Large population limit - A law of large numbers

Theorem [Kurtz, 1971]

When $K \to \infty$ *, the stochastic process* $(Z_t^{A,K}, Z_t^{a,K})_{t\geq 0}$ *converges in probability to the deterministic and continuous solution* $(n_t^A, n_t^a)_{t\geq 0}$ *of the ODE's system*

$$\frac{dn^A}{dt} = \Big(r(A) - C(A,A)n^A - C(A,a)n^a + \frac{\alpha(A,a)}{(n^A+n^a)}\, n^a\Big) n^A = P(n^A, n^a)$$

$$\frac{dn^a}{dt} = \Big(r(a) - C(a,A)n^A - C(a,a)n^a - \frac{\alpha(A,a)}{(n^A+n^a)}\, n^A\Big) n^a = Q(n^A, n^a).$$

Idea of the proof : Uniform control of moments ; Tightness (compactness of the laws) ; Identification of the limit and uniqueness.

If there is only one type a, we recover the logistic equation

$$\frac{dn^a}{dt} = \Big(r(a) - C(a,a)n^a\Big)n^a.$$

There is a unique stable equilibrium

$$\bar{n}^a = \frac{r(a)}{C(a,a)}.$$

Study of the dynamical system

- If $C(A,A) > 0$ and $C(a,a) > 0$, no cycle in $(\mathbb{R}_+^*)^2$. Indeed $\varphi(z^1,z^2) = \frac{1}{z^1 z^2}$ is a Dulac function, i.e.

$$\Big(\partial_u(\varphi P) + \partial_v(\varphi Q)\Big)(u,v)$$

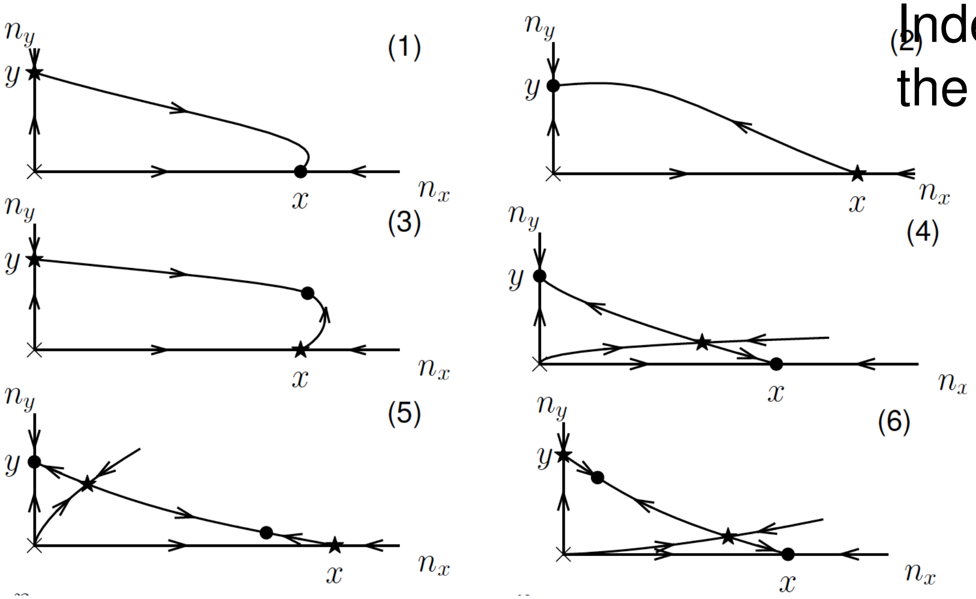
  has the same sign on the whole domain $(\mathbb{R}_+^*)^2$. We apply Dulac's Theorem.

- To find the fixed points in the positive quadrant: easier to consider the system " population size and frequencies".

$$n(t) = n^a(t) + n^A(t) \quad ; \quad q(t) = \frac{n^a(t)}{n^a(t) + n^A(t)}.$$

$$\begin{aligned}\frac{dn}{dt} &= n\Big(q\,r(A) + (1-q)\,r(a) - C_{AA}\,q^2 n - (C_{Aa} + C_{aA})\,q(1-q)n \\ &\qquad - C_{aa}\,(1-q)^2 n\Big) \\ \frac{dq}{dt} &= q\,(1-q)\,\Big(r(A) - r(a) + nq(C_{aA} - C_{AA}) + n(1-q)(C_{aa} - C_{Aa}) + \\ &\qquad + \alpha(a,A)\Big).\end{aligned}$$

Stability Analysis



Index Poincaré Theorem to obtain the sinks and sources.

- Without transfer (Lotka-Volterra competitive system): only the four first pictures.

The stability is governed by the function, called invasion fitness function

$$S(y;x) = r(y) - C(y,x)\bar{n}^x + \alpha(y,x) = r(y) - \frac{C(y,x)}{C(x,x)} r(x) + \alpha(y,x).$$

- A can invade a resident population with trait a if $S(A;a) > 0$.
- Trade-off between demography-ecology and transfer.

The case when C is constant

- The system becomes

$$\frac{dn}{dt} = n\left(q\,r(A) + (1-q)\,r(a) - Cn\right)$$
$$\frac{dq}{dt} = q\,(1-q)\,\left(r(A) - r(a) + \alpha(A,a)\right) = q(1-q)\,S(A;a)$$

where $n = n^a + n^A$ and $q = n^a/n$ and

$$S(A;a) = r(A) - r(a) + \alpha(A,a).$$

In this case $S(a;A) = -S(A;a)$.

- We cannot obtain long time co-existence: Invasion-Implies-Fixation Principle (IIF).

Central Limit Theorem

We define the fluctuation process:

$$(\eta_{\cdot}^{K,A}, \eta_{\cdot}^{K,a}) = \left(\sqrt{K}(Z_{\cdot}^{A,K} - n_{\cdot}^{A},\ Z_{\cdot}^{a,K} - n_{\cdot}^{a})\right)_{K\in\mathbb{N}^*}.$$

We get

$$\begin{aligned}
\eta_t^{K,A} &= \sqrt{K}(Z_0^{A,K} - n_0^A) + \int_0^t \sqrt{K}\Big(P_K(Z_s^{A,K}, Z_s^{a,K}) - P(n^A, n^a)\Big) ds + \sqrt{K} M_t^{K,A}, \\
\eta_t^{K,a} &= \sqrt{K}(Z_0^{a,K} - n_0^a) + \int_0^t \sqrt{K}\Big(Q_K(Z_s^{A,K}, Z_s^{a,K}) - Q(n^A, n^a)\Big) ds + \sqrt{K} M_t^{K,a}.
\end{aligned}$$

Theorem :

The sequence of processes $(\eta_{\cdot}^{K,A}, \eta_{\cdot}^{K,a})_{K\in\mathbb{N}^*}$ *converges in law to the unique continuous solution of the diffusion equation*

$$\begin{pmatrix} \eta_t^A \\ \eta_t^a \end{pmatrix} = \begin{pmatrix} \eta_0^A \\ \eta_0^a \end{pmatrix} + \begin{pmatrix} M_t^A \\ M_t^a \end{pmatrix} + \int_0^t J(n_s^A, n_s^a) \begin{pmatrix} \eta_s^A \\ \eta_s^a \end{pmatrix} ds$$

where

$$J(u,v) = \begin{pmatrix} J_{11}(u,v) & J_{12}(u,v) \\ J_{21}(u,v) & J_{22}(u,v) \end{pmatrix}$$

with

$$\begin{aligned}
J_{11}(u,v) =& r(A) - 2C(A,A)u - C(A,a)v + \alpha(A,a)\frac{v^2}{(u+v)^2} \\
J_{12}(u,v) =& - C(A,a)u + \alpha(A,a)\frac{u^2}{(u+v)^2} \\
J_{21}(u,v) =& - C(a,A)v + \alpha(a,A)\frac{v^2}{(u+v))^2} \\
J_{22}(u,v) =& r(a) - 2C(a,a)v - C(a,A)u + \alpha(a,A)\frac{u^2}{(u+v)^2}.
\end{aligned}$$

Further, the continuous martingale $(M_t^A, M_t^a)_{t\geq 0}$ satisfies:

$$\mathbb{E}((M_t^A)^2) =$$

$$\int_0^t \Big[\big(b(A) + (d(A) + C(A,A)n_s^A + C(A,a)n_s^a)\big)n_s^A + (\tau(A,a) + \tau(a,A))\frac{n_s^A n_s^a}{(n_s^A + n_s^a)}\Big] ds$$

$$\mathbb{E}((M_t^a)^2) =$$

$$\int_0^t \Big[\big(b(a) + (d(a) + C(a,A)n_s^A + C(a,a)n_s^a)\big)n_s^a + (\tau(A,a) + \tau(a,A))\frac{n_s^A n_s^a}{(n_s^A + n_s^a)}\Big] ds$$

$$\mathbb{E}(M_t^A M_t^a) = -\int_0^t (\tau(A,a) + \tau(a,A))\frac{n_s^A n_s^a}{(n_s^A + n_s^a)}\; ds.$$

One can show that $(M_t^A, M_t^a)_{t\geq 0}$ has a Gaussian distribution.

The process (η_t^A, η_t^a) is a generalized Ornstein-Uhlenbeck process.

From the observations of the fluctuations of population sizes, one could obtain information on the coefficients.

Eco-evolutionary Modeling

Adaptive biology (for micro-organisms)- Eco-evolutionary mechanisms

Individuals are characterized by genetic or phenotypic information that influences their ability to reproduce and their probability of survival.

• Heredity. Vertical transmission of this information to descendants in cell division.

• Mutation. creates variability in the trait distribution.

• Selection. Individuals with a higher probability of survival or a better ability to reproduce will invade the population over time (population genetics), as will those most able to survive in competition with others (ecology).

• Horizontal Gene Transfer (HGT): The bacteria or cells exchange genetic information.

Our aim : modeling of the emergence of successful advantageous mutations on long-term.

Asexual populations (cells, bacteria).

Usual biological assumptions:

- large populations
- rare mutations
- small mutation effects
- long (evolutionary) time scale.

Remark: The evolution time scale can be very fast with respect to the human time scale. For example, bacteria E. Coli become resistant to an antibiotic by an evolutive procedure in less than 5 years. From a virus, its shorter ($\sim$ 6 months).

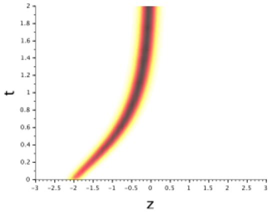
The main goal:

- predict the long term evolutionary dynamics.
- model and quantify the population dynamics and the successive invasions of successful mutants.

That is a multi-scale question : different mathematical approaches using different analytical tools.

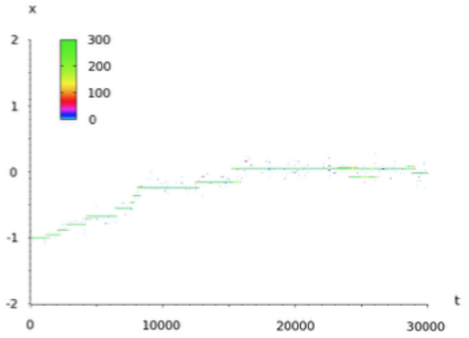
- Game Theory - Dynamical Systems: Maynard-Smith 1974, Hofbauer-Sigmund 1990, Marrow-Law-Cannings 1992, Metz-Geritz-Meszéna et al. 1992, 1996, Dieckmann-Law 1996, Diekmann 2004.
- Partial or integro-differential and Hamilton-Jacobi equations (Hopf-Cole transformation): Perthame-Barles-Mirrahimi 07-10, Jabin, Desvillettes, Raoul, Mischler 08-10.

  Concentration phenomenon on advantageous mutants but evolution seemed too fast.



- **Stochastic individual-based processes** (birth and death processes with mutation and selection) : Bolker-Pacala 97, Kisdi 99, Dieckmann-Law 00, Fournier-M. 04, Ferrière-Champagnat-M. 06, Champagnat 06, Champagnat-M. 10.

  Concentration phenomenon on advantageous mutants but evolution seemed too slow.



Stochastic individual-based model

- Population structured by a trait x belonging to a subset $\mathcal{X}$ of $\mathbb{R}$ or $\mathbb{R}^d$.
  The trait is a quantitative information on a genotype or a phenotype.
  Each individual is characterized by its trait.

- The parameter K scales the population size or of the resources amount (carrying capacity).

- Population of $N^K(t)$ individuals weighted by $\dfrac{1}{K}$.

- The population dynamics is described by a pure jump Markovian measure-valued process $(\nu_t^K, t \in \mathbb{R}_+) \in \mathbb{D}(\mathbb{R}_+, M_F(\mathcal{X}))$ defined by

  $$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N^K(t)} \delta_{X_i(t)} \quad ; \quad N^K(t) = K \, \langle \nu_t^K, 1 \rangle,$$

  where $X_i(t)$ is the trait of the individual i alive at time t.

- **Dynamics:**
  - The demography is regulated by birth and death.
  - The trait variability comes from mutation and transfer.

Transitions

BIRTHS:

Each individual with trait x gives birth to a single individual at rate $b(x)$.
The function b is continuous on $\mathcal{X}$.

p_K scales the mutation probability.

At each birth time:

- with probability $1 - p_K$, the offsprings inherits of x.
- with probability p_K , a mutation occurs.
- Trait mutation: the new trait is z chosen according to $m(x, z)dz$.

  The mutation measure $m(., z)dz$ is continuous.

  For example $m(., z)dz = \mathcal{N}(x, \sigma^2)$.

HORIZONTAL TRANSFER

Bacteria conjugation: the donor transfers its trait to the recipient.

- In a population ν, an individual with trait x chooses a partner with trait y at frequency-dependent rate

$$\frac{\tau(x,y)}{K\langle \nu, 1\rangle},$$

where τ is a continuous function.

- The new traits are (x, x).
- *Unilateral plasmid transfer:* $\tau(x,y) = 0$ for $x < y$.

DEATHS:

- Each individual with characteristics x dies at rate

$$d(x) + \frac{1}{K} \sum_{i=1}^{N^K(t)} C(x, x_i) = d(x) + C * \nu_t^K(x).$$

- $\dfrac{C(x, x_i)}{K}$: competition pressure between two individuals.
- The functions d and C are bounded continuous and

$$r(x) = b(x) - d(x) > 0 \; ; \;\; C(x, y) \geq \underline{c} > 0.$$

A toy model:

$$\mathcal{X} = [0, 1] \, ; \; b(x) = 1 - x \, ; \; d(x) = d < 1 \, ; \; m = \mathcal{N}(0, \sigma^2) \, ; \; \tau(x, y) = \tau \mathbf{1}_{x>y}.$$

Trade-off between demography and horizontal transfer.

Infinitesimal generator of ν^K

For any measurable bounded function F on $M_F(\mathcal{X})$ and $\nu = \frac{1}{K}\sum_{i=1}^{n}\delta_{x_i}$,

$$
\begin{aligned}
L^K F(\nu) = & \sum_{i=1}^{n} b(x_i)(1-p_K)\big(F(\nu + \frac{1}{K}\delta_{x_i}) - F(\nu)\big) \\
& + \sum_{i=1}^{n} b(x_i)\,p_K \int_{\mathcal{X}} \big(F(\nu + \frac{1}{K}\delta_z) - F(\nu)\big)\, m(x_i, dz) \\
& + \sum_{i=1}^{n} \big(d(x_i) + KC_K * \nu(x_i)\big)\big(F(\nu - \frac{1}{K}\delta_{x_i}) - F(\nu)\big) \\
& + \sum_{i,j=1}^{n} \frac{\tau(x_i, x_j)}{K\langle \nu, 1\rangle}\big(F(\nu + \frac{1}{K}\delta_{x_i} - \frac{1}{K}\delta_{x_j}) - F(\nu)\big).
\end{aligned}
$$

In particular, for $G_f(\nu) = \langle \nu, f\rangle$,

$$
\begin{aligned}
G^K F_f(\nu) = & \int_{\mathcal{X}} \nu(dx)\Big[b(x)\Big((1-p_K)f(x) + p_K \int_{\mathcal{X}} f(z)m(x,dz)\Big) \\
& - \big(d(x) + C * \nu(x)\big)f(x) + \frac{1}{\langle \nu, 1\rangle}\int_{\mathcal{X}} \tau(x,y)\big(f(x) - f(y)\big)\nu(dy)\Big].
\end{aligned}
$$

Semi-martingale decomposition

For some $p \geq 2$,

$$\mathbb{E}\left(\langle \nu_0^K, 1\rangle^p\right) < +\infty.$$

Moment conditions propagate and imply the existence and uniqueness of the process.

$$\int f(x)\nu_t^K(dx) = \int f(x)\nu_0^K(dx) + M_t^{K,f} + \int_0^t G^K F_f(\nu_s^K)ds,$$

where $M^{K,f}$ is a square integrable martingale such that

$$\mathbb{E}\big(\sup_{t\leq T}(M_t^{K,f})^2\big) = \frac{1}{K}\,\mathbb{E}\bigg(\int_0^T \int_{\mathcal{X}} \Big\{\Big(((1-p_K)b(x) + d(x) + C * \nu_s^K(x)\Big)f^2(x)$$

$$+ p_K b(x)\int_{\mathcal{X}} f^2(z)\,m(x,dz) + \int_{\mathcal{X}} \frac{\tau(x,y)}{\langle \nu_s^K, 1\rangle}\Big(f(x) - f(y)\Big)^2 \nu_s^K(dy)\Big\}\nu_s^K(dx)ds\bigg).$$

Large population, time scale $O(1)$

$K \to \infty\,,\; p_K \to p\,.$

Let us introduce the transfer flux $\alpha(x,y) = \tau(x,y) - \tau(y,x)$.

Proposition: *Let* $T > 0$. *If* $\nu_0^K \Longrightarrow n_0 \ll$ *leb meas. when* $K \to +\infty$, *the sequence* $(\nu^K)_{K\geq 1}$ *converges in probability to the solution* $n(.,x)dx \in \mathcal{C}([0,T],\mathcal{M}_F(\mathcal{X}))$, *weak positive solution of*

$$\partial_t n(t,x) = \big(b(x)(1-p) - d(x) - C * n(t,x)\big)\, n(t,x) + p\int_{\mathcal{X}} b(y)m(y,x)n(t,y)dy + \frac{n(t,x)}{\|n(t,.)\|_1}\int_{\mathcal{X}} \alpha(x,y)n(t,y)dy,$$

with $C * n(t,x) = \int C(x,y)n(t,y)dy\,,\; \|n(t,.)\|_1 = \int n(t,y)dy$.

Proof: Compactness-identification-uniqueness using moment estimates.

Long time behaviour? (Cf. Desvillettes, Jabin, Mischler, Raoul '08 ($\alpha = 0$), Hinow, Le Foll, Magal, Webb '09, Magal, Raoul '15).

Example: Kisdi's model (1999).

$$\mathcal{X} = [0,4]\ ;\ b(x) = 4 - x\ ;\ d(x) = 0\ ;\ p_K(x) = p\ ;\ \tau(x,y) = 0.$$

and

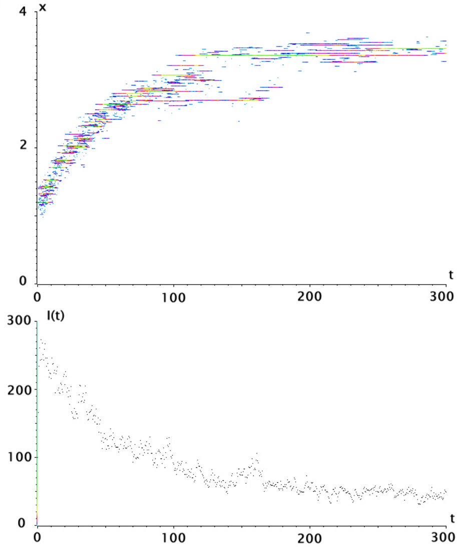
$$C(x,y) = C(x-y) = 2\left(1 - \frac{1}{1 + \exp(-4(x-y))}\right)$$

and

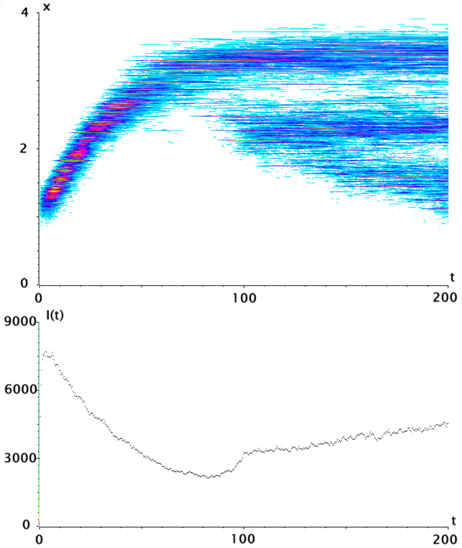
$$m(x,z)dz = \mathcal{N}(x, \sigma^2).$$

Trade-off between demography and competition.

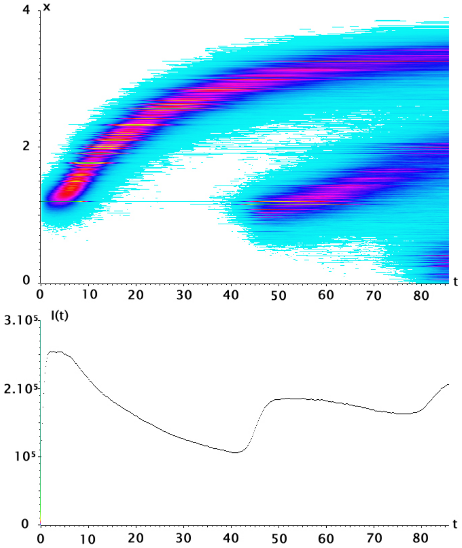
Kisdi's model



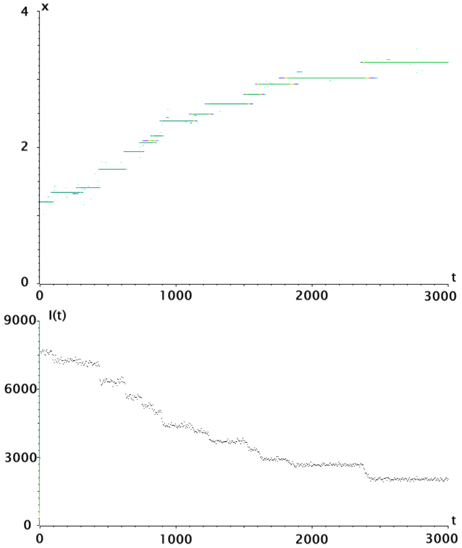
$p = 0.03; \sigma = 0.1; K = 100$



$p = 0.03; \sigma = 0.1; K = 3000$



$p = 0.03; \sigma = 0.1; K = 100000$



$p = 0.00001; \sigma = 0.1; K = 1000$

Evolutionary scaling

Rare mutations : $p_K \to 0$.

Small mutations : $m = \delta_0$

The integro-differentiel equation becomes

$$\begin{aligned}\partial_t n(t,x) =& \big(b(x) - d(x) - C * n(t,x)\big)\, n(t,x) \\ &+ \frac{n(t,x)}{\|n(t,.)\|_1} \int_{\mathcal{X}} \alpha(x,y) n(t,y) dy,\end{aligned}$$

Evolution cannot be captured at this time scale. We have to wait a longer time to capture the mutational effects.

Evolutionary point of view - Occurence of a mutant

- A mutant A occurs in a monomorphic population of trait a at equilibrium.
- The dynamics of the mutant population is modeled by a Birth and Death process in the environment given by the $\bar{n}^a$ individuals of trait a.
- Invasion fitness of an individual with trait A in a resident a-population :

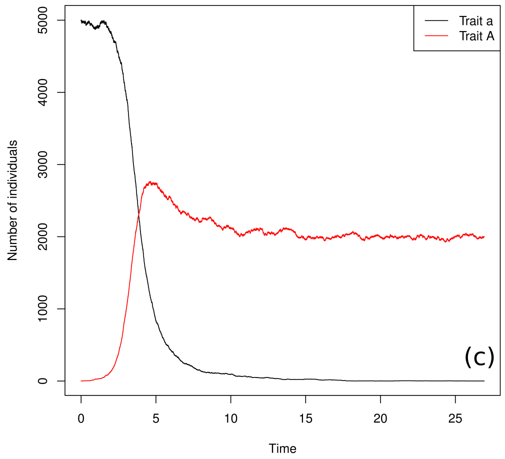
$$S(A;a) = f(A;a) + \alpha(A,a),$$

where $f(A;a) = r(A) - \frac{C_{Aa}}{C_{aa}} r(a)$.

- A can invade the population if and only if $S(A,a) > 0$.
- Trade-off between the signs of $f(A;a)$ and $\alpha(A,a)$.

Invasion, fixation or co-existence for a costly plasmid

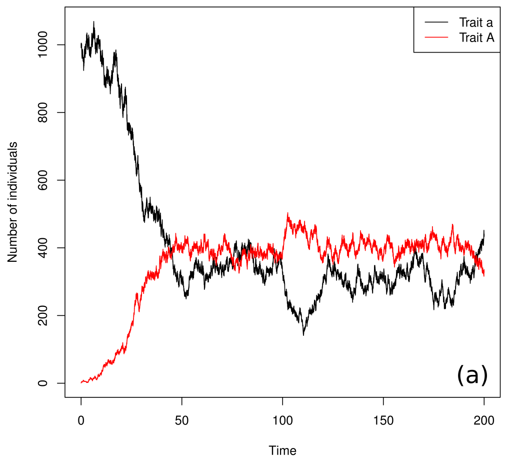
Unilateral transfer.



$b(A) = 0.5$; $b(a) = 1$; $\tau(A, a) = \alpha(A, a) = 0,7$; $K = 1000$; $C = 1$; $d \equiv 0$.

Fixation of a deleterious mutant.

A highly costly mutant



$b(A) = 0.8$; $b(a) = 1$; $\tau(A, a) = \alpha(A, a) = 0.5$; $K = 5000$; $C_{Aa} = C_{aa} = 2$; $C_{AA} = 4$; $C_{aA} = 1$; $d \equiv 0$.

Polymorphism.

- **Invasion probability of A in a resident a-population** : $S(A;a) > 0$.

$$P_{Aa} = \frac{[S(A;a)]_+}{b(A)+\tau(A,a)} = \frac{[r(A) - C_{Aa}\frac{r(a)}{C_{aa}} + \tau(A,a)]_+}{b(A)+\tau(A,a)}.$$

The unilateral horizontal transfer increases the invasion probability of A.

Duration for the A-population size to become of order K: $\log K/S(A;a)$.

$$\mathbb{E}(Z_t^{K,A}) = Z_0^{K,A} e^{S(A;a)t} = \varepsilon K \quad \text{and} \quad Z_0^{K,A} = c.$$

- **Competition**: dynamics close to the dynamical system - Duration of order 1.

- **Fixation** (when the deterministic system converges to $(\bar{n}^A, 0)$): the a-population size dynamics is driven by a Birth and Death process processus de with negative growth rate $S(a;A) < 0$.

Duration of order $\log K/|S(a;A)|$.

$$\mathbb{E}(Z_t^{K,a}) = \varepsilon K e^{S(a;A)t} = c.$$

The fixation times decrease with horizontal transfer.

Rare mutation: a first scaling

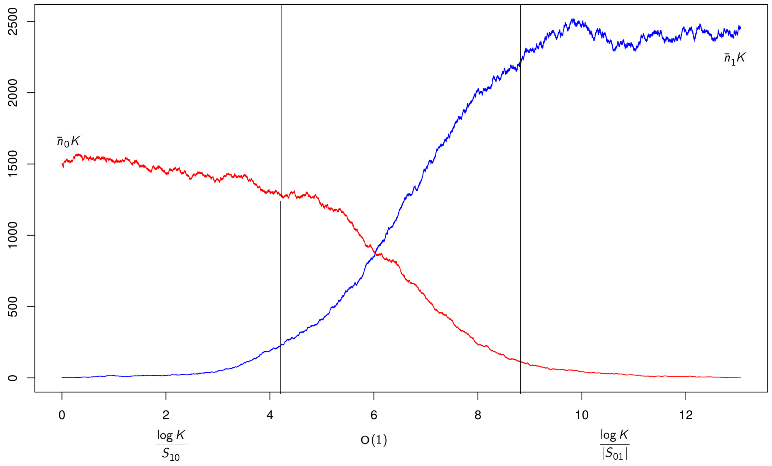
(Metz et al. 1996, Champagnat 2006).

Hypothesis:

$$Kp_K \to 0 \quad : \quad \log K \ll \frac{1}{Kp_K} \ll e^{KV}, \forall V > 0.$$

Through this assumption : separation of time scales, between competition phases and occurence of mutations.

We have seen that when C constant, one has the "Invasion Implies Fixation" principle and the time to fixation is of order $\log K$.



Before the first mutation mutation, $K \to \infty$

- $\frac{1}{K} N_t^{K,x}$ close to $\bar{n}(x)$.

- Large deviations: time to left a neighborhood of this equilibrium of order $\exp(KV)$, with $V > 0$.

- If $\frac{1}{Kp_K} \ll e^{KV}$, the first mutation occurs before this exit time with large probability.

- Before this exit time, the mutation rate from the x-population is close to $p_K \, b(x) \, K \, \bar{n}(x)$.

- On the time scale $\frac{t}{Kp_K}$: $b(x) \, \bar{n}(x)$.

- **Between** times **0 and** 4 (see Figure): the number of mutants with trait y is close to a branching process with birth rate $b(y) + \tau(y,x)$ and death rate $d(y) + C(y,x)\bar{n}(x) + \tau(x,y)$.

  Survival Probability : $[S(y;x)]_+ / \big(b(y) + \tau(y,x)\big)$.

- Between 0 and 12 (see figure): time of order $\log K$.

- Since $\log K \ll \frac{1}{K\mu_K}$, then at the time scale of mutations ($\frac{1}{K\,p_K}$), the three phases will be reduced to a jump from $\bar{n}(x)$ individuals with trait x to $\bar{n}(x+h)$ individuals with trait $x+h$.

- If $\log K \ll \frac{1}{K\mu_K}$, the next mutation will occur after these three invasion-fixation phases with large probability.

- One reiterate the procedure with Markovian arguments.

- $\Longrightarrow$ succession of fast invasion phases and occurence of rare mutations.

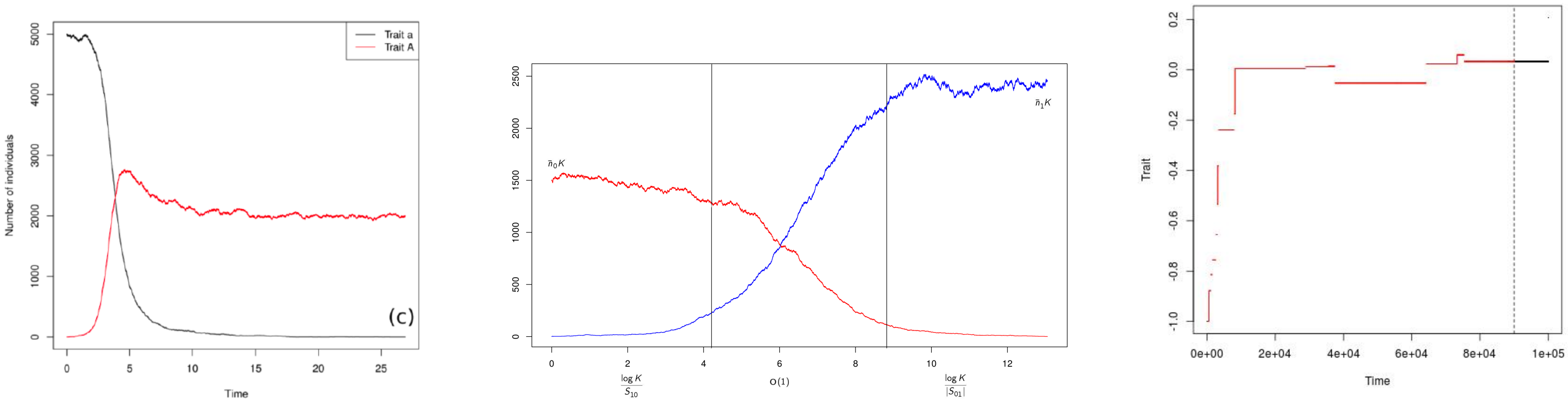
- At the mutation time scale ($\frac{1}{K\,p_K}$), the population process is close to a pure jump process describing the successive substitutions of traits (Trait Substitution Sequence (TSS).

Assume that (IIF) is satisfied (C constant).

Theorem[TSS]

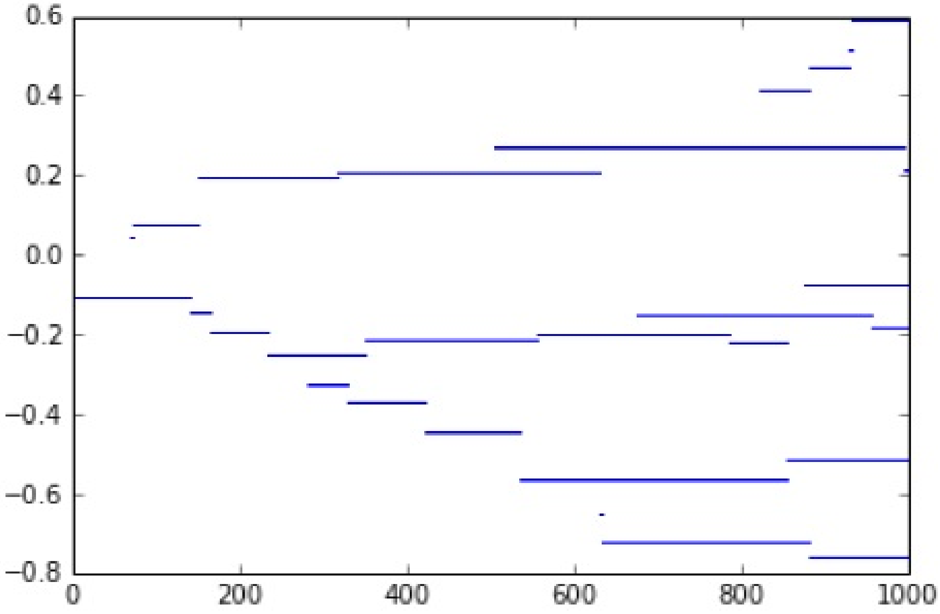
The population process $\nu^K_{\frac{t}{Kp_K}}$ converges, when K tends to infinity to a pure jump Markov process, which jumps from $\bar{n}_x$ individuals with trait x to $\bar{n}_y$ individuals with trait y chosen according to the distribution m, at rate

$$b(x)\,\bar{n}_x\,\frac{[S(y;x)]_+}{b(y)+\tau(y,x)}.$$



(S. Billiard - C. Smadi)

Without (IIF) : Polymorphic Evolution Sequence.



Let us come back to the TSS.

Dynamics of the limiting process: its support is $\mathcal{X}$ and at each time t, the process writes

$$\bar{n}_{X_t}\,\delta_{X_t}.$$

The support process $(X_t, t \in [0,T])$ is then a pure jump Markov process with generator

For φ a bounded measurable test function,

$$L\varphi(x) = b(x)\,\bar{n}_x \int_{\mathcal{X}} \frac{[S(x+h;x)]_+}{b(x+h)+\tau(x+h,x)}(\varphi(x+h)-\varphi(x))\mathcal{N}(x,\sigma^2(x))(dh).$$

Assume now that the mutation amplitudes are scaled by a coefficient $\varepsilon > 0$.
We replace h by εh.
Then

$$L_\varepsilon\varphi(x) = b(x)\,\bar{n}_x \int_{\mathcal{X}} \frac{[S(x+\varepsilon h;x)]_+}{b(x+\varepsilon h)+\tau(x+\varepsilon h,x)}(\varphi(x+\varepsilon h)-\varphi(x))\mathcal{N}(x,\sigma^2(x))(dh).$$

Then

$$S(x+\varepsilon h; x) = r(x+\varepsilon h) - r(x) + \tau(x+\varepsilon h, x) \; - \tau(x, x+\varepsilon h).$$

When $\varepsilon \to 0$,

$$S(x+\varepsilon h; x) = \varepsilon h\Big(r'(x) + \partial_1\tau(x,x) \; - \partial_2\tau(x,x)\Big) + o(\varepsilon).$$

The generator L_ε is approximated by

$$\varepsilon^2\, \bar{n}_x \left(r'(x) + \partial_1\tau(x,x) \; - \partial_2\tau(x,x)\right) \varphi'(x)\sigma^2(x).$$

In a new time scale t/ε^2, the approximated generator becomes

$$\mathcal{L}\varphi(x) = \bar{n}_x\, \sigma^2(x) \left(r'(x) + \partial_1\tau(x,x) \; - \partial_2\tau(x,x)\right) \varphi'(x).$$

We have proven that when mutations are of order ε, the process $(X^{\varepsilon}_{t/\varepsilon^2}, t \in [0,T])$ converges to the deterministic dynamics $(x_t, t \in [0,T])$ solution of

$$x'(t) = \bar{n}_{x(t)}\,\sigma^2(x(t))\Big(r'(x(t)) + \partial_1\tau(x(t),x(t)) - \partial_2\tau(x(t),x(t))\Big)\ .$$

Canonical Equation of the Adaptive Dynamics.

RemarK: Using an expansion at a higher level, one can also prove that

$$X(t) \sim x(t) + G(\varepsilon, t),$$

where $G(\varepsilon, t)$ models Gaussian fluctuations.

Evolutionary Scenario - No HGT

A toy model : $x \in [0, 4]$. $b(x) = 4 - x$; $d \equiv 1$, $C(x, y) \equiv C$ and

$$\bar{n}_x = \frac{3 - x}{C} \, .$$

• The invasion fitness is given by

$$f(y; x) = r(y) - r(x) = x - y > 0 \Longleftrightarrow y < x.$$

A mutant trait y will invade the population $\Longleftrightarrow$ $y < x$.

The evolution leads to trait 0.

Simulations:

- $C = 0,5$; $p = 0,03$; $\sigma = 0,1$; $K = 1000$.
- Initial state: 1000 individuals with trait 1.

  Equilibrium : $1000 \times \frac{b(1)-d(1)}{C} = 4000$ individuals.
- Optimal trait 0 . Equilibrium : $1000 \times \frac{b(0)-d(0)}{C} = 6000$ individuals.

$\tau = 0$

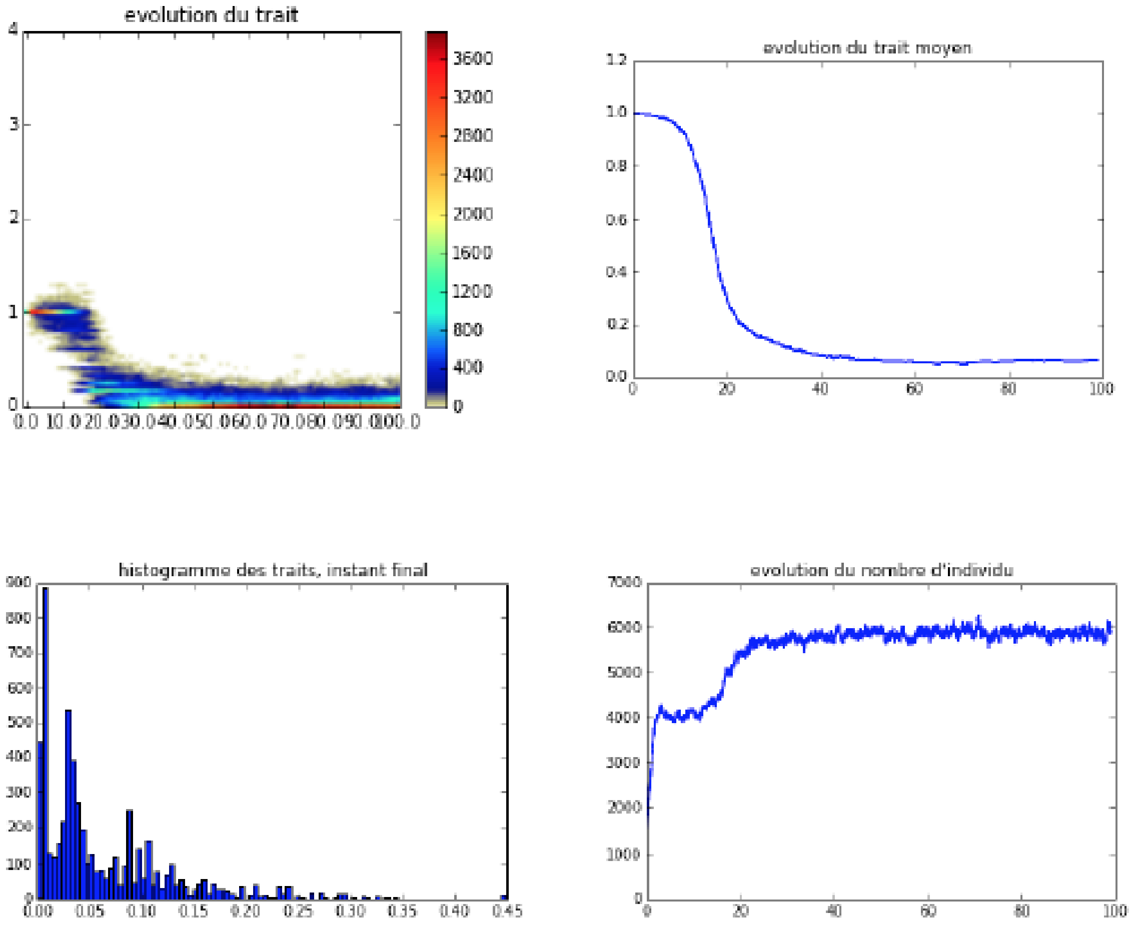


FIGURE 7 – Simulations pour $\tau = 0$.

Evolutionary Scenario - With HGT

- Assume $\tau(x, y) = \tau\,\mathbf{1}_{x>y}$.

Transfer favors large traits: trade-off between reproduction and transfer.

We have

$$\begin{aligned} S(y; x) &= r(y) - r(x) + \alpha(y, x) \\ &= x - y + \tau\,\frac{y - x}{|y - x|} \end{aligned}$$

$$S(y; x) > 0 \iff y > x \text{ and } \tau > y - x \quad \text{or} \quad x > y \text{ and } x - y > \tau.$$

Large values of τ : the evolution can lead the population to traits larger and larger and possibly to evolutionary suicide.

$\tau = 0, 2$ - Almost no modification

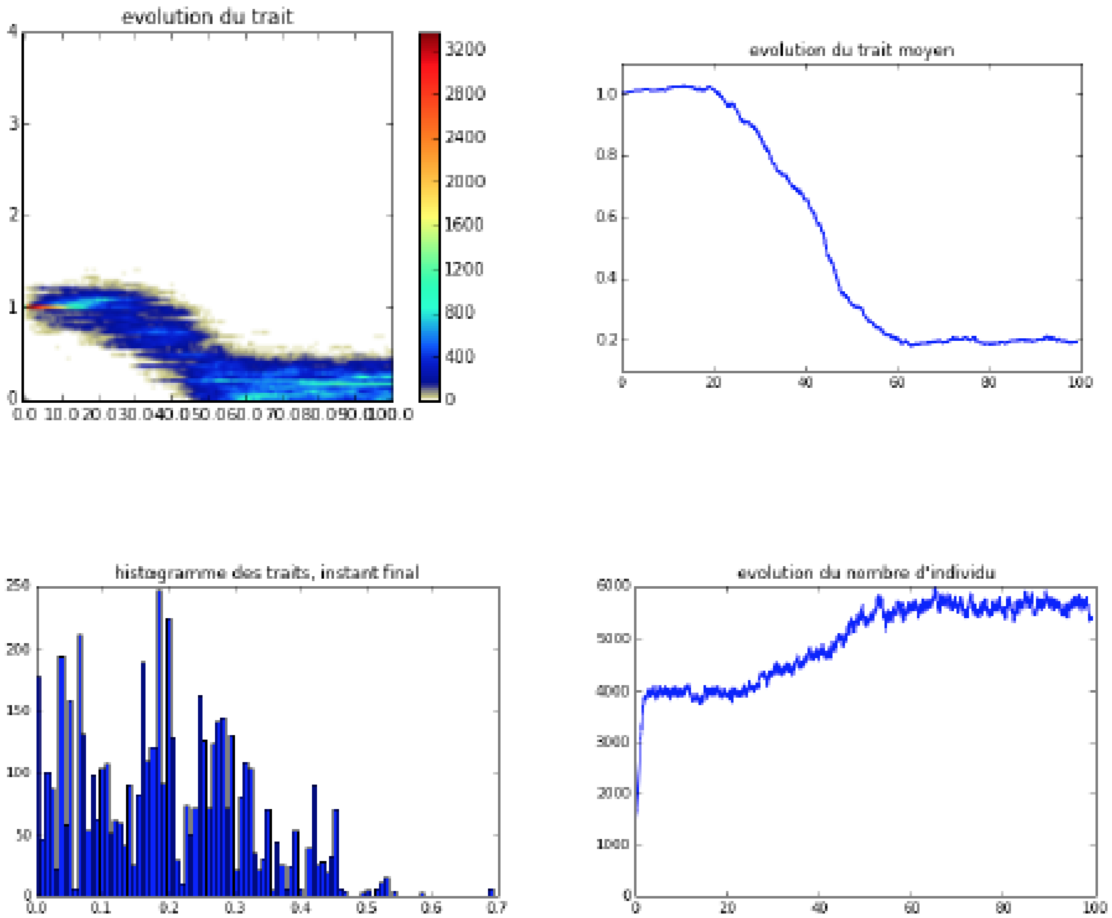


FIGURE 8 – Simulations pour $\tau = 0.2$

$\tau = 1$ - Evolutionary suicide

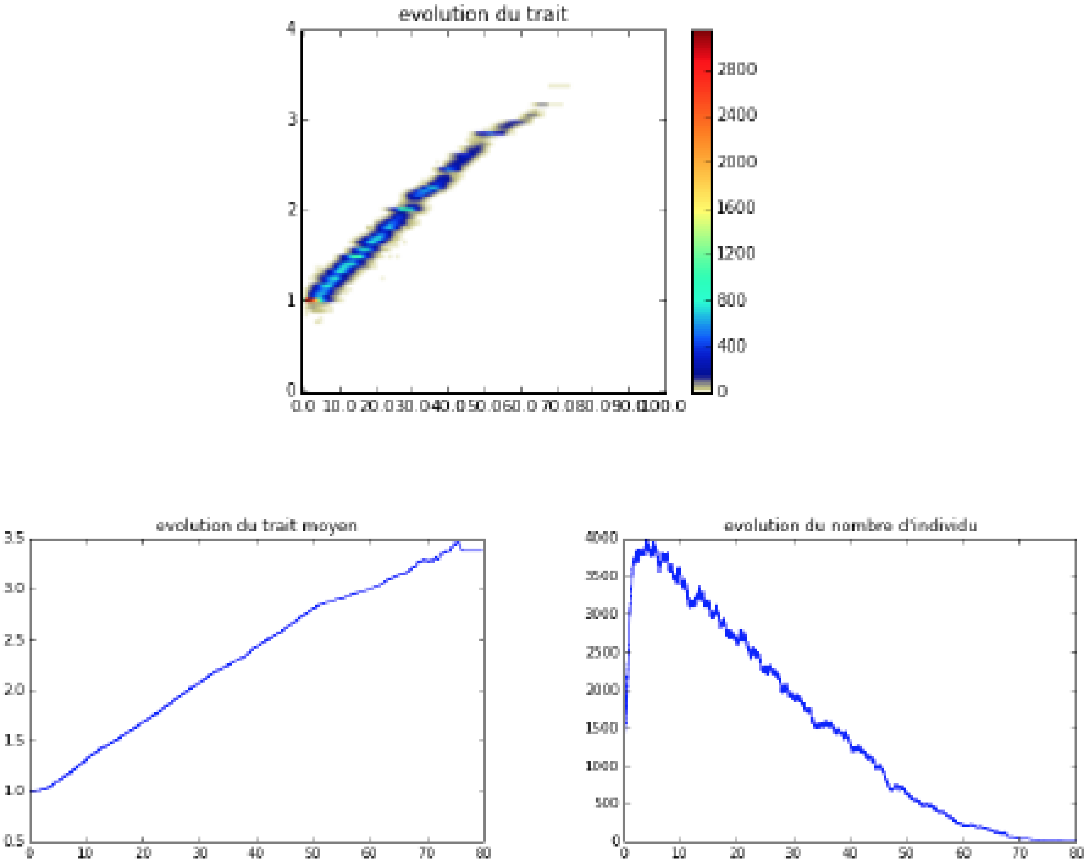


FIGURE 17 – Simulations pour $\tau = 1$

Intermediate rate : $\tau = 0,6$

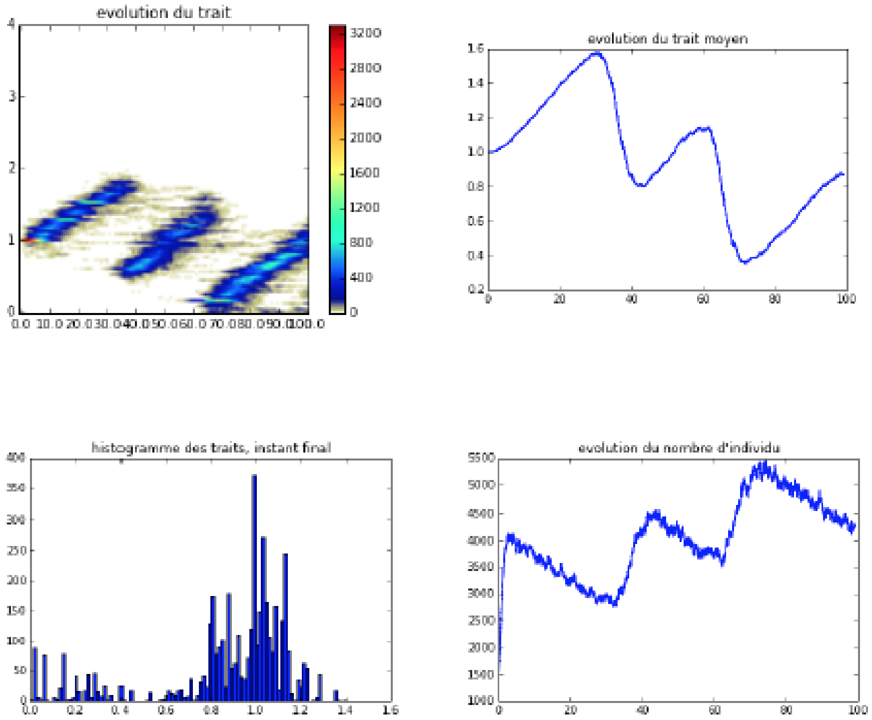


FIGURE 9 – Simulations pour $\tau = 0.6$ sur un temps de 100

- Population size decreases. For a given trait x, the population size at equilibrium is $N_{eq} = \frac{b(x)-d}{C} \times 1000 = 2000(3-x)$.
- One observes the brutal occurence of new strains.

$\tau = 0,7$

4 simulations with the same parameters. The differences are due to the possibility for a mutant to create a new strain.