Qsd in large populations birth and death processes, can we see them (it) ? are they (is it) useful for something ?

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Joint work with J.R.Chazottes and S.Méléard.

We consider a continuous time process (b.d.p.) (N_t) on $\mathbb{N}$ with transition rates

$$\begin{aligned}\mathbb{P}\big(N_{t+dt} = n+1 \mid N_t = n\big) =& \lambda_n \, dt \ , \\ \mathbb{P}\big(N_{t+dt} = n-1 \mid N_t = n\big) =& \mu_n \, dt \ , \\ \mathbb{P}\big(N_{t+dt} = n \mid N_t = n\big) =& 1 - (\lambda_n + \mu_n) \, dt \ .\end{aligned}$$

N_t is the size of the population at time t, λ_n is the birth rate in a population of size n and μ_n the death rate (in a population of size n).

We will assume $\lambda_0 = 0$ (no spontaneous generation) and $\mu_0 = 0$, hence the state $n = 0$ is invariant.

We will assume

$$\lim_{n \to \infty} \frac{\lambda_n}{\mu_n} = 0 \ ,$$

and $\lambda_n > 0$ and $\mu_n > 0$ for all $n > 0$.

Let T_0 be the extinction time, namely the time the process reaches $n = 0$ (afterwards it stays there). From the above assumption it follows that for any $n > 0$

$$\mathbb{P}_n\big(T_0 < \infty\big) = 1 \ .$$

A measure ν on $\mathbb{N}^*$ is a Yaglom limit if for any $n > 0$ and any set $A \subset \mathbb{N}^*$ we have

$$\lim_{t\to\infty} \mathbb{P}_n\big(N_t \in A \,\big|\, T_0 > t\big) = \nu(A) \; .$$

A measure ν on $\mathbb{N}^*$ is a quasi stationary distribution (q.s.d.) if for any $t > 0$ and any set $A \subset \mathbb{N}^*$ we have

$$\mathbb{P}_\nu\big(N_t \in A \,\big|\, T_0 > t\big) = \nu(A) \; .$$

For b.d.p., if ν is a q.s.d. there exists $\rho_0 > 0$ such that for any $t > 0$

$$\mathbb{P}_\nu\big(T_0 > t\big) = e^{-\rho_0\, t} \; .$$

A necessary and sufficient condition for the existence of a (unique) q.s.d. is known for b.d.p.processes in terms of the sequences (λ_n) and (μ_n).

Carrying capacity.

We will assume that λ_n and μ_n have the functional forms

$$\lambda_n = n\,\lambda\big(n/K\big) = K\,B(n/K)\ ,$$

$$\mu_n = n\,\mu\big(n/K\big) = K\,D(n/K)\ ,$$

where K will be a large number. K is called the carrying capacity and gives the scale of the population size that can be sustained by the input food rate.

For a given (large) K the process will be denoted by N^K.

We consider the case where $\lambda_n >> \mu_n$ for small n (with respect to K) and $\lambda_n << \mu_n$ for large n (with respect to K).

If the population is small there is a lot of food available and the population grows (except for stochastic fluctuations).

If the population is large, there is a lot of competition, not enough food for everybody and the population decays.

We want to investigate the "equilibrium".

It is convenient to state the hypotheses on the functions B and D (on $\mathbb{R}^+$) which do not depend on K ($\lambda_n = K\,B(n/K)$, $\mu_n = K\,D(n/K)$). We will assume

$B(0) = D(0) = 0$ ($\lambda_0 = \mu_0 = 0$)

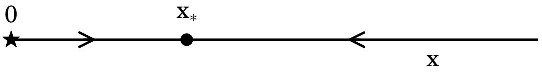
B and D are regular

$$\lim_{x\to\infty} D(x) = \infty\,, \quad \lim_{x\to\infty} \frac{B(x)}{D(x)} = 0$$

$B'(0) > D'(0) > 0$.

The function $B - D$ has a unique strictly positive zero x_* with $B'(x_*) - D'(x_*) < 0$ (stable fixed point).

Therefore the o.d.e.
$$\frac{dx}{dt} = B(x) - D(x)$$
has the stable fixed point x_* as a global attractor on $\mathbb{R}^+$.



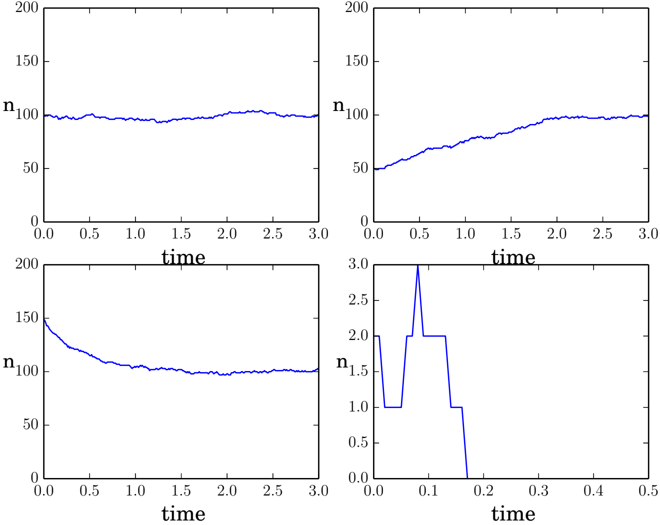
The process (N_t^K) is supercritical at low population (with respect to K) because $B'(0) > D'(0)$ but subcritical at large population because $\lim_{x\to\infty} B(x)/D(x) = 0$.

Theorem

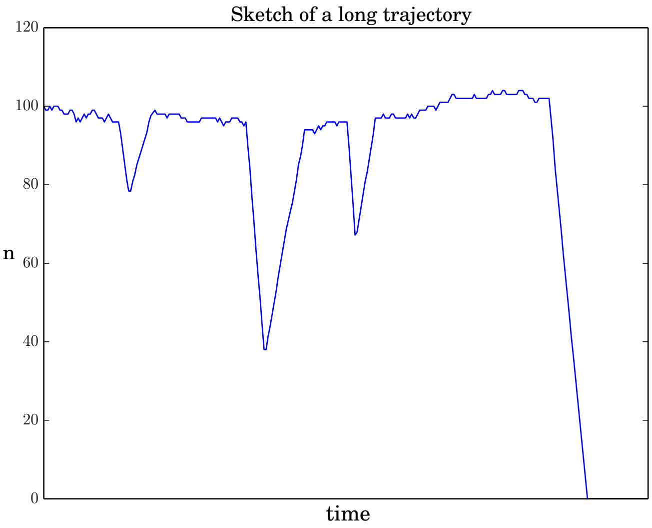
The process (N_t^K/K) converges a.s. to $x(t)$ solution of the o.d.e. on any finite time interval (provided N_0^K/K converges to a fixed quantity).

Under some technical hypothesis the process N_t^K has a unique q.s.d. ν^K.

Let us look at trajectories of the process N_t^K for large K and different initial conditions.



However the process will almost surely reach $n = 0$ in a finite time and stay there forever (extinction).



Sketch of a long trajectory
120
100
80
60
40
20
0
n
time

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Since $\mathbb{P}_{\nu^K}\big(T_0 > t\big) = e^{-\rho_0(K)\,t}$, the extinction time is of order $1/\rho_0(K)$. If the time it takes to reach the "q.s.d. regime" is much smaller than $1/\rho_0(K)$, then we will "see" the q.s.d. .

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We proved that there is another time scale $1/\rho_1(K)$ which describes the time it takes to reach the "q.s.d. regime" and satisfies

$$\frac{1}{\rho_1(K)} << \frac{1}{\rho_0(K)} \qquad \text{for large } K$$

We need a lower bound on $\rho_1(K)$ and an upper bound on $\rho_0(K) > 0$ to prove that $\rho_1(K) >> \rho_0(K)$.

Theorem

For K large enough we have

$$\rho_0(K) = \left(a + \mathcal{O}\left(\frac{(\log K)^3}{\sqrt{K}} \right) \right) \sqrt{K}\, e^{-b\,K}$$

$$a = \frac{1}{\sqrt{2}\,\pi} \left(\sqrt{\frac{B'(0)}{D'(0)}} - \sqrt{\frac{D'(0)}{B'(0)}} \right) \sqrt{\frac{D'(x_*)}{D(x_*)} - \frac{B'(x_*)}{B(x_*)}}\, x_*\, B(x_*)\ ,$$

$$b = \int_0^{x_*} \frac{B(x)}{D(x)}\ ,$$

$$\textit{and} \qquad \rho_1(K) \ge \frac{c_1}{\log K}\ ,$$

with $c_1 > 0$ independent of K. Moreover

$$\sup_{n\in\mathbb{N}^*} d_{\mathrm{TV}}\Big(\mathbb{P}_n\Big(N_t^K \in \cdot \;\Big|\; T_0 > t\Big)\,,\, \nu^K\Big) \le c_2\, e^{-\rho_1(K)\, t}$$

$c_2 > 0$ independent of K.

We also have results without conditioning.

There exists a sequence

$$\alpha_n(K) = 1 - \left(\frac{D'(0}{B'(0)}\right)^n + \frac{\mathcal{O}(1)}{K}$$

such that for any K large enough, for any $n \in \mathbb{N}^*$ and for any $t \geq 0$

$$d_{TV}\big(\mathbb{P}_n\big(N_t^K \in \,\cdot\,\big)\,,\; \alpha_n(K)\,\nu^K + (1-\alpha_n(K))\,\delta_0\big) \leq \mathcal{O}(1) \times$$

$$\left(\sqrt{K}\;\log K\; e^{-c\,K} + \big(1-e^{-\rho_0\,t}\big) + Ke^{-a\,t/4} + K^{3/4}\,e^{b\,K}\,e^{-\rho_1\,t/2}\right)\;,$$

where a and b are positive constants independent of K.

In other words, starting from $n \in \mathbb{N}^*$ the system goes rapidly to extinction with probability $1 - \alpha_n$ or stays for a long time in the "q.s.d. regime" with probability α_n.

The numbers $-\rho_0(K)$ and $-\rho_1(K)$ are eigenvalues of the infinitesimal generator L^K of a C^0 semi-group in the Hilbert space $\ell^2(\pi)$ with $\pi_1 = 1/\mu_1$ and for $n \geq 2$

$$\pi_n = \frac{\lambda_1 \cdots \lambda_{n-1}}{\mu_1 \ldots \mu_n}$$

In this space the operator L^K is self-adjoint with a compact resolvent and spectrum consisting only of simple eigenvalues on the negative real axis.

The number $\rho_1(K) - \rho_0(K)$ is the spectral gap.

The q.s.d. ν^K satisfies

$$L^{K\dagger} \nu^K = -\rho_0(K)\, \nu^K$$

but here the duality is for the flat ℓ^2 space.

Let $n_* = \nu^K(n)$.

We conjecture that

1) If $0 < a < 1$, and if we denote by $T_a^{(1)},\ T_a^{(2)}, \ldots$ the sequence of successive down crossings of $a\, n_*$ with upcrossing of say $n_*\ (1+a)/2$ in between, then if $0 < b < a$ for K large

$$T_b^{(1)} >> T_a^{(1)},\ T_a^{(2)},\ \ldots$$

2) Moreover when correctly normalized the process $T_a^{(1)},\ T_a^{(2)}, \ldots$ converges in law to a Poisson point process of intensity one when K tends to infinity.

3) The normalization should be given by a formula analogous to $\rho_0(K)$.

In dimension $d > 1$ (several species competing for the same food resources) we have similar but less sharp results.

For the moment we assume mutations at the boundary, i.e. if a population disappears it can reappear by mutation from another species (provided there is still some alive). This is related to a technical problem of proving the descent from infinity.

Theorem

There exists constants $a_1 > 0, \dots, a_4 > 0$ such that for any K large enough

$$e^{-a_1 K} \le \rho_0(K) \le e^{-a_2 K} , \qquad \rho_1(K) \ge \frac{a_3}{\log K} .$$

There exists a unique q.s.d. ν^K, its death rate is $\rho_0(K)$, and

$$\sup_{\vec{n} \in \mathbb{N}^d \backslash \{\vec{0}\}} d_{TV}\left(\mathbb{P}_{\vec{n}}\left(\vec{N}_t^K \in \cdot \;\middle|\; T_0 > t\right), \nu^K\right) \le a_4 \, e^{-\rho_1(K)\, t} .$$

Linear Resilience.

Joint Work with S.Méléard and S.Martínez.

Recall the infinite limit population dynamical system (in 1d)

$$\frac{dx}{dt} = B(x) - D(x) \, .$$

The stability of the fixed point x_* is given by the quantity

$$B'(x_*) - D'(x_*) < 0 \, .$$

This number is the inverse of the relaxation time to x_* starting from a close initial condition. It is also related to the change of x_* due to a (small) change of the environment (i.e. the functions B and D). It is the (linear) resilience in the ecological terminology. Can it be estimated from a population time sample?

Linear Resilience estimation.

In dimension 1

$$\text{linear resilience} = B'(x_*) - D'(x_*) = -\frac{\langle\text{jump rate}\rangle_{\nu^K}}{2\,\mathrm{Var}_{\nu^{\mathrm{K}}}(n)} + \frac{\mathcal{O}(1)}{\sqrt{K}}\ .$$

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In dimension larger than one we need to look at the fluctuations of the birth rates and of the death rates of the different species and there is no such simple formula.

The relation between the variance of the fluctuations and the stability of the deterministic system has been known for a long time in Physics.

It is called the second Fluctuation Dissipation Theorem or the Einstein relation.

For the Langevin equation it takes the well known form

$$
\begin{aligned}
dq &= v\ dt\ , \\
m\ dv &= -\gamma\ v\ dt - U'(q)\ dt + \sqrt{2\,\gamma\,k\,m\,T}\,dW_t
\end{aligned}
$$

with q the position, v the velocity, γ the friction coefficient, U the potential energy, k the Boltzmann constant, m the mass of the particle and T the temperature. The invariant measure has the Gibbs density $e^{-\beta\ H} = e^{-\beta\ (m\,v^2/2+U(q))}$ with $\beta = k\ T$, and Einstein relation is also related to equipartition $< m\,v^2/2 >= k\ T/2$.

Proofs.

In dimension one we used a matching (WKB) argument to estimate $\rho_0(K)$, namely we guess a good approximation of $(L^K u)(n) = -\rho_0(K)\, u(n)$ for $n \leq K\, x_*$.
For $n \geq K\, x_*$ we use Levinson's Theorem to get the right asymptotic behavior (with all needed corrections).
The matching condition (at $n = [K\, x_*]$) of the two approximations gives an equation for $\rho_0(K)$.
For $\rho_1(K)$, we established a Poincare inequality, namely for any $y \in \ell^2(\pi)$ with finite support we have

$$-\langle y\,,\, L^K\, y\rangle_{\ell^2(\pi)} \geq \left(\rho_0(K) + \frac{\mathcal{O}(1)}{\log K}\right)\, \|y\|^2_{\ell^2(\pi)}\,.$$

Resilience

With $n_* = \nu^K(n)$

$$\nu^K\big(L^K(n-n_*)^2\big) = \rho_0 \nu^K\big((n-n_*)^2\big) = \rho_0\ \mathcal{O}(1)\ K \simeq 0\ .$$

We have

$$L^K(n-n_*)^2 = KB(n/K)\ \big(1+2\ (n-n_*)\big) + KD(n/K)\ \big(1-2\ (n-n_*)\big)$$

$$= K\big(B(n_*/K)+D(n_*/K)\big) + 2\ \big(B'(n_*/K)-D'(n_*/K)\big)\ (n-n_*)^2$$

$$+\mathcal{O}(1)\ \big(|n-n_*| + |n-n_*|^3/K\big)\ .$$

It follows that

$$K\big(B(n_*/K)+D(n_*/K)\big) + 2\ \big(B'(n_*/K)-D'(n_*/K)\big)\ \nu^K\big((n-n_*)^2\big)$$

$$= \mathcal{O}(1)\ \sqrt{K}\ . \qquad qed$$

In dimension $d > 1$ we use a necessary and sufficient condition for the existence and uniqueness of a q.s.d. together with the convergence in total variation recently established by N.Champagnat and D.Villemonais.

They require two conditions.

Condition A1: there exists two positive numbers b_1 and t_0 and a positive probability measure θ on $\mathbb{N}^d \backslash \{\vec{0}\}$ such that for any subset A of $\mathbb{N}^d \backslash \{\vec{0}\}$

$$\inf_{\vec{n} \in \mathbb{N}^d \backslash \{\vec{0}\}} \mathbb{P}_{\vec{n}}\big(N_{t_0}^K \in A \,\big|\, T_0 > t\big) \geq b_1 \,\theta(A) \,.$$

Note that in general θ is not the q.s.d. , in our case we chose the uniform distribution of the ball of radius $\sqrt{K}$ centered in $K\,\vec{x}_*$.

Condition A2: there exists a positive number b_2 such that

$$\mathbb{P}_\theta\big(T_0 > t\big) \geq b_2 \sup_{\vec{n} \in \mathbb{N}^d \backslash \{\vec{0}\}} \mathbb{P}_{\vec{n}}\big(T_0 > t\big) \,.$$

Under these two hypothesis they prove existence and uniqueness of a q.s.d. ν^K and

$$\sup_{\vec{n}\in\mathbb{N}^d\setminus\{\vec{0}\}} d_{\mathrm{TV}}\big(\mathbb{P}_{\vec{n}}\big(N_t^K\in\,\cdot\,\big)\,,\,\nu^K\big)\leq\big(1-b_1\,b_2\big)^{t/t_0}\;.$$

We have to prove that for large K the constants b_1 and b_2 can be chosen independent of K while

$$t_0=\mathcal{O}(1)\,\log K\;.$$

A simpler proof gives $t_0=\mathcal{O}(1)\,K$.

Note that the order of t_0 ($\log K$) is independent of the dimension while the prefactor may depend on d.

The proof relies on descent from infinity, onion lemma and lower bounds on transition probabilities (but the problem is generically not self adjoint, no Harnack inequality available, no Gaussian bound known).

Resilience

Using the same idea as in dimension 1 we get

$$D\vec{X}(\vec{x}_*)\ V + V\ D\vec{X}(\vec{x}_*)^t + 2\ K\ \mathfrak{D}_D = 0\ ,$$

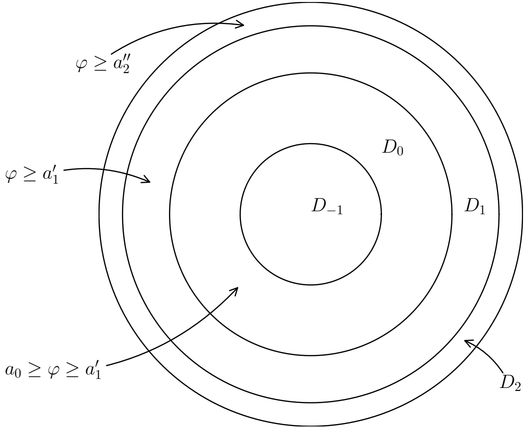
where $\mathfrak{D}_D$ is the $d \times d$ diagonal matrix with

$$\mathfrak{D}_D(j,j) = D_j(\vec{x}_*) = B_j(\vec{x}_*)\ .$$

and V is the $d \times d$ covariance matrix of $\vec{n}$.
This equation implies some constraint on the spectrum of the matrix $D\vec{X}(x_*)$ but is not sufficient to determine the largest real part of this spectrum. We need to extract some other quantities from the data.

The onion Lemma

A useful estimate for entrance and exit times if a Lyapunov function φ is available (can be generalized to other spaces).



$$\inf_{\vec{n} \in D_0 \setminus D_{-1}} \mathbb{P}_{\vec{n}}\big(T_{D_{-1}} \leq t\,,\ T_{D_2 \setminus D_1} > T_{D_{-1}}\big) \geq 1 - \frac{a_0}{a_2''} - \frac{a_0}{a_1'}\ e^{-\Lambda\,t}\ .$$

Lemma

Let $D_{-1} \subsetneq D_0 \subsetneq D_1 \subsetneq D_2 \subsetneq \mathbb{N}^d \backslash \{\vec{0}\}$ *, with* D_2 *a compact subset. Assume* $D_2 \backslash D_1 \cap D_{-1} = \emptyset$ *. Assume that there exists a positive function* φ *defined in* $\mathbb{N}^d \backslash \{\vec{0}\}$ *such that*

$$\Lambda = - \sup_{D_2 \backslash D_{-1}} \frac{\mathscr{L}_K \varphi(\vec{n})}{\varphi(\vec{n})} > 0.$$

Let $a_0 = \sup_{\vec{n} \in D_0 \backslash D_{-1}} \varphi(\vec{n})$ $a_2'' = \inf_{\vec{n} \in D_2 \backslash D_1} \varphi(\vec{n})$ *, and* $a_1' = \inf_{\vec{n} \in D_1 \backslash D_{-1}} \varphi(\vec{n})$ *. Then*

$$\inf_{\vec{n} \in D_0 \backslash D_{-1}} \mathbb{P}_{\vec{n}}\big(T_{D_{-1}} \leq t \, , \; T_{D_2 \backslash D_1} > T_{D_{-1}} \big) \geq 1 - \frac{a_0}{a_2''} - \frac{a_0}{a_1'} \; e^{-\Lambda \, t} \; .$$

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