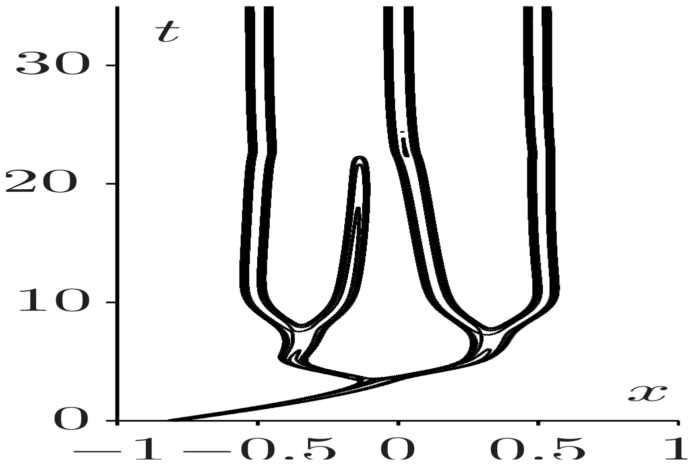
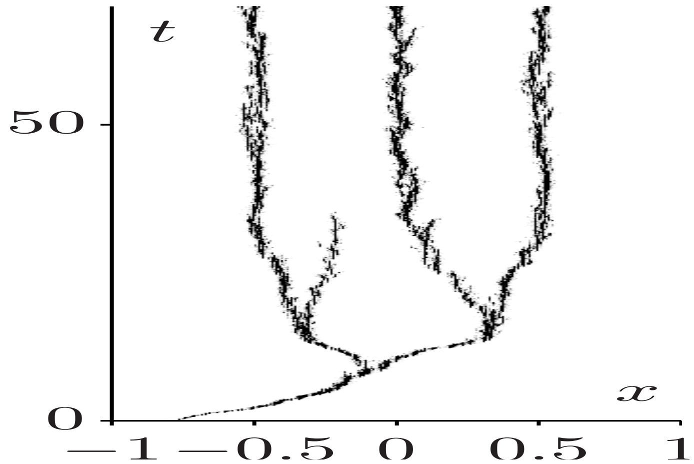
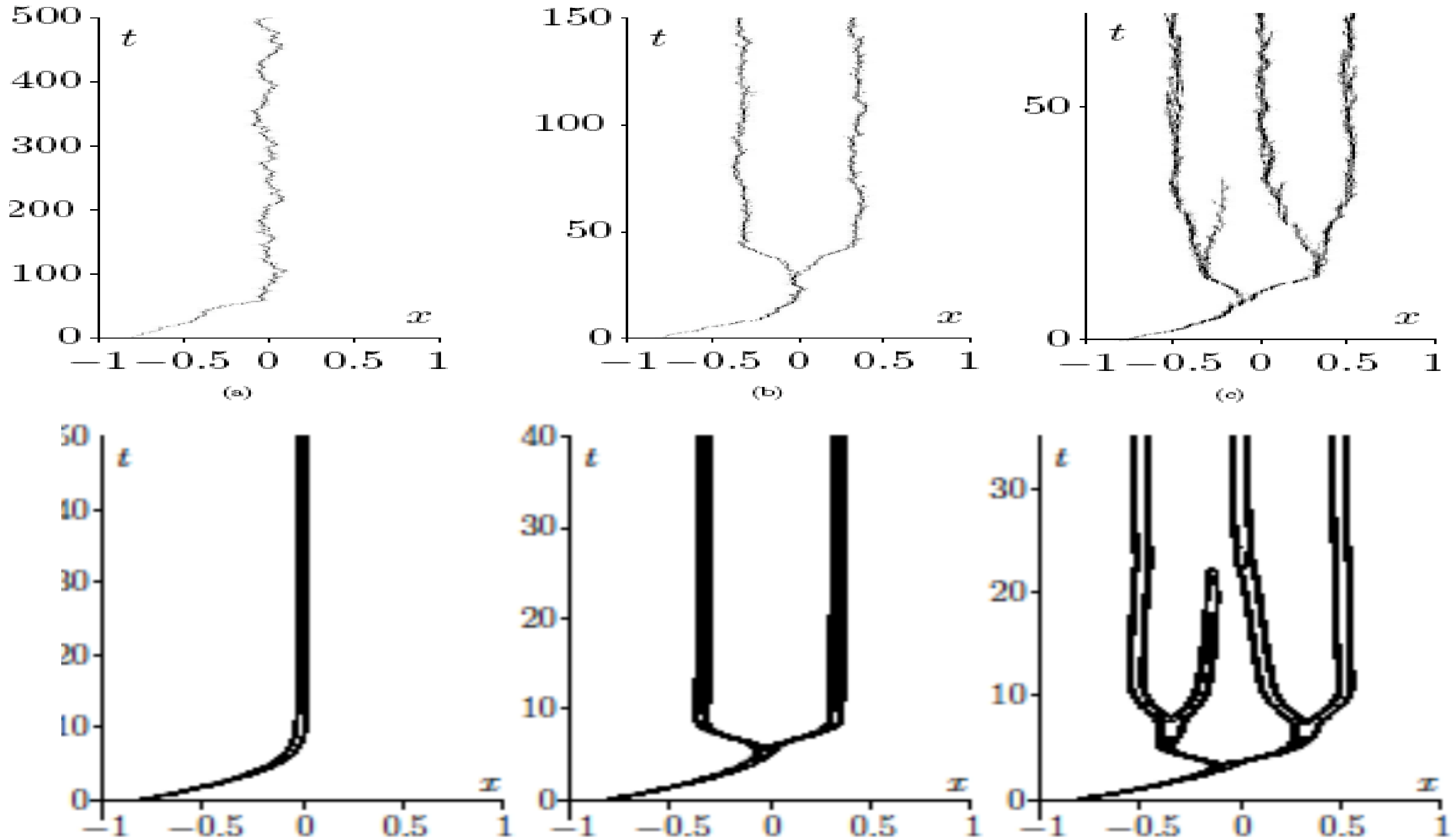
Adaptive evolution : a population approach

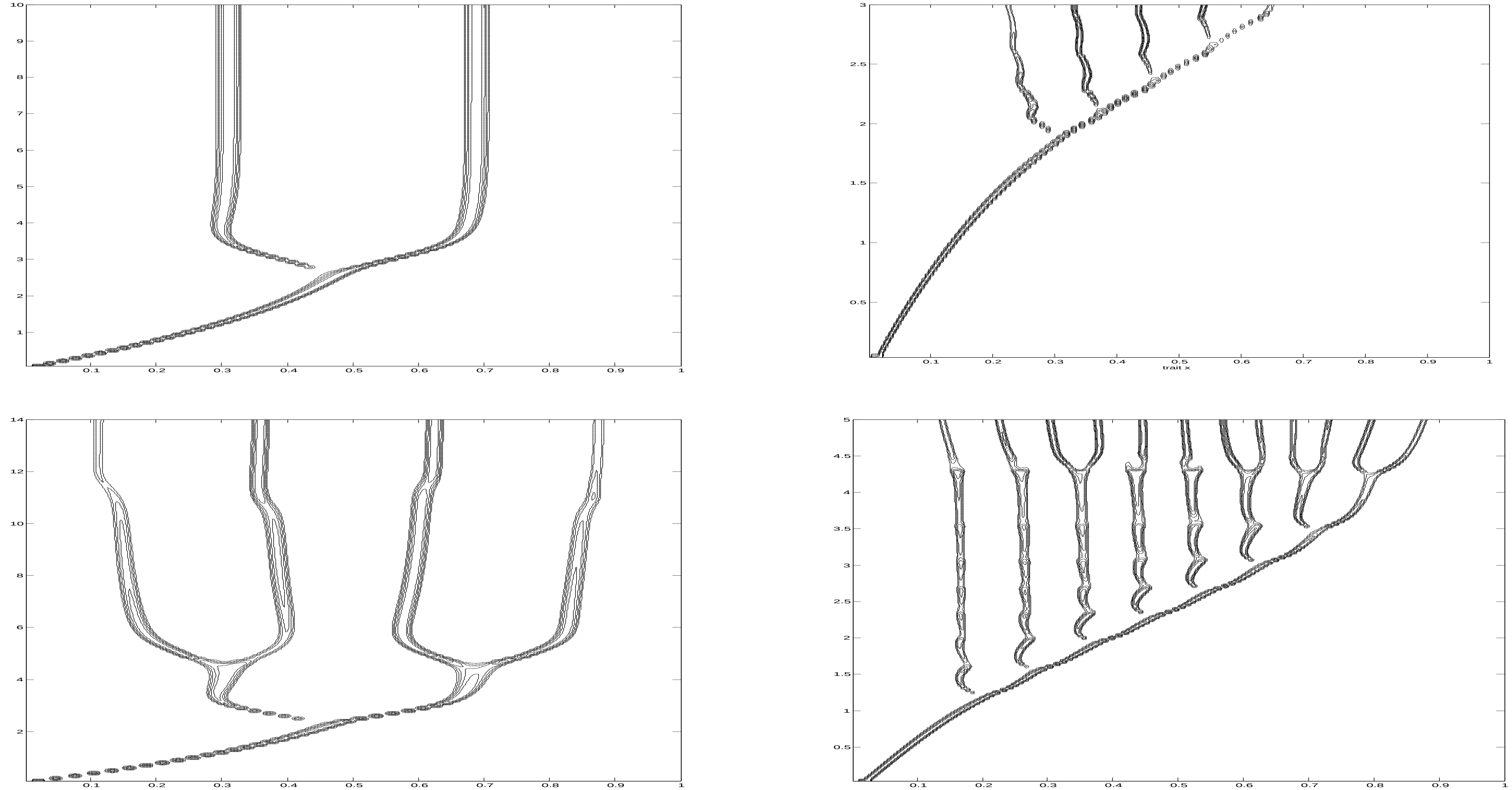
Benoît Perthame





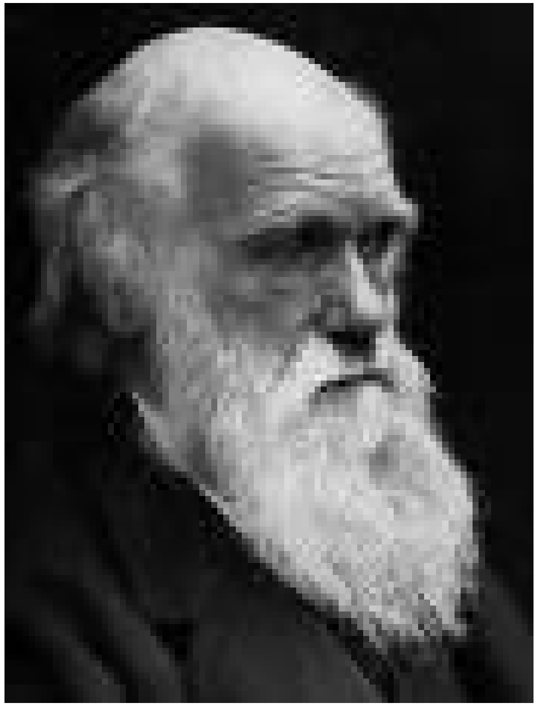
Motivation 1 : population adaptive evolution

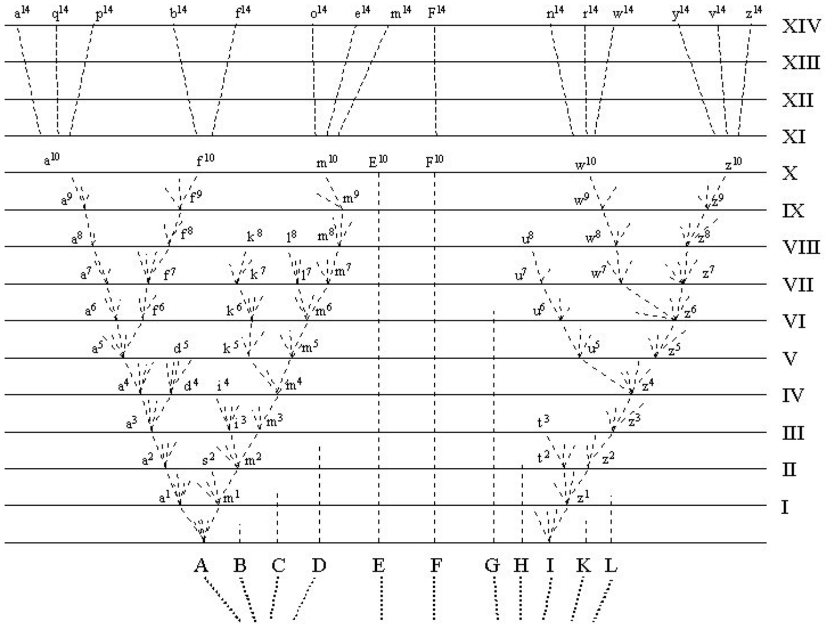



trait x

Motivation 1 : Short history

- Darwin (1809-1882) 'On the origin of species' (1859)





Motivation 1 : adaptive evolution

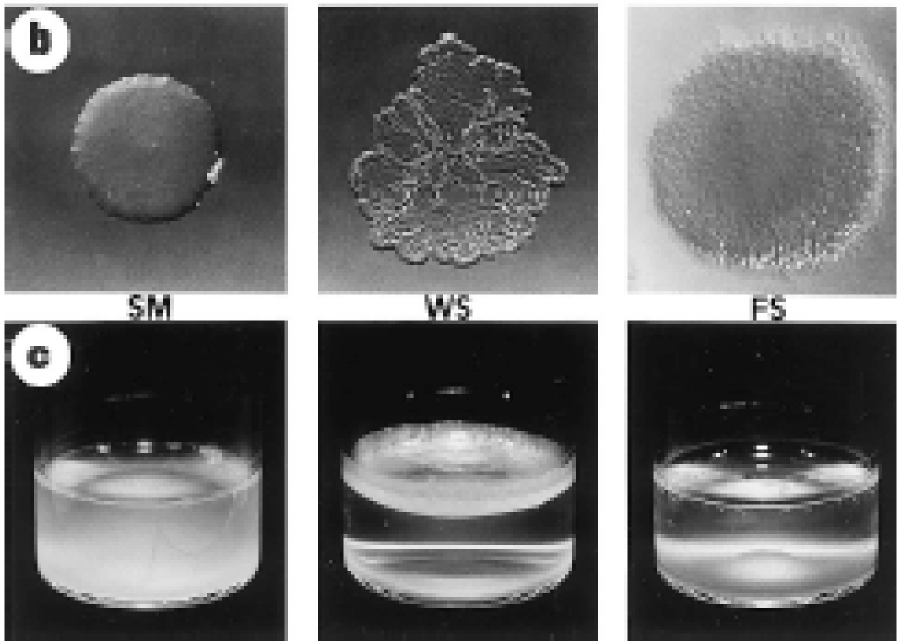
But adaptation can be seen on shorter times scales

- Bacterial resistance to antibiotics

- Resistance of tumor cells to chemotherapy

- Lab experiments on bacteria...

Motivation 1 : adaptive evolution



Phenotypic diversity for *Pseudomonas fluoresens*.

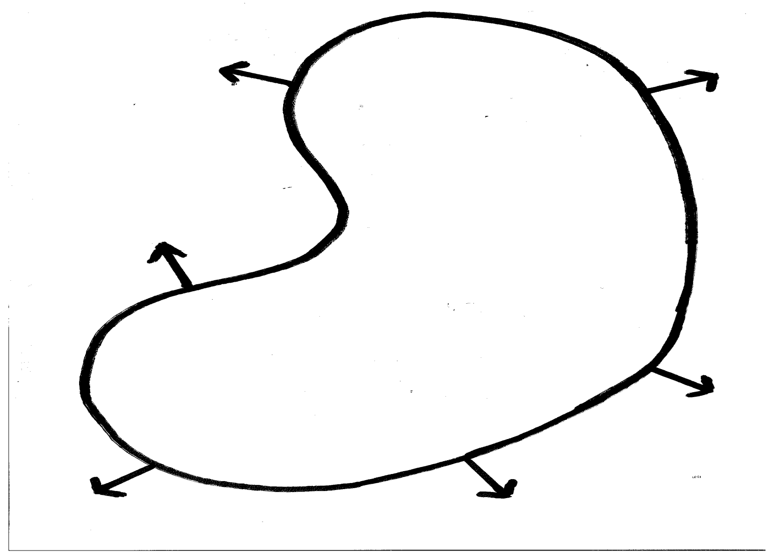
Populations were founded from single morph cells.

From Rainey and Travisano, Letters to Nature, 1998

Motivation 2 : geometric motion

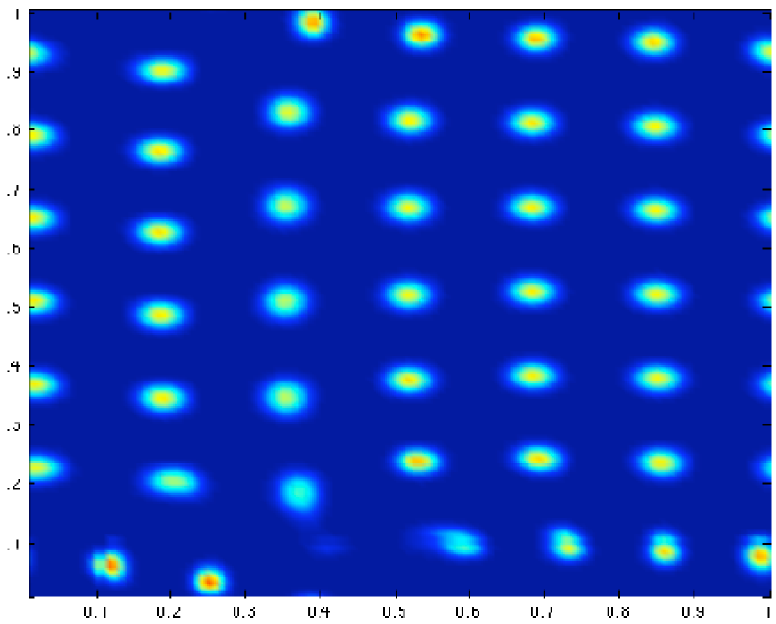
Combustion or invasion fronts lead to sharp moving interfaces described by geometric equations

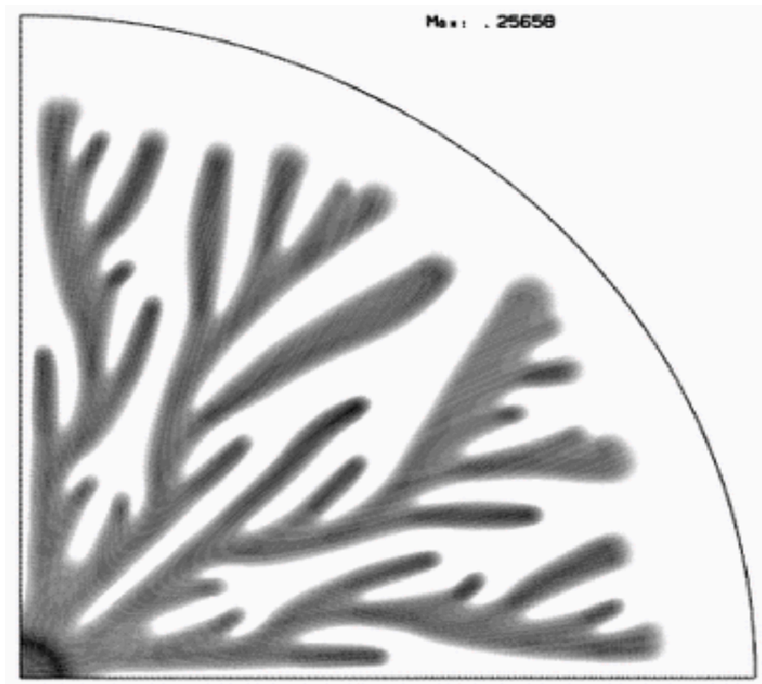
$$\frac{\partial u}{\partial t} + V|\nabla u| = 0,$$



These are hypersurfaces. Is it possible to describe 0 dimension motion as well ?

Motivation 3 : Turing patterns - Dentritic patterns





OUTLINE OF THE LECTURE

I. How to model evolution ?
II. Asymptotic method and the constrained H.-J. equation
III. Canonical equation
IV. Polymorphism
V. Evolution by non-proliferative advantage

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II. Asymptotic method and the constrained H.-J. equation
III. Canonical equation
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V. Evolution by non-proliferative advantage

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Adaptive dynamic : selection principle

Consider a structured population model

$$\begin{cases} \frac{d}{dt} n(t,x) = n(t,x) R\Big(x, \varrho(t)\Big), \\ \\ \varrho(t) = \int_{\mathbb{R}^d} n(t,x)dx. \end{cases}$$

Examples type 1 :

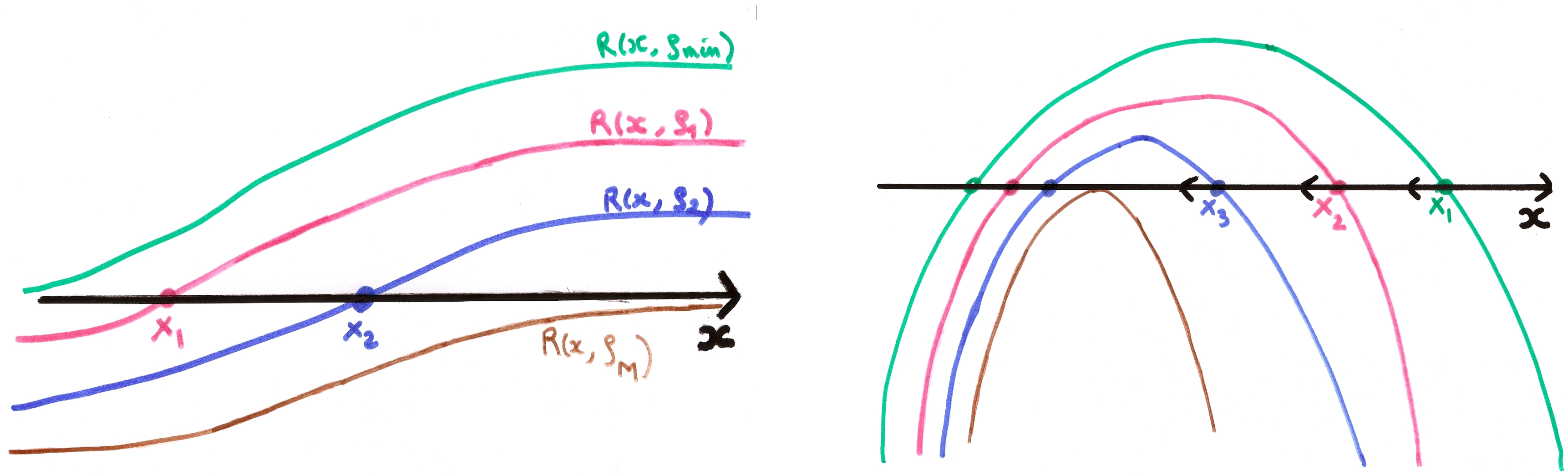
$R\Big(x, \varrho(t)\Big) := b(x) - d(x)\varrho(t), \qquad R\Big(x, \varrho(t)\Big) := \frac{b(x)}{1+\varrho(t)} - d(x)$

Examples type 2 : $R\Big(x, \varrho(t)\Big) := \frac{b(x)}{1+\varrho(t)} - d(x)\varrho(t)$

Keep in mind : • R changes sign, $R_\varrho(x, \varrho) < 0$,

• $\varrho(t) \leq \varrho_{Max}$ when $R\Big(x, \varrho_{Max}\Big) < 0, \ \forall x$

Motivation : general setting for adaptive evolution



Examples of growth rates $R(x, \varrho_i)$

Adaptive dynamic : selection principle

$$\begin{cases} \frac{d}{dt}n(t,x) = n(t,x)R\Big(x,\varrho(t)\Big), \\ \\ \varrho(t) = \int_{\mathbb{R}^d} n(t,x)dx, \end{cases}$$

with $\quad \frac{\partial}{\partial\varrho}R(x,\varrho) < 0, \qquad R\Big(x,\varrho_{Max}\Big) < 0 \quad \forall x.$

Theorem Assume $n^0(x) > 0$ then

$$\varrho(t) \to \varrho_\infty \qquad as \quad t \to \infty,$$

$$n(t,x) \underset{t\to\infty}{\longrightarrow} \varrho_\infty \, \delta(x = x_\infty) \qquad \text{(Competitive Exclusion Principle)}$$

and (assuming uniqueness)

$$\min_{\varrho\leq\varrho_\infty} \max_x R(x,\varrho) = 0 = R(x_\infty,\varrho_\infty) \qquad \text{(pessimism principle)}$$

Adaptive dynamic : selection principle

Proof. 1. bounds on $\varrho(t)$

$$\begin{cases} \frac{d}{dt}n(t,x) = n(t,x)\Big(b(x) - \varrho(t)d(x)\Big), \\ \varrho(t) = \int_{\mathbb{R}^d} n(t,x)dx. \end{cases}$$

We have the a priori estimate

$$\frac{d}{dt}\varrho(t) = \int b(x)n(t,x)dx - \varrho(t)\int d(x)n(t,x)dx \leq \varrho(t)[\max b - \min d\ \varrho(t)],$$

$$\frac{d}{dt}\varrho(t) = \int b(x)n(t,x)dx - \varrho(t)\int d(x)n(t,x)dx \geq \varrho(t)[\min b - \max d\ \varrho(t)],$$

This implies

$$\min(\varrho(0), \min b/d) \leq \varrho(t) \leq \max(\varrho(0), \max b/d).$$

Adaptive dynamic : selection principle

Proof. 2. $\lim_{t\to\infty} \varrho(t)$

Next, we prove BV bounds on $\varrho(t)$

$$\int_0^\infty \left|\frac{d}{dt}\varrho(t)\right| dt < \infty$$

Therefore $\varrho(t) \to \varrho_\infty$ as $t \to \infty$.

Adaptive dynamic : selection principle

Proof. 3. $\lim_{t\to\infty} n(t)$

The, BV estimates show that $\varrho(t)$ has a limit ϱ_∞ as $t \to \infty$.

$$\frac{d}{dt} n(t,x) \approx n(t,x)\Big[R\Big(x,\varrho_\infty\Big) \pm o(t)\Big],$$

This contradicts $R\Big(x,\varrho_\infty\Big) > 0$ for some x (finite population)

This contradicts $R\Big(x,\varrho_\infty\Big) < 0$ for all x (non extinction).

Adaptive dynamic : selection principle

$$\begin{cases} \frac{d}{dt} n(t,x) = n(t,x) R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}^d} n(t,x) dx. \end{cases}$$

Remark There are many steady states. For any $\bar{x}$

$$\bar{n}(x) = \bar{\varrho}\ \delta(x - \bar{x})$$

choosing $\bar{\varrho}$ such that $$R(\bar{x}, \bar{\varrho}) = 0.$$

The limit depends on the initial support

Adaptive dynamic : selection principle

$$\begin{cases} \frac{d}{dt} n(t,x) = n(t,x) R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}^d} n(t,x) dx. \end{cases}$$

given $\bar{x}$, $\qquad \bar{n}(x) = \bar{\varrho}\ \delta(x - \bar{x}), \qquad R(\bar{x}, \bar{\varrho}) = 0, \quad \bar{\varrho}(\bar{x}).$

- They are stable by perturbation of the weight $\bar{\varrho}$ (strong topology)

$$\frac{d}{dt}\varrho(t) = \varrho(t) R(\bar{x}, \varrho(t)).$$

Adaptive dynamic : selection principle

$$\begin{cases} \frac{d}{dt}n(t,x) = n(t,x)R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}^d} n(t,x)dx. \end{cases}$$

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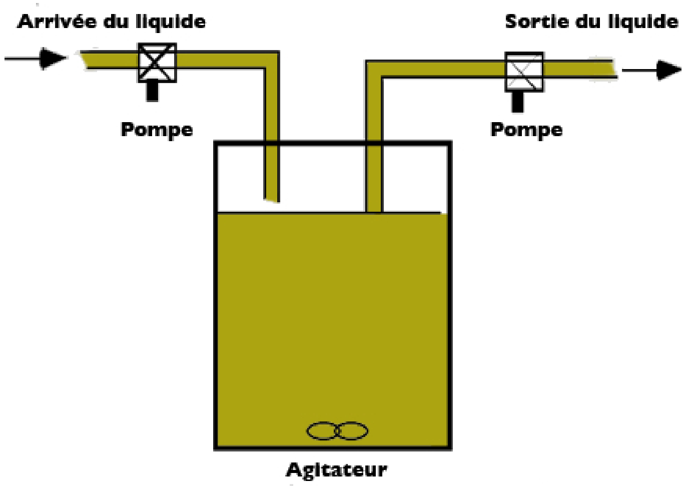
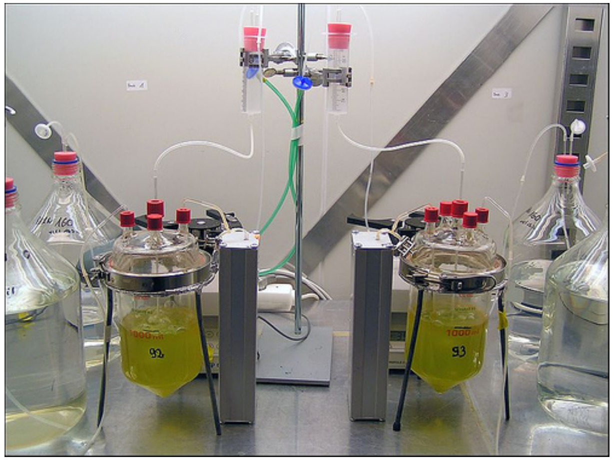
• They are stable by perturbation of the weight $\bar{\varrho}$ (strong topology)

$$\frac{d}{dt}\varrho(t) = \varrho(t)R(\bar{x}, \varrho(t)).$$

• But they are unstable by approximation in measures (weak topology), and by mutation (structural)...

Model derivation : the chemostat





$$
\begin{cases}
\overbrace{\frac{d}{dt}S(t)}^{\text{nutrient variation}} = \overbrace{r[S_0 - S(t)]}^{\text{inflow-outflow}} - \overbrace{S(t)\int b(x)n(t,x)dx}^{\text{consumption}} \\
\underbrace{\frac{d}{dt}n(t,x)}_{\text{population variation}} = n(t,x)\left(\underbrace{S(t)b(x)}_{\text{proliferation}} - \underbrace{r}_{\text{outflow}} \right)
\end{cases}
$$

Model derivation : the chemostat

The quasi-stastic approximation is mathematically more tractable

$$\frac{d}{dt}S(t) = r[S_0 - S(t)] - S(t)\int b(x)n(t,x)dx,$$

$$S(t) = \frac{rS_0}{r + \int b(x)n(t,x)dx} \leq S_0$$

$$\begin{cases} S(t) &= \dfrac{rS_0}{r + \int b(x)n(t,x)dx} \\ \frac{d}{dt}n(t,x) &= n(t,x)\,\Big(S(t)b(x) - r\Big) \end{cases}$$

Model derivation : the chemostat

$$\begin{cases} S(t) &= \dfrac{rS_0}{r + \int b(x)n(t,x)dx} \\ \\ \frac{d}{dt}n(t,x) &= n(t,x)\,\Big(S(t)b(x) - r\Big) \end{cases}$$

Theorem (Gause competitive exclusion principle)
Assume $n^0 \in L^1$, $\mathbf{n^0 > 0}$ and $\bar{b} := \max b = b(\bar{x}_\infty)$ uniquely, then

(i) For $r \geq S_0\bar{b}$ then $n(t,x) \underset{t\to\infty}{\longrightarrow} 0$,

(ii) For $r < S_0\bar{b}$

$$\int b(x)n(t,x)dx \underset{t\to\infty}{\longrightarrow} \bar{\rho}_\infty, \qquad n(t,x) \underset{t\to\infty}{\longrightarrow} \bar{\rho}_\infty\delta(x - \bar{x}_\infty)$$

Model derivation : the chemostat

$$\begin{cases} S(t) &= \dfrac{rS_0}{r + \int b(x)n(t,x)dx} \\ \frac{d}{dt}n(t,x) &= n(t,x)\Big(S(t)b(x) - r\Big) \end{cases}$$

Proof of (i) (Extinction) : Because $S(t) < S_0$ we have

$$\begin{aligned} \tfrac{d}{dt}n(t,x) &< n(t,x)\Big(S_0 b(x) - r\Big) \\ &< n(t,x)\Big(S_0 \max(b) - r\Big) \\ &< 0 \qquad\qquad \text{because } r \geq S_0 \max(b) \end{aligned}$$

One easily concludes : $n(t,x)$ converges to $N(x)$ and by contradiction

$$\int b(x)N(x)dx = 0.$$

Model derivation : the chemostat

The model can be extended to several nutrients

$$\begin{cases} \frac{d}{dt}S_j(t) &= r[S_{0,j} - S_j(t)] - S_j(t) \int b_j(x) n(t,x) dx, \qquad 1 \leq j \leq J \\ \frac{d}{dt}n(t,x) &= n(t,x) \left(\sum_{j=1}^{J} S_j(t) b_j(x) - r \right) \end{cases}$$

And with the quasi-static assumption

$$\begin{cases} S_j(t) &= \frac{r S_{0,j}}{r + \int b_j(x) n(t,x) dx} \\ \frac{d}{dt}n(t,x) &= n(t,x) \left(\sum_{j=1}^{J} S_j(t) b_j(x) - r \right) \end{cases}$$

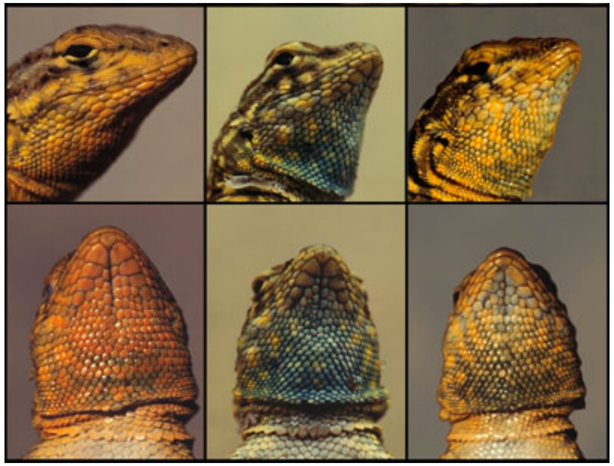
Claim (Gause competitive exclusion principle) Generically there can be J traits represented.

Population model of adaptive dynamics : related approaches

- Evolutionary game theory

Blue (stronger),
Orange (middle size),
Yellow (smaller)

compensate by mating **strategies**



from B. Sinervo. *http://bio.research.ucsc.edu/barrylab*

NATURE VOL. 246 NOVEMBER 2 1973

The Logic of Animal Conflict

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Population model of adaptive dynamics : related approaches

• Evolutionary game theory

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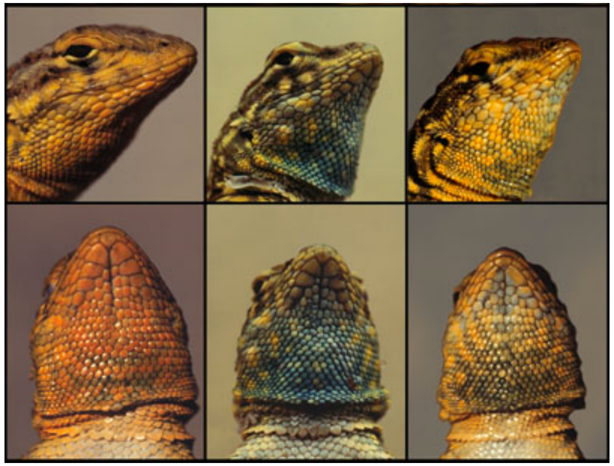
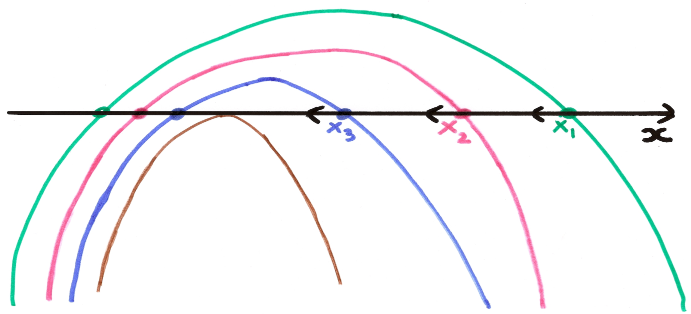


from B. Sinervo. *http : //bio.research.ucsc.edu/barrylab*

The relation can be seen by

$$\max_{\mathcal{S}} R(x, \bar{\rho}) = 0 = R(\bar{x}, \bar{\rho})$$

$$\min_{\rho} \ \max_{\mathcal{S}} R(x, \rho) = 0, \quad \text{(ESS)}$$



Population model of adaptive dynamics : related approaches

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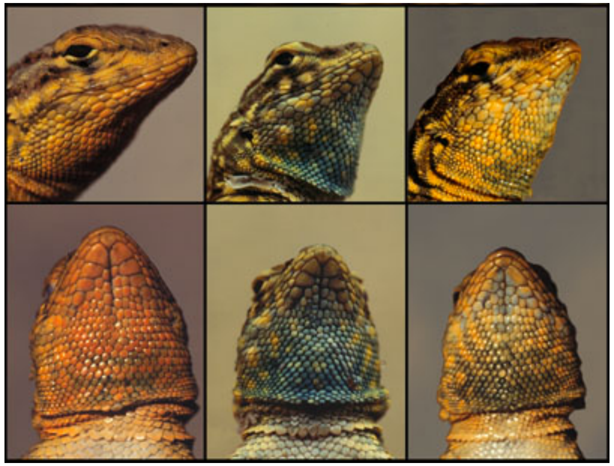


from B. Sinervo. $http://bio.research.ucsc.edu/barrylab$

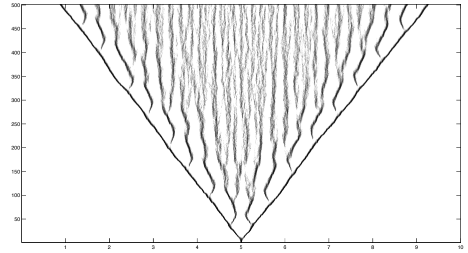
• Stochastic models, Individual Based Models

N individuals,

rescale mutation, birth, death rates

U. Dieckmann- R. Law, R. Ferriere

N. Champagnat, S. Méléard



Open questions

- We can prove (Chung, Lorz, BP) :

$$\begin{cases} \frac{d}{dt}n(x,t) & = n(x,t)R(x,I(t)), \\ \frac{d}{dt}I(t) & = \lambda[\varrho(t) - I(t)] \end{cases}$$

for λ large $\qquad \varrho(t),\ I(t) \to \varrho_\infty,\ I_\infty$

- Prove convergence of $n(x,t)$ when there is no uniqueness
- Multiple species, multiple nutrients,
- Uniqueness for the constrained Hamilton-Jacobi equation