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INTRODUCTION TO BRANCHING PROCESSES

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Structures with a branched form are very prevalent in a huge variety of organisms (Thompson, 1971). Theoretical studies of branching forms have been made for aquatic invertebrates (Cheetham, et al., 1980), trees (Honda, 1971; Leopold, 1971), lungs (Horsfield, 1980), rhizomes and stolons of plants (Bell et al., 1979), and plant stems from a phyllotaxis view (Jean, 1978). At a very different level, the phyllogenies of various taxonomic groups are branched structures, and in cladistics, models of this branched form have been constructed (Raup & Gould, 1974). Essentially all of the work on branched forms has been of a deterministic nature, with simulation models constructed to mimic such attributes, as number of branches, interbranch lengths, and branching ratios. See Bell et al. (1979) for a review of such models. There has been no real attempt to to analyze branching structures through the use of stochastic branching processes, though the framework of these processes would seem to underly the branching patterns observed. In fact, branching processes had their origin in the demographic study of the extinction of family names and their main utility in biological theories to date has been on questions of population growth. It is my opinion that a variety of problems regarding organism growth forms have the potential to be fruitfully attacked through the use of branching processes.

My aim here is to give a brief summary of some basic results of the theory of branching processes, mainly following Karlin & Taylor (1975). A number of excellent books have been written on this subject, the most comprehensive coverage being in Harris (1963) and Athreya & Ney (1972). For an excellent introduction see Karlin & Taylor (1975). Jagers (1975) gives a fine history of the theory along with applications to demography and cell kinetics. Much of the current interest in branching processes deals with random environments, which I briefly discuss at the end of this lecture.

Discrete Time Branching Processes

Suppose individuals in a population all act independently of each other and can reproduce regularly at fixed time intervals. If all individuals in the population are the same age, then the population size is given by the random variable X_n, representing the number of individuals alive at generation n. Each individual gives rise to k offspring with probability p_k, $k=0,1,2,\ldots$ and $\{p_k\}$ will be refered to as the offspring distribution. Assume the population starts with one individual, $X_0=1$, and then

$$X_{n+1} = \sum_{j=1}^{X_n} \eta_j \qquad (1)$$

where η_j are independent, identically distributed random variables with $P[\eta_j = k] = p_k$, $k=0,1,2,\ldots$, $\sum_{k=0}^{\infty} p_k = 1$. The branching process $\{X_n\}$, often called the Galton-Watson process, is a Markov chain since the distribution of X_{n+1} depends only on X_n, not on X_i for $i<n$. This model may be applied to investigate the number of descendents of a given family after many generations, or the survival of a mutant gene in a population.

Much of the analysis of this process utilizes the probability generating function

$$\varphi(s) = E[s^\eta] = \sum_{k=0}^{\infty} p_k s^k \qquad (2)$$

$$\varphi_n(s) = E[s^{X_n}] = \sum_{k=0}^{\infty} P[X_n=k]\, s^k \qquad n=0,1,2\cdots$$

where $\varphi_0(s) \equiv s$ and $\varphi_1(s) = \varphi(s)$. Making use of the fact that $\eta_1+\eta_2+\cdots+\eta_j$ has generating function $(\varphi(s))^j$ for $j=1,2,\ldots$ and by conditioning on the value of X_n, one gets

$$\begin{aligned}\varphi_{n+1}(s) &= \sum_{k=0}^{\infty}\sum_{j=0}^{\infty} P[X_{n+1}=k \mid X_n=j]\, s^k\, P[X_n=j] \\ &= \sum_{j=0}^{\infty} P[X_n=j] \sum_{k=0}^{\infty} P[\eta_1+\cdots+\eta_j=k]\, s^k \\ &= \sum_{j=0}^{\infty} P[X_n=j]\,(\varphi(s))^j = \varphi_n(\varphi(s)) \, . \qquad (3)\end{aligned}$$

By iterating and applying induction to (3), it follows that

$$\varphi_{n+1}(s) = \varphi_{n-k}(\varphi_{k+1}(s)) \qquad k=0,1,\ldots,n \qquad (4)$$

Under the assumption that $m = E[\eta_1] < \infty$ and

$\sigma^2 = \mathrm{Var}[\eta_1] = E[(\eta_1 - m)^2] < \infty$, it is possible to compute $E[X_n]$ and $\mathrm{Var}[X_n]$. By differentiating (3) at $s=1$, one gets

$$E[X_{n+1}] = \varphi_{n+1}'(1) = \varphi'(1)\,\varphi_n'(1) = (\varphi'(1))^2\,\varphi_{n-1}'(1)$$
$$= \cdots = (\varphi'(1))^{n+1} = m^{n+1}. \qquad (5)$$

It is also easy to show that

$$\mathrm{Var}[X_n] = \begin{cases} \sigma^2 m^{n-1} \dfrac{m^n - 1}{m-1} & , \text{if } m \neq 1 \\ n\sigma^2 & , \text{if } m = 1 \end{cases} \qquad (6)$$

Thus the mean population size either grows or decays geometrically depending upon the mean of the offspring distribution, and the variance increases if $m > 1$ and decreases if $m < 1$. If the initial population size $X_0 > 1$, similar results to the above can be derived with the exception that (4) doesn't hold.

One of the most frequently investigated aspects of branching processes are their extinction probabilities, i.e. $q_n = P[X_n = 0] = \varphi_n(0)$. By (4) above,

$$q_{n+1} = \varphi_{n+1}(0) = \varphi(\varphi_n(0)) = \varphi(q_n) \qquad (7)$$

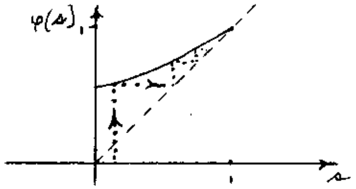
and letting $n \to \infty$ and using the fact that $\varphi(\cdot)$ is continuous, one sees that $\rho = \lim_{n\to\infty} q_n$ = probability of eventual extinction, satisfies

$$\rho = \varphi(\rho) = \sum_{j=0}^{\infty} p_j \rho^j \qquad (8)$$

This follows intuitively since for extinction to occur, all the families founded by the offspring of the single ancestor must themselves go extinct. If there are j offspring of the founder (which occurs with probability p_j) then due to the independence of individuals, the probability that all the families of these offspring eventually go extinct is ρ^j. There are two cases for the extinction probability:

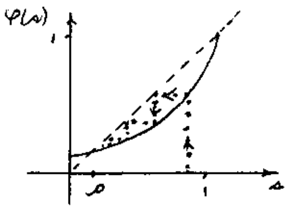
(a)

$m = \varphi'(1) \leq 1$



(b)

$m = \varphi'(1) > 1$



In case (a), the mean number of offspring is less than or equal to one, and the iterates in (7) approach $\rho = 1$, so ultimate extinction occurs with probability one. In case (b), the mean number of offspring is greater than one, and the iterates of (7) approach a value $0 < \rho < 1$, independent of $q_1 = p_0$. Thus in case (b), extinction doesn't occur with certainty.

From the above figures it is clear that in both cases

$$\lim_{n\to\infty} \varphi_n(s) = \rho \qquad \text{for } 0 \leq s \leq 1 \qquad (9)$$

Since $\varphi_n(s)$ is a power series which converges as $n \to \infty$ to a constant independent of s, this implies that $\lim_{n\to\infty} P[X_n = 0] = \rho$ and $\lim_{n\to\infty} P[X_n = j] = 0$ for all $j \neq 0$. When $m > 1$, so that $\rho < 1$, this says that the probability the population approaches any finite size as $n \to \infty$ is zero, so $X_n \to \infty$ with probability $1 - \rho$. To investigate the asymptotic behavior of X_n, let $S_n = \dfrac{X_n}{m^n}$. Then since

$$E[X_{n+1} \mid X_n, X_{n-1}, \ldots, X_0] = E[X_{n+1} \mid X_n] = m X_n$$

one has $E[S_{n+1} \mid S_n] = S_n$, so $\{S_n\}$ is a martingale. If $\sigma^2 < \infty$, then from (6)

$$E[S_n^2] < \frac{\sigma^2 - m + m^2}{m(m-1)} < \infty \quad \text{for } m \neq 1 \qquad (10)$$

and thus $\{S_n\}$ is a mean-square bounded martingale, and the martingale convergence theorem (Feller, 1966, Page 236) guarantees that S_n converges with probability one to a random variable S_∞. Thus if $m > 1$, conditioned on non-extinction, the population grows geometrically, i.e. a fraction ρ of populations go extinct and a fraction $1 - \rho$ grow geometrically. A similar result may be obtained for the case $m = 1$, in which the population goes to extinction with probability one, but conditioned on non-extinction, the population grows. (Ludwig, 1974, Page 28).

Multi-type Branching Processes

In the above, the population consisted of only one type of individual, and this is now extended to the case of several different types in the population. This allows the structure of the population, in terms of age or size classes, or mutant genotypes, to be investigated. It is assumed that individuals still act independently and may give rise to offspring of any type. For simplicity, I here deal with only two types, though the extension to more types is straightforward. For a complete overview of multi-type branching, see Mode (1971).

Let X_n and Y_n be the number of type 1 and type 2 individuals at time n respectively. Then

$$\begin{aligned} X_{n+1} &= \sum_{j=1}^{X_n} \eta_j^{(1)} + \sum_{j=1}^{Y_n} \eta_j^{(2)} \\ Y_{n+1} &= \sum_{j=1}^{X_n} \xi_j^{(1)} + \sum_{j=1}^{Y_n} \xi_j^{(2)} \end{aligned} \qquad (11)$$

where $(\eta_j^{(i)}, \xi_j^{(i)})$, $i=1,2$, are independent, identically distributed random vectors with distribution

$$p_i(k,l) = P[\eta_j^{(i)} = k,\ \xi_j^{(i)} = l] \qquad \begin{array}{l} i=1,2 \\ k,l = 0,1,2,\dots \\ j=1,2,\dots \end{array}$$

So $p_i(k,l)$ is the probability an individual of type i produces k offspring of type 1 and l offspring of type 2. Analogous to the generating function (2) is the pair of functions

$$\varphi^{(i)}(s,t) = \sum_{k,l=0}^{\infty} p_i(k,l)\, s^k t^l, \quad i=1,2 \qquad (12)$$

Here, the i^{th} case gives the generating function for the offspring of a single individual of type i, and defining

$$\varphi_0^{(1)}(s,t) = s,\quad \varphi_0^{(2)}(s,t) = t,$$

$$\varphi_1^{(i)}(s,t) = \varphi^{(i)}(s,t) \qquad i=1,2$$

it is easily seen that

$$\varphi_{n+m}^{(i)}(s,t) = \varphi_m^{(i)}\left(\varphi_n^{(1)}(s,t),\ \varphi_n^{(2)}(s,t)\right) \qquad (13)$$

$$\text{for } i=1,2, \quad n,m = 0,1,2,\dots$$

which is analogous to (4).

Letting $m_{11} = E[\eta^{(1)}]$, $m_{12} = E[\xi^{(1)}]$, $m_{21} = E[\eta^{(2)}]$, $m_{22} = E[\xi^{(2)}]$ and $\overline{M} = \begin{pmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{pmatrix}$ be the matrix of these expectations, then if $\vec{Z}_n = (X_n, Y_n)$,

$$E[\vec{Z}_{n+r} \mid \vec{Z}_n] = (X_n, Y_n)\,\overline{M}^r = \vec{Z}_n \cdot \overline{M}^r \qquad (14)$$

$$r = 0,1,2,\dots$$

This is analogous to the geometric growth condition for a single-type process in (5). For extinction probabilities, let

$$\rho^{(1)} = P[X_n = Y_n = 0 \text{ for some } n \mid X_0 = 1,\ Y_0 = 0]$$

$$\rho^{(2)} = P[X_n = Y_n = 0 \text{ for some } n \mid X_0 = 0,\ Y_0 = 1]$$

and $\vec{\rho} = (\rho^{(1)}, \rho^{(2)})$. Following Karlin and Taylor (1975, page 407), let

$$\vec{u} = (s,t),\quad \vec{\varphi}(\vec{u}) = (\varphi^{(1)}(s,t),\ \varphi^{(2)}(s,t))$$

$$\vec{\varphi}_n(\vec{u}) = (\varphi_n^{(1)}(s,t),\ \varphi_n^{(2)}(s,t)) \text{ and } \vec{1} = (1,1).$$

The Frobenius theory of non-negative matrices guarantees that if all $m_{ij} > 0$, the largest magnitude eigenvalue of $\overline{M}$ is real and positive. Call this eigenvalue λ. Under these conditions, the following Theorem holds: If the components of $\vec{\varphi}(\vec{u})$ are not linear functions of s and t, then $\vec{\rho} = \vec{1}$ if $\lambda \le 1$, and $\rho^{(i)} < 1$, $i=1,2$, if $\lambda > 1$. When $\lambda > 1$, $\vec{\rho}$ is the smallest non-negative solution of $\vec{u} = \vec{\varphi}(\vec{u})$. Thus the extinction probabilities are fixed points of the 2-dimensional generating function analogous to (8). Also it is possible to show that, similar to (9), if $\vec{q}$ is any vector in the unit square, $\vec{q} \ne \vec{1}$, then $\lim_{n\to\infty} \vec{\varphi}_n(\vec{q}) = \vec{\rho}$ if the conditions of the above theorem hold

Continuous-time Branching Processes

The above processes all have fixed generation times at which every individual in the population produces offspring. A more general analysis allows individuals to reproduce at any time, not necessarily in synchrony with the rest of the population. Again, it is assumed that all individuals act independently of each other, and thus there is no density-dependance in this case. Let X_t be the number of individuals present at time t, $t \geq 0$. There are basically two alternative derivations of a continuous-time branching process. In one of these, the infinitesimal transition probabilities of the process are specified as:

$$P[X_{t+h} = k \mid X_t = 1] = a_k h + o(h) \quad k = 0, 2, 3, \ldots$$
$$P[X_{t+h} = 1 \mid X_t = 1] = 1 + a_1 h + o(h) \quad \text{as } h \to 0^+ \qquad (15)$$

where $a_1 \leq 0$, $a_k \geq 0$ for $k = 0, 2, 3, \ldots$ and $\sum_{k=0}^{\infty} a_k = 0$.

Since the a_k's do not depend on the time t, the process is a Markov process with stationary transition probabilities. The independence of individuals assumption and (15) lead to

$$P[X_{t+h} = n+k-1 \mid X_t = n] = a_k n h + o(h) \quad k = 0, 2, 3, \ldots \qquad (16)$$
$$P[X_{t+h} = n \mid X_t = n] = 1 + n a_1 h + o(h) \quad \text{as } h \to 0^+$$

since in small time intervals h, at most one particle on average will split. Here $\frac{o(h)}{h} \to 0$ as $h \to 0^+$.

A second view towards defining the above process may be taken by supposing that each individual lives for a random time, then produces offspring according to a certain distribution function. The lifetime of each individual is exponentially distributed, with mean

$$\frac{1}{\lambda} = a_0 + a_2 + a_3 + \cdots \qquad (17)$$

The exponential lifetime distribution guarantees that the process is Markov, and although more general lifetime distributions may be considered, the analysis becomes more difficult (Karlin and Taylor, 1975, page 431). The number of offspring produced, D, at the end of a lifespan follows

$$P[D = k] = \frac{a_k}{a_0 + a_2 + a_3 + \cdots} \quad k = 0, 2, 3, \ldots \qquad (18)$$

in order to agree with (15). It should be noted at this point that the actual construction of a process with infinitesimal transitions given by (16) involves certain difficulties I do not consider. The reader should consult Harris (1963) for details. I here assume that the transition function

$$P_{ij}(t) = P[X_{t+s} = j \mid X_s = i]$$

is well-defined. Note that this process is essentially an extension of birth and death processes to the case which allows an individual to give birth to any number of offspring.

Define the generating functions

$$\varphi(t,s) = \sum_{j=0}^{\infty} P_{1j}(t)\, s^j$$
$$u(s) = \sum_{k=0}^{\infty} a_k s^k. \qquad (19)$$

Since individuals act independently

$$\sum_{j=0}^{\infty} P_{ij}(t)\, s^j = (\varphi(t,s))^i \qquad (20)$$

and making use of the Chapman-Kolmogorov equation for $h > 0$,

$$P_{ij}(t+h) = \sum_{k=0}^{\infty} P_{ik}(t)\, P_{kj}(h)$$

with a bit of rearrangement in (20), one gets

$$(\varphi(t+h,s))^i = [\varphi(t, \varphi(h,s))]^i$$

or for $i = 1$,

$$\varphi(t+h,s) = \varphi(t, \varphi(h,s)). \qquad (21)$$

This is analogous to (3) from the discrete case. Now for h small, formally

$$\varphi(h,s) = \sum_{j=0}^{\infty} P_{1j}(h)\, s^j = s + h u(s) + o(h) \qquad (22)$$

by the use of (15). Thus

$$\varphi(t+h,s) = \varphi(t, s + h u(s) + o(h)) \qquad (23)$$

and expanding in a Taylor's series in the second variable, dividing by h, and taking limits, one gets

$$\frac{\partial \varphi(t,s)}{\partial t} = \frac{\partial \varphi(t,s)}{\partial s}\, u(s) \qquad (24)$$

with initial condition

$$\varphi(0,s) = \sum_{j=0}^{\infty} P_{1j}(0)\, s^j = s. \qquad (25)$$

This is essentially a forward Kolmogorov equation, and a backwards equation may also be derived using (21) and (22):

$$\frac{\partial \varphi(t,s)}{\partial t} = u(\varphi(t,s)) \tag{26}$$

which is an ordinary differential equation with initial condition (25).

Using (24), (25), and (26) it is possible to derive several results about the behavior of the process. By differentiating (24) with respect to s at $s=1$, one gets

$$E[X_t] = e^{u'(1)t}$$

so the mean population size grows or decays exponentially depending upon the sign of $u'(1)$. The extinction probability

$$\rho = \lim_{t \to \infty} P_{10}(t)$$

may be found by observing X_t at periodic fixed times, generating a discrete-time branching process which is analyzed as described earlier. The result is that ρ is the smallest non-negative root of $u(s) = 0$ and $\rho = 1$ if and only if $u'(1) \le 0$. An analysis of (26) allows the long-term distribution of the process, conditioned on non-extinction, to be derived (Karlin and Taylor, 1975, Page 423).

An Example with Immigration

Consider a bacteria colony growing according to the above continuous-time branching process. Suppose bacteria also immigrate into the colony, after which they reproduce in the same independent manner, with the same offspring distribution, as previous members of the colony. If immigrants arrive at times $0 \le t_1 \le t_2 \le t_3 \le \cdots \le t_N$, then the generating function at time t for the family derived from the j^{th} immigrant is $\varphi(t-t_j, s)$, $j = 1, 2, \ldots, N$. Due to independence, the total population size at time t has generating function

$$(\varphi(t,s))^{n_0} \prod_{j=1}^{N} \varphi(t-t_j, s) \tag{27}$$

if N immigrants arrive in $[0,t]$, and the initial population size of the colony was n_0. Suppose that immigrations occur at random times according to a Poisson process, so the interarrival times between immigrants is exponentially distributed with parameter β. The generating function for the total population size will be derived.

Let $N(t)$ = number of immigrants arriving in $[0,t]$, which has a Poisson distribution with parameter βt. Let $Y_j(t,t_j)$ be the population size at time t derived from a single immigrant arriving at t_j, and define

$$Y_t = \sum_{j=1}^{N(t)} Y_j(t,t_j) \tag{28}$$

which is the population at time t derived totally from immigrants and their descendants. Now using the fact that the joint distribution of arrival times of a Poisson process, conditioned on the number of arrivals, is that of the order statistics, one gets

$$\begin{aligned}
E[s^{Y_t}] &= \sum_{k=0}^{\infty} E[s^{Y_t} \mid N(t) = k]\, P[N(t) = k] \\
&= \sum_{k=0}^{\infty} \frac{k!}{t^k} \int_0^t dt_1 \int_{t_1}^t dt_2 \cdots \int_{t_{k-1}}^t dt_k \, E\left[s^{\sum_{j=1}^{k} Y_j(t,t_j)}\right] e^{-\beta t} \frac{(\beta t)^k}{k!} \\
&= \sum_{k=0}^{\infty} \frac{1}{t^k} \int_0^t dt_1 \int_0^t dt_2 \cdots \int_0^t dt_k \left(\prod_{j=1}^{k} E\left[s^{Y_j(t,t_j)}\right] \right) e^{-\beta t} \frac{(\beta t)^k}{k!} \\
&= \sum_{k=0}^{\infty} \frac{1}{t^k} \left(\prod_{j=1}^{k} \int_0^t \varphi(t-t_j, s)\, dt_j \right) e^{-\beta t} \frac{(\beta t)^k}{k!} \\
&= \sum_{k=0}^{\infty} \left(\beta \int_0^t \varphi(t-\tau, s)\, d\tau \right)^k \frac{1}{k!} e^{-\beta t} \\
&= \exp\left\{ \beta \int_0^t [\varphi(t-\tau, s) + 1]\, d\tau \right\}
\end{aligned} \tag{29}$$

So from (27), the generating function for total population size is

$$g(s,t) = (\varphi(t,s))^{n_0} \exp\left\{ \beta \int_0^t [\varphi(t-\tau, s) - 1]\, d\tau \right\} \tag{30}$$

From this it is possible to compute all moments of the population size.

Environmental Variation

The above models are all extensions of simple deterministic exponential growth models to situations with finite population sizes. The stochastic aspects enter strictly due to the potential sampling effects of finite populations, so called demographic stochasticity. The mean populations always grow or decay exponentially, and the additional element introduced is the potential for extinction to occur. An alternative manner in which stochastic elements come into play in population models is when the environment is viewed as randomly varying. These random environment models involve situations in which growth rates are stochastic processes which are influenced by an unpredictable environment. See for example Ricciardi (1977) and Turelli (1978). The majority of work on random environment models has been an application of the diffusion processes which result from adding noise to a deterministic population growth model. I here give a brief introduction to an alternative approach, that of branching processes in random environments, following Keiding (1975).

Consider first a discrete time branching process in a periodically varying environment such that the offspring distributions vary periodically in successive generations with means $m_1, m_2, \ldots, m_k, m_1, m_2, \ldots, m_k, m_1, \ldots$ If the branching process is X_n, define $Z_n = X_{nk}$, $n = 0, 1, 2, \ldots$, and then Z_n is itself a branching process with generating function of the offspring distribution

$$\phi(s) = \varphi_k(\varphi_{k-1}(\cdots \varphi_1(s)\cdots)) \qquad (31)$$

where $\varphi_i(\cdot)$ is the offspring generating function for the i^{th} year of the periodic cycle. Thus, from our above results, the extinction probability of the Z_n process

$$\rho = P[Z_n = 0 \text{ for some } n]$$

depends upon the mean of the offspring distribution, which is

$$\phi'(1) = \varphi_k'(1)\, \varphi_{k-1}'(1) \cdots \varphi_1'(1) = m_1 m_2 \cdots m_k .$$

So $\rho = 1$ if and only if $m_1 m_2 \cdots m_k \le 1$ or equivalently

$$\frac{1}{k} \sum_{i=1}^{k} \log m_i \le 0 . \qquad (32)$$

Similarly, if $\frac{1}{k} \sum_{i=1}^{k} \log m_i > 0$, $\rho < 1$ and Z_n is asymptotically distributed as $(m_1 m_2 \cdots m_k)^n W$ where W is a random variable with $P[W = 0] = \rho$. So the behavior in a periodic environment depends upon the product of the means, or the geometric mean, of the offspring distributions.

As another example, consider the deterministic growth in a random environment model investigated by Lewontin & Cohen (1969). Here the population grows multiplicatively with population size at generation t given by

$$N_t = l_1 l_2 \cdots l_t N_0 \qquad (33)$$

where the l_i's are independent, identically distributed non-negative random variables with mean λ and variance σ^2, and $P[l_i = 0] = 0$. The environment is thus stationary, unlike the periodic case above, and there is no real demographic stochasticity in this model since no sampling phenomena are considered. Note that

$$E[N_t] = N_0 E[l_1 l_2 \cdots l_t] = N_0 \lambda^t \qquad (34)$$

so the population grows or decays exponentially in expectation depending only upon the mean offspring produced per individual each generation.

Now for any $K_1 < K_2$

$$\begin{aligned} P[K_1 \le N_t < K_2] &= P[\ln K_1 \le \ln N_t < \ln K_2] \\ &= P\Big[\ln K_1 \le \ln N_0 + \sum_{i=1}^{t} \ln l_i < \ln K_2\Big] \\ &= P\Big[\tfrac{1}{t} \ln\Big(\tfrac{K_1}{N_0}\Big) \le \tfrac{1}{t} \sum_{i=1}^{t} \ln l_i < \tfrac{1}{t} \ln\Big(\tfrac{K_2}{N_0}\Big)\Big] \end{aligned} \qquad (35)$$

But $\ln l_i$ are independent, identically distributed with mean $\mu = E[\ln l_i]$ and variances $\xi^2 = Var(l_i)$, so by the Central Limit theorem, for t large

$$P[K_1 \le N_t < K_2] \approx P\left[\frac{\frac{1}{t}\ln\left(\frac{K_1}{N_0}\right) - \mu}{\xi/\sqrt{t}} \le Z < \frac{\frac{1}{t}\ln\left(\frac{K_2}{N_0}\right) - \mu}{\xi/\sqrt{t}}\right] \qquad (36)$$

where Z is a standard normal random variate. If $\mu < 0$, as $t \to \infty$ the right hand endpoint in (36) grows without bound for any positive K_1, and thus with probability one the population size goes to zero. If $\mu > 0$, as $t \to \infty$ in (36) it is clear that with probability one the population grows without bound. Thus the probability the population goes to extinction or grows without depends upon $\mu = E[\ln l_i]$, while the expected population size $E[N_t]$ depends upon $\lambda = E[l_i]$. By Jensen's inequality

$$\mu = E[\ln l_i] \le \ln E[l_i] = \ln \lambda$$

which says that the geometric mean e^{μ} is always less than the arithmetic mean λ. Thus situations can arise in which the geometric mean growth rate is less than one ($\mu < 0$), so the population goes to extinction with probability one, while the arithmetic mean growth rate is greater than one,

$\alpha > 1$), and so the expected population size grows without bound. This illustrates the care which must be used in stochastic models — expected population sizes may be meaningless for determining the behavior of the majority of populations.

Branching Processes in Random Environments (BPRE)

In the earlier discussion of branching processes, the offspring distributions were fixed and unvarying. It is possible to relax this assumption by considering a sequence of random variables $\xi = (\xi_0, \xi_1, \ldots)$, representing environments in various generations, such that the offspring distribution in generation i is a function of ξ_i, $p_i(\xi_i)$. Although individuals in the i^{th} generation produce offspring independantly according to the distribution $p_i(\xi_i)$, their reproductive output is no longer stochastically independent, being correlated due to the common environmental value ξ_i. This process, a BPRE, was described by Smith & Wilkinson (1969), and extensively analyzed in Athreya & Karlin (1971 a, b). With restrictions on the environmental sequence ξ, it is possible to derive conditions for extinction and non-extinction, determine the behavior of the mean, and establish the limit distributions in cases when the population doesn't go extinct.

The above model of Lewontin & Cohen (1969) is a special case of a BPRE with similar results concerning the differences in population behavior induced by geometric versus arithmetic mean growth rates as those in more general models (Keiding, 1975). Keiding (1975) uses a diffusion process approximation of a BPRE to compare the relative effects of environmental and sampling variations on populations with large sizes. Goettge (1975) derives some further limit theorems for BPRE, given non-extinction, utilizing martingale theory. Agresti (1975) derives bounds on extinction times of a BPRE in which the environments ξ_i are assumed independent, but not necessarily identically distributed.

Essentially all of the processes discussed above are density independent, since the offspring distributions do not vary with population size. Thus, populations tend to either grow exponentially or go to extinction. The majority of work to date on density dependent stochastic population models has been through the analysis of stochastic differential equation analogs of deterministic ordinary differential equation growth models (Feldman & Roughgarden, 1975; Turelli, 1978). Alternatively some work has been done on BPRE models in which the offspring distributions in generation n are conditioned on the population size then, e.g.

$$P[\eta = k \mid X_n = z] = p_k(z)$$

is used as the offspring distribution for the n^{th} generation (Lipow, 1977; Tier & Hanson, 1981). The analysis makes use of rescalings of time and population size to produce a diffusion approximation. The results are generalizations of many of the diffusion process solutions of stochastic differential equation models, and allow such questions as the persistence, or time to extinction, of the populations to be analyzed (Tier & Hanson, 1981).

An alternative method to introduce random environments in a branching process model is used by Kaplan et. al. (1975). They consider a continuous-time branching process with disasters, meaning that at random times, a phenomenon occurs (earthquake, epidemic, radiation, etc.) which kills a certain fraction of the population. The disasters are assumed to occur according to a renewal process, and conditions may be derived under which eventual extinction occurs with certainty.

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