HOW MIGHT A POPULATION HAVE STARTED?

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(Joint work with F. C. Klebaner and P. Chigansky)

From little (unobservable) to big,
From scattered to dense.
From independence between elements to interaction and ultimate deterministic behaviour, after suitable norming.

- Think warts, tumours, species invading a habitat, or a set of replicating DNA molecules, small but growing quickly. Or, think the early universe!
- ‘Populations’, of individuals/elements, creating new individuals – first independently, then under increasing influence from outside/others, when the population grows big and dense, and usually less and less successfully, as space and/or nourishment per individual decreases.

Fixed (unknown?) start → little population of free (random) elements → deterministic (even continuous) system (after norming)

- From (almost) branching processes to differential equations. But in between ?!
- Classical example: spread of epidemics.
- But our starting point was different: a model of DNA replication in the Polymerase Chain Reaction (PCR).
- How many were the perpetrators?

Problem

- From how many elements did the population start?
- Data: The density (x = number/K) can be seen only when $\geq \rho > 0$.
- Idea: While the density is small, the population size at time n, Z_n, will be like an ordinary, supercritical GW process.
- The carrying capacity K is some system size measure. Sometimes the population is supercritical when < K and subcritical above – but not necessarily.

Heuristics

- Let z_0 be the number of ancestors and $a > 1$ the mean reproduction when density $x=0$.
- For this classical process "reproduction as though $x=0$", $Z_n \sim W(z_0)a^n$, $W(z_0)$ the sum of z_0 i.i.d. random variables with mean 1.
- Similarly, if n is large but x still smaller than $O(\log K)$, say $n = n_K = \epsilon \log K << \rho K$ for K large,
- At later times, by Markov, Z_n is thus a function of $W(z_0)a^{n_K}$, maybe deterministic due to large number effects.
- $z_0 = W(z_0) \Leftrightarrow Var[W]=0 \Leftrightarrow$ reproduction variance $= 0 \Leftrightarrow$ deterministic future.

From sounds to things!

- $\{\xi_{ni}; i \in N\}$, $n \in N$ integer valued ≥ 0.
- $F_n := \sigma(\{\xi_{ki}; i \in N\}, k \leq n\}$, $\xi_{ni}; i \in N \,|F_{n-1}$ iid.
- $Z_n = Z(n) = \sum_{i=1}^{Z(n-1)} \xi_{ni}$, $X_n = Z_n/K$, the density at n, which is Markov for given K.
- $E[\xi_{ni}|\, F_{n-1}] = m^K(X_{n-1})$, $Var[\xi_{ni}|\, F_{n-1}] = \sigma^2{}_K(X_{n-1})$
- $E[X_n|X_{n-1}=x] = f^K(x) = xm^K(x)$

Smoothness assumptions

1. As $K\to\infty$, $m^K\to m\in C^1(R_+)$, , uniformly. $|xm^K(x)-xm(x)|^2 = O(1/K)$, $K\to\infty$
2. $f(x)=xm(x)$ increases strictly. Note: $f(0)=0$.
3. m' is uniformly continuous around 0.
4. As $K\to\infty$, X_0 has a limit in probabiliy.
5. The variances $\sigma^2_K(x)$, are uniformly bounded and, as $K\to\infty$, $\sigma^2_K(x)\to$ some $\sigma^2(x)$.
6. The $\xi_{ni}|X_{n-1}=x$ increase in distribution with K and decrease in x.
7. $1<m(0)=a\geq m^K(x)=a(1-Cx+o(x))$, $x\to 0$

That is:

- For each carrying capacity K and density x, a branching type behaviour.
- Natural assumptions as K and x vary, including the limit and convergence rate as $K \to \infty$.
- The interest is in K large, as compared to the population, i.e. $K \to \infty$.

So, what happens?

- Write $f_n = f \circ f \circ \ldots f$, n times.
- Klebaner's Threshhold Thm: If…, then $X_n \to f_n(x_0)$, as $K \to \infty$, in probability (or L^1), provided $X_0 \to x_0$ in the same sense.
- But this is for fixed n. In our case z_0 is fixed, so $X_0 \to 0$, and $f(0)=0$!
- Only around time log K will the density be positive, cf. the heuristics. (log with base a.)
- But $f_n(x/a^n)$ has a uniform and strictly increasing limit $h(x)$.

$X_{\log K}$?

- Write $Y(n) = \sum_{i=1}^{Y(n-1)} \eta_{ni}$, the summands iid with the limiting reproduction distribution at $x=0$, as $K\to\infty$. Let $W(z_0) = \lim Y_n/a^n$.
- Recall $f_n = f\circ f \circ \ldots f$, n times, $f_n(x/a^n) \to h(x)$.
- And as $K\to\infty$, $X_{\log K} \to h(W(z_o))$, in distribution.
- Proof by a two step approximation, first $Z_n \approx Y(n)$ up to $\epsilon \log K$. Then a restart from $x=W(z_0)$ and Klebaner's theorem.

And the whole process?

- Main result: $X_{\log_a K + n} \to f_n \circ h(W(z_0)) = h(a^n W(z_0))$, in distribution, $n \in N$, as $K \to \infty$, (functional convergence).
- Here, with W=W(1), $E[e^{-saW}] = g \circ E[e^{-sW}]$, where g is the generating function of η, i.e. the limiting reproduction at density 0, as $K \to \infty$, and W(z) is the sum of z iid W-copies
- $1 < a = m(0) = E[\eta]$, $\sigma^2 = \sigma^2(0) = Var[\eta]$, $E[W]=1$, $Var[W]=\sigma^2/a(a-1)$.

Properties

- Observe the density X at time t = log K +n.
- Then the number of original elements was
- $z_0 = E[W(z_0)] \approx E[h^{-1}(X)]/a^n$, for K large.
- And $z_0 \approx h^{-1}(X)/a^n \Leftrightarrow W(z_0)=E[W(z_0)] \Leftrightarrow Var[W]=0 \Leftrightarrow \sigma^2=0$.
- Similarly, the future is determined by $W(z_0)$, and hence by $h^{-1}(X)a^{k-n}$, k=n, n+1, ….

A corresponding time change

- Now, change also time scale to unit K:
- $X_t = Z_{tK}/K$, the density in intrinsic time.
- Then, $X_{(\log\ K)/K} \approx h \circ W(z_0)$, by our earlier result.
- Since K is large, $(\log K)/K \approx 0$, and the process seems to start from $X_0 \approx h \circ W(z_0)$.
- The real start from z_0 elements has been concealed by the random veil of $h \circ W(z_0)$.

Conclusion

- We have considered populations which start small and scattered. Hence, individuals multiply freely (=randomly).
- As the population and whole system grow, at the same pace, law of large numbers' effects render a deterministic macroscopic description natural.
- And randomness appears only at the very beginning of the system (though that was actually deterministic!) but has lasting effects.
- A general phenomenon of nature?

Klebaner's Threshold Theorem

simplified version

- Branching structure. $Z_{n+1}= \sum_{j=1}^{Z(n)} \xi_{jn}$, where $Z(n)=Z_n$, ξ_{jn} may depend on K, and are i.i.d. integer valued ≥ 0, given the past (Markov).
- Scale. $E[X_{n+1}|X_n=x] = xm^K(x) = xE[\xi|X_n=x]$
- Stabilisation. $X_0 \to x \geq 0$ (P) (or L^1), as $K\to\infty$; $m^K(x + o(1)) \to m(x)$ (P), and similarly $Var[\xi|X_n=x + o(1)] = o(K)$.
- Then, $X_n \to f_n(x)$, as $K\to\infty$, in probability (or L^1 or even L^2); $f(x):= xm(x)$.