Quasi-stationarity and applications to models of population adaptation

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Introduction

I extend the approach of [1] to obtain results of quasi-stationarity for models where the extinction has a stabilizing effect. I apply it notably to an elementary model for the adapatation of a population to changing environmental conditions.

Among the major questions :
Under which condition can we say that the population is adapting ?
What is the importance for this adaptation of the different mutation effects involved ?

Averaged over a long time, by looking back at the ancestral line of a surviving population, a specific profile of mutation effects shall arise. We notably want to investigate how this profile is constrained.

Notations

Extinction happens at time τ_∂
Interest in comparing the extinction rate λ to the convergence rate to the QSD γ .

For any set $\mathcal{D}$, we defined its exit and its hitting times as :

$$
\begin{aligned}
T_{\mathcal{D}} &:= \inf\{t \geq 0\,;\; X_t \notin \mathcal{D}\}\\
\tau_{\mathcal{D}} &:= \inf\{t \geq 0\,;\; X_t \in \mathcal{D}\}\,.
\end{aligned}
$$

Quasi-ergodic measure :
$\beta(dx, dn) = h(x, n)\, \alpha(dx, dn)$
Quasi-ergodic jump measure : $J(dx, dw)$
$= \int_{\mathbb{R}_+} \alpha(dx, dn)\, f(n)\, g(x, w) h(x + w, n)$
$\{\times \exp[\theta F(x, w)]$ if jumps are biased$\}$

References

[1] Champagnat, N., Villemonais, D.; Exponential convergence to quasi-stationary distribution and Q-process, Probab. Theory Relat. Fields, V. 164, pp. 243–283 (2016)

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A set of generic conditions

There exists a sequence $(\mathcal{D}_\ell)_{\ell \geq 1}$ of closed subsets of $\mathcal{X}$ s. t. : $\forall\, \ell \geq 1,\ \mathcal{D}_\ell \subset \mathcal{D}_{\ell+1}^{\circ}$ and $\cup_{\ell \geq 1} \mathcal{D}_\ell = \mathcal{X}$.
$(A1)$: **"Mixing property" :** There exists a probability measure $\zeta \in \mathcal{M}_1(\mathcal{X})$ such that, for any $\ell \geq 1$, there exists $L > \ell$ and $c, t > 0$ such that :

$$\forall\, x \in \mathcal{D}_\ell, \qquad \mathbb{P}_x\left[X_t \in dx\,;\; t < \tau_\partial \wedge T_{\mathcal{D}_L}\right] \geq c\, \zeta(dx).$$

$(A2)$: **"Escape from the Transitory domain" :** *For a $\rho > \rho_S$ and $\mathcal{D}_E \in \mathbf{D}$:*

$$\sup_{\{x \in \mathcal{X}\}} \mathbb{E}_x\left(\exp\left[\rho\left(\tau_\partial \wedge \tau_{\mathcal{D}_E}\right)\right]\right) < \infty.$$

This exponential moment is compared to the following **"survival estimate"** :

$$\rho_S := \sup\left\{\rho \geq 0 \,\middle|\, \sup_{\{L \geq 1\}} \liminf_{\{t > 0\}}\ e^{\rho t}\, \mathbb{P}_\zeta(t < \tau_\partial \wedge T_{\mathcal{D}_L}) = 0\right\} \vee 0.$$

$(A3)$: **"Asymptotic comparison of survival" :** $\displaystyle \limsup_{t \to \infty}\ \sup_{x \in \mathcal{D}_E} \frac{\mathbb{P}_x(t < \tau_\partial)}{\mathbb{P}_\zeta(t < \tau_\partial)} < \infty.$

These conditions $(A1 - 3)$ are sufficient for our theorems.
This last condition $(A3)$ might be difficult to prove directly for processes that are not strong Feller.
A method is proposed in [6] to ensure $(A3)$ given the other assumptions and an additional estimate.

Theorem of Quasi-Stationarity

Convergence to the Quasi-Stationary Distribution α :

$$\left\|\, \mathbb{P}_\mu\left[X_t \in dx \mid t < \tau_\partial\right] - \alpha(dx) \,\right\|_{TV} \leq C \frac{\inf_{\gamma > 0} \|\mu - \gamma \alpha\|_{TV}}{\langle \mu \,|\, h \rangle}\, e^{-\zeta\, t}.$$

The function h, the "survival capacity" , is described as the limit of the following functions :

$$h_t(x) := e^{\lambda\, t}\mathbb{P}_x(t < \tau_\partial) = \mathbb{P}_x(t < \tau_\partial)/\mathbb{P}_\alpha(t < \tau_\partial), \quad x \in \mathcal{X}.$$

The convergence of h_t to h is uniform over $\mathcal{X}$ at exponential rate.

Illustration on a model of population

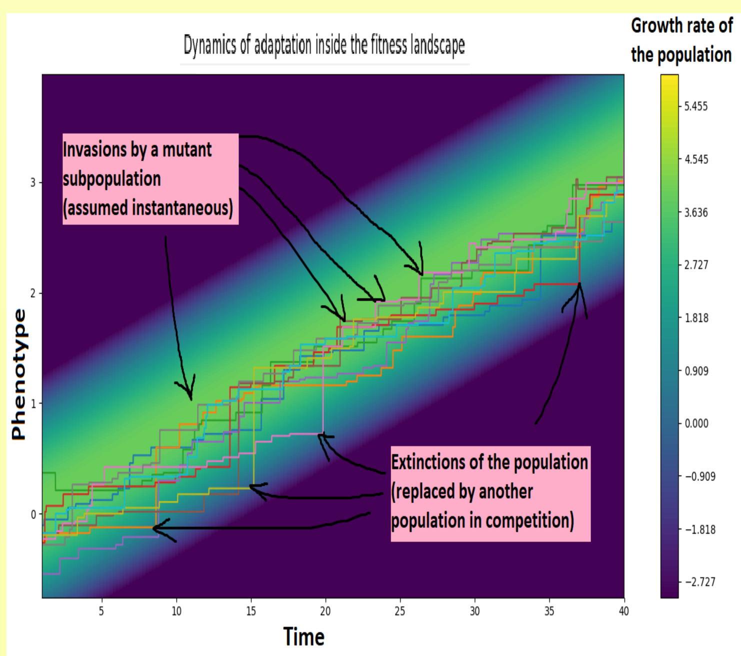
The dynamics of the adaptation parameter X is driven by the environmental change at speed v and by the fixation of new mutations in the population, whose success rate is encoded through the Poisson Point Process M with intensity $ds\, \nu(dw)\, du$.

$$X_t = x - v\, t + \int_{[0,t] \times \mathbb{R}^d \times \mathbb{R}_+} w\, \mathbf{1}_{\{u \leq f(N_s)\; g(X_{s-},\, w)\}}\, M(ds, dw, du),$$

Extinction happens at time τ_∂ as soon as N_t reaches 0 (no more individuals in the population),

$$\text{with } N_t = n + \int_0^t \left(r(X_s)\, N_s - c\,(N_s)^2\right) ds + \sigma \int_0^t \sqrt{N_s}\, dB_s,$$

where B is a Brownian Motion and $r(x) \underset{|x| \to \infty}{\longrightarrow} -\infty$
(extreme values of X_t are not viable)



Population following the environmental change

Large deviation extensions

What we intend to prove is that at least for some test functions F, g, we have the following large deviations estimate :

$$\tfrac{1}{t} \log \mathbb{P}_\mu\left[\Delta_t(F, g) \geq \epsilon \mid t < \tau_\partial\right] \to -I(F, g, \epsilon), \quad \text{as } t \to \infty$$
$$\text{where } t \times \Delta_t(h) := \textstyle\sum_{s \leq t} F(X_{s-}, \Delta X_s) + \int_0^t g(X_s)\, ds - \langle J \,|\, F \rangle - \langle \alpha \,|\, h \times g \rangle$$

uniform over the initial condition.
From the literature on Large Deviation theory, such an estimate of $I(h, \epsilon)$ is related to the quasi-stationarity of X_t when the natural probability law $\mathbb{P}_\mu$ is biased to favor larger values of $\Delta_t(F, g)$ (see notably [2]) : the weight $\exp[\theta\, t\, \Delta_t(F, g)]$ with the renormalization plays a role very similar to the one of conditioning that the process is not extinct. The proof that the biased process is quasi-ergodic may rely on the same criteria as for the unbiased process.
In a paper in preparation, I show that convergence results for the biased processes are sufficient to imply the Gartner-Ellis conditions, thus the large deviation estimates. When the bias on the jumps may be positive, there is still an issue of weight explosion.
Numerically, looking at the deviation produced by specific values of θ, we can see which directions are the most rigid, so possibly under stronger selective effects.