Adaptation to a gradual environment - Research of lineages

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Climate change adaptation

- One observes rapid phenotypic changes in invasive or natural populations that are subject to environmental changes.
- Such fast evolution may result in adaptation of these populations facing changing environment.

Our aim:

- To model the response of a population to a gradual change in environment, based on an individual-based model.
- To capture the dynamics in the past of the lineage (genetic history) of an individual chosen at random at a fixed time.

The population process

- Each individual is characterized by a quantitative genetic or phenotypic real parameter, usually called trait.
- The parameter K scales the population size. It will be large.
- Population of $N^K(t)$ individuals weighted by $\frac{1}{K}$ and traits

$$(X_t^1, \cdots, X_t^{N^K(t)}) \in \mathbb{R}^{N^K(t)}.$$

- The population is described by the point measure

$$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N^K(t)} \delta_{X_t^i}.$$

$$\int \varphi(x)\nu_t^K(dx) = \frac{1}{K} \sum_{i=1}^{N^K(t)} \varphi(X_t^i) \quad ; \quad \int \nu_t^K(dx) = \frac{N^K(t)}{K}$$

- The population process $(\nu_t^K, t \geq 0)$ is a Markov process with values in $\mathbb{D}(\mathbb{R}_+, \mathcal{M}_F(\mathbb{R}))$.

The transitions

- BIRTH

  Clonal reproduction at rate 1 from each individual of trait x : the offsprings inherits of x.

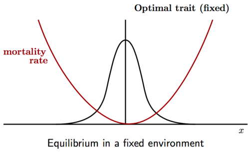
- MUTATION: two different modeling

  1) During its life time, the trait of the individual is submitted to many very small centered mutations.
  Its behavior is modeled by a Brownian motion with variance σ^2.

  2) At rate 1, there is a reproduction event with mutation.
  The offspring of an individual with trait x will inherit the trait $x + \sigma h$, where h is distributed according to a symmetric law $G(h)dh$.
  (Ex: $G(h)dh$ is a centered reduced Gaussian law).

The mortality rate

- Without environmental effect: mutation-selection balance



Each individual with trait x dies at rate

$$\frac{x^2}{2} + \frac{N^K(t)}{K} = \frac{x^2}{2} + \int \nu_t^K(dx).$$

The intrinsic death rate $\frac{x^2}{2}$ depends on the trait x of the individual.

$\frac{1}{K}$: competition pressure between two individuals.

The term $\int \nu_t^K(dx)$ represents the interaction between individuals.

Effect of the environment

• The environment evolves linearly in time at the velocity σc.

• The optimal trait is driven by the environment: the optimal trait at time t will be σct.

• In our modeling, we will replace the death rate $x^2/2$ by $(x - \sigma ct)^2/2$.

• Moving optimal trait: $x = \sigma ct$.

The stochastic population process

The population process ν^K is solution of a stochastic differential equation driven by Poisson point measures governing birth and death events and Brownian motions or Poisson processes governing mutations.

Semi-martingale decomposition.

$$
\begin{aligned}
\int \varphi(x)\nu_t^K(dx) &= \int \varphi(x)\nu_0^K(dx) + M_t^K(\varphi) \\
&\quad + \int_0^t \int \left(1 - \frac{(x-\sigma cs)^2}{2} - \int \nu_s^K(dx)\right) \varphi(x)\nu_s^K(dx)ds \\
&\quad + \begin{cases} \int_0^t \int \frac{\sigma^2}{2}\varphi''(x)\,\nu_s^K(dx)ds \\ \int_0^t \int \int \varphi(x+\sigma h) - \varphi(x))G(h)dh\,\nu_s^K(dx)ds \end{cases}
\end{aligned}
$$

where $M^K(\varphi)$ is a square integrable martingale with

$$\mathbb{E}((M_t^K(\varphi))^2) = \frac{C(\varphi,t)}{K}.$$

Large population approximation

Proposition: *Let $T > 0$. Under appropriate assumptions, the population process ν^K is approximated on $[0,T]$ by the unique weak solution of*

$$\partial_t u(t,x) = \Big(1 - \frac{(x-\sigma ct)^2}{2} - \int u(t,x)dx\Big)u(t,x) + \begin{cases} \frac{\sigma^2}{2}\partial^2_{xx} u(t,x) \\ \int (u(t,x+\sigma h) - u(t,x))G(h)dh \end{cases} .$$

That means that $\forall \varepsilon > 0$, $\forall \varphi \in C_b^2$,

$$\lim_{K\to+\infty} \mathbb{P}(\sup_{t\leq T} |\int \varphi(x)\nu_t^K(dx) - \int \varphi(x)u(t,x)dx| > \varepsilon) = 0.$$

In particular,

$$\lim_{K\to+\infty} \mathbb{P}(\sup_{t\leq T} |\int \nu_t^K(dx) - \int u(t,x)dx| > \varepsilon) = 0.$$

Moving Framework - Gaussian case

Let us define $\widetilde{Z}^K$ as the image-measure of ν^K by the map $x \longrightarrow x - \sigma c t$.

Then for all C_b^2 function φ,

$$\int \varphi(x)\widetilde{Z}_t^K(dx) = \int \varphi(x)\nu_0^K(dx) + \widetilde{M}_t^K(\varphi)$$
$$+ \int_0^t \int \left(\left(1 - \frac{x^2}{2} - \int \widetilde{Z}_s^K(dx)\right) \varphi(x) - \sigma c \varphi'(x) + \frac{\sigma^2}{2}\varphi''(x)\right)\widetilde{Z}_s^K(dx)ds.$$

where $\widetilde{M}^K(\varphi)$ is a square integrable martingale with second order moment of the form $\frac{C(T,\varphi)}{K}$.

The macroscopic approximation when K is large is given by the density profile $f(t,x) = u(t, x + \sigma c t)$, solution of

$$\begin{aligned} \partial_t f(t,x) &= \left(1 - \frac{x^2}{2} - \int f(t,x)dx\right) f(t,x) + \sigma c \partial_x f(t,x) \\ &\quad + \frac{\sigma^2}{2}\partial^2_{xx} f(t,x). \end{aligned}$$

with $f(0,x) = u_0(x)$.

The stationary distribution

Theorem: Gaussian case.

There is a unique positive stationary distribution, solution of

$$\frac{\sigma^2}{2}F'' + \sigma c F' + \left(1 - \frac{x^2}{2} - \int F\right)F = 0,$$

if and only if

$$1 - \frac{\sigma}{2} - \frac{c^2}{2} > 0.$$

It is given by

$$F(x) = \frac{\lambda}{\sqrt{2\pi\sigma}} \exp\left(-\frac{(x+c)^2}{2\sigma}\right) \text{ and } \int F(x)dx = \lambda = 1 - \frac{\sigma}{2} - \frac{c^2}{2}.$$

Remark: If $u_0 = F$, then for any $\varepsilon > 0$,

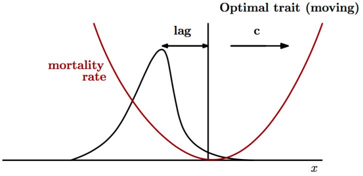
$$\lim_{K\to+\infty} \mathbb{P}(\sup_{t\leq T} |\int \widetilde{Z}_t^K(dx) - \lambda| > \varepsilon) = 0.$$

The population follows the optimum that moves to the right at the constant speed σc.

The shape of the wave that follows this movement "stabilizes" to become

$$u(x,t) = F(x - \sigma c t).$$

In the Gaussian case, F has its maximum in -c in the moving reference frame. The population is always "behind" its environment.

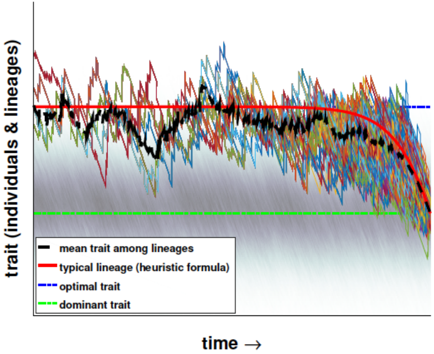


Equilibrium in a changing environment

Stationary dynamics - Research of genetic lineages in a gradual environment

Assume that the population is at equilibrium in the moving reference frame.

Question: **what is the internal dynamics in the stationary distribution**?



The grey background is the stationary density of individuals F. The y axis represents the phenotype z in the moving frame ($z = x - ct$).

The maladaptive individuals of yesterday have become more adapted today and these phylogenies can be seen as a "trace" of past environmental change.

The associated branching-diffusion process: the nonlinearity is frozen

We construct on the same probability space a branching-diffusion process $(Z^K_t, t \geq 0)$, issued from the same initial condition where the nonlinearity is fixed to $\lambda = \|F\|_1$.

For any $\varphi \in C^2_b(\mathbb{R})$,

$$\int \varphi(x) Z^K_t(dx) = \int \varphi(x) \nu^K_0(dx) + M^K_t(\varphi)$$
$$+ \int_0^t \int \Big(\big(1 - \frac{x^2}{2} - \lambda\big) \varphi(x) - \sigma c \varphi'(x) + \frac{\sigma^2}{2} \varphi''(x) \Big) Z^K_s(dx) ds.$$

• We assume that ν^K_0 converges in law to F. (For example, the r.v. X^i_0 are independent with law F).

Then

$$\lim_{K \to +\infty} \mathbb{E}\Big(\sup_{t \leq T} \Big| \int \varphi(x) Z^K_t(dx) - \int \varphi(x) \widetilde{Z}^K_t(dx) \Big|^2 \Big) = 0.$$

We will approximate the nonlinear process by the branching-diffusion process which has beautiful properties based on the branching property.

In particular, it's enough to consider one initial individual taking $K = 1$.

An auxiliary one-dimensional process

One initial individual and $K = 1$.

We can easily observe (using Itô's Formula) that for any bounded continuous function φ, for $t \geq 0$ and $x \in \mathbb{R}$,

$$\mathbb{E}_{\delta_x}\Big[\int \varphi(x) Z_t(dx)\Big] = \mathbb{E}_x\Big[\exp\Big(\int_0^t \Big(1 - \frac{1}{2}Y_s^2 - \lambda\Big)\,ds\Big)\varphi(Y_t)\Big],$$

where Y is the drifted Brownian motion

$$dY_t = \sigma(dB_t - c\,dt).$$

Then, $m_t(x) = \mathbb{E}_{\delta_x}\Big[\int Z_t(dx)\Big]$ satisfies

$$m_t(x) = \mathbb{E}_x\Big[\exp\Big(\int_0^t \Big(1 - \frac{1}{2}Y_s^2 - \lambda\Big)\,ds\Big)\Big],$$

and then $m \in C_b^{1,\infty}([0, T] \times \mathbb{R})$.

From Feynman-Kac formula, we deduce that $(m_t(x), x \in \mathbb{R}, t \geq 0)$ is the unique strong solution of

$$\begin{cases} \partial_t m = \frac{\sigma^2}{2}\partial_{xx} m - \sigma c \partial_x m + (1 - \frac{x^2}{2} - \lambda) m \\ m_0(x) = 1. \end{cases}$$

That implies that for any $t \geq 0$,

$$\int m_t(x) F(x) dx = \int F(x) dx = \lambda.$$

Moreover, following Fitzsimmons-Pitman-Yor arguments using Girsanov's transform, one can explicitely compute m_t:

$$m_t(x) = \sqrt{1 + \tanh(\sigma t)} \exp\left(-\frac{(x + e^{-\sigma t} c)^2}{2\sigma} (1 + \tanh(\sigma t)) + \frac{(x + c)^2}{2\sigma} \right).$$

The historical particle system

We extend the previous formula to the historical system until a fixed (observation) time T.

- V_T denotes the set of individuals alive at time T.
- Let us take $i \in V_T$ and $t < T$.

  $X^i(t)$ denotes the historical lineage of the individual i in the following sense:

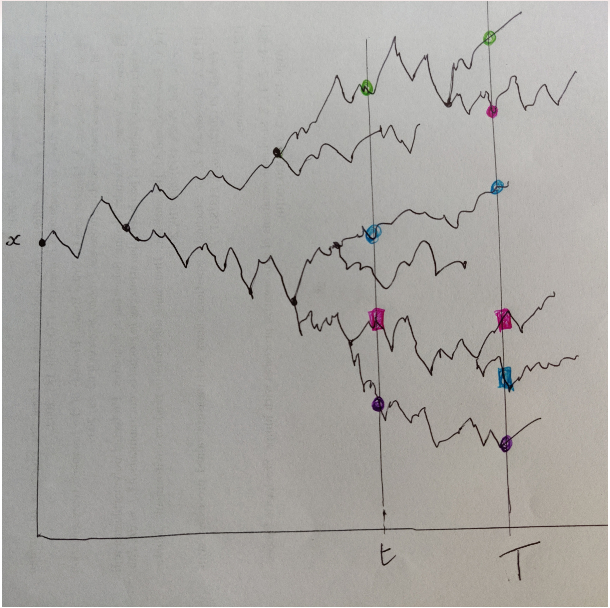
  If the individual i was born at time t, then $X^i(t)$ denotes the trait of i at t.

  But if the individual i was not born at time t, then $X^i(t) = X^j(t)$ where j is the most recent ancestor of i living at time t.

  We write $(j, t) \preceq (i, T)$.

Theorem: *For any $t_1 < t_2 < \cdots < t_n \leq T$, for any $x \in \mathbb{R}$,*

$$\mathbb{E}_{\delta_x}\left[\sum_{i \in V_T} \varphi(X^i_{t_1}, \ldots, X^i_{t_n})\right] = \mathbb{E}_x\left[\exp\left(\int_0^T \left(1 - \frac{1}{2}Y_s^2 - \lambda\right) ds\right) \varphi(Y_{t_1}, \ldots, Y_{t_n})\right].$$


x
t
T

The spinal approach - the typical trajectory

Theorem:
For $x \in \mathbb{R}$ and Φ a continuous bounded function on $\mathcal{C}([0,T],\mathbb{R})$, we have

$$\begin{aligned}\lim_{K\to+\infty} \mathbb{E}_{K\delta_x}\left[\frac{1}{N_T^K}\sum_{i\in V_T^K}\Phi(X_s^i,\ s\le T)\right] &= \frac{1}{m_T(x)}\mathbb{E}_{\delta_x}\left[\sum_{i\in V_T}\Phi(X_s^i,\ s\le T)\right]\\ &= \mathbb{E}_x\left[\Phi(\widetilde{Y}_s,\ s\le T)\right],\end{aligned}$$

where $\widetilde{Y}$ is an inhomogeneous Markov Process (depending on T) with infinitesimal generator given for $f \in C_b^2(\mathbb{R})$ by

$$\mathcal{G}_t f(x) = \frac{L(m_{T-t}f)(x) - f(x)Lm_{T-t}(x)}{m_{T-t}(x)},$$

where L is the infinitesimal generator of the drifted Brownian Y.

The process $\widetilde{Y}$ describes the behavior of the phenotypic trajectory of an individual uniformly sampled among the individuals alive at time T, in a large population.

The biaised initial distribution

Taking $s = 0$, we obtain that the initial value of $\tilde{Y}$ is not distributed according to $\frac{1}{\lambda} F$ but according to the biaised distribution $\frac{1}{\lambda} m_T F$.

Proof: (Cf. A. Marguet).
Markov property and Itô's Formula applied to $f(Y_t) m_{T-t}(Y_t)$.

Using the explicit value of $m_t(x)$, we deduce that for $0 \leq t \leq T$,

$$\begin{aligned}\widetilde{Y}_t &= \frac{\cosh(\sigma(T-t))}{\cosh(\sigma T)} \widetilde{Y}_0 + c \cosh(\sigma(T-t)) \big(\tanh(\sigma(T-t)) - \tanh(\sigma T) \big) \\ &\quad + \sigma \cosh(\sigma(T-t)) \int_0^t \frac{dB_s}{\cosh(\sigma(T-s))}.\end{aligned}$$

- For any $t \geq 0$, the random variable $\widetilde{Y}_t$ is a Gaussian variable.

- Computation gives that for any $0 \leq t \leq T$,

$$\widetilde{Y}_t \sim \mathcal{N}\Big(- c\, e^{-\sigma(T-t)}, \frac{\sigma}{1 + \tanh(\sigma(T-t))}\Big)$$

- Then the density $p(t, y)$ of $\widetilde{Y}_t$ satisfies

$$\partial_y \log p(t, y) = -\frac{x + c\, e^{-\sigma(T-t)}}{\sigma} \big(1 + \tanh(\sigma(T-t))\big).$$

Time-reversion of the process: the phenotypic lineage equation to the ancestor

We can now apply a result of Haussmann and Pardoux.

The reverse-time process of a diffusion $b(t, \widetilde{Y}_t)dt + \sigma dB_t$ is a diffusion process whose drift is given by

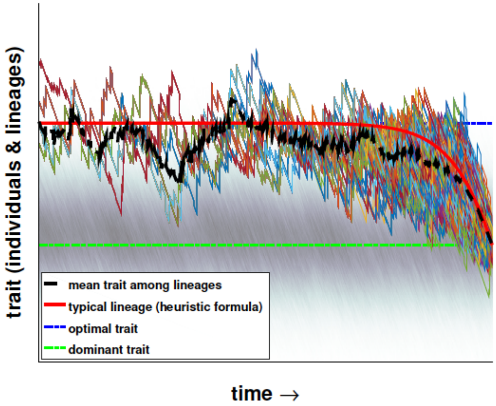
$$b^r(t, y) = -b(T - t, y) + \sigma^2 \partial_y \log p(T - t, y)$$

and the diffusion part stays unchanged.

Here we obtain that the time-reverse diffusion process of $\widetilde{Y}$ is the Ornstein-Uhlenbeck process

$$dX_t = -\sigma X_t dt + \sigma dB_t,$$

which is homogeneous and independent of T !!



The grey background is the stationary density of individuals F. The y axis represents the phenotype z in the moving frame ($z = x - ct$).

Dominant trait: $-c$.
Optimal trait: 0.

Work in progress - The non local case

In this case, we have seen that the pde is

$$\begin{aligned}\partial_t f(t,x) &= \int \left(f(t,x+\sigma h) - f(t,x)\right) G(h)dh + \left(1 - \frac{x^2}{2} - \int f(t,x)dx\right) f(t,x)\\ &+\sigma c \partial_x f(t,x)\end{aligned}$$

with $f(0,x) = u_0(x)$.

In what follows, we will denote by $G_\sigma * f$ the operator

$$G_\sigma * f(x) = \int f(x+\sigma h) G(h) dh.$$

The stationary distribution

Theorem: (Coville-Hamel, Velleret)

Let us define the operator A for any smooth function f by

$$Af = f - G_\sigma * f - c\sigma\partial_x f + \frac{1}{2}x^2 f.$$

Then
(i) There exists a unique $\lambda \geq 0$ and a unique positive function $\phi \in H^1(\mathbb{R})$ satisfying $\int \phi = 1$ and $x^2\phi \in L^2$ satisfying that

$$A\phi = \lambda\phi.$$

In addition, the function ϕ is a smooth function.

(ii) There exists a unique non zero stationary distribution F for our non local problem if and only if

$$\lambda < 1.$$

Moreover, $\int F = 1 - \lambda$.

A part of the previous approach stays valid but without explicit computations.

- The auxiliary process is now

$$dY_t = \sigma\left(- cdt + \int hN(dt, dh)\right) ,$$

with N a Poisson point measure on $\mathbb{R}_+ \times \mathbb{R}$ with intensity $G(h)dh\, dt$.

- Approach based on additive functionals (Dynkin) and reverse time for general Markov processes (Reinhard-Roynette).

Let (P_t) the semigroup defined by

$$P_t\varphi(x) = \mathbb{E}_x\Big[\exp\Big(\int_0^t \Big(1 - \frac{1}{2}Y_s^2 - \lambda\Big)\, ds\Big)\varphi(Y_t)\Big].$$

- One can show that since F is stationary, then

$$P_t^* F = F.$$

We deduce that the law of $\widetilde{Y}_t$ issued from $m_T F$ is $m_{T-t}.F$.
Moreover, using reverse time technics, we obtain that the semigroup of the reverse time process of $\widetilde{Y}$ satisfies

$$P_t^R\varphi = \frac{P_t^*(F\varphi)}{F}.$$

This semigroup does not depend on m_t!

Thank you for your attention!