Time scales in some large population birth and death processes, quasi stationary distribution and resilience.

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Joint work with J.-R.Chazottes and S.Méléard, together with S.Martínez for the second part.

Population dynamics of d interacting species is often modeled by a vector field $\vec{X}(\vec{x})$ on $\mathbb{R}^d_+$, x_j representing the concentration of species j ($1 \leq j \leq d$).

There is often a built-in splitting $\vec{X}(\vec{x}) = \vec{B}(\vec{x}) - \vec{D}(\vec{x})$ (birth and death rates) coming from the details of individual interactions. $\vec{B}(\vec{x})$ and $\vec{D}(\vec{x})$ have non-negative components and $\vec{B}(\vec{0}) = \vec{D}(\vec{0}) = \vec{0}$ reflect the absence of spontaneous generation.

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We will consider a situation where the number of individuals is large. This is represented by a parameter $K > 0$ (large) giving the order of magnitude of the number of individuals (a scale) maintained by the available resources.

We will denote by n_j the number of individuals of specie j, and $x_j = n_j / K$.

The vector field is associated (coming from) a microscopic time evolution of a birth and death (b.d.) process $\vec{N}(t) \in \mathbb{Z}_+^d$ ($\vec{N}(K, t)$) given by its transition rates

$$\mathbb{P}\big(N_j(t + dt) = n_j + 1, \, N_q(t + dt) = n_q \, \forall q \neq j \,\big|\, \vec{N}(t) = \vec{n}\big) = K \, B_j(\vec{n}/K) \, dt$$

$$\mathbb{P}\big(N_j(t + dt) = n_j - 1, \, N_q(t + dt) = n_q \, \forall q \neq j \,\big|\, \vec{N}(t) = \vec{n}\big) = K \, D_j(\vec{n}/K) \, dt$$

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For example if $B_j(\vec{x}) = \lambda_j\, x_j$, we have

$$\mathbb{P}\big(N_j(t + dt) = n_j + 1 \,\big|\, \vec{N}(t) = \vec{n}\big) = \lambda_j\, n_j$$

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Note that for populations of order K, the jump rate of the process $\vec{N}$ is of order K, hence the time interval between two consecutive jumps is of order $1/K$.

We will now distinguish different time scales ($\gg 1/K$).

On a time scale of order 1, we have convergence of the process to the time evolution of the vector field (Kurtz). Namely, for any $T > 0$ for any $\vec{x}_0 \in \mathbb{R}_+^d$, if $\lim_{K \to +\infty} \frac{\vec{N}(K, 0)}{K} = \vec{x}_0$, then for any $\epsilon > 0$

$$\lim_{K \to +\infty} \mathbb{P} \left(\sup_{t \leq T} \left| \frac{\vec{N}(K, t)}{K} - \vec{x}(t) \right| > \varepsilon \right) = 0;$$

where $d\vec{x}(t)/dt = \vec{X}(\vec{x})$ and $\vec{x}(0) = \vec{x}_0$.

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On a larger time scale, the trajectory of the process $\vec{N}(K, t)/K$ stay close to the trajectory of the diffusion process $\vec{Z}$ given by

$$dZ_j = X_j(\vec{Z})\, dt + \frac{\sqrt{B_j(\vec{Z}) + D_j(\vec{Z})}}{\sqrt{K}}\, dW_t$$

where $\vec{W}$ is the standard Brownian motion and $\vec{Z}(0) = \vec{N}_K(0)/K$. This is standard stochastic perturbation.

What about very large (infinite) time scale?

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We introduce a hypotheses of "descent from infinity", namely if the population is too large, the death rates (strongly) dominate the birth rates, namely $\lim_{\vec{x}\to\infty} \sup_j B_j(\vec{x})/\inf_j D_j(\vec{x}) = 0$. This is a consequence of competition, there is not enough food for everybody.

Under this hypothesis the process reaches $\vec{0}$ almost surely in finite time. If $T_{\vec{0}}$ denotes the first (and last) time the process $\vec{N}$ reaches $\vec{0}$, for any initial point $\vec{n}$ we have $\mathbb{P}_{\vec{n}}(T_{\vec{0}} < \infty) = 1$. This holds even if the fixed point $\vec{0}$ of the vector field $\vec{X}$ is repulsive. "In the long run we are all dead" (J.M.Keynes).

How long does it take for the process to reach $\vec{0}$? In other words what is the time scale of $T_{\vec{0}}$? In order to answer this question we have to make more hypothesis. They are tailored to make the model "as simple as possible" and can certainly be relaxed.

Besides the descent from infinity, we assume that $\vec{0}$ is a repeller and there is a unique fixed point $\vec{x_*}$ for the vector field $\vec{X}$, lying in the interior of $\mathbb{R}_+^d$, linearly stable and globally attracting. This is not a very interesting dynamical system but a rather frequent situation in ecology.

It turns out that $T_{\vec{0}} \sim \exp(\mathcal{O}(1)K)$, namely a very long time scale. I will make this statement more precise later on but before let us consider some numerical simulations to get a feeling of the behavior of the process. They were done with only one specie ($d = 1$), $K = 100$ and using different initial conditions, three of order K and the last one of order 1. Notice in this last case a behavior very different from the prediction of the vector field.
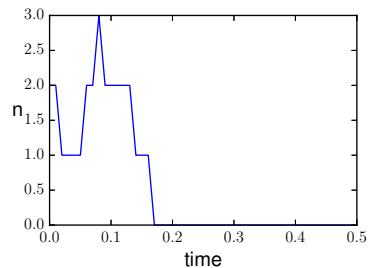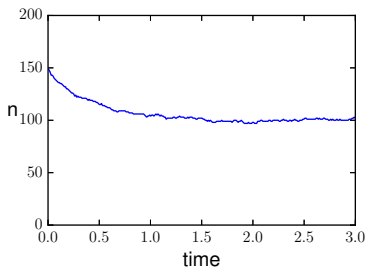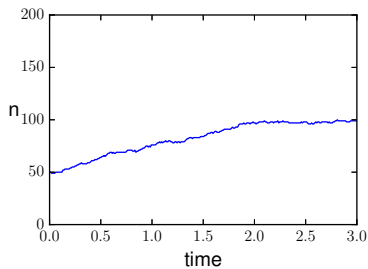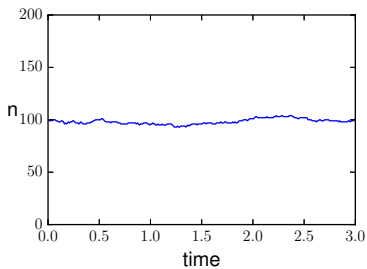
However the process will almost surely reach $n = 0$ in a finite time and stay there forever (extinction).

Sketch of a long trajectory
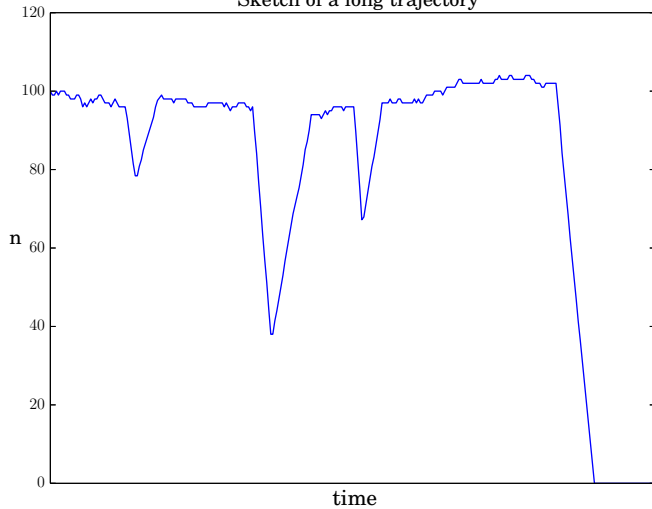
Summarizing:

1. If we start with $\vec{n}$ of order K, the size of the population stays of order K for a very long time with fluctuations (some eventually large ones) until a catastrophic event. A sort of "temporary stationarity" sets in.

2. If we start with $\vec{n}$ of order 1, there is a sizable probability (independent of K) such that $\vec{0}$ is reached in a time or order one (note the different scale of the graph).

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1. If we start with $\vec{n}$ of order K, the size of the population stays of order K for a very long time with fluctuations (some eventually large ones) until a catastrophic event. A sort of "temporary stationarity" sets in.

2. If we start with $\vec{n}$ of order 1, there is a sizable probability (independent of K) such that $\vec{0}$ is reached in a time or order one (note the different scale of the graph).

How to describe more precisely the first case? A measure ν (ν_K) on $\mathbb{Z}_+^d \setminus \{\vec{0}\}$ is a quasi stationary distribution (q.s.d.) if for any $t > 0$ and any set $A \subset \mathbb{Z}_+^d \setminus \{\vec{0}\}$ we have

$$\mathbb{P}_\nu\big(\vec{N}(t) \in A \mid T_{\vec{0}} > t\big) = \nu(A) .$$

The notion of q.s.d. replaces the notion of invariant measure when there is "leaking". For a b.d.p., if ν is a q.s.d. there exists $\rho_0 > 0$ such that for any $t \geq 0$, $\mathbb{P}_\nu\big(T_{\vec{0}} > t\big) = e^{-\rho_0\, t}$.

A necessary and sufficient condition for the existence of a (unique) q.s.d. for b.d.p. processes was established by N. Champagnat and D. Villemonais. They provide in particular an estimate for the rate of convergence (spectral gap). For $d > 1$ we used their result in our model and quantified the K dependence of the estimates. For $1/\rho_0$, the time scale of extinction in the q.s.d. $\left(\mathbb{P}_\nu \left(T_{\vec{0}} > t \right) = \exp(-\rho_0\, t) \right)$, we get

$$\frac{1}{\rho_0} \simeq e^{\mathcal{O}(1)\, K}$$

with a very precise estimate for $d = 1$ using WKB methods.

For the rate of convergence we get for some $a > 0$ independent of K

$$\sup_{\vec{n} \in \mathbb{Z}_+^d \setminus \{\vec{0}\}} \left\| \mathbb{P}_{\vec{n}}(\vec{N}(t) \in \cdot) - \mathbb{P}_{\vec{n}}\left(T_{\vec{0}} > t \right) \nu_K(\cdot) \right\|_{\mathrm{TV}} \leq 2\, e^{-a\, t/\log K}\,.$$

In our case TV is just the ℓ^1 norm.

This can be rephrased as (for all $\vec{n}$)

$$\left\| \mathbb{P}_{\vec{n}}(\vec{N}(t) \in \cdot) - \nu_K(\cdot) \right\|_{\mathrm{TV}} \leq 2\, e^{-a\, t/\log K} + \mathbb{P}_{\vec{n}}(T_{\vec{0}} < t)\,,$$

a kind of (pseudo) uniform ergodic theorem saying that the law of $\vec{N}$ approaches ν_K if we can ensure that the r.h.s. is small (note that $\delta_{\vec{0}}$ is the unique ergodic measure).

We proved that there exists $b > 0$, $c > 0$, $d > 0$ and $D > 0$, independent of K such that any $\vec{n} \in \mathbb{Z}_+^d$ and any $t \geq 0$

$$\mathbb{P}_{\vec{n}}\left(T_{\vec{0}} \leq t\right) \leq e^{-b(\|\vec{n}\|_1 \wedge (c\, K))} + t\, D\, e^{-d\, K}\,.$$

Therefore we get the error estimate for the uniform approach to the *q.s.d.*
$$\sup_{\vec{n} \in \mathbb{Z}_+^d \setminus \{\vec{0}\}} \left\| \mathbb{P}_{\vec{n}}(\vec{N}(t) \in \cdot) - \nu_K(\cdot) \right\|_{\mathrm{TV}} \leq$$
$$e^{-b(\|\vec{n}\|_1 \wedge (c\, K))} + 2\, e^{-a\, t/\log K} + t\, D\, e^{-d\, K}\,.$$

This error estimate $e^{-b(\|\vec{n}\|_1 \wedge (c\,K))} + 2\,e^{-a\,t/\log K} + t\,D\,e^{-d\,K}$ reflects what we saw in the simulations.

1. If the starting point $\vec{n}$ is of order one, the error is not small and the population can disappear in a time of order one (but it has also a sizable probability to survive for a long time).

2. If the starting point $\vec{n}$ is of order K, the error decreases with time at an exponential rate of order $1/\log K$ and becomes small if $t \ll \exp(dK)$.

3. If $t \approx \exp(dK)$ the error becomes large again.

4. Hence if $\log K \ll t \ll \exp(dK)$, the distribution of $\vec{N}(t)$ is very near to ν_K (for a starting point of order K).

Note the huge difference of time scales between $\log K$ (rate of convergence to ν_K), and $\exp(dK)$ (lower bound on the time scale of extinction), if K is "large".

Properties of the q.s.d. and of the process.

1. Exponential moments exists $\nu_K\big(\exp(\|\vec{N}\|)\big) \leq \exp\big(\mathcal{O}(1)K\big)$.

2. $\nu_K(\vec{N}) = K\,\vec{x}_* + \mathcal{O}(1)$, the carrying capacity.

3. Centered moments. For any $\ell \in \mathbb{Z}_+$, there exists $C_\ell > 0$ such that for any $K \geq 1$ $\nu_K\big(\|\vec{N} - \nu_K(\vec{N})\|^{2\ell}\big) \leq C_\ell\, K^\ell$.

4. There exists $\mathfrak{C} > 0$ such that for any $K \geq 1$, $\nu_K\big(\|\vec{N} - \nu_K(\vec{N})\|^2\big) \geq \mathfrak{C}\, K$.

5. There is a Gaussian approximation of ν_K near $\nu_K(\vec{N})$ with variance of order K (kind of C.L.T.).

Let $S_t(f)(\vec{n}) = \mathbb{E}_{\vec{n}}\big(f(\vec{N}(t))\big)$ be the Markov semi-group, then for some $C > 0$ independent of $K > 1$

$$\sup_{\vec{n} \in \mathbb{Z}_+^d} S_1\left(e^{\|\cdot\|}\right)(\vec{n}) \leq e^{C\,K}\,.$$

In particular, S_1 maps polynomially growing functions to bounded functions and is a compact operator in such Banach spaces.

Properties of the q.s.d. for one specie ($d = 1$).

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

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

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

$$d_{TV}\big(\mathbb{P}_n\big(N(t) \in \cdot\big)\,,\, \alpha_n(K)\,\nu_K + (1 - \alpha_n(K))\,\delta_0\big) \leq \mathcal{O}(1) \times$$

$$\left(\sqrt{K}\,\log K\,e^{-\mathfrak{c} K} + \big(1 - e^{-\rho_0 t}\big) + K e^{-\mathfrak{d} t/4} + K^{3/4}\,e^{\mathfrak{e} K}\,e^{-\rho_1 t}\right)\,,$$

where $\mathfrak{c}$, $\mathfrak{d}$ and $\mathfrak{e}$ are positive constants independent of K, and

$$\alpha_n(K) = 1 - \left(\frac{D'(0)}{B'(0)}\right)^n + \frac{\mathcal{O}(1)}{K}, \qquad \rho_1 \geq \frac{\mathcal{O}(1)}{\log K} \,.$$

Resilience.

Back to the dynamical system. Let
$$\mathcal{M} = D\vec{X}(\vec{x}_*) \,.$$

The engineering resilience is defined by (recall we assumed $\vec{x}_*$ to be a stable fixed point)

$$\mathcal{R} = - \sup_{z \in \mathrm{Sp}(\mathcal{M})} \mathrm{Re}(z) \; > 0,$$

The ecological resilience measures the size of the basin of attraction, a quantity more difficult to quantify (see Holling). Engineering resilience is useful for at least two major purposes:

1) It gives the exponential rate of relaxation to the equilibrium after a (small) perturbation. Large resilience means more stability.

2) It gives an estimation of the change of the equilibrium after a (small) perturbation of the system.

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One can prove a $\textsf{Einstein relation}$ (fluctuation dissipation relation)

$$\mathcal{M}\,\Sigma + \Sigma\,\mathcal{M}^t + 2\,\mathcal{D} = \mathcal{O}(\sqrt{K})\,. \tag{1}$$

where $\mathcal{D}$ is the diagonal matrix with entries $\mathcal{D}_{i\,i} = K\,D_i(\vec{x_*}) = K\,B_i(\vec{x_*})$ and Σ is the convariance matrix of ν_K

$$\Sigma_{i,j} = \int \left(n_i - \mu_i\right)\left(n_j - \mu_j\right)d\nu_K(\vec{n})\,, \qquad \vec{\mu} = \int \vec{n}\,d\nu_K(\vec{n})\,.$$

Note that each term on the l.h.s. of (1) is of order K. The Einstein result from 1905 was

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

relating friction (resilience, dissipation) to fluctuations.

Given an observed trajectory of the process $\vec{N}(t)_{0 \le t \le T}$, with $K^2 \ll T \ll \exp(\mathcal{O}(1)\, K)$ one can estimate Σ and $\mathscr{D}$.
If $d = 1$ (only one specie) we get

$$\mathcal{R} = \frac{\mathscr{D}}{\Sigma}.$$

If $d > 2$ (several species), the equation $\mathcal{M}\, \Sigma + \Sigma\, \mathcal{M}^t + 2\, \mathscr{D} = 0$ has many solutions for $\mathcal{M}$ (this is called a Sylvester equation). There is a unique symmetric solution but generically $\mathcal{M}$ is not symmetric.

Note that in statistical mechanics, the matrix $\mathcal{M}\, \Sigma$ is the matrix of kinetic coefficients. This matrix is symmetric if the system is reversible (Onsager). In ecological models this is in general not the case.

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One can use the time correlations. Define for $\tau > 0$

$$\Sigma_{i,j}(\tau) = \mathbb{E}_{\nu_K}\left(\left(N_i(\tau) - \mu_i\right)\left(N_j(0) - \mu_j\right)\right) .$$

Note that $\Sigma(0) = \Sigma$. One can prove that

$$e^{\tau\mathcal{M}} = \Sigma(\tau)\,\Sigma(0)^{-1} + O\left(\frac{1}{\sqrt{K}}\right) .$$

The matrices $\Sigma(\tau)$ and $\Sigma(0)$ can be estimated from the data $\vec{N}(t)_{0 \le t \le T}$, and choosing for example $\tau = 1$ one can estimate the matrix $\mathcal{M}$ and hence the resilience.

Note that the Einstein relation should still be valid providing some kind of verification of the result.

Note also that in the Einstein relation and in the above relation, the scale K does not appear explicitly, it is not an observable quantity.

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One can also integrate $\Sigma(\tau)$ from $\tau = 0$ to $\log K$ to get

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Note that estimation of the ecological resilience (size of the basin of attraction) requires the observation of large excursions (deviations) which only occur after a very long time, unless the system is near instability.

Statistics.

One can introduce statistics to estimate the various quantities of interest from the data. For $T > 0$ let

$$S_p^{\vec{\mu}} = \frac{1}{T} \int_0^T \vec{N}_p(s) \, ds \, ,$$

$$S_{p,\,q}^{\Sigma} = \frac{1}{T} \int_0^T \left(\vec{N}_p(s) - S_p^{\vec{\mu}} \right) \left(\vec{N}_q(s) - S_q^{\vec{\mu}} \right) \, ds \, ,$$

$$S_p^{\mathscr{D}} = \frac{1}{T} \, \# \big[\text{birth of specie } p \text{ for } 0 \le t \le T \big] \, ,$$

$$S_{p,\,q}^{*}(\tau) = \frac{1}{T-\tau} \int_0^{T-\tau} \left(\vec{N}_p(s+\tau) - S_p^{\vec{\mu}} \right) \left(\vec{N}_q(s) - S_q^{\vec{\mu}} \right) \, ds \, .$$

We will use the statistics $S^{\vec{\mu}}$ to infer $\vec{\mu}$, S^{Σ} to infer Σ, $S^{\mathscr{D}}$ to infer $\mathscr{D}$ and $S^*(\tau)$ to infer $\Sigma(\tau)$. From S^{Σ} and $S^*(\tau)$, we obtain an estimate of $\mathcal{M}$ as explained before. For one specie $(d = 1)$, S^{Σ} and $S^{\mathscr{D}}$ allow also to infer $\mathcal{M}$ using the Einstein relation.

Rates of convergence of the statistics.

The errors in the inferences depend on T and the starting point.
We have estimates for the L^2-distance between each of the above
statistics and the quantities to infer, starting in the q.s.d. or from
an initial condition. For example there exists $C > 0$, $\theta > 0$, $\mathfrak{f} > 0$,
$\mathfrak{g} > 0$, $\mathfrak{h} > 0$, and $\mathfrak{l}$ such that for any $K > 2$ and $T > 0$

$$\mathbb{E}_\nu \big(\big\| S^{\vec{\mu}}(T) - \nu(\vec{n}) \big\|^2 \big) \leq C \, K^2 \, \left(\frac{1 + \log K}{T} + (1 + T) \, e^{-\theta \, K} \right)$$

and

$$\mathbb{E}_{\vec{n}} \big(\big\| S^{\vec{\mu}}(T) - \nu(\vec{n}) \big\|^2 \big) \leq$$
$$C \, (\|\vec{n}\|_1 + K) \, \left[\frac{\|\vec{n}\|_1 + K \log K}{T \vee 1} + K \, e^{-\mathfrak{f} \left(\mathfrak{g} \frac{\|\vec{n}\|_1}{K} \wedge \mathfrak{h} \right) K} + T K \, e^{-\theta \, K} \right] .$$

Similar variance estimates hold for the other statistics.

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