EXTINCTION (AND A LITTLE ABOUT EVOLUTION)

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Extinction and Evolution

- "Extinction and natural selection...go hand in hand."Darwin in Origin, p. 172
- "Extinction is the motor of evolution." Stephen Jay Gould (?)
- Formalised into Adaptive Dynamics: A resident, (pseudo-)stable population, size = carrying capacity K, experiences a (slightly) beneficial mutation . If the latter does not die out, it overtakes the habitat in a short ("ecological") time span , and the old resident dies out. At critical points speciation might occur.
- An "evolutionary" era of pseudo-stability follows.

Approaches

- "Classical" AD (Metz, Diekmann, Gyllenberg, Geritz, Kisdi.....): General deterministic, differential equations, heuristic ... But the ideas are there.
- French school (Méléard, Champagnat, Lambert): Multi-type, population size dependent birth-and-death, strictly individual based, first pop size carrying capacity $\rightarrow \infty$, then mutational steps $\rightarrow 0$. Extinction explains movement in trait space. Time to evolutionary branching VERY long.....
- Other formulations?

The Binary Lotka-Volterra-Gauss Toy Model

- In discrete time, given that the population consists of z_1 individuals with trait x_1 , ... , z_k with trait x_k , there is binary splitting of an x_j – individual with probability
- $p_2(j) = NK(x_j)/(NK(x_j) + z_j + \sum_{i \neq j} \alpha(x_j,x_i)z_i)$, no children otherwise.
- Mutation probability u_N, and then a new trait according to a (Gaussian) distribution around the old, cf. Méléard-Champagnat.
- Classically K and α have Gaussian forms.

One trait – no mutation

- $p = K/(K+z)$ – also of direct interest in PCR, (though there the alternative to replication is that the molecule remains, J. Theoret. Biol. 2003).
- $Z < K$ implies $p > \frac{1}{2}$, supercritical, z=K critical and z>K subcritical.
- Since the mean reproduction 2K/(K+z) is >1, for finitely many z only, the process must die out.
- If T is extinction time, for any $\delta > 0$, there is a c > 0; $P(e^{K(c-\delta)} < T < e^{K(c+\delta)}) \rightarrow 1$, as $K \rightarrow \infty$. (Klebaner and Zeitouni, Ann. Appl. Prob. 1994)

Growth vs Early Extinction

- By comparison with a binary branching process with p = 1/(1+d) = K/(K+dK), it is clear that the probability of reaching dK, 0<d<1 is larger than $1 - d^n$, if the population starts from n individuals, and grows exponentially to that level.
- Hence, if early extinction is avoided, the population grows to a small band around K in time O(logK), remains there for a time of exponential order, and finally, as we shall see dies out in a time of O(log K).

Extinction and Competition

- But more than 99.9% of all species are extinct, many of them successful (Raup , 1991, 1994).
- Maybe much extinction is unrelated to competition?
- Mass extinctions (many, but not Darwin)?
  - Catastrophes (the Chixculub meteorite, killing all dinosaurs?) – and catastrophes (El Niño).
- Environmental variation . (Vatutin et al.)
- The Malthus-Châteauneuf-Bienaymé-Galton, Watson-Haldane-Steffensen insight and blunder, 1798-1930): 75-100% of all family lines die out , often during growth of the total population (biomass) !

A Seal Example

- Survival probabilities for seals look like
          0.6 0.8 0.95 0.95 ...... 0.95,
  possibly slightly lower after 30 years or so.
- The first three years no children are born. The fourth year, the probability of a daughter is 0.2, and then it is 0.45 per year.
- The extinction probability for the family line from one female is q=0.65. The imbedded GW m=3, (The Malthusian parameter is $\alpha = 0.11$. Doubling time 6 years!)

Time to extinction

- European noble families seem to persist some 300 years (Galton and several others).
- A long living family: Kung Fu-tse's (500 B.C.) 77:th direct male descendant Kung Te-chen, died October 2008.
- 22% of all Chinese share three surnames. 50 % of all Koreans are Lee, Park, or Kim. A result of frequent extinction amidst massive growth?

More Relistic Time Structure

- The family extinction problem can be solved without a time structure, by the generation counting Galton-Watson process. First things can be said about the time to extinction
- But actually more refined models are needed for this, if not to understand evolution, at least for conservation biology: general branching.
- In this individuals are independent, have arbitrary life span distributions, and give birth at events of a point process.

Markov structure, not in time but in the pedigree
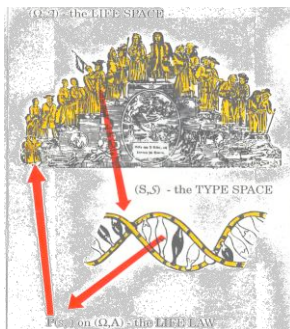
The quintessential population is a multi-type branching process. If it dies out for intrinsic reasons, it is subcritical

Branching process experts: Naturally!

- General public: Strange – extinction induces a global restriction on the whole population, which should be incompatible with independence .
- But the branching people (though naive) are right!

Theorem

A (general multitype) branching process conditioned on extinction, remains a branching process. Its life law is

$$Q(s, A) = P_s(A \times \Omega^{T \setminus \{a\}} \mid E) .$$

In this:

- s is any type (with a positive extinction probability),
- A is any subset of the life space , Ω,
- P_s is the population measure, defined on the population space Ω^T by the original life law $P(s,A)$,
- T is the Ulam-Harris space of all possible individuals, a is the ancestor, and E the set of extinction.

Properties

- The new process has extinction probability one.
- If the original process is Malthusian, so is the new, and subcritical (i.e. has a negative Malthusian parameter),
- In terms of Radon-Nikodym derivatives

$$Q(s,A) = \int_A \Pi_k q_{\sigma(k)} P(s,d\omega)/q_s,$$

where the product is over realised children of the ancestor, the latter of type s, the type of child k being $\sigma(k)(\omega)$.

FROM NOW: A SINGLE TYPE

- Each life-span is distributed like λ and reproduction like a point process ξ on R_+.
- Then $\xi(a) = \xi([0,a))$ is the number of children born up to age a, $\xi(\infty)$ is the total off-spring, $\mu(a):= E[\xi(a)]$ is the reproduction measure, and $m = E[\xi(\infty)] = \mu(\infty)$.
- Assumptions: $E[\xi(0)] < 1$, $m < \infty$, and $\sigma^2 = Var[\xi(\infty)] < \infty$, mostly.
- The process is supercritical if m>1, critical or subcritical otherwise.
- Supercritical processes survive with a probability $1-q > 0$ (but often small!). The others die out.

The Malthusian parameter

- is the exponential rate of population increase, postulated by Malthus.
- Mathematically defined, in the single-type case, by $E[\int_0^\infty e^{-\alpha t} \xi(dt)]=1$.
- In supercritical, non-lattice cases, population size $\sim$ random variable $\times e^{\alpha t}$.
- In subcritical: Yaglom's (generalised) theorem holds (under simple conditions): $P(Z_t>0) \sim ce^{-rt}$, c>0, r=$-\alpha$.

Little is known about the constant c!

- However , $C=\lim e^{rt}E[Z_t]$ and $b=\lim E[Z_t|Z_t>0]$ both exist. For exponentially distributed life spans, C=1.
- Hence, in $P(Z_t>0) \sim ce^{-rt}$, c = C/b.
- If $C \approx 1$ and b is large, c must be small.
- For geometric reproduction in GW with m<1 expected number of children per individual c = 1-m.

The time to extinction in large subcritical populations

- General, non-lattice, single-type branching process Z_t^x starting from x, $Z_t=Z_t^1$,
- subcritical with the Malthusian parameter –r.
- $T_x =T= \inf \{t \geq 0; Z_t^x =0\}$
- $P(T_x>t) =1-P(T_1 \leq t)^x = 1- P(Z_t=0)^x = 1-(1-c_t e^{-rt})^x$, $c_t \to c$.
- $E[T_x]=\int_0^\infty P(T_x>t)dt =(\ln x +\ln c +\gamma_x)/r$, $\gamma_x \to$ Euler's γ .
- $T_x =(\ln x +\ln c +\eta_x)/r$, $P(\eta_x < y) \to$??

The Actual Time to Extinction

- $T_x = (\ln x + \ln c + \eta_x)/r$,
- Since $P(\eta_1 < y)$ has an exponential tail, and η_x is the maximum of x independent family survival times $\sim \eta_1$:
- $P(\eta_x < y) \to \exp(-e^{-y})$, $y \in R$, $x \to \infty$. Gumbel!
- $\ln x = 10$ for large x (Old Oxford saying, Hammersley? - Etheridge).
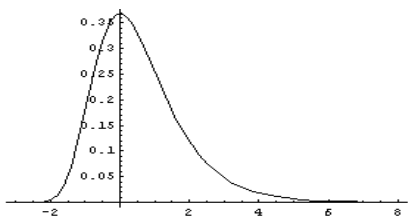
Between Dawn and Demise

- $x^{u-1} Z^x{}_{uT} \to^d C^{1-u} b^u e^{-u\eta}$, $0<u<1$, as $x \to \infty$, in distribution.
- Typically, the normed shape is thus exponentially decreasing, provided $\eta > \ln (b/C)$.
- The expected path is $C^{1-u} b^u \Gamma(u+1)$:


b=1.1, C=1   b=5, C=1
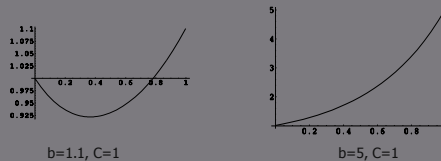
The Markov Case

- avails itself to a more transparent analysis, and also to an investigation of the last trembling minutes:
- Exponentially distributed life spans, with parameter a,
- splitting into k children with probability p_k.
- $m = \sum k p_k < 1$.
- Indicate the starting number on P and E.
- Then, $E_x[Z_t] = xe^{-rt}$, $r = a(1-m)$.

Population size u-ways to death

- If G is the distribution of T from one ancestor, $P_y(T \leq t) = G(t)^y$.
- Hence, with $G' = g$, $P_x(Z_{uT}=y) = \int_0^\infty P_x(Z_{ut}=y) P_y(T \in dt(1-u)) = \int_0^\infty P_x(Z_{ut}=y) y G^{y-1}(t(1-u)) g(t(1-u)) dt$.
- The same for multidimensional distributions and generating functions yields $x^{u-1} Z^x{}_{uT} \to^d b^u e^{-u\eta}$, $0<u<1$, as $x \to 1$.

And realisations:
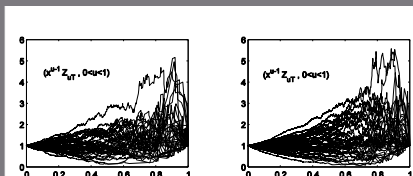
Markov branching with $p_0 = 0.75$ and $p_2 = 0.25$, life expectancy =1, x = 1 000 and 10 000, respectively. Biologically small (threatened) can be mathematically large.

On the eve of extinction

- Close to extinction the approximation is bad. Consider $T_x - u$ instead.
- Let $f(s) = \sum_k p_k s^k$ be the reproduction generating function,
- $\pi(s) = \sum \pi_i s^i$, where $0 \leq s \leq 1$ and

$$\pi(s) = \int_0^s \frac{dv}{a(f(v) - v)}$$

Then:

- under "xlogx", $Z^x_{T-u} \to Y_u$, $u > 0$, (functionally), as $x \to \infty$.
- $Y_0 = 1$ and $\{Y_u, \in R_+\}$ is Markov with
- expected holding time $1/a_i$ in state i
- and jump distribution $j\pi_j p_{i-j+1}/(i\pi_i)$, for j = 1,2, ... i+1.
- As $u \to \infty$, $e^{-ru}Y_u \to^d$ an exponential random variable with mean b = lim $E[Z_t|Z_t > 0]$.

But all this disregards inbreeding

The smaller the population the greater the risks for inbreeding... ...accelerating extinction.

How to model this?

This is joint work with

- Fima Klebaner and Serik Sagitov (extinction in subcritical branching. PNAS 104: 15, 6107-6111, 2007, Adv. Appl. Prob. 2008.)
- Andreas Lagerås (supercritical processes conditioned to die out are subcritical, Elect. Comm. Prob. 13, 540-547, 2008).
- Serik, Fima, and Volodya Vatutin (Lotka-Volterra-Gauss) models for trait substitution and sympatric speciation.
- Fima, Andreas, and Serik and Donald Blomqvist (inbreeding – ongoing work).

Brunswick Street, Fitzroy, Melbourne, Vic.
26 February 2009   (Picture: E. Mayer)