

Selection-mutation models: diversification of populations

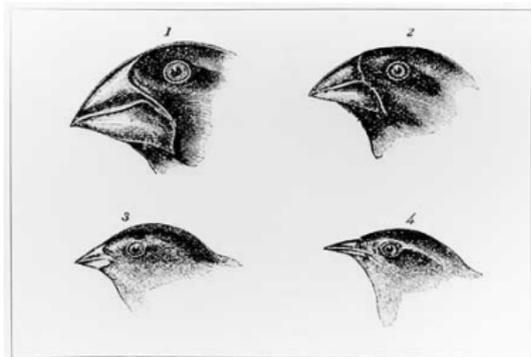
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CMAP, Ecole Polytechnique

Ecole Polytechnique, Chaire MMB, 27 Juin 2012

Darwinian evolution of a structured population density

- We study the **Darwinian** evolution of a population structured by **phenotypical traits**, and(or) **space**, under **selection** and **mutation**



- We study the **long time** behavior of a population density, assuming that mutations are **rare** or **small**.
- We expect to observe: **speciation**, **extinction** and **branching**

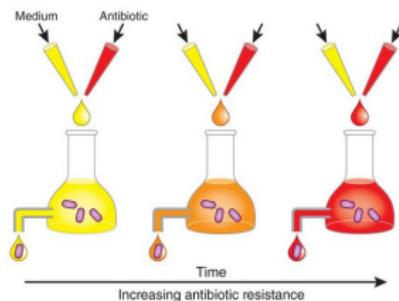
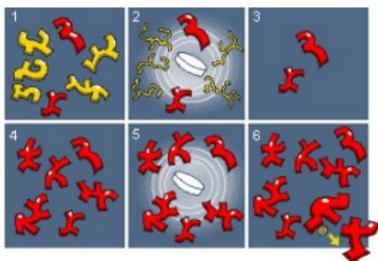


Figure: Morbidostat : a selective pressure is applied continuously to the bacterial population

Rosenthal et Elowitz, Nature Genetics
2012

- **Game theory:** Maynard Smith, Hofbauer, Sigmund,...
- **Classical adaptive dynamics:** Dieckmann, Gertiz, J. A. J. Metz, Kisdi, Meszéna, Diekmann, Jacobs, Gyllenberg, H. Metz,...
- **Stochastic methods:** Méléard, Champagnat, Ferrière, Fournier, Bolker, Pacala, Lambert,...
- **Integro-differential models:** Perthame, Desvillettes, Jabin, Mischler, Carrillo, Calsina, Cuadrado, Barles, Raoul, Génieys,...

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A model with a single nutrient

$$\begin{cases} \frac{\partial}{\partial t} n_\varepsilon = \frac{n_\varepsilon}{\varepsilon} R(x, l_\varepsilon) + \frac{1}{\varepsilon} \int \frac{1}{\varepsilon^d} K\left(\frac{y-x}{\varepsilon}\right) b(y, l_\varepsilon) n_\varepsilon(y, t) dy, \\ n_\varepsilon(\cdot, t=0) = n_\varepsilon^0(\cdot), \end{cases}$$

$$l_\varepsilon(t) = \int_{\mathbb{R}^d} \eta(x) n_\varepsilon(x, t) dx.$$

- $x \in \mathbb{R}^d$: phenotypical trait
- $n_\varepsilon(x, t)$: density of trait x
- $K(z)$: mutation probability kernel
- $\eta(x)$: consumption rate
- $l_\varepsilon(t)$: total consumption
- $R(x, l_\varepsilon)$: growth rate
- $b(x, l_\varepsilon)$: mutation birth rate
- ε : a small parameter

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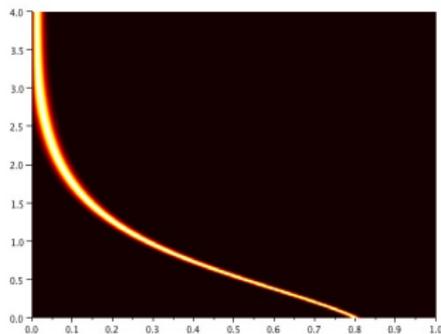
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Another way to model the mutations

$$\begin{cases} \frac{\partial}{\partial t} n_\varepsilon - \varepsilon \Delta n_\varepsilon = \frac{n_\varepsilon}{\varepsilon} R(x, l_\varepsilon), \\ n_\varepsilon(\cdot, t=0) = n_\varepsilon^0(\cdot), \end{cases}$$

$$l_\varepsilon(t) = \int_{\mathbb{R}^d} \eta(x) n_\varepsilon(x, t) dx.$$

A simple typical growth rate: $R(x, l) = 1 - \frac{x^2}{2} - l$



Dynamics of the dominant trait

No blow up, no extinction

$$\min_{x \in \mathbb{R}^d} [R(x, I_m) + b(x, I_m)] = 0, \quad \max_{x \in \mathbb{R}^d} [R(x, I_M) + b(x, I_M)] = 0,$$

$$I_m \leq I_\varepsilon(0) \leq I_M.$$

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Limited resource \implies **competition between traits.**

Further assumptions

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- and some regularity assumptions...

\implies after extraction of a subsequence, $(I_\varepsilon)_\varepsilon$ converges a.e. to $I(t)$.

Some notations

- $n(x, t)$: weak limit of $n_\varepsilon(x, t)$ as ε vanishes

- We expect n to concentrate as **Dirac masses**

- Hopf-Cole transformation: $n_\varepsilon(x, t) = \exp\left(\frac{u_\varepsilon(x, t)}{\varepsilon}\right)$

Theorem (Barles, M., Perthame - 2009)

Under the previous assumptions, after extraction of a subsequence, u_ε **converges locally uniformly** to a continuous function u , a viscosity solution to

$$\begin{cases} \frac{\partial}{\partial t} u = R(x, I(t)) + b(x, I(t)) \int K(z) \exp(\nabla u \cdot z) dz, \\ \max_{x \in \mathbb{R}^d} u(x, t) = 0, \\ u(0, x) = u^0(x), \end{cases}$$

$$I_\varepsilon(t) \xrightarrow{\varepsilon \rightarrow 0} I(t) \quad \text{a.e.}, \quad \int \eta(x) n(x, t) dx = I(t) \quad \text{a.e.}$$

The case of Laplacian

After extraction of a subsequence, u_ε **converges locally uniformly** to a continuous function u , a viscosity solution to

$$\begin{cases} \frac{\partial}{\partial t} u = |\nabla u|^2 + R(x, l(t)) \\ \max_{x \in \mathbb{R}^d} u(x, t) = 0, \\ u(0, x) = u^0(x). \end{cases}$$

Barles, M., Perthame - 2009

Consequences...

$$\bar{x}(t) \in \text{supp } n(t, \cdot)$$

$$\implies u(\bar{x}(t), t) = 0$$

$$\implies R(\bar{x}(t), I(t)) = 0$$

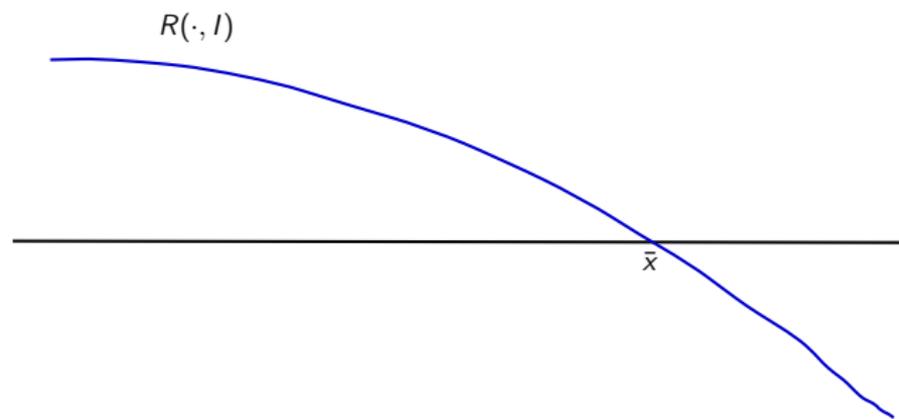
Convergence to a monomorphic population

In 1-d : Under **monotonicity** conditions on R , weakly in the sense of measures and after extraction of a subsequence, we have

$$n_\varepsilon(x, t) \xrightarrow{\varepsilon \rightarrow 0} n(x, t) = \bar{\rho}(t) \delta(x - \bar{x}(t)),$$

with $R(\bar{x}(t), I(t)) = 0$ and $\bar{\rho}(t) = \frac{I(t)}{\eta(\bar{x}(t))}$.

G. Barles, B. Perthame - 2008



Multi-d: Concavity assumptions

$$-2\underline{K}_1 \leq D^2 R(x, l) \leq -2\overline{K}_1 < 0$$

as symmetric matrices for $0 \leq l \leq l_M$,

$$-2\underline{L}_1 \leq D^2 u_\varepsilon^0 \leq -2\overline{L}_1,$$

$$4\overline{L}_1^2 \leq \overline{K}_1 \leq \underline{K}_1 \leq 4\underline{L}_1^2.$$

Convergence to a monomorphic population [competitive exclusion]

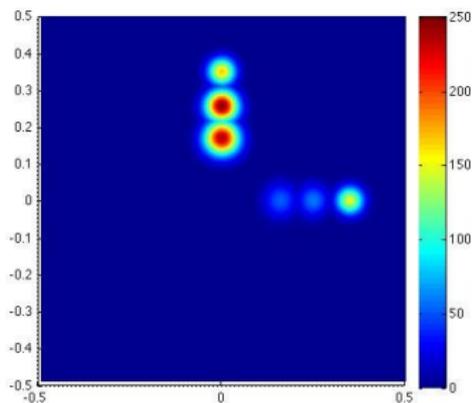
Theorem (Lorz, M., Perthame - 2011)

Under the previous assumptions, after extraction of a subsequence, the sequence $(n_\varepsilon)_\varepsilon$ converges weakly in the sense of measures to a single Dirac mass

$$n_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \rho(t) \delta(x - \bar{x}(t)),$$

$$\rho(t) = \frac{I(t)}{\eta(\bar{x}(t))}, \quad R(\bar{x}(t), I(t)) = 0 \quad \text{a.e.},$$

and $I(t)$ is non-decreasing.



$$R(x, y, l) = 3 - 1.5l - 5.6(y^2 + 1.1x^2).$$

Canonical equation

"**Canonical equation**" refers to a differential equation for the position of the dominant trait(s) in trait space.

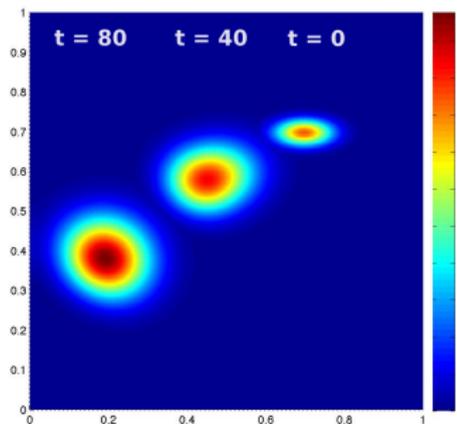
$$D^3 R(\cdot, I) \in L^\infty(\mathbb{R}^d), \quad D^3 u_\varepsilon^0 \in L^\infty(\mathbb{R}^d).$$

Theorem (Lorz, M., Perthame - 2011)

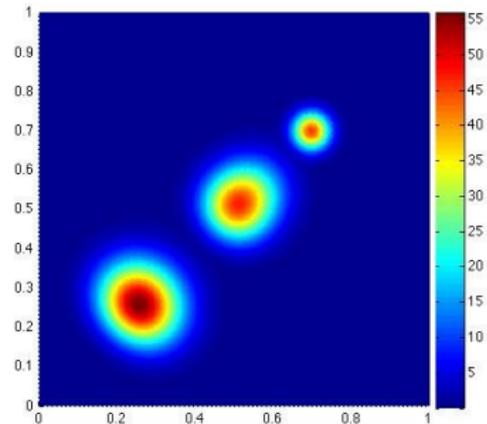
Under the previous assumptions, $\bar{x}(\cdot)$ belongs to $W^{1,\infty}(\mathbb{R}^+; \mathbb{R}^d)$ and satisfies

$$\dot{\bar{x}}(t) = (-D^2 u(\bar{x}(t), t))^{-1} \cdot \nabla_x R(\bar{x}(t), I(t)), \quad \bar{x}(0) = \bar{x}^0.$$

Furthermore, we have $I(t) \in W^{1,\infty}(\mathbb{R}^+)$.



(a) asymmetric I.D.



(b) symmetric I.D.

$$R(x, y, l) = 2 - l - 0.6(x^2 + y^2).$$

Dynamics of the density n with asymmetric initial data (left) and symmetric initial data (right).

A model with several resources

$$\begin{cases} \frac{\partial}{\partial t} n_\varepsilon - \varepsilon \Delta n_\varepsilon = \frac{n_\varepsilon}{\varepsilon} R(x, l_\varepsilon^1, \dots, l_\varepsilon^K), \\ n_\varepsilon(\cdot, t=0) = n_\varepsilon^0(\cdot), \end{cases}$$

$$l_\varepsilon^j(t) = \int_{\mathbb{R}^d} \eta^j(x) n_\varepsilon(x, t) dx.$$

In this model we can observe **polymorphism** and **branching**.

Champagnat, Jabin, 2011

Spatial models

x : space, v : trait

$$\partial_t n - \alpha \Delta_x n - \beta \Delta_v n = \frac{n}{\gamma} R(x, v, I(t, x)),$$

$$I(t, x) = \int \psi(v) n(t, x, v) dv.$$

A model with two favorable habitable zones:

$$\begin{cases} \partial_t n_\varepsilon^1 - \varepsilon \Delta n_\varepsilon^1 &= \frac{1}{\varepsilon} n_\varepsilon^1 R^1(x, l_\varepsilon^1) + \frac{1}{\varepsilon} \nu^2 n_\varepsilon^2 - \frac{1}{\varepsilon} \nu^1 n_\varepsilon^1, \\ \partial_t n_\varepsilon^2 - \varepsilon \Delta n_\varepsilon^2 &= \frac{1}{\varepsilon} n_\varepsilon^2 R^2(x, l_\varepsilon^2) + \frac{1}{\varepsilon} \nu^1 n_\varepsilon^1 - \frac{1}{\varepsilon} \nu^2 n_\varepsilon^2, \end{cases}$$

$$l_\varepsilon^1 = \int \psi(x) n_\varepsilon^1 dx, \quad l_\varepsilon^2 = \int \psi(x) n_\varepsilon^2 dx.$$

- One can write a similar model for K favorable habitable zones.

The stationary problem

$$\left\{ \begin{array}{ll} -\varepsilon^2 \Delta n_\varepsilon^1 = n_\varepsilon^1 R^1(x, I_\varepsilon^1) + \nu^2 n_\varepsilon^2 - \nu^1 n_\varepsilon^1 & \text{in } B_L(0), \\ -\varepsilon^2 \Delta n_\varepsilon^2 = n_\varepsilon^2 R^2(x, I_\varepsilon^2) + \nu^1 n_\varepsilon^1 - \nu^2 n_\varepsilon^2 & \text{in } B_L(0), \\ \nabla n_\varepsilon^i \cdot \vec{n} = 0 & \text{in } \partial B_L(0), \end{array} \right.$$

$$I_\varepsilon^1 = \int \psi(x) n_\varepsilon^1 dx, \quad I_\varepsilon^2 = \int \psi(x) n_\varepsilon^2 dx.$$

$$n_\varepsilon^i = \exp\left(\frac{u_\varepsilon^i}{\varepsilon}\right), \quad i = 1, 2.$$

Theorem (M. - 2012)

Under some assumptions, after extraction of a subsequence, both sequences $(u_\varepsilon^1)_\varepsilon$ and $(u_\varepsilon^2)_\varepsilon$ converge to a continuous function u that is a viscosity solution to the following equation

$$\begin{cases} -|\nabla u|^2 = H(x, I^1, I^2), & \text{in } B_L(0), \\ \max_{x \in B_L(0)} u(x) = 0, \end{cases}$$

with $H(x, I^1, I^2)$ the largest eigenvalue of the matrix

$$A = \begin{pmatrix} R^1(x, I^1) - \nu^1 & \nu^2 \\ \nu^1 & R^2(x, I^2) - \nu^2 \end{pmatrix}.$$

Consequences...

$$n_\varepsilon^1 \xrightarrow{\varepsilon \rightarrow 0} n^1, \quad n_\varepsilon^2 \xrightarrow{\varepsilon \rightarrow 0} n^2.$$

$$\text{supp } n^i \subset \Omega \cap \Gamma, \quad \text{for } i = 1, 2$$

$$\Omega = \{x \in B_L(0) \mid u(x) = 0\}$$

$$\Gamma = \{x \in B_L(0) \mid H(x, I^1, \dots, I^K) = \max_{x \in B_L(0)} H(x, I^1, \dots, I^K) = 0\}$$

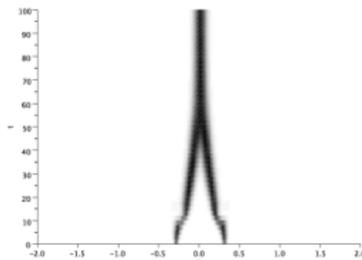
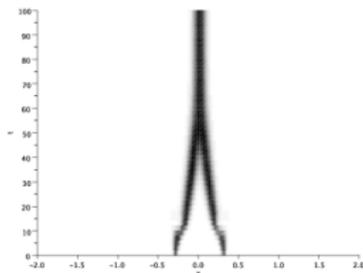
In particular, the population has an Evolutionary Stable Distribution (ESD)

If the support of n^i , for $i = 1, 2$, is a set of distinct points:
 $\text{supp } n^i \subset \{x_1, x_2, \dots, x_l\}$, we then have

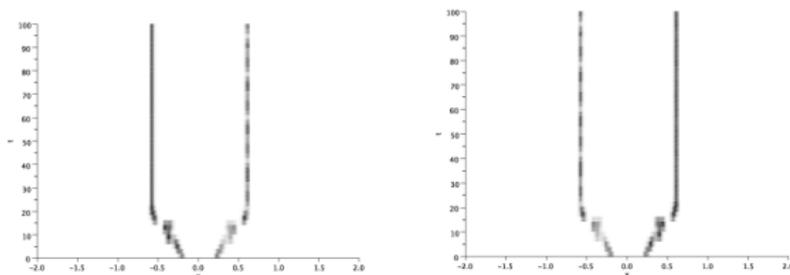
$$n^i = \sum_{j=1}^l \rho_j^i \delta(x - x_j), \quad \text{for } i = 1, 2,$$

with $\begin{pmatrix} \rho_j^1 \\ \rho_j^2 \end{pmatrix}$ is the **eigenvector** corresponding to the **largest eigenvalue** of the matrix \mathcal{A} at the point x_j , which is 0, and

$$\sum_j \rho_j^i \psi(x_j) = l^i.$$



- The gray layers represent the value of n_ε^1 (left) and n_ε^2 (right).
- Migration rates : $\nu^1 = \nu^2 = 1$.
- $R^1(x, l) = 5 - (x + 1)^2 + x - l$, $R^2(x, l) = 5 - (x - 1)^2 - x - l$
- The **optimal trait** in the first patch is $x = -0.5$ and in the second patch is $x = 0.5$.
- **Initially**: the trait in the first patch is $x = -0.3$ and in the second patch is $x = 0.3$.
- **At the final time**: the trait in both patches is $x = 0$.



- The gray layers represent the value of n_{ε}^1 (left) and n_{ε}^2 (right).
- **Migration rates** : $\nu^1 = \nu^2 = 0.5$.
- $R^1(x, l) = 3.2 - (x + 1)^2 + .1 \times x - l$,
 $R^2(x, l) = 3.2 - (x - 1)^2 - .1 \times x - l$
- The **optimal trait** in the first patch is $x = -0.95$ and in the second patch is $x = 0.95$.
- **Initially**: the trait in the first patch is $x = -0.2$ and in the second patch is $x = 0.2$.
- **At the final time**: two traits $x = -0.6$ and $x = 0.6$ are present in both patches.

Thank you for your attention !