

Population Size Dependent, Age Structured Branching Processes Linger around their Carrying Capacity

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New Frontiers in Applied Probability

Branching Processes – and Søren

- Long before queuing Søren, simulating Søren, ruin Søren – there was **Branching Søren!**
 1. Convergence rates for branching processes. Ann. Probab. 4, 139-146 (1976).
 2. (with N. Kaplan) Branching random walks I. Stoch. Proc. Appl. 4, 1-13 (1976).
 3. (with N. Kaplan) Branching random walks II. Stoch. Proc. Appl. 4, 15-31 (1976).
 4. (with H. Hering) Strong limit theorems for general supercritical branching processes.....
.....
 12. On some two-sex population models. Ann. Probab. 8, 727-744 (1980).
 13. (with H. Hering) Branching Processes. Birkhäuser, Boston Basel Stuttgart (1983).
- Like queuing etc, branching makes extensive use of regeneration properties, and thus Markov Renewal Theory.
- Unlike it, branching deals with (natural) science.

Branching processes – from a population theoretic viewpoint

- Unlike deterministic theory, branching processes can handle finite populations of individuals with varying behaviour.
- Closed real populations change at the initiative of members.
- Independence is a natural but (too) far-reaching idealisation of this.

Independence leads to:

- The Malthusian dichotomy between extinction and exponential growth.
- The probability of extinction can be determined,
- as well as the rate of growth.
- During exponential growth the population composition – from age distribution to pedigree - stabilises.

What if the independence requirement is relaxed?

- Deterministic theories with a feedback loop individual \rightarrow population \rightarrow environment \rightarrow individual can create stable populations asymptotically.
- But no reasonable finite stochastic population models (even with environmental feedback) can stabilise; very weak Markovianness suffices to yield the explosion-or-extinction dichotomy. So, what are the stabilities we seem to observe?

The New Frontier: Carrying Capacity

- What can be obtained if the basic ecological concept of a carrying capacity is introduced?
- Assume that there is a (large) number K such that the population is supercritical, when the population is $< K$ and subcritical, otherwise – whatever that means....
- Background:
 - Age- and size-dependent general branching (PJ & FK, SPA 2000). Earlier papers by Kersting and FK. Explanation of linear growth in PCR (PJ & FK, JTB 224, 2003)
 - Sylvie Méléard and the French school, notably Tran, ESAIM (2008): age-dependent birth-and-death, with the death rate population dependent.
- Similar ideas in queuing?

What is the basic pattern? A toy example.

- Z_n = population size at time (generation) n ,
- ξ = offspring random variable, = 0 or 2.
- K = carrying capacity.
- $P(\xi = 2 \mid Z_1, Z_2, \dots, Z_n) = K/(K + Z_n)$. (Like PCR.)
- The probability of splitting is $> \frac{1}{2}$ if Z_n is small
– reproduction is supercritical – and it is $< \frac{1}{2}$,
if $Z_n > K$ –subcritical.
- Such a population must die out.
- Will it ever take off? (Come close to K ?)
- And then, will it stay there (long)?

If the starting number $Z_0 = z$, $T =$ time to extinction, and $T_d =$ time to reaching size dK , $0 < d < 1$, then $P(T < T_d) \leq d^z$.

- Easy to see: at any size $k < dK$, the probability of no children $= k/(K+k) < dK/(K+dK) = d/(1+d)$.
- Hence the probability of dying out without crossing dK must be smaller than the same probability for binary G-W $\{Y_n\}$ with $P(\xi=0) = d/(1+d)$. But $P_z(Y_n = 0 \text{ before } dK) \leq P_z(Y_n \rightarrow 0) = q^z$.
- And $q = d/(d+1) + (1/(d+1))q^2$, yielding $q = d$.

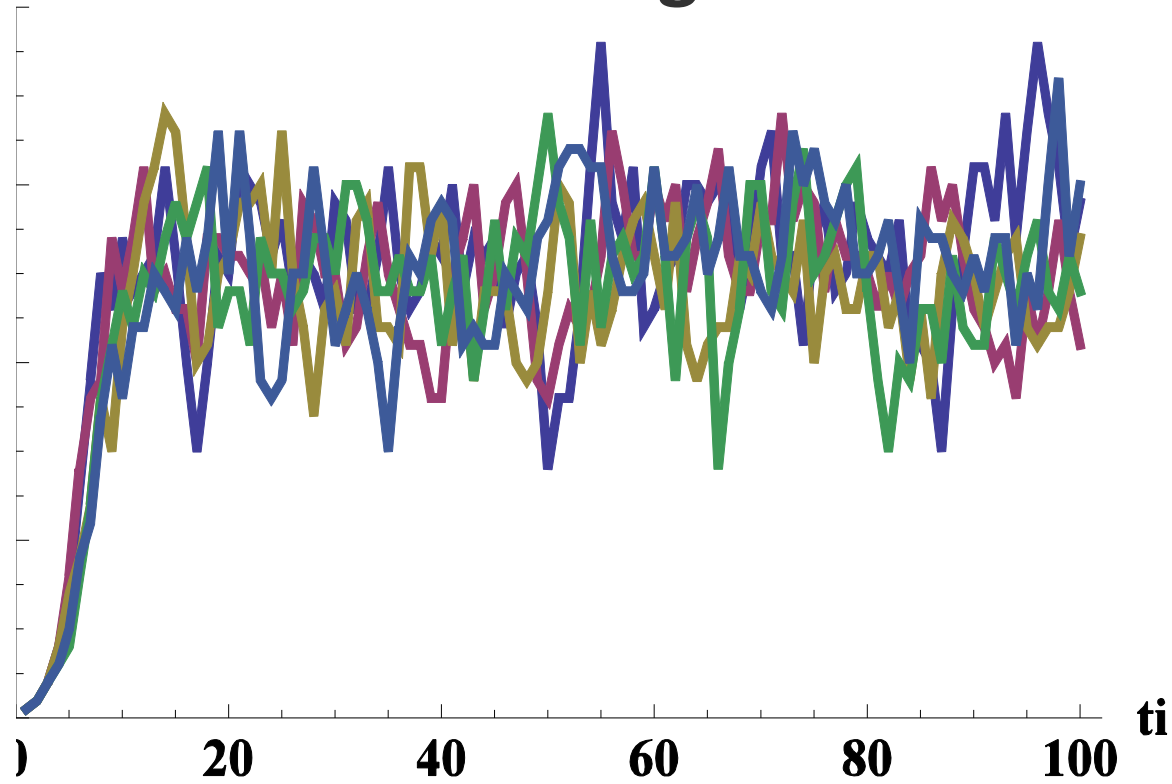
Similarly: $T_d = O(\log K)$

- $Z_n \geq Y_n$ on $\{T_d \geq n\}$.
- Hence, $dK \approx Z_{T_d} \geq Y_{T_d} \approx W(2/(1+d))^{T_d}$ and
- $T_d = O(\log K)$.
- Further, $E[T_1] \leq CK$ for some C (Vatutin, to appear).

Lingering around K

- And once in a band around K , it stays there for a long time, of the order e^{cK} for some $c > 0$, with a probability that $\rightarrow 1$, as $K \rightarrow \infty$ (Large Deviation Theory).
- This example is much more elementary – large deviations for binomial r. v., (Janson) and c can be calculated,
- $c = d(1-d)^2 / 8(1+d)$.
- Actually, for any K , the expected time to leaving a band $(1 \pm d)K$ is $\geq e^{cK}$.
- FK, Sagitov, Vatutin, PJ and Haccou: J. Biol. Dyn. March 2011.

And this is what things look like



K=50, and not one direct extinction among 10 simulations.

Is this behaviour general?

- Birth during life, and/or split at death, after a life span with an arbitrary distribution, all dependent upon population size, in this way:
- If the age structure is $A=(a_1, a_2, \dots, a_z)$, the birth rate of an a -aged individual is $b_A(a)$ and the death rate is $h_A(a)$.
- Litter size then is 1 (for simplicity).
- At death ξ (bounded) children are produced . The distribution may depend on mother's age at death and on A . Expectation and variance: $m_A(a)$, $v_A(a) < \infty$.
- **Population size dependence:** $b_A=b_z$, $h_A=h_z$, etc.

Markovianness

- The process is **Markovian in the age structure**, A_t = the array of ages at t , $Z_t = (1, A_t)$, $(f, A) = \sum f(a_i)$, $A = (a_1, \dots, a_z)$.
- $L_z f = f' - h_z f + f(0)(b_z + h_z m_z)$
 - $f'(a)$ reflects linear growth in age.
 - $h_z(a)$ the risk of disappearing,
 - $b_z(a)$ the birth intensity, resulting on a 0-aged individual, and
 - $h_z(a)m_z(a)$ is the splitting intensity.
- Dynkin's formula: For $f \in C^1$,
- $(f, A_t) = (f, A_0) + \int_0^t (L_{Z(s)} f, A_s) ds + M_t^f$, where $Z(s) = Z_s$ and M_t^f is a local square integrable martingale (PJ & FK 2000)
- In particular,
- $Z_t = (1, A_t) = Z_0 + \int_0^t (b_{Z(s)} + h_{Z(s)}(m_{Z(s)} - 1), A_s) ds + M_t^f$.

Growth

- $Z_t = Z_0 + \int_0^t (b_{Z(s)} + h_{Z(s)}(m_{Z(s)} - 1), A_s) ds + M_t^f$
means that there is a growth trend at t iff
- $(b_{Z(t)} + h_{Z(t)}(m_{Z(t)} - 1), A_t) > 0$.
- The most natural criticality concept is thus **criticality in the age distribution**:
- $(b_{Z(t)} + h_{Z(t)}(m_{Z(t)} - 1), A_t) = 0$.
- A stronger concept is **strict criticality at population size z** :
- $b_z(a) + h_z(a)(m_z(a) - 1) = 0$ for all a .

Criticality

- Finally, a population can be called **annealed critical** at a size z if the expected number of children during a whole life in a population of that size is $= 1$.
- The three concepts coincide in the Bellman-Harris case, where b_A vanishes and $m_A(a)$ is constant in a .
- We assume strict criticality at K .
- Then it is also annealed critical there and critical in the age distribution.

The risk of direct extinction

- Assume monotonicity in the sense that if $\{Z_t'\}$ and $\{Z_t\}$, are annealed at sizes $z' \leq z$, but start at the same size and age distribution, then $Z_t' \geq Z_t$ in distribution.
- Then, the probability of direct extinction, without reaching dK , $0 < d < 1$, is $\leq q_d^z$, where:
 - $q_d < 1$ is the extinction probability of a supercritical branching process with the fixed reproduction determined by size dK – the annealed extinction probability and
 - z is the starting number.
- The chance of reaching dK is $\geq 1 - q_d^z$, if $Z_0 = z$.
- With m_d and v_d the reproduction mean and variance of the embedded GW-process, annealed at pop size dK , $q_d \leq 1 - 2(m_d - 1) / (v_d + m_d(m_d - 1))$ (Haldane).

And otherwise:

- By the assumed monotonicity in parameters, Z_t grows quicker to dK than does the process annealed there (if it does not die out before).
- Hence, the time to reach the level is $O(\log K)$.
- And once there, we would expect it to remain for a time of order e^{cK} , $K \rightarrow \infty$, for some $c > 0$, by large deviation theory.

What we actually prove

- Introduce the criticality function $\chi_{z/K} = b_z(a) + h_z(a)(m_z(a) - 1)$ and assume it is Lipschitz in the density $x = z/K$ around the carrying capacity, $|\chi_x| < C|x - 1|$. Write $X_t^K = Z_t / K$.
- Then, if $X_0^K \rightarrow 1$, then $X_t^K \rightarrow 1$ uniformly in probability on compacts, as $K \rightarrow \infty$.
- Assume that exponential reproduction moments exist, that the number of children at splitting is bounded (and a technical condition) then, the expected time around K is $O(e^{cK})$.

The age (etc) distribution (under work)

- Write A_s^K for the age structure at time s for fixed K and also normed by K .
- Assume that parameters $b_A^K(a)$, the death rate $h_A^K(a) > c > 0$, and the mean number of children at split, $m_A^K(a)$, all are “smooth enough” and that
- $\sup_K E[|A_0^K|] < \infty$ and $A_0^K \rightarrow$ some A_0 , as $K \rightarrow \infty$.
- Then, as $K \rightarrow \infty$, the random measure function $t \mapsto A_t^K$ converges weakly on any compact to the solution of
- $(f, A_t) = (f, A_0) + \int_0^t (L_{A(s)} f, A_s) ds$, $A(s) = A_s$, $L_A f = f' - h_A f + f(0)(b_A + h_A m_A)$, in terms of parameter limits, as $K \rightarrow \infty$.
- Randomness only in the start, the rest is McKendrick-von Foerster.

What if the population starts small?

- Then $A_0^K \rightarrow 0$.
- But the population size will reach any vicinity dK , $0 < d < 1$, of the carrying capacity in time $O(\log K)$ with positive probability, whereas it will die out only after time $O(e^{cK})$.
- Study the process in an evolutionary time scale K , $\{A_{uK}^K; 0 < u < \infty\}$. Then it stays around K .
- This is the right limit, rather than $\lim_K A_t^K!$

The End.

- The general case is joint work with F. C. Klebaner, Monash, and will appear in the Journal of Applied Probability 48A, 2011.
- The “fluid approximation” is ongoing work with Fima Klebaner and K. Hamza.
- The binary splitting is due to Klebaner, Sagitov, Vatutin, Haccou, and PJ in J. Biol. Dyn. 5, 2011.
- A more mathematical version of the latter is under way, and will also include simple adaptive dynamics (of evolution).