Influence of a spatial structure on phenotypic evolution
-
With Sepideh Mirrahimi and Sylvie Méléard

Hélène Leman

April 2013

ANR MANEGE

Plan

Aim : We try to understand the interplay between migration and local competition in the evolution of the phenotypic composition of a population.

First example : heterogeneous environment favors diversity

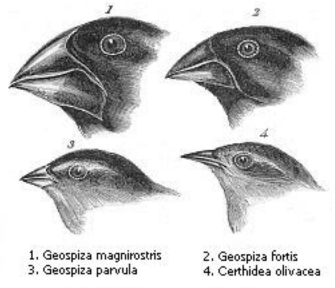

FIGURE : Finches from the Galapagos Archipelago

Second example : impact of mutation on invasion

FIGURE : Female cane toad

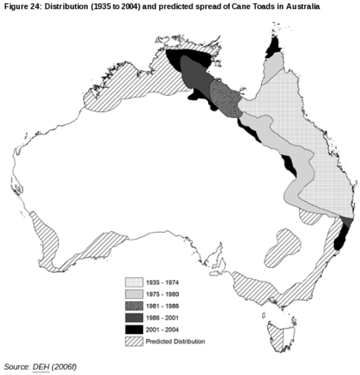

FIGURE : Distribution (1935 to 2004) and predicted spread of Cane Toads in Australia. Source : www.environment.gov.au

Plan

- asexual reproduction,
- spatially explicit individual-based model,
- $X_t^i \in \mathcal{X}$ is the location of individual i at time t, where $\mathcal{X}$ is an open bounded subset of $\mathbb{R}^d$.
- $U_t^i \in \mathcal{U}$ is the trait of individual i at time t, where $\mathcal{U}$ is a compact set of $\mathbb{R}^q$.

Definition

The population is modeled by the finite measure

$$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N_t} \delta_{(X_t^i, U_t^i)}$$

where N_t is the number of individuals alive at time t and $K > 0$ is a parameter which will be specified later.

Space evolution

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

$$\begin{cases} dX_t & = & \sqrt{2m(X_t,u)}Id \cdot dB_t + b(X_t,u)dt - dk_t \\ |k|_t & = & \int_0^t 1_{\{X_s \in \partial\mathcal{X}\}} d|k|_s; \; k_t = \int_0^t n(X_s)d|k|_s \end{cases}$$

where k is a continuous, increasing process and B is a d-dimensional Brownian motion.

Phenotypic evolution

- **Birth** : An individual described by (x, u) gives birth to a clonal child at rate $\lambda_1(x, u)$,
- **Death** : An individual described by (x, u) dies at rate $\lambda_2(x, u)$.

We denote its growth rate by $a(x, u) = \lambda_1(x, u) - \lambda_2(x, u)$.

- **Birth with mutation** : Each individual gives birth to mutant child at a certain rate, the trait of the child is chosen according to a Gaussian law.

- **Competition** : If the population is described by $\nu = \dfrac{1}{K}\sum_{i=1}^{n} \delta_{(x_i)}$, the spatial competition against an individual (x, u) is given by :

$$\mu(x,u) I \star \nu(x,u) = \mu(x,u)\frac{1}{K}\sum_{i=1}^{n} I(x - x^i)$$

where I is a competition kernel.

Simulations

We can then simulate with a computer the behaviour of this population. We present an example here :

- the space $\mathcal{X}$ is $(0,1)$, and individuals move according to a symmetric diffusion (m is constant, $b \equiv 0$),
- the space of traits $\mathcal{U}$ is equal to $[0,1]$,
- the growth rate is $a(x,u) = \max(-1, 1 - 20(x-u)^2)$,
- two individuals are in competition if and only if their distance is smaller than $\delta = 0.1$.

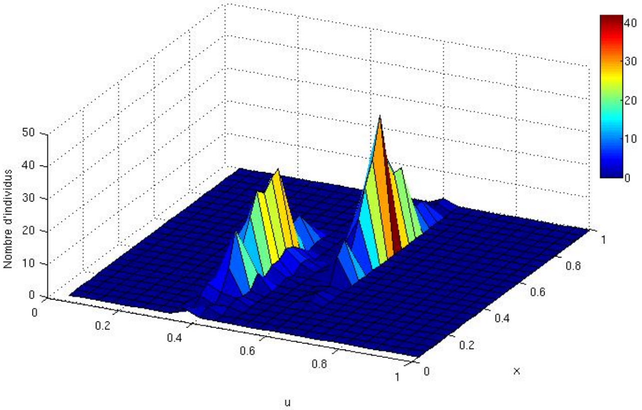

FIGURE : (a) t=300

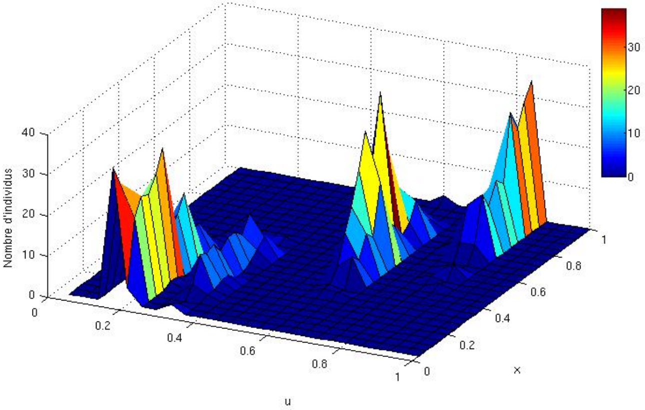

FIGURE : (b) t=600

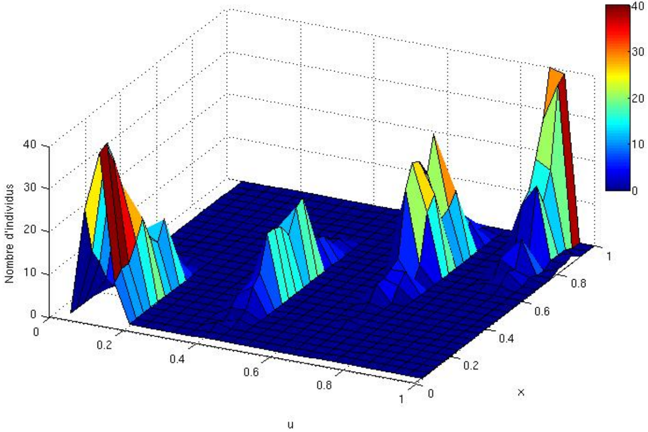

FIGURE : (c) t=1500

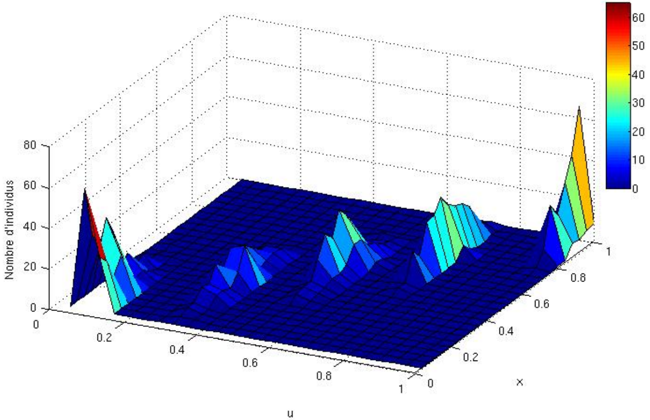

FIGURE : (d) t=4000

Large population approximation : $K \to +\infty$

If the coefficients are bounded and if m has a positive lower bound, the following theorem holds.

Theorem (Champagnat-Méléard 2007)

For all $T > 0$, if $(\nu_0^K)_{K>0}$ converges in law to some deterministic finite measure ξ_0 which has a density with respect to Lebesgue measure dxdu then $(\nu^K)_{K>0}$ converges in law as a process in $\mathbb{D}([0,T], M_F(\bar{\mathcal{X}} \times \mathcal{U}))$ to a deterministic function $\xi \in \mathbb{C}([0,T], M_F(\bar{\mathcal{X}} \times \mathcal{U}))$. For all t, ξ_t has a density with respect to Lebesgue measure.

The density function $g_t(x,u)$ is a weak solution to the partial differential equation :

$$\begin{cases} \partial_t g_t(x,u) = \Delta(m(x,u)g_t(x,u)) - \nabla(b(x,u)g_t(x,u)) \\ \qquad + a(x,u)g_t(x,u) \\ \qquad + \mu(x,u)\int_{\mathcal{X}} I(x-y)g_t(y,u)dyg_t(x,u), \\ g_0 \text{ is the density function of } \xi_0, \\ \partial_n g_t(x,u) = 0 \ \ \forall (t,x,u) \in [0,T] \times \partial\mathcal{X} \times \mathcal{U}. \end{cases}$$

Plan

In the case of a monomorphic population, the evolution equation is

$$\begin{cases} \partial_t g_t(x) = \Delta(m g_t)(x) + a(x) g_t(x) \\ \qquad\qquad - \mu(x)\left(\int_{\mathcal{X}} I(x-y) g_t(y) dy\right) g_t(x), \ \forall x \in \mathcal{X} \\ \partial_n g_t(x) = 0, \ \forall x \in \partial\mathcal{X}, \ \forall t \in \mathbb{R}, \end{cases}$$

where g_t is the density at time t of the population on $\mathcal{X}$.

Result : if $I \equiv 1$, g_t tends to a stationary state when t tends to $+\infty$.

Lemma

If

$$\min_{u\in K^1} \frac{1}{\|u\|_{L^2}^2}\left[\int_{\mathcal{X}} m|\nabla u|^2 dx - \int_{\mathcal{X}} a(x)u^2(x)dx\right] = -C_a < 0,$$

then

$$\begin{cases} -\Delta(mg)(x) = \left(a(x) - \mu(x)\int_{\mathcal{X}} I(x-y)g(y)dy\right) g(x) \text{ sur } \mathcal{X} \\ \partial_n g(x) = 0 \text{ pour tout } x \in \partial\mathcal{X}. \end{cases}$$

has a positive solution in $L^2(\mathcal{X})$.

Lemma

If

$$\min_{u\in K^1}\frac{1}{\|u\|_{L^2}^2}\left[\int_{\mathcal{X}} m|\nabla u|^2dx-\int_{\mathcal{X}} a(x)u^2(x)dx\right]=-C_a<0,$$

then

$$\begin{cases} -\Delta(mg)(x)=\left(a(x)-\mu(x)\int_{\mathcal{X}} I(x-y)g(y)dy\right)g(x) \text{ sur } \mathcal{X} \\ \partial_n g(x)=0 \text{ pour tout } x\in\partial\mathcal{X}. \end{cases}$$

has a positive solution in $L^2(\mathcal{X})$.

Proof : Find a **fixed-point** of a function χ.

Using the Krein-Rutman theorem,

Theorem (Krein-Rutman)

Let E be a Banach space, and $A : \begin{pmatrix} E & \mapsto & E \\ f & \to & g \end{pmatrix}$.

If A is continuous, compact, and if there exists a closed cone K such that :

$$\text{if } g \in K, \text{ then } A(g) \in Int\{K\},$$

then there exists a simple positive eigenvalue of A with eigenvector in $Int\{K\}$.

we conclude that for all $f \in L^2$, there exist $c_f \in \mathbb{R}$ and $g \in C^2$, positive, such that

$$\begin{cases} L_f(g) = c_f g & \forall x \in \mathcal{X} \\ \partial_n g(x) = 0 & \forall x \in \partial\mathcal{X}. \end{cases}$$

where $L_f(g) = -\Delta(mg) - (a - \mu(I * f))g$.

We construct a function $\chi : \begin{pmatrix} L^2(\mathcal{X}) & \mapsto & L^2(\mathcal{X}) \\ f & \rightarrow & g \end{pmatrix}$,

g is the positive eigenvector, defined previously, such that

$$c_g = 0.$$

We construct a function $\chi : \begin{pmatrix} L^2(\mathcal{X}) & \mapsto & L^2(\mathcal{X}) \\ f & \to & g \end{pmatrix}$,

g is the positive eigenvector, defined previously, such that

$$c_g = 0.$$

$$c_g = \min_{\substack{u \in H^1,\, u > 0, \\ \partial_n u = 0}} \frac{1}{\|u\|_{L^2}^2} \Big[\int_{\mathcal{X}} m |\nabla u|^2 dx - \int_{\mathcal{X}} a(x) u^2(x) dx + \int_{\mathcal{X}} \mu(x)(I * g)(x) u^2(x) dx \Big].$$

If χ has a fixed point g, then $\chi(g) = g$, so

$$\begin{cases} L_g(g) = c_g\, g & \forall x \in \mathcal{X} \\ \partial_n g(x) = 0 & \forall x \in \partial\mathcal{X} \end{cases}$$

$$\text{and} \quad c_g = 0.$$

i.e.

$$\begin{cases} -\Delta(mg) = (a - \mu(I * g))g & \forall x \in \mathcal{X} \\ \partial_n g(x) = 0 & \forall x \in \partial\mathcal{X} \end{cases}$$

Fixed-point theorem

We used this fixed point theorem.

Theorem (Schaefer)

Let E be a Banach space, $\chi : E \mapsto E$, continuous, compact and such that there exists $R > 0$ satisfying :

$$\text{if } \exists g \in E,\ g = t\chi(g),\ \text{ with } t \in [0,1[,\ \text{then } \|g\|_E \leq R,$$

then χ has a fixed point in E.

Smoothness of χ

- χ is compact :
  We take $A = \{f \in L^2, \|f\|_{L^2} \leq M\}$ and show that $\chi(A)$ is a bounded set of H^1, so it is a compact of L^2.

- χ is continuous :
  To show this, we write χ as a composition of continous functions.

Smoothness of χ

- χ is compact :
  We take $A = \{f \in L^2, \|f\|_{L^2} \leq M\}$ and show that $\chi(A)$ is a bounded set of H^1, so it is a compact of L^2.

- χ is continuous :
  To show this, we write χ as a composition of continous functions.

Degree hypothesis

Let t be in $]0,1[$ and g be in L^2 such that $g = t\chi(g)$.

- If $\mathcal{X} \subset \mathbb{R}$ then
$$\|g\|_{L^2} \leq C\|g\|_\infty \leq R.$$
So χ has a fixed point, i.e. there exists a positive stationary solution.

- If $\mathcal{X} \subset \mathbb{R}^d$, $d > 1$, and if we add the hypothesis
$$(\mathrm{H})\ \exists k, k' > 0 / \ \forall x \in \mathcal{X},\ k \leq I(x) \leq k',$$
then
$$\|g\|_{L^2} \leq R.$$
So χ has a fixed point, i.e. there exists a positive stationary solution.

Degree hypothesis

Let t be in $]0,1[$ and g be in L^2 such that $g = t\chi(g)$.

- If $\mathcal{X} \subset \mathbb{R}$ then
$$\|g\|_{L^2} \leq C\|g\|_\infty \leq R.$$
So χ has a fixed point, i.e. there exists a positive stationary solution.

- If $\mathcal{X} \subset \mathbb{R}^d$, $d > 1$, and if we add the hypothesis
$$\text{(H) } \exists k, k' > 0 / \; \forall x \in \mathcal{X}, \; k \leq I(x) \leq k',$$
then
$$\|g\|_{L^2} \leq R.$$
So χ has a fixed point, i.e. there exists a positive stationary solution.

Plan

- Define the probability for a mutant to survive and invade an established monomorphic population,
- Study the evolution of a population with two or more traits.

- Define the probability for a mutant to survive and invade an established monomorphic population,
- Study the evolution of a population with two or more traits.

Thank you !