Quasi-stationary distributions and diffusion models in population dynamics

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Quasi-stationary Distributions

The aim : To study the asymptotic behavior of the size $(Z_t)_t$ of some isolated biological population.

- No immigration
- Competition for limited resources implies extinction after some finite time T_0.
- $Z_t \geq 0, \ \forall t$ and 0 is an absorbing point.
- The population size fluctuates for large amounts of time before extinction : captured by the notion of quasi-stationarity.

References : Pollett, Seneta ;Vere-Jones, Van Doorn, Ferrari ;Kesten ; Martinez ;Picco, Collet ;Martinez ;San Martin, Gosselin, Steinsaltz ;Evans, Lambert

Quasi-stationary distribution

Definition : ν quasi-stationary distribution (QSD) if $\forall A \subset (0, +\infty)$, $\forall t$,

$$P_\nu(Z_t \in A | T_0 > t) = \nu(A).$$

Example : If $\exists \mu$ probability measure on $\mathbb{R}_+^*$ such that

$$\lim_{t \to +\infty} P_x(Z_t \in A | T_0 > t) = \mu(A), \quad x \text{ fixed population size},$$

then μ is a QSD. μ is called Yaglom limit.

Definition : Q-process : law of the process conditioned to be never extinct.

$$\forall B_s \in \mathcal{F}_s, Q_x(B_s) = \lim_{t \to +\infty} P_x(Z \in B_s | T_0 > t).$$

Question : Long time behavior of this process ?

Population Dynamics

Our aim : To study QSD and Q-processes for population dynamics obtained as scaling limits of generalized birth-death processes.

- Birth-death process $(Z_t^N)_t$ with absorbing state 0.
- renormalized by weights $\frac{1}{N}$: values in $\frac{1}{N}\mathbb{N}$.
- birth rates $b_N(z)$, $b_N(0) = 0$.
- death rates $d_N(z)$, $d_N(0) = 0$.

Convergence Theorem

Assumptions :

- $\exists \gamma \geq 0$ and a smooth funtion h with $h(0) = 0$, such that

$$\frac{b_N(z) - d_N(z)}{N} \to h(z) \; ; \; \frac{b_N(z) + d_N(z)}{N^2} \to \gamma z.$$

- The function h is the limiting growth rate.
- γ is a demographic parameter describing the ecological timescale.
- $(Z_0^N)_N$ converges as $N \to \infty$: population size of order N.
- Then, (Lipow or Joffe-Métivier),

$$(Z_t^N, t \geq 0) \Rightarrow (Z_t, t \geq 0).$$

The limiting process

- If $\gamma = 0$, dynamical system $dZ_t = h(Z_t)dt.$
  - 0 (unstable) equilibrium ($h(0) = 0$),
  - Existence of a non-trivial stable equilibrium.

- If $\gamma > 0$,

$$dZ_t = \sqrt{\gamma Z_t}dB_t + h(Z_t)dt.$$

  - Acceleration of ecological process $\Rightarrow$ noise (demographic stochasticity).
  - The function $\frac{h(z)}{z}$ is the mean individual growth rate.
  - If the growth function $h \equiv 0$, Z is a Feller diffusion.
  - The process Z is called a generalized Feller diffusion.

Examples

- $h(z) = rz$: continuous state branching process.
- $h(z) = rz - cz^2$: logistic branching process (Lambert).
- $h(z) = (rz - cz^2)\left(\frac{z}{K_0} - 1\right)$: Allee effect, the individual growth rate $\frac{h(z)}{z}$ increases, then decreases. (Cooperation, then competition).

Continuous state branching process (Lambert) :

- subcritical case $r < 0$: infinite number of QSD
- critical case $r = 0$: no QSD
- supercritical case $r > 0$: no sense but

$$\mathcal{L}(Z|\text{extinction}) \sim CSBP(-r).$$

More generally, if there exists $h_\infty = \lim_{z\to\infty} h(z) \in [-\infty, +\infty]$, then h_∞ determines the long time behavior of the process.

3 cases :

- If $h_\infty = -\infty$, subcritical case, process a.s. absorbed at 0 in finite time. Existence of a Yaglom limit.
- If $h_\infty \in (-\infty, +\infty)$, critical case. Nothing known concerning QSD.
- **Proposition :** If $\lim_{z\to+\infty} h(z) = +\infty$, then the generalized Feller diffusion Z conditioned on eventual extinction satisfies

$$dY_t = \sqrt{\gamma Y_t}dB_t + \left(h(Y_t) + \gamma Y_t \frac{u'(Y_t)}{u(Y_t)}\right) dt,$$

where $u(y) = P_y(\lim_t Z_t = 0)$ and

$$h(y) + \gamma y \frac{u'(y)}{u(y)} \sim_{y\to\infty} -h(y).$$

Existence and uniqueness of a QSD in the subcritical case

Theorem :
Assume

$$\lim_{z\to\infty} \frac{h(z)}{\sqrt{z}} = -\infty \quad \text{(strong competition in large population)},$$

$$\lim_{z\to\infty} \frac{zh'(z)}{h(z)^2} = 0 \quad \text{(technical assumption, fulfilled for most}$$

classical biological models).

Then there exists a probability measure ν such that

- For each initial law with bounded support (in particular for each Dirac measure),

$$\mathcal{L}(Z_t | T_0 > t) \Rightarrow \nu, \quad \text{exponentially fast.} \tag{1}$$

$\Rightarrow$ existence of a QSD (Yaglom limit).

- The Q-process is well defined and converges, when $t \to +\infty$, to a measure absolutely continuous w.r.t. ν.
- If

$$\int_1^\infty \frac{1}{-h(z)} dz < \infty \ ,$$

then Z comes down from infinity and (1) holds for all initial law :

$\Rightarrow$ uniqueness of the QSD.

The associated Kolmogorov equation

We introduce $X_t = 2\sqrt{\frac{Z_t}{\gamma}}$. Then

$$dX_t = dB_t - \frac{1}{2X_t}dt + \frac{2}{\gamma X_t} h\left(\frac{\gamma X_t^2}{4}\right) dt.$$

Example : $h(z) = rz - cz^2$,then

$$dX_t = dB_t - \frac{1}{2X_t}dt + \left(\frac{rX_t}{2} - \frac{c\gamma X_t^3}{8}\right) dt.$$

The diffusion has the form :

$$dX_t = dB_t - q(X_t)dt,$$

where $q(x) \sim_{x\to 0} \frac{1}{2x}$ and $q(x) \mapsto_{x\to+\infty} +\infty$.

Study of QSD for the diffusion

$$dX_t = dB_t - q(X_t)dt.$$

Mandl (1961), Collet, Martinez, San Martin (1995) and Evans, Steinsaltz (2007) under Mandl's conditions : q is C^1 up to 0 and doesn't grow to fast to infinity at ∞.

Here

- $q \in C^1(]0, +\infty[)$.
- Define T_y : first time the process hits y.
- Explosion time : $\tau = T_0 \wedge T_\infty$.

Assumption (H1) :

$$\forall x, \quad P_x(\tau = T_0 < +\infty) = 1.$$

Remark : (H1) satisfied if X comes as previously from a generalized Feller diffusion.

Reference measure :

For $Q(x) = \int_1^x 2q(u)du$, let us define on $(0, +\infty)$ the measure

$$\mu(dx) = e^{-Q(x)}dx.$$

Remark : μ is not necessarily bounded : $Q(x) \sim_{x\to 0} \ln x$ if $q(x) \sim_{x\to 0} -\frac{1}{2x}$.

Nevertheless $L^2(\mu)$ is the natural space to work with.

Theorem : (By Girsanov's theorem)

$$P_t g(x) = E(g(X_t)\mathbf{1}_{t<T_0}) \;=\; \int_0^\infty g(y) r(t,x,y)\mu(dy)$$

and if $\exists\ C > 0$ such that $\forall y > 0,\ q^2(y) - q'(y) \geq -C$, then $r \in L^2(\mu)$ and

$$\int_0^\infty r^2(t,x,y)\mu(dy) \leq \frac{1}{\sqrt{2\pi t}} e^{Ct} e^{Q(x)}.$$

Define :

$$< f, g >_\mu = \int_0^\infty f(y)g(y)\mu(dy).$$

Define the symmetric form defined for $f, g \in C_c^\infty((0, +\infty))$ by

$$\mathcal{E}(f, g) =< f', g' >_\mu,$$

Dirichlet forms theory (Fukushima) :

- P_t extends to a symmetric sub-Markovian semi-group of contractions on $L^2(\mu)$.
- Its generator L is non-positive self-adjoint on $L^2(\mu)$ with domain $D(L)$ and for $f \in C_c^\infty((0, +\infty))$, $Lf = \frac{1}{2}f'' - qf'$.

Spectral theory

Assumption (H2) : (i) $\exists\ C > 0$ such that $\forall y > 0$, $q^2(y) - q'(y) \geq -C$.
(ii) $\lim_{y\to+\infty} q^2(y) - q'(y) = +\infty$.

Spectral Theory in $L^2(\mu)$: Assume (H1) and (H2), then

- $(-L)$ has a purely discontinuous spectrum $0 < \lambda_1 < \ldots < \lambda_n \ldots$, each λ_k is simple.
- (η_k) BON of eigenfunctions, and $\eta_1(x) > 0$, $\forall x > 0$.
- For $f \in L^2(\mu)$, $P_t f =_{L^2} \sum_k e^{-\lambda_k t} < \eta_k, f >_\mu \eta_k$.
- $< P_t f, g >_\mu \sim_{t\to\infty} e^{-\lambda_1 t} < \eta_1, f >_\mu < \eta_1, g >_\mu$.

Proof : We transform the spectral theory for a Fokker-Planck operator in a spectral theory for a Schrödinger operator.

For $f \in L^2(dx)$, we set

$$\tilde{P}_t f(x) = e^{-Q/2} P_t(f \; e^{Q/2}).$$

$\tilde{P}_t$ is a strongly continuous semi-group on $L^2(dx)$ with generator

$$\tilde{L} = \frac{1}{2}\Delta - \frac{1}{2}(q^2 - q'),$$

on $C_c^\infty((0, +\infty))$.

Rem : The potential $q^2 - q'$ is not in L^∞_{loc} near 0. Adaptation of Berezin-Shubin.

The Yaglom limit

For $f \in L^2(\mu)$,

$$P_t f =_{L^2} \sum_k e^{-\lambda_k t} < \eta_k, f >_\mu \eta_k.$$

Heuristically,

$$\begin{aligned} P_t \mathbf{1}_A &\sim_{t\to\infty} e^{-\lambda_1 t} < \eta_1, \mathbf{1}_A >_\mu \eta_1, \\ P_t \mathbf{1}_{\mathbb{R}_+^*} &\sim_{t\to\infty} e^{-\lambda_1 t} < \eta_1, 1 >_\mu \eta_1. \end{aligned}$$

Then if $x > 0$,

$$\frac{P_t \mathbf{1}_A(x)}{P_t \mathbf{1}_{\mathbb{R}_+^*}(x)} \longmapsto_{t\to\infty} \frac{< \eta_1, \mathbf{1}_A >_\mu}{< \eta_1, 1 >_\mu}.$$

A good candidate to be the Yaglom limit is $\nu_1 = \frac{\eta_1 d\mu}{<\eta_1, 1>_\mu}$, if $\eta_1 \in L^1(\mu)$.

Theorem : Assume (H1), (H2), and $\eta_1 \in L^1(\mu)$, and consider $\nu_1 = \frac{\eta_1 d\mu}{<\eta_1, 1>_\mu}$. Then

- $P_x(T_0 > t) \sim_{t\to\infty} e^{-\lambda_1 t}\eta_1(x) < \eta_1, 1 >_\mu$.
- ν_1 is a Yaglom limit :

$$\forall x > 0, \lim_{t\to\infty} P_x(X_t \in A | T_0 > t) = \nu_1(A).$$

- ν_1 is a QSD and $P_{\nu_1}(T_0 > t) = e^{-\lambda_1 t}$.
- Speed of convergence : If moreover $\eta_2 \in L^1(\mu)$,

$$\lim_{t\to\infty} e^{(\lambda_2-\lambda_1)t}\left(P_x(X_t \in A | T_0 > t) - \nu_1(A)\right) < +\infty.$$

The Q-process

Theorem : 1) Assume $B_s \in \mathcal{F}_s$. Then for all $x > 0$,

$$\lim_{t \to +\infty} P_x(X \in B_s | T_0 > t) = Q_x(B_s).$$

Q_x has the transition probability densities (w.r.t. Lebesgue measure)

$$q(s, x, y) = e^{\lambda_1 s} \frac{\eta_1(y)}{\eta_1(x)} r(s, x, y) e^{-Q(y)}.$$

2) For any Borel set A,

$$\lim_{s \to +\infty} Q_x(\omega_s \in A) = \int_A \eta_1^2(y) \mu(dy).$$

The stationary measure of the Q-process is absolutely continuous w.r.t. ν_1.

Domain of attraction and uniqueness

Definition : X comes down from ∞ if

$$\exists t_0,\ \exists y_0, s.t.\ \lim_{x\to\infty} P_x(T_{y_0} < t_0) > 0.$$

Definition : We say that (H3) is satisfied if

$$\int_1^\infty e^{Q(y)} \left(\int_y^\infty e^{-Q(z)} dz \right) < \infty.$$

Theorem : Assume (H1), (H2), and that $\eta_1 \in L^1(\mu)$. The following conditions are equivalent.

- X comes down from ∞.
- (H3).
- ν_1 is the unique limiting conditional distribution, namely

$$\lim_{t\to\infty} P_\nu(X_t \in A | T_0 > t) = \nu_1(A),$$

for any Borel set A and any initial distribution ν, and then ν_1 is the unique QSD.

Proof : Condition (H3) allows us to construct a Lyapounov function to obtain the intermediary result : for any $A > 0$, there exists $y_A > 0$, such that $\sup_{x>y_A} E_x(e^{AT_{y_A}}) < +\infty$.

Remarks : 1) Our result is very different of the previous ones obtained under the Mandl's conditions, for which there is an infinite number of QSD.

2) If $q'(x) \geq 0$ for $x > 0$ and $q(x) \mapsto_{x\to+\infty} +\infty$, then

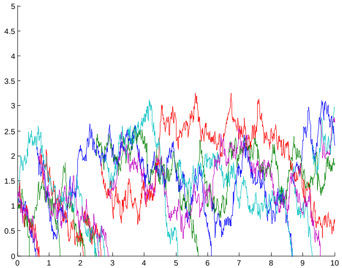
$$(H3) \Leftrightarrow \int^{\infty} \frac{1}{q(x)} dx < \infty.$$

It's true in the logistic case.

3) As corollary, we obtain that for all $\lambda < \lambda_1$, $\sup_{x>0} E_x(e^{\lambda T_0}) < \infty$, generalizing Lambert's result $\sup_x E_x(T_0) < \infty$ obtained in the logistic case.

Works in Progress.

- Generalization to multi-type populations : d-dimensional equations.
- Evolution : each individual is characterized by an heritable trait, (except when a mutation occurs). Birth and death process with mutation and selection, nonlinear super-processes : Infinite-dimensional problems.
- Approximation of the QSD by Fleming-Viot systems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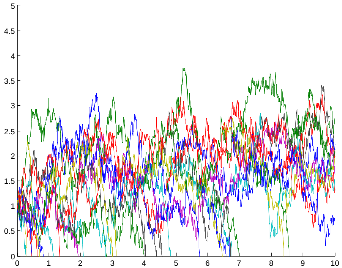
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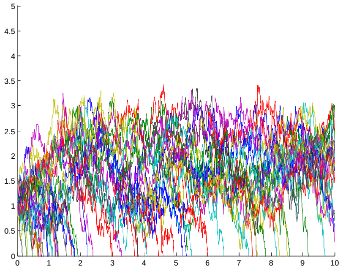
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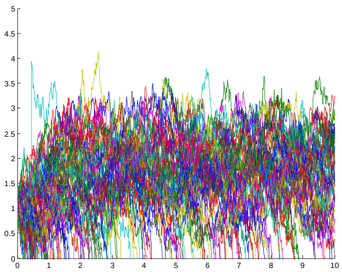

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