Time scales for quasi-stationary distributions in large populations.

Sylvie Méléard, Ecole Polytechnique, France

GDR Mamovi, Lyon , September 2017

Joint work with Jean-René Chazottes and Pierre Collet.

A main question in the conservation of endangered species:

From which population size can we consider that the population will go "fast" to extinction with large probability?

We want to give a quantitative answer in terms of the demographic and ecological parameters of the population.

Our aim: to revisit limit theorems with a more quantitative point of view.
Cf. Diaconis and Miclo '15, '16.

The birth and death process

$(N_t^K, t \geq 0)$ is a continuous time birth-and-death process on $\mathbb{N}$.

K gives the scale of the population size and will be a large number.

The process starts from a state $[x_0 K]$ with $x_0 > 0$.

λ_n^K is the birth rate and μ_n^K the death rate for a state *n*.

$$\lambda_n^K = n\,\lambda(n/K) = K\,B(n/K)\ ;\ \mu_n^K = n\,\mu(n/K) = K\,D(n/K)\ ,$$

where

- $B(0) = D(0) = 0$ *($\lambda_0^K = \mu_0^K = 0$ and 0 is an absorbing point).*
- *B and D are regular*
- $\lim_{x\to\infty} D(x) = +\infty$, $\quad \lim_{x\to\infty} \dfrac{B(x)}{D(x)} = 0.$
- $B'(0) > D'(0) > 0.$
- *$B - D$ has a unique strictly positive zero x_* with* $B'(x_*) - D'(x_*) < 0.$

Example: logistic birth and death process

$$B(x) = b\,x \ ; \ D(x) = x(d + cx) \ ; \ x^* = (b - d)/c.$$

The process $(N_t^K, t \geq 0)$ is supercritical at low population (positive growth rate) but subcritical at large population.

One can easily show that for any $n \in \mathbb{N}^*$

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

We have almost-sure extinction.

Quasi-stationary distribution

(Van Doorn '91): For a fixed K, there exists a unique quasi-stationary distribution ν^K (QSD): probability measure on $\mathbb{N}^*$ such that

$$\mathbb{P}_{\nu^K}\left(N_t^K \in A \,\middle|\, T_0 > t\right) = \nu^K(A) \qquad \forall t > 0, A \subset \mathbb{N}^*.$$

Moreover, there exists $\rho_0(K) > 0$ such that for any $t > 0$

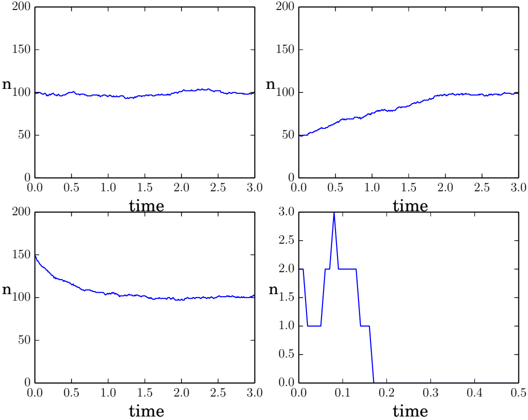
$$\mathbb{P}_{\nu^K}\left(T_0 > t\right) = e^{-\rho_0(K)\,t}\,.$$

$\rho_0(K)$ is the extinction rate starting from the QSD and

$$\mathbb{E}_{\nu^K}(T_0) = 1/\rho_0(K).$$

- Can we obtain the exact dependence of ρ_0 on K, for large K?

Trajectories of the process N_t^K



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

Large K

Theorem (Kurtz '70)

When $K \to +\infty$, $(N_t^K/K, t \geq 0)$ converges a.s. on any finite time interval to $(x(t), t \geq 0)$ solution of the o.d.e.

$$\frac{dx}{dt} = B(x) - D(x)\ ;\ x(0) = x_0,$$

which has the unique stable fixed point x_* on $\mathbb{R}^+$.

Then N_t^K is close to $[x_* K]$ for large t.

The limits in t and K are not commutative.

• Are the statistical properties of the process before extinction related to the QSD ν^K? Can we see the QSD?

We prove that there is another time scale $1/\rho_1(K)$ which describes the time it takes to reach the "QSD regime" and satisfies

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

Theorem

For K large enough we have

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

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

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

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

with $c_1 > 0$ independent of K. Moreover

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

$c_2 > 0$ independent of K.

We also prove that the QSD is close to a Gaussian law centered in $[Kx^*]$ with variance $2K\sigma^2$ with

$$\sigma = 1/\sqrt{\frac{D'(x_*)}{D(x_*)} - \frac{B'(x_*)}{B(x_*)}}.$$

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 K large enough and t with $\frac{K \log K}{\rho_1(K) - \rho_0(K)} \ll t \ll \frac{1}{\rho_0(K)}$, we have

$$\sup_{n \in \mathbb{N}^*} d_{TV}\left(\mathbb{P}_n(N_t^K \in \cdot\,)\ ,\ \alpha_n(K)\,\nu^K + (1 - \alpha_n(K))\,\delta_0\right) \ll 1.$$

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 “QSD regime” with probability α_n.

Proof: *the generator of the killed process is self-adjoint in some* $\ell^2(\pi)$ *with discrete spectrum.* $-\rho_0(K)$ *is the maximal eigenvalue, the analysis of* $Lu = -\rho_0 u$ *is inspired by matching techniques (Levinson) and* $\rho_1(K) - \rho_0(K)$ *is the spectral gap - Poincaré inequality.*

The logistic case

$$\mathbb{E}_{\nu^K}(T_0) = \frac{\sqrt{2\pi dc}}{(b-d)^2\sqrt{K}} e^{\frac{K}{c}(b-d+d\log\frac{d}{b})}\Big(1 + O\Big(\frac{(\log K)^3}{\sqrt{K}}\Big)\Big)$$

and the QSD ν^K is close to a Gaussian law centered in $[K\frac{b-d}{c}]$ with variance $2K\frac{b}{c}$.

For

$$\alpha_n(K) = 1 - \left(\frac{d}{b}\right)^n + \frac{\mathcal{O}(1)}{K}$$

and for K large enough and t with

$$K\log^2 K \ll t \ll \frac{1}{\sqrt{K}} e^{\frac{K}{c}(b-d+d\log\frac{d}{b})},$$

we have

$$\mathbb{P}_n(N_t^K \in \cdot\,) = \left(1 - \left(\frac{d}{b}\right)^n\right)\nu^K(\cdot) + \left(\frac{d}{b}\right)^n \delta_0(\cdot) + \frac{\mathcal{O}(1)}{K}.$$

How to get information from the data?

K is large.

- We observe the (fluctuating) population size on $[t_1; t_2]$.
- With high probability, the law of N_t^K is close to $N([K\frac{b-d}{c}], 2K\frac{b}{c})$.
- Ergodic theorem: the random variable

$$S_1(K) = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} N_s^K ds$$

  is a statistics for $[K\frac{b-d}{c}]$.
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$$S_2 = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} (N_s^K - S_1(K))^2 ds$$

  is the statistics of $2K\frac{b}{c}$.

Multi-type population process ; $d > 1$

We have $d > 1$ species competing for the same food resources.

$$N_t^K = (N_t^{K,1}, \cdots, N_t^{K,d}) \in (\mathbb{N})^d.$$

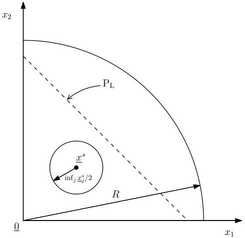
The generator is given by

$$\mathcal{L}_K f(\vec{n}) = K \sum_{j=1}^{d} \left[B_j(\frac{\vec{n}}{K})\big(f(\vec{n} + e^{(j)}) - f(\vec{n})\big) + D_j(\frac{\vec{n}}{K})\big(f(\vec{n} - e^{(j)}) - f(\vec{n})\big) \right].$$

The vector field $B - D$ has a unique fixed point $\vec{x}_* \in (\mathbb{R}_+)^d$ and any trajectory starting from $B(0,R) \cap (\mathbb{R}_+)^d \setminus \{0\}$ converges to $\vec{x}_*$.

Coming down from infinity:

$$\sup_{s>L} \frac{B_{max}(s)}{D_{min}(s)} > 1/2.$$



$$\forall\ \|x\| \leq R,\ \langle B(x) - D(x), x - x^* \rangle \leq -\beta \|x\| \|x - x^*\|^2.$$

Theorem

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

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

There exists a unique QSD ν^K, its death rate is $\rho_0(K)$, and

$$\sup_{\vec{n} \in \mathbb{N}^d \setminus \{\vec{0}\}} d_{TV}\Big(\mathbb{P}_{\vec{n}}(\vec{N}_t^K \in \cdot \mid T_0 > t), \nu^K\Big) \leq a_4\, e^{-\rho_1(K)\, t}.$$

and there exists $p_K(\vec{n}) \in (0,1]$ such that for

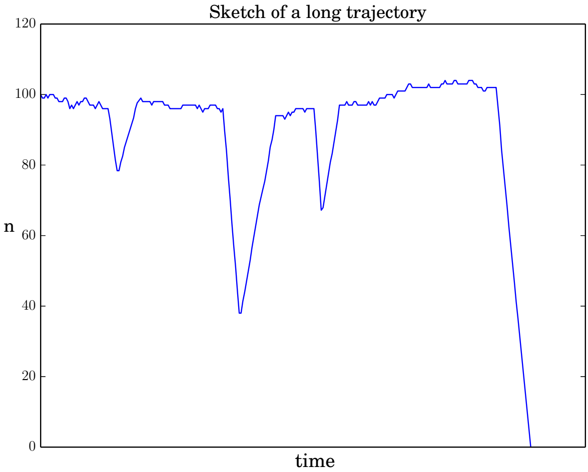
$$\log K \ll t \ll 1/\rho_0(K),$$

$$\sup_{\vec{n} \in \mathbb{N}^d \setminus \{\vec{0}\}} d_{TV}\Big(\mathbb{P}_{\vec{n}}(N_t^K \in \cdot), \; e^{-\rho_0(K)t} p_K(\vec{n})\, \nu^K + (1 - e^{-\rho_0(K)t} p_K(\vec{n}))\, \delta_0\Big) \ll 1.$$

We use a necessary and sufficient condition for the existence and uniqueness of a QSD together with the convergence in total variation established by N. Champagnat and D. Villemonais, 2016.

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

Thank you for your attention!



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

Remark that $u_n^0 = 1 + \sum_{j=1}^{n-1} \frac{1}{\lambda_j \pi_j}$ satisfies $(L_K u^0)(n) = 0$ for all $n \geq 1$ but $u^0 \notin \ell^2(\pi)$ and that the constant sequence 1 satisfies $(L_K 1)(n) = 0$ for all $n \geq 2$.

For small ρ, we guess a good approximation of $(L_K u)(n) = -\rho\, u_n$, of the form
$u_n = u_n^0 (1 + \delta_n)$ for $n \leq K\, x_*$
and of the form
$1 + w_n$ for $n \geq K\, x_*$.

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

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