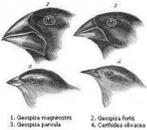


## Motivations

A number of stochastic studies have been developed to understand precisely the phenotypic evolution of a population. This poster focus on the **spatial aspect** which is an important issue in Darwinian evolution. Ecological researches ([1]) conclude that a heterogeneous environment can induce some diversifications within species, as observed in the example of the Darwinian finches.

Our objective is to understand the framework of a large population evolving in a bounded space domain when the mutations are rare.



## I. Stochastic Model

The stochastic model, proposed in [2], is an individual based model with spatially dependent coefficients, which represents an asexual population.

Each individual  $i$  is characterized at time  $t$  by

- its **trait** :  $U_i^t$  in a compact subset  $\mathcal{U}$  of  $\mathbb{R}^d$ ,
- its **position** :  $X_i^t$  in an open bounded subset  $\mathcal{X}$  of  $\mathbb{R}^d$ .

Thus the population is modeled by a process with values in the space of finite measures,  $M_F(\mathcal{X} \times \mathcal{U})$ ,

$$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N_t} \delta_{(X_i^t, U_i^t)},$$

where  $N_t$  is the number of individuals alive at time  $t$ , and  $K > 0$  is a scaling parameter.

**Spatial evolution** : the **migration** of an individual is described by a diffusion process normally reflected at the boundary of  $\mathcal{X}$  :

$$dX_t = \sqrt{2mU_t} Id \cdot dB_t - dk_t$$

with  $k$  a continuous, increasing process that represents the normal reflexion at the boundaries of  $\mathcal{X}$  and  $B$  a  $d$ -dimensional Brownian motion.

**Phenotypic evolution** : an individual of trait  $u$  and position  $x$  has

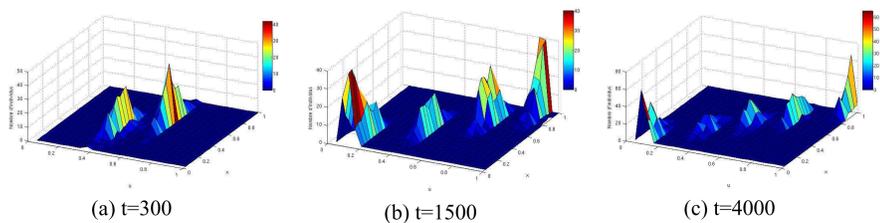
- a **birth** rate :  $b_u(x)$ . For each event of birth, with probability
  - \*  $r_K \cdot p_u(x)$ , the child is a mutant, its new trait  $v$  is chosen thanks to a law  $\theta(x, u, v)dv$ ,
  - \*  $1 - r_K \cdot p_u(x)$ , the child is a clone of its parent,
- a **natural death** rate :  $d_u(x)$ ,
- a death rate, coming from the **competition** exerted by the individual  $(x^j, u^j)$  :  $\frac{1}{K} I_{u, u^j}(x - x^j)$ .

## II. Stochastic simulations

In that simulation,  $\mathcal{U} = [0, 1]$  and  $\mathcal{X} = (0, 1)$ . Initially, all individuals have the same trait and position,  $u_0 = 0.5$  and  $x_0 = 0.5$ .

This simulation illustrate an example of niche differentiation : natural selection drives the population into sub-populations that have different patterns of trait and that live in different spatial niches. As time increases, we observe more and more niches, then the pattern is stabilizing.

- Parameters :
- $m_u \equiv 0.003$ ,
  - $b_u(x) = \max\{2 - 20(x - u)^2, 0\}$ ,
  - $d_u(x) = 1$ ,
  - $I_{u, v}(x) = C \mathbb{1}_{|x| < 0.1}$ ,
  - $\theta(x, u, v)dv$  is a gaussian law  $\mathcal{N}(u, 0.01)$  conditioned on staying in  $\mathcal{U}$ ,
  - $K = 500, r_K = 0.01$ .



(a) t=300

(b) t=1500

(c) t=4000

## III. Large population and rare mutations

Here, we study a limit of **large population** to understand some mean behaviour of the population ; in the same time, we suppose that mutation is a really **rare event** : we suppose

$$K \rightarrow +\infty \quad \text{and} \quad r_K \xrightarrow{K \rightarrow \infty} 0.$$

Under some assumptions of regularity of the parameters and  $\sup_K \mathbb{E} \left[ \int_{\mathcal{X} \times \mathcal{U}} \nu_0^K(dx, du) \right] < +\infty$ .

**Theorem 1 (see [2])** For all  $T > 0$ , if  $(\nu_0^K)_{K > 0}$  converges in law to some deterministic finite measure with a density  $g_u(0, x)dxdu$  then the process  $(\nu_t^K)_{K > 0}$  in  $\mathbb{D}([0, T], M_F(\mathcal{X} \times \mathcal{U}))$  converges in law to a deterministic continuous function  $\xi \in \mathcal{C}([0, T], M_F(\mathcal{X} \times \mathcal{U}))$  such that for each  $t, \xi_t$  admits a density  $g_u(t, x)dxdu$ .

The density function  $g$  is a weak solution to the partial differential equation on  $[0, T] \times \mathcal{X} \times \mathcal{U}$  with Neumann's boundary condition and initial condition  $g_u(0, x)$  :

$$\begin{cases} \partial_t g_u(t, x) = m_u \Delta_x (g_u(t, x)) + (b_u(x) - d_u(x) - \int_{\mathcal{X} \times \mathcal{U}} I_{u, v}(x - y) g_v(t, y) dy dv) g_u(t, x), \\ \partial_n g_u(t, x) = 0 \quad \text{on } [0, T] \times (\partial \mathcal{X}) \times \mathcal{U}, \end{cases}$$

Thanks to the assumption of rare mutations, there is no mutation in the limit. Thus, if a finite number of traits  $\{u_1, u_2, \dots, u_k\}$  are represented in the population initially, then this is true for all time  $t$ .

**Question** : What is the **long time behaviour** of such a deterministic population with a finite number of traits ?

## IV. Monomorphic population

In the case of one trait, the spatial density  $g(t, \cdot)$  of the population at time  $t$  satisfies this equation with a easier competition kernel

$$\begin{cases} \partial_t g(t, x) = m \Delta_x g(t, x) + [(b - d)(x) - \int_{\mathcal{X}} I(y) g(t, y) dy] g(t, x), \\ \partial_n g(t, x) = 0. \end{cases} \quad (1)$$

Let  $H$  be the **principal eigenvalue** (i.e. the largest eigenvalue) of the linear elliptic operator  $\mathcal{L}$ , defined for all functions  $h$  by  $\mathcal{L}h = m \Delta_x h + (b - d)h$ .

Under some assumptions of regularity and positivity,

**Theorem 2** For any positive  $C^2$ -solution,  $g$ , to (1),

- if  $H > 0$ ,  $g(t, \cdot) \xrightarrow{L^\infty} \bar{g}$ , as  $t \rightarrow \infty$  with  $\bar{g}$  the unique positive steady state of (1),
- if  $H \leq 0$ ,  $g(t, \cdot) \xrightarrow{L^\infty} 0$  as  $t \rightarrow \infty$ .

Thus  $H > 0$  is a **necessary and sufficient condition for the survival of the population**, that is, **only the diffusion parameter and the natural growth rate have an influence on the non-extinction**. The competition rate affects only the total size of the population in the limit.

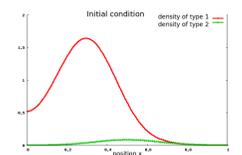
## V. Dimorphic population

The system of parabolic equations satisfied by the density functions in the case of two types is

$$\begin{cases} \partial_t g_1(t, x) = m_1 \Delta_x g_1(t, x) + \left( (b_1 - d_1)(x) - \int_{\mathcal{X}} I_{11}(y) g_1(t, y) dy - \int_{\mathcal{X}} I_{12}(y) g_2(t, y) dy \right) g_1(t, x), \\ \partial_n g_1(t, x) = 0, \quad \text{on } \mathbb{R}^+ \times \partial \mathcal{X}, \\ \partial_t g_2(t, x) = m_2 \Delta_x g_2(t, x) + \left( (b_2 - d_2)(x) - \int_{\mathcal{X}} I_{21}(y) g_1(t, y) dy - \int_{\mathcal{X}} I_{22}(y) g_2(t, y) dy \right) g_2(t, x), \\ \partial_n g_2(t, x) = 0, \quad \text{on } \mathbb{R}^+ \times \partial \mathcal{X}, \end{cases}$$

This system admits **4 nonnegative steady states** depending on the ecological parameters :

- \* the trivial state  $(0, 0)$ ,
- \* two states with no coexistence  $(\bar{g}_1, 0)$  and  $(0, \bar{g}_2)$ ,
- \* one state with coexistence  $(\hat{g}_1, \hat{g}_2)$ .



Parameters :  
 $(b_i - d_i)(x) = \max\{\bar{a}_i(1 - 20(x - u_i)^2), -1\}$ ,  
 $m_1 = m_2 = 0.01, \bar{a}_1 = 1, u_1 = 0.3, u_2 = 0.5$ ,  
different values of  $\bar{a}_2$  will be explored,  
 $I_{ij}(x) = 0.1 + 0.9 \cdot \mathbb{1}_{|x - u_j| < 0.25, |x - u_i| < 0.25}$ .

**Problem** : Initially we suppose that a population of type 1 is well established, its density is closed to the steady state in the case of a monomorphic population that survive. But there exists also a mutant population of type 2 with a small density. Thus, the initial condition is near the state  $(\bar{g}_1, 0)$ . What are the conditions to observe invasion by the mutants ?

**Theorem 3** For any initial condition in  $L^2(\mathcal{X})$ , the unique solution of the previous system of parabolic equations tends in  $L^\infty(\mathcal{X})$  to one of the nonnegative steady states.

To understand the long time behaviour and identify the limit, we have first studied the limit of the population densities normalized by the masses. Then we have analyzed the dynamics of the masses described by a perturbed Lotka-Volterra system. Finally, to clarify some uncertain cases, we have used methods with spectral decompositions.

The steady state reached after a long time is characterized by the following parameters for  $i = 1, 2$  :

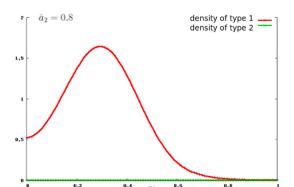
- \*  $H_i$  the **principal eigenvalue** of  $\mathcal{L}_i = m_i \Delta_x (\cdot) + (b_i - d_i) \cdot$ ,
- \*  $h_i$  the **principal eigenvector** of  $\mathcal{L}_i$  such that  $\int_{\mathcal{X}} h_i(y) dy = 1$ , that is, for all  $x \in \mathcal{X}$ ,  
 $m_i \Delta_x (h_i(x)) + (b_i - d_i)(x) h_i(x) = H_i h_i(x)$ ,
- \*  $\mu_{ji} = \int_{\mathcal{X}} I_{ji}(y) h_i(y) dy$ , for  $j = 1, 2$ , the **competition** kernels applied on the eigenvector.

Here, we only present three different behaviors for our problem :

$$\text{If } H_1 > 0, \quad H_2 \mu_{11} - H_1 \mu_{21} < 0,$$

the steady state  $(\bar{g}_1, 0)$  is **stable**. Thus, the mutant population goes extinct rapidly and we have fixation of type 1.

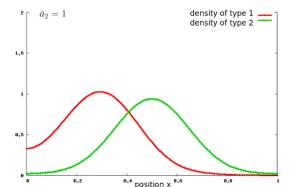
(Moreover, if  $H_1 \mu_{22} - H_2 \mu_{12} > 0$ , for any initial condition, the solution tends to  $(\bar{g}_1, 0)$ , i.e. it is globally asymptotically stable).



$\bar{a}_2 = 0.8, H_2 \mu_{11} - H_1 \mu_{21} = -0.155, H_1 \mu_{22} - H_2 \mu_{12} = 0.383$

$$\text{If } H_1 > 0, H_2 > 0, H_2 \mu_{11} - H_1 \mu_{21} > 0, H_1 \mu_{22} - H_2 \mu_{12} > 0$$

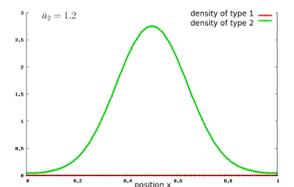
the steady state  $(\hat{g}_1, \hat{g}_2)$  is **globally asymptotically stable**. That is, as  $t$  approaches  $+\infty$ , we observe a coexistence between the two populations. The competition of the mutant on the population of type 1 is revealed by the diminution of the total number of type 1 compared with the previous case.



$\bar{a}_2 = 1, H_2 \mu_{11} - H_1 \mu_{21} = 0.164, H_1 \mu_{22} - H_2 \mu_{12} = 0.181$

$$\text{If } H_2 > 0, H_2 \mu_{11} - H_1 \mu_{21} > 0, H_1 \mu_{22} - H_2 \mu_{12} \leq 0$$

the steady state  $(0, \bar{g}_2)$  is **globally asymptotically stable**. The mutant population has invaded the space. Notice that it does not live on the same spatial position as the type 1. From an ecological point of view, that example is interesting because it shows a change of spatial niche due to a selection event.



$\bar{a}_2 = 1.2, H_2 \mu_{11} - H_1 \mu_{21} = 0.487, H_1 \mu_{22} - H_2 \mu_{12} = -0.037$

## Perspectives

Our objective now is to understand the framework of adaptive dynamics for this spatially structured population. The theory of adaptive dynamics, developed by Metz et al. and Dieckmann and Law, supposed that the time scale of the selective events is faster than the time scale of mutation events. Thus, we want now to understand the time scale of mutation events : between two mutations is the dynamic driven by the previous system of differential equations? What is the effect of the spatial structure on that kind of dynamics ?

[1] Doebeli M. and Dieckmann U. Speciation along environmental gradients. *Nature*, 421 :259-263 (2003).

[2] Champagnat N., Méléard S. Invasion and adaptive evolution for individual-based spatially structured populations. *J. Math. Biol.*, 55 :147-188 (2007)

[3] Leman H., Mirrahimi S., Méléard S. Influence of a spatial structure on the long time behavior of a competitive system of integro-differential equations. *Disc. Cont. Dyn. Syst. - B* 20 (2) (2015), 469-493.