = \ell - 1 - \frac{1}{2}(\ell-1)^2 + \dots$$

so that, approximately,

$$E\{\log \ell\} = E(\ell - 1) - \frac{1}{2}E\{(\ell-1)^2\}$$

Now

$$E\{(\ell-1)^2\} = \text{Var}(\ell) + \{E(\ell) - 1\}^2$$

and, therefore, by the assumptions above,

$$E\{\log \ell(n)\} \sim \frac{\alpha}{n} - \frac{\omega^2}{2n} + \frac{\alpha^2}{n^2} \sim \frac{1}{n} \left(\alpha - \frac{\omega^2}{2} \right)$$

showing the agreement of the two conditions. We commented in Section 2 above on the history of the criticality condition for discrete time (Lewontin and Cohen (1969), Smith and Wilkinson (1969)). In the form $\alpha = \omega^2/2$ the condition states that certain extinction (or at least certain attraction of the boundary 0) will happen not only for negative growth rates, but also for positive growth rates less than half the environmental variance. This bears a remarkable similarity to a conclusion by May (1973) in his study of random carrying capacity.

e. Further consequences for the theory of BPRE.

The result concerning the extinction probability of the supercritical case $\alpha > \omega^2/2$

$$q_x = P\{X_t \rightarrow 0 \mid X_0 = x\} = \left(1 + \frac{\omega^2}{\tau^2} x\right)^{1-2\alpha/\omega^2}$$

may prove of some general interest, in particular in view of the

scarcity of exact explicit results on extinction probabilities for BPPE, cf. Wilkinson (1969) and Keiding and Nielsen (1975). It is seen that, as expected, q_x is increasing in the sampling variance τ^2 and the environmental variance ω^2 but decreasing in the initial population size x and the growth parameter α . As $\omega^2 \rightarrow 0$,

$$q_x \rightarrow \exp\left(-\frac{2\alpha}{\tau^2} x\right)$$

which is the well-known result for the Feller diffusion approximation of a Galton-Watson process.

In Smith and Wilkinson's (1969) and Wilkinson's (1969) basic papers, considerable attention was given to the dual process X_n of a BPPE Z_n defined by

$$X_0 = s_0, X_{n+1} = \varphi_{\zeta_n}(X_n)$$

where $s_0 \in [0,1]$ is arbitrary and fixed and φ_{ζ_n} is the probability generating function of the offspring distribution parametrized by the n 'th environment ζ_n . In particular, it was shown that for all $k = 1, 2, \dots$

$$E(X_n^k | X_0 = s_0) \rightarrow P\{Z_n \rightarrow 0 | Z_0 = k\}$$

as $n \rightarrow \infty$. Thus, the extinction probability

$$q_k = P\{Z_n \rightarrow 0 | Z_0 = k\} = \int_0^1 q^k F(dq)$$

where F is the stationary distribution of the dual process. We

We remark that for the diffusion approximation

$$q_x = P\{X_t = 0 \text{ for some } t | X_0 = x\} = \left(1 + \frac{\omega^2}{\tau^2} x\right)^{1 - \frac{2\alpha}{\omega^2}}$$

$$= \left(\frac{\omega^2}{\tau^2}\right)^{1 - 2\alpha/\omega^2} \Gamma\left(\frac{2\alpha}{\omega^2} - 1\right)^{-1} \int_0^1 q^x q^{\frac{\tau^2}{\omega^2} - 1} (-\log q)^{\frac{2\alpha}{\omega^2} - 2} dq$$

which is of the form $E(Q^X)$ with $-\log Q$ following a Γ -distribution with parameters $2\alpha/\omega^2 - 1$ and ω^2/τ^2 , that is,

$$E(-\log Q) = \frac{2\alpha - \omega^2}{\tau}$$

$$\text{Var}(-\log Q) = \frac{2\alpha\omega^2 - \omega^4}{\tau^2}$$

It is apparent that this suggests the following limiting distribution results. Let

$$Q_k(nx) = Q_k^{nx}(1) = P\{Z_m(k) \rightarrow 0 \text{ as } m \rightarrow \infty \mid Z_0(k) = nx, \zeta(k)\}$$

be the extinction probability of the k 'th approximating BPPE given its environmental sequence $\zeta(k)$ and an initial population size of nx . Then $Q_n(nx) \Rightarrow Q^X$ in distribution as $n \rightarrow \infty$, where Q has the distribution described above.

It seems an interesting research problem to investigate this scheme further.

Appendix 1. The growth of supercritical branching processes with weakly dependent environments.

Assume that the environmental sequence $\zeta = (\zeta_0, \zeta_1, \dots)$ is stationary and ergodic, let $\mu = E\{\log l(\zeta_0)\}$ and suppose that $0 < \text{Var}\{\log l(\zeta_0)\} < \infty$. For $0 \leq a < b \leq \infty$, let \mathcal{G}_a^b denote the σ -algebra generated by $l(\zeta_a), \dots, l(\zeta_b)$ and define the uniform mixing coefficients

$$\varphi(n) = \sup_k \sup_{A \in \mathcal{G}_0^k, B \in \mathcal{G}_{n+k}^\infty} \frac{1}{P(A)} \left| P(A \cap B) - P(A)P(B) \right|.$$

If $\sum_{n=1}^{\infty} \varphi(n) < \infty$, then

$$\lim_{n \rightarrow \infty} \frac{1}{n} \text{Var} \left\{ \sum_{i=0}^{n-1} \log l(\zeta_i) \right\} = \sigma^2 < \infty$$

and if $\sigma^2 > 0$,

$$\left(Z_n e^{-n\mu} \right) n^{-\frac{1}{2}} \xrightarrow{\mathcal{L}} U e^V$$

where U and V are independent, $P\{U=0\} = 1 - P\{U=1\} = P\{Z_n \rightarrow 0\}$ and V is normal $(0, \sigma^2)$.

Proof. The conditions ensure that Heyde's (1973) results on central limit theory for stationary processes may be applied, and the proof may, therefore, be adapted, step by step, from Keiding and Nielsen (1973), the only difference being the independence of U and V .

Thus let

$$Z_n e^{-n\mu} = \frac{Z_n}{l(\xi_0) \dots l(\xi_{n-1})} \frac{l(\xi_0) \dots l(\xi_{n-1})}{e^{n\mu}} = W_n Y_n.$$

Let $k_n \rightarrow \infty$ such that $k_n n^{-\frac{1}{2}} \rightarrow 0$, define $U_n = I\{Z_{k_n} > 0\}$ and $X_n = l(\xi_{2k_n}) \dots l(\xi_{n-1}) e^{-n\mu}$. Then as in the case of independent environments $W_n n^{-\frac{1}{2}} \Rightarrow U$ a.s. so that $W_n n^{-\frac{1}{2}} - U_n \rightarrow 0$ a.s. and hence in probability. Further, by Heyde's central limit results, $Y_n n^{-\frac{1}{2}} \Rightarrow e^V$ in distribution and it is easily seen that $X_n n^{-\frac{1}{2}} - Y_n n^{-\frac{1}{2}} \rightarrow 0$ in probability. The result is, therefore, proved when we have shown that X_n and U_n are asymptotically independent. But

$$\left| P(\{X_n \in A\} \cap \{U_n \in B\}) - P\{X_n \in A\}P\{U_n \in B\} \right| \leq \phi(k_n) \rightarrow 0$$

as $n \rightarrow \infty$, since $\{X_n \in A\} \in \mathcal{G}_{2k_n}^\infty$ and $\{U_n \in B\} \in \mathcal{G}_0^{k_n}$.

Remark. The result as given here will remain true for strongly mixing environmental sequences satisfying the central limit theorem, cf. Ibragimov and Linnik (1970, Chapter 18).

Appendix 2. The growth of supercritical birth-and-death processes with stationary weakly dependent environments.

In this Appendix, we use another version of the central limit theorem for weakly dependent stationary processes, partly to illustrate the remark at the end of Appendix 1 above, but mainly since only strong mixing as opposed to uniform mixing will apply to the example which we shall give below.

Consider a birth-and-death process X_t with stationary, ergodic random birth and death rates $\lambda(t)$ and $\mu(t)$ defined according to Kaplan (1973) and discussed in Section 3 above. Let $r(t) = \lambda(t) - \mu(t)$ be the random Malthusian parameter and assume that $\rho = E\{r(t)\} > 0$ so that the process is supercritical. Assume also that $0 < \text{Var}\{r(t)\} < \infty$, and define the strong mixing coefficients of $r(t)$ by

$$\alpha(t) = \sup_{\tau} \sup_{A \in \mathcal{G}_\tau^0, B \in \mathcal{G}_{\tau+t}^\infty} |P(A \cap B) - P(A)P(B)|$$

where \mathcal{G}_a^b is the σ -algebra generated by all vectors $(r(t_1), \dots, r(t_n))$, $a < t_i < b$ for all i . If for some $\delta > 0$

$$E |r(t)|^{2+\delta} < \infty \tag{A2.1}$$

and

$$\int_0^\infty \alpha(t)^{\delta/(2+\delta)} dt < \infty$$

then

$$\sigma^2 = \lim_{T \rightarrow \infty} \frac{1}{T} \text{Var} \left\{ \int_0^T r(t) dt \right\} < \infty$$

and if $\sigma^2 > 0$, then

$$(X_t e^{-\rho t}) t^{-\frac{1}{2}} \xrightarrow{\text{d}} U e^V$$

where U and V are independent, $P\{U=0\} = 1 - P\{U=1\} = P\{Z_n \rightarrow 0\}$ and V is normal $(0, \sigma^2)$.

Proof. The conditions ensure that the continuous time analogue of theorem 18.5.3 of Ibragimov and Linnik (1970) may be applied, and the rest of the proof is then analogous to the proof of Appendix 1. In the proof we use the existence, established by Kaplan (1973, Section 4) of a random variable W such that as $t \rightarrow \infty$

$$X_t \exp\left\{-\int_0^t r(u) du\right\} \rightarrow W$$

almost surely, where under the present conditions $\{W=0\} = \{X_t \rightarrow 0\}$ a.s.

Example. It may not be completely obvious at the outset that there at all exists a process $r(t)$ satisfying the given requirements.

Following an idea due to Barndorff-Nielsen and Yeo (1969) who studied a special example of Poisson processes with random parameter (so-called negative binomial processes), we shall show here that if $\lambda(t)$ and $\mu(t)$ are independent gamma processes, the results apply.

Let $Y_1(t), \dots, Y_k(t)$ be independent Ornstein-Uhlenbeck processes, that is, each $Y_i(t)$ is a stationary Gaussian process with mean zero and covariance function

$$E\{Y_1(s) Y_1(s+t)\} = R(t) = \tau_Y^2 \exp\left\{-\frac{\beta_Y}{2} t\right\},$$

$0 < \tau_Y^2 < \infty$, $0 < \beta_Y < \infty$. Let then

$$\lambda(t) = Y_1^2(t) + \dots + Y_k^2(t) + \eta.$$

Obviously the one-dimensional distributions of $\lambda(t) - \eta$ are gamma-distributions with parameters $(k/2, \tau_Y^2)$. Similarly, let $Z_1(t), \dots, Z_m(t)$ be independent Ornstein-Uhlenbeck processes, independent of the $Y_i(t)$'s, with parameters τ_Z^2 and β_Z . Let

$$\mu(t) = Z_1^2(t) + \dots + Z_m^2(t) + \xi.$$

Then $E\{\lambda(t)\} = \frac{k}{2} \tau_Y^2 + \eta$ and $E\{\mu(t)\} = \frac{m}{2} \tau_Z^2 + \xi$ and the positivity condition for $\rho = E\{r(t)\} = E\{\lambda(t) - \mu(t)\}$ is exhibited as $\frac{k}{2} \tau_Y^2 + \eta > \frac{m}{2} \tau_Z^2 + \xi$. Now for an Ornstein-Uhlenbeck process Y_t with parameters τ^2 and β , it is a standard result (cf. Ibragimov and Linnik (1970, p.313)) that the mixing coefficients $\alpha_Y(t)$ satisfy $\alpha_Y(t) \leq R(t) = \tau^2 \exp\{-\beta t/2\}$. Let \mathcal{B}_a^b be the σ -algebra generated by all vectors $(Y(t_1)^2, \dots, Y(t_n)^2)$, $a < t_i < b$ for all i . Then clearly $\mathcal{B}_a^b \subset \mathcal{A}_a^b$ where \mathcal{A}_a^b is the corresponding σ -algebra for $Y(t)$, and thus the mixing coefficients $\alpha_{Y^2}(t)$ satisfy

$$\alpha_{Y^2}(t) \leq \alpha_Y(t) \leq R(t).$$

It is, therefore, also obvious that the mixing coefficients $\alpha_r(t)$ of the random Malthusian parameter $r(t)$ are dominated

$$\alpha_r(t) \leq C \exp\{-\beta t/2\} \quad (A2.2)$$

where $\beta = \min(\beta_Y, \beta_Z)$ and C is a constant. All moments of $r(t)$ are finite, so we may choose δ of the condition freely, let $\delta = 1$.

The finiteness of

$$\int_0^\infty \alpha(t)^{\delta/(2+\delta)} dt = \int_0^\infty \alpha(t)^{1/3} dt$$

is now obvious from (A2.2), and we may compute σ^2 by

$$\sigma^2 = \lim_{T \rightarrow \infty} 2 \int_0^T \left(1 - \frac{t}{T}\right) R_r(t) dt$$

where

$$R_r(t) = \frac{k}{2} \tau_Y^4 \exp(-\beta_Y t) + \frac{m}{2} \tau_Z^4 \exp(-\beta_Z t)$$

is the auto-covariance function of the random Malthusian parameter $r(t)$.

Thus

$$\sigma^2 = \frac{k\tau_Y^2}{\beta_Y} + \frac{m\tau_Z^2}{\beta_Z} .$$

Let us finally notice that by a standard result for gamma- and beta-distributions, $\lambda(t) + \mu(t)$ and $\lambda(t) / \{\lambda(t) + \mu(t)\}$ will be independent if and only if $\lambda(t)$ and $\mu(t)$ have common scale parameters, that is, if $\tau_Y^2 = \tau_Z^2$. In that case, Kaplan's (1973) results will apply without modification, and the present example may, therefore, also be seen as an example pertaining directly to his analysis.

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References

- ATHREYA, K.B. and KARLIN, S., 1971a. On branching processes with random environments: I. Extinction probabilities. Ann. Math. Statistics 42, 1499-1520.
- ATHREYA, K.B. and KARLIN, S., 1971b. Branching processes with random environments, II: Limit theorems. Ann. Math. Statistics 42, 1843-1858.
- BARNDORFF-NIELSEN, O. and YEO, G.F., 1969. Negative binomial processes. J. Appl. Prob. 6, 633-647.
- CAPOCELLI, R.M. and RICCIARDI, L.M., 1974. A diffusion model for population growth in random environment, Theor. Pop. Biol. 5, 28-41.
- FELDMAN, M.W. and ROUGHGARDEN, J., 1974. Remarks on certain diffusion models in ecology. Manuscript.
- FELLER, W., 1951. Diffusion processes in genetics. Proc. Second Berkeley Symp. Math. Statist. Prob. 227-246.
- FELLER, W., 1952. The parabolic differential equations and the associated semi-groups of transformations. Ann. Math. 55, 468-519.
- HEYDE, C.C., 1973. On the central limit theorem for stationary processes. Techn. Rep. Department of Statistics, Stanford University.
- IBRAGIMOV, I.A. and LINNIK, Yu.V., 1970. "Independent and stationary sequences of random variables." Groningen: Wolters-Noordhoff.
- JIRINA, M., 1969. On Feller's branching diffusion processes. Cas. pěst. mat. 94, 84-90.
- KAPLAN, N., 1973. A continuous time Markov branching model with random environments. Adv. Appl. Prob. 5, 37-54.
- KEIDING, N. and NIELSEN, J.E., 1973. The growth of supercritical branching processes with random environments. Ann. Probability 1, 1065-1067.
- KEIDING, N. and NIELSEN, J.E., 1975. Branching processes with varying and random geometric offspring distributions. J. Appl. Prob. 12 (to appear).
- LEVINS, R., 1969. The effect of random variations of different types on population growth. Proc. Nat. Acad. Sci. 62, 1061-1065.
- LEWONTIN, R.C., and COHEN, D., 1969. On population growth in a randomly varying environment. Proc. Nat. Acad. Sci. 62, 1056-1060.
- MAY, R.M., 1973. "Stability and complexity in model ecosystems," Princeton University Press.

- MOUNTFORD, M.D., 1971. Population survival in a variable environment. J. Theor. Biol. 32, 75-79.
- MOUNTFORD, M.D., 1973. The significance of clutch-size. In: The mathematical theory of the dynamics of biological populations (M.S. Bartlett and R.W. Hiorns, ed.) London: Academic Press, 315-323.
- PROHOROV, Yu.V. and ROZANOV, Yu.A., 1969. "Probability theory." Berlin: Springer.
- SMITH, W.L. and WILKINSON, W.E., 1969. On branching processes in random environments. Ann. Math. Statist. 40, 814-827.
- TUCKWELL, H.C., 1974. A study of some diffusion models of population growth. Theor. Pop. Biol. 5 (to appear).
- WILKINSON, W.E., 1969. On calculating extinction probabilities for branching processes in random environments. J. Appl. Prob. 6, 478-492.