On the Persistence of Populations

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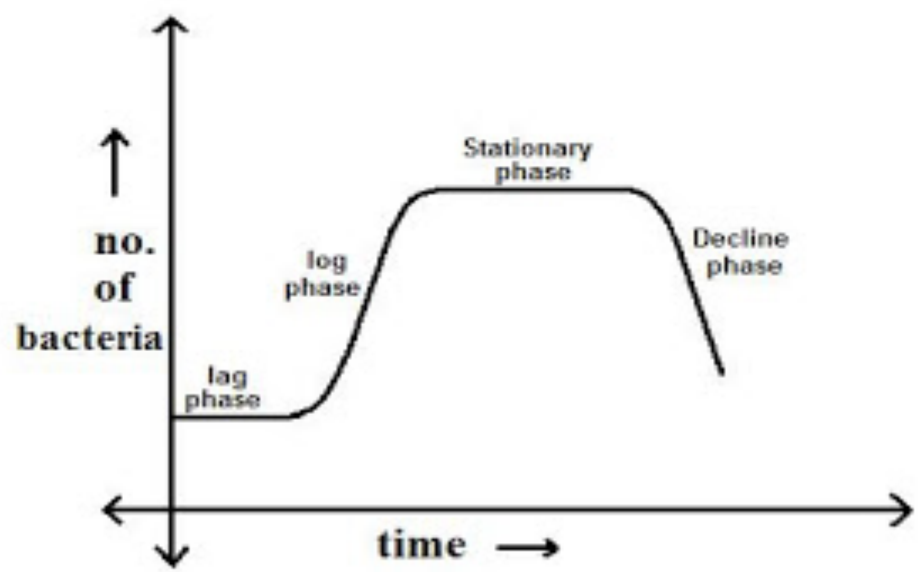
(Joint work with and Fima Klebaner et al.)

We all know what it is like…



The growth curve of bacteria
showing different phases

After some hesitation, we either die out or increase in numbers, until we have filled the eart. We persist, and we die out.

But branching processes teaches

- that a (small) population either dies out or grows exponentially,
- that large ectinction probability does not preclude rapid growth, where it occurs,
- that there may thus well be frequent extinction during growth,
- and that the composition (age-distribution, type-, pedigree…) stabilises during infinite growth.
- But what about (real) populations that either die out or display a long quasi-stationary phase, and then die out?

What's lacking in branching?

- Individual reproduction -> population change -> environment -> individual reproduction.
- Each habitat ("island") has a Carrying Capacity K (for the species) such that reproduction turns subcritical whenever population size $Z_t > K$.
- In discrete time, the meaning is obvious: individuals beget children independently, given generation size z, and the offspring mean m(z) is a decreasing (no cooperation) function of z; m(1) > 1 and m(K) = 1.
- Toy example: $p_2(z)=K/(K+z)$, $p_0=1-p_2$.
- Klebaner, Sagitov, Vatutin, Haccou, and PJ in J. Biol. Dyn. 5, 2011.

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

- At any $k<dK$, $p_0(k) = k/(K+k) < dK/(K+dK) = d/(1+d)$.
- Hence the probability of dying out without crossing dK must be smaller than the same probability for a binary G-W $\{Y_n\}$ with P(no children) = $d/(1+d)$. 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 $q=d$.

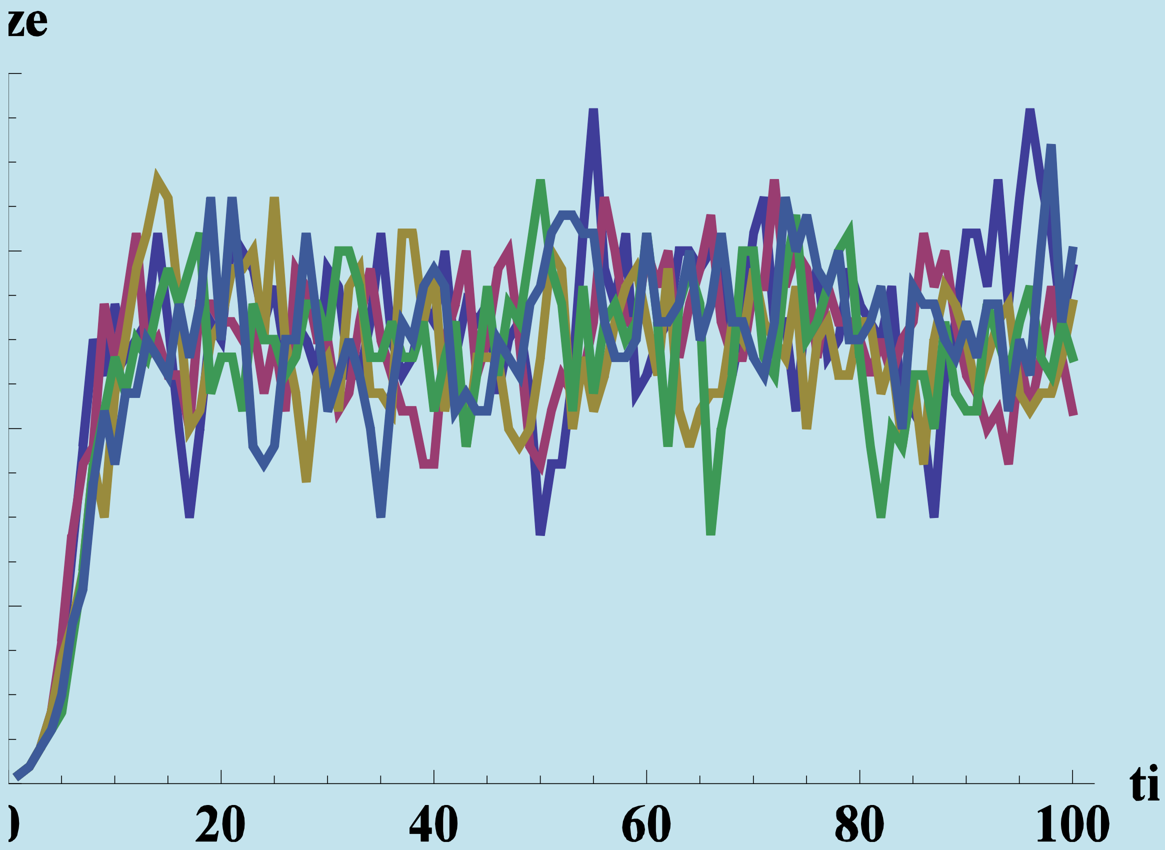
Lingering around K

- And once in a band around K, the population 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).
- In this example c can be calculated – large deviations for binomial r. v., (Janson),
- $c=d(1-d)^2 /8(1+d)$.
- For any K, the expected time to leaving a band $(1\pm \delta)K$ is $O(e^{cK})$, $\delta = 1-d$.

The time of ascent $T_a = O(\log K) = T_d$, the time of descent

- $Z_n \geq Y_n$ on $\{T_a \geq n\}$, where $\{Y_n\}$ binary G-W with P(no children) = $d/(1+d)$.
- Hence, $dK \approx Z_{T_a} \geq Y_{T_a} \approx W(2/(1+d))^{T_a}$ and
- $T_a = O(\log K)$.
- At least for non-population-dependent general branching processes, also $T_d = O(\log K)$ (PJ and Klebaner: On the Path to Exinction, PNAS, 2007).

And this is what things look like in a simulated world:



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

Is this behaviour general, and what happens during the long plateau phase?

- 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 $A=(a_1, a_2, ..., a_z)$, 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.
- 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, $Z_t = (1, A_t)$, $(f, A) = \sum f(a_i)$, $A = (a_1, \ldots a_z)$.
- $L_z f = f' - h_z f + f(0)(b_z + h_z m_z)$
  - $f'(a)$ 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 $f \in C^1$,
- $(f, A_t) = (f, A_0) + \int_0^t (L_{Z(s)} f, A_s) ds + M^f_t$, where $Z(s) = Z_s$ and M^f_t is a local square integrable martingale (PJ & FK 2000)
- In particular,
- $Z_t = (1, A_t) = Z_0 + \int_0^t (b_{Z(s)} + h_{Z(s)}(m_{Z(s)} - 1), A_s) ds + M^f_{t.}$

Growth

- $Z_t = Z_0 + \int_0^t (b_{Z(s)} + h_{Z(s)}(m_{Z(s)} - 1), A_s)ds + M^f_t.$ 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 and Monotonicity

- 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 for Bellman-Harris type age-dependent branching processes.
- We work with strict criticality at K.
- Assume monotonicity in the sense that if $\{Z_t'\}$ and $\{Z_t\}$, are annealed at sizes $z' \leq z$, but start the same, then $Z_t' \geq Z_t$ in distribution.

The risk of direct extinction

- 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 still expect it to remain for a time of order e^{cK}, $K \to \infty$, for some c>0, by large deviation theory.
- This is proved under technical assumptions in Klebaner and PJ (Journ. Appl. Prob. 48A, 2011).

Now, let's have a look at the population behaviour around the carrying capacity.

Write $M(R^+)$ for the set of finite measures on R^+, and assume that

- the population starts from around K individuals: $(a_1, \ldots a_z)/K = A^K_0 \rightarrow A_0$, as $K \rightarrow \infty$.
- the support of A^K_0 and its total mass are bounded: $\sup_K \inf\{t>0: A^K_0((t,+\infty))=0\}<\infty$ and $\sup_K A^K_0<\infty$.
- If $\exists\, C>0\,;\ \forall\, A\in M(R^+)\ |(L_A f, A)| \leq C(1+f,A)$, where C may depend on f, then for any A, (f,A_t) is integrable and its expectation is bounded,
- All demographic parameters are uniformly bounded .

(If the population starts small it will reach any vicinity of the carrying capacity in time $O(\log K) \ll K$.)

Then:

- $\{A^K{}_t, t \geq 0\}_K$ is tight in $D(R^+, M(R^+))$.
- Proof by Jakubowski's criteria, compact containment + tightness of integrals of a separating family of continuous functions closed under addition (coordinate tightness).

Stabilisation

- Add to earlier assumptions of boundedness of parameters and stabilisation of the initial age distribution A^K_0, as $K \to \infty$, that
- parameters are Lipschitz in the Levy-Prohorov distance ρ: $|b_A^K(u)-b_B^K(u)| \leq \mathcal{C}\rho(A/K,B/K)$ and the same for h_A^K and m_A^K (Lipschitz density dependence).
- Then, the processes $A^K = \{A^k_t; t \geq 0\} \to$ some A^∞, weakly in $D(R^+,M(R^+))$, as $K \to \infty$.

What is the limit?

- If $\mu^K/K \Rightarrow \mu$, then the demographic parameters also converge: $b_{\mu^K}{}^K \longrightarrow$ some b_μ *etc.* and so does the infinitesimal operator corresponding to them, $L_{\mu^K}{}^K \longrightarrow L_\mu$, $L_\mu{}^K f = f' - h_\mu{}^K f + f(0)(b_\mu{}^K + h_\mu{}^K m_\mu{}^K)$.
- The limit $A = A^\infty$ satistfies
- $(f, A_t) = (f, A_0) + \int_0^t (L_{A_s} f, A_s)ds$.
- This is a weak form of the classical McKendrick-von Foerster differential equation for the density $a(t,u) = A_t'(u)$ of A_t:
- $(\partial/\partial t + \partial/\partial u)a(t,u) = -a(t,u)h_{A_t}(u)$, which can be solved in special cases, like when $h_{A_t}(u)$ is constant or only depends upon $|A_t|$.

Summary

- A population in a habitat that can carry a large number of individuals K, and where parameters stabilise as $K \to \infty$,
- grows to around K in time log K
- lingers there for a time e^{cK}, while its age distibution stabilises to $A = A^{\infty}$, given by the McKendrick-von Foerster equations,
- and then it dies out in time log K (?).