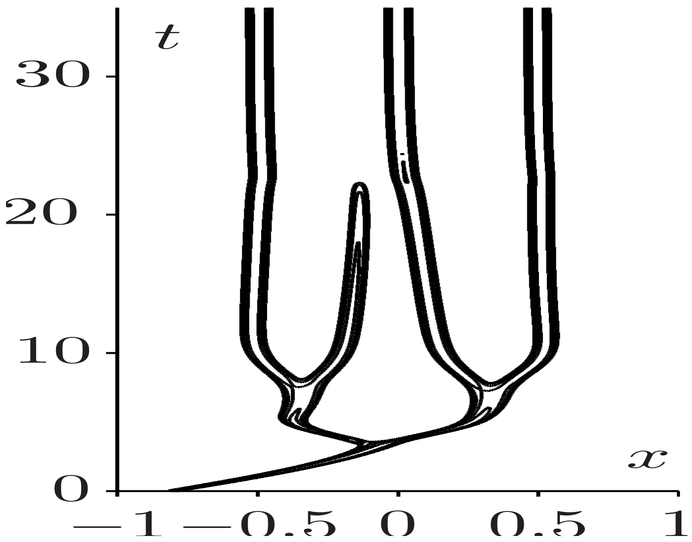
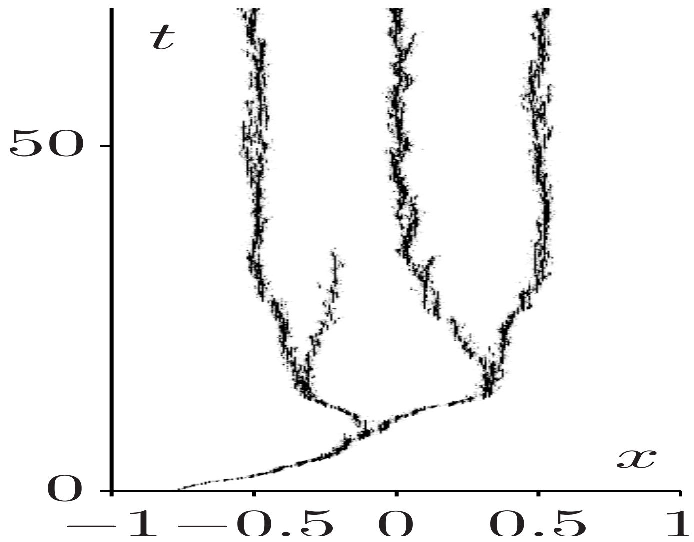
Adaptive evolution : a population approach

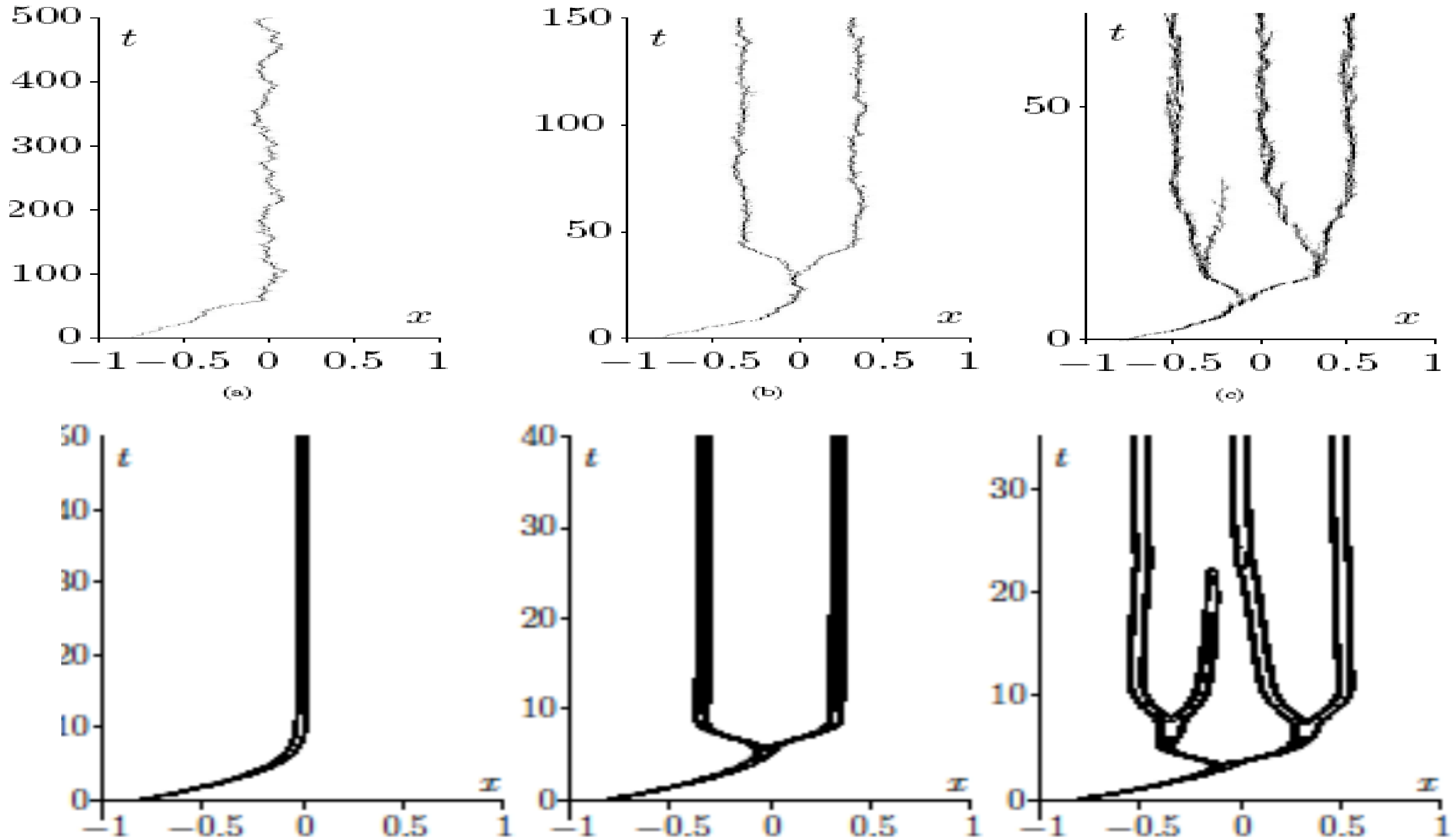
Benoît Perthame

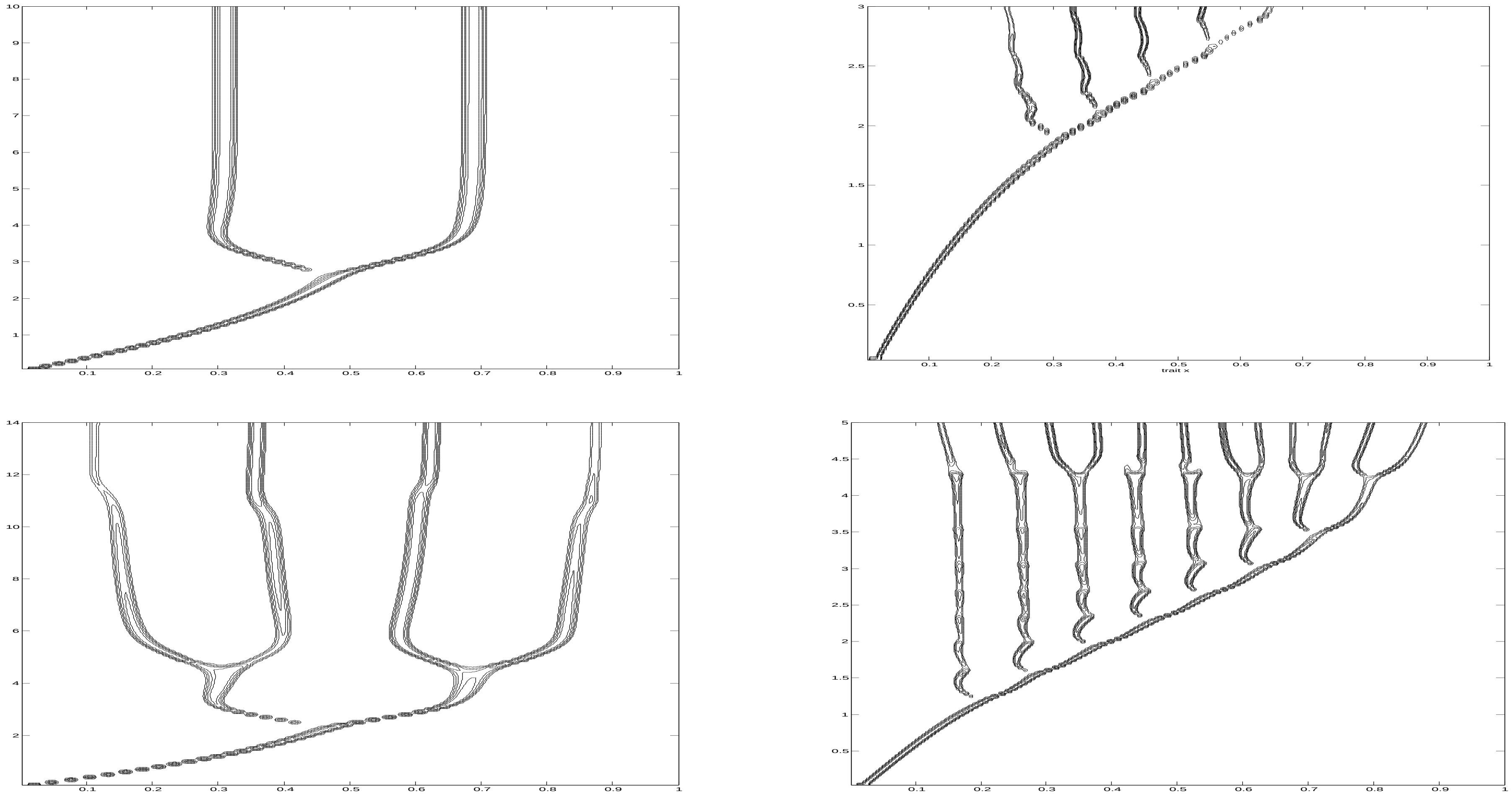
Labo. J.-L. Lions, INRIA





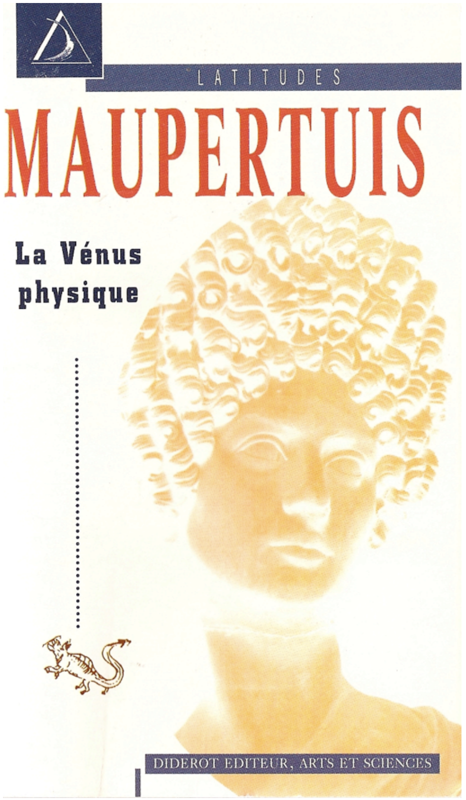
Motivation 1 : population adaptive evolution




trait x

Motivation 1 : Short history

- Maupertuis (1698-1759) 'La Venus Physique' (1745)



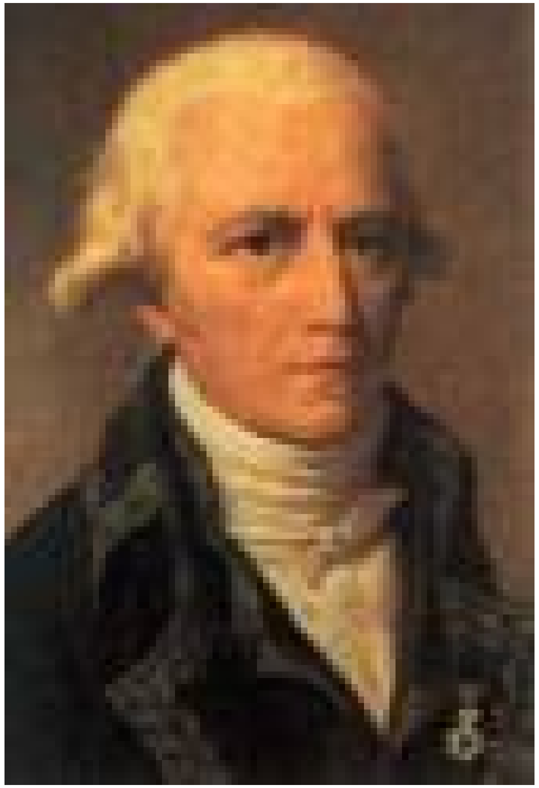
Chapitre III

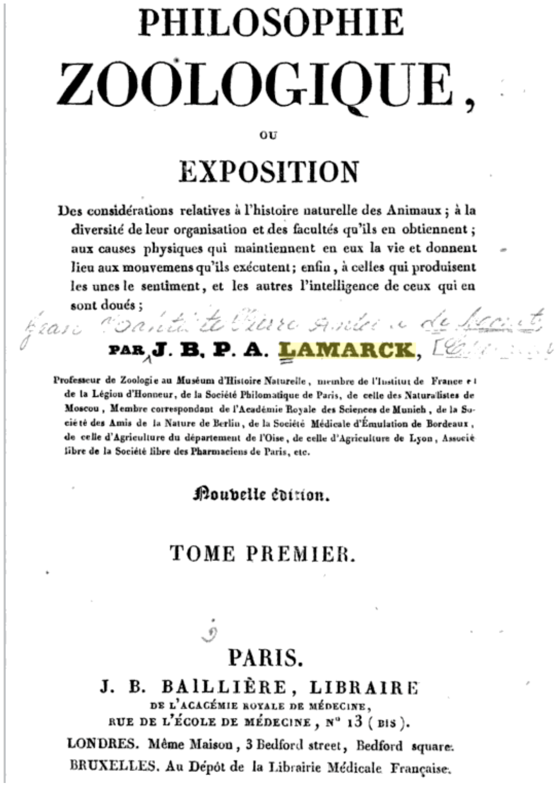
PRODUCTIONS DE NOUVELLES ESPECES

"La nature contient le fonds de toutes ces variétés : mais le hasard ou l'art les mettent en oeuvre... Nous voyons paraître des races de chiens, de pigeons, de serins qui n'étaient point auparavant dans la nature. Ce n'ont été d'abord que des individus fortuits ; l'art et les générations répétées en ont fait des espèces."

Motivation 1 : Short history

- Lamarck (1744-1829) 'Philosophie Zoologique' (1809)





PHILOSOPHIE

ZOOLOGIQUE,

OU

EXPOSITION

Des considérations relatives à l'histoire naturelle des Animaux ; à la diversité de leur organisation et des facultés qu'ils en obtiennent ; aux causes physiques qui maintiennent en eux la vie et donnent lieu aux mouvemens qu'ils exécutent ; enfin, à celles qui produisent les unes le sentiment, et les autres l'intelligence de ceux qui en sont doués ;

PAR J. B. P. A. LAMARCK,

Professeur de Zoologie au Muséum d'Histoire Naturelle, membre de l'Institut de France et de la Légion d'Honneur, de la Société Philomatique de Paris, de celle des Naturalistes de Moscou, Membre correspondant de l'Académie Royale des Sciences de Munich, de la Société des Amis de la Nature de Berlin, de la Société Médicale d'Émulation de Bordeaux, de celle d'Agriculture du département de l'Oise, de celle d'Agriculture de Lyon, Associé libre de la Société libre des Pharmaciens de Paris, etc.

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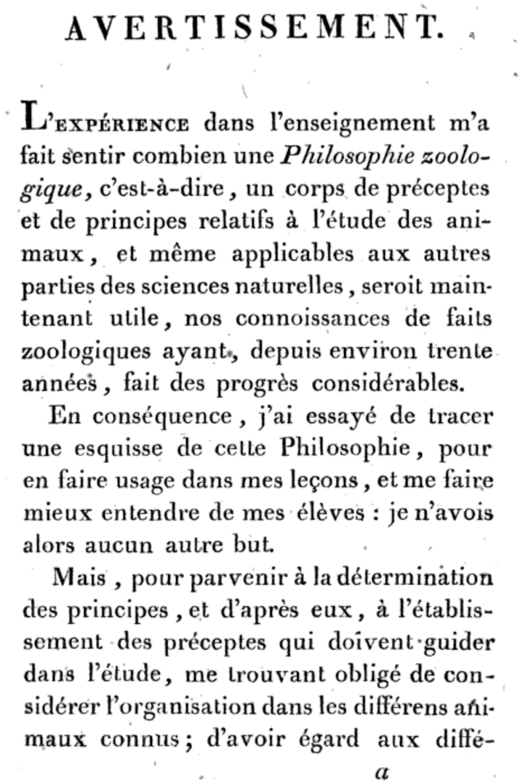


AVERTISSEMENT.

L'EXPÉRIENCE dans l'enseignement m'a fait sentir combien une *Philosophie zoologique*, c'est-à-dire, un corps de préceptes et de principes relatifs à l'étude des animaux, et même applicables aux autres parties des sciences naturelles, seroit maintenant utile, nos connoissances de faits zoologiques ayant, depuis environ trente années, fait des progrès considérables.

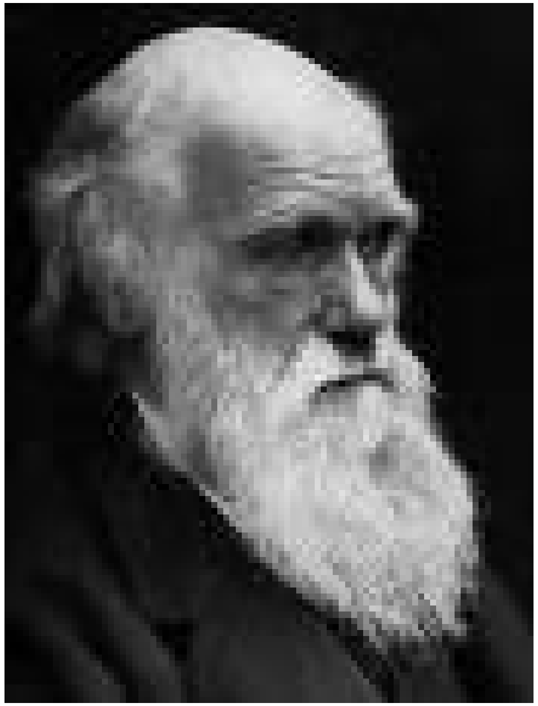
En conséquence, j'ai essayé de tracer une esquisse de cette Philosophie, pour en faire usage dans mes leçons, et me faire mieux entendre de mes élèves : je n'avois alors aucun autre but.

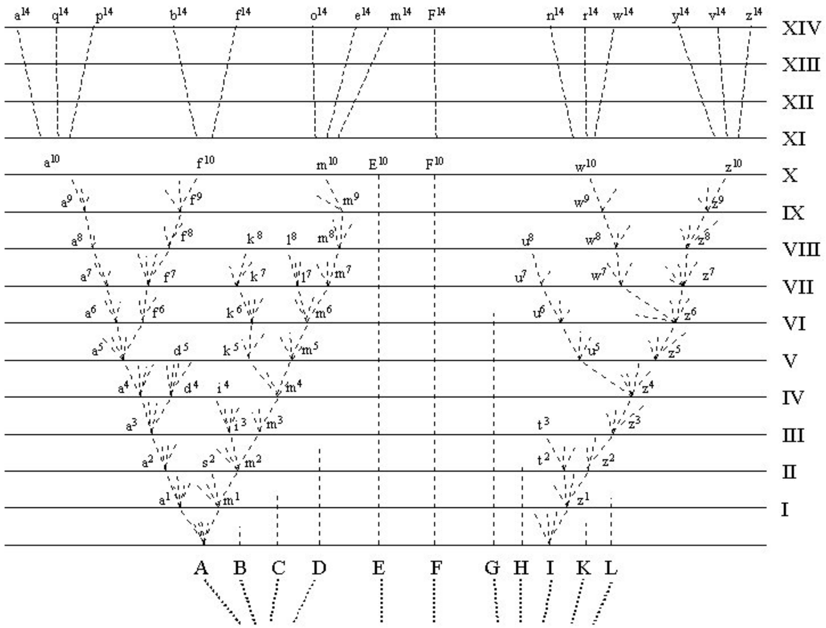
Mais, pour parvenir à la détermination des principes, et d'après eux, à l'établissement des préceptes qui doivent guider dans l'étude, me trouvant obligé de considérer l'organisation dans les différens animaux connus ; d'avoir égard aux diffé-

a

Motivation 1 : Short history

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



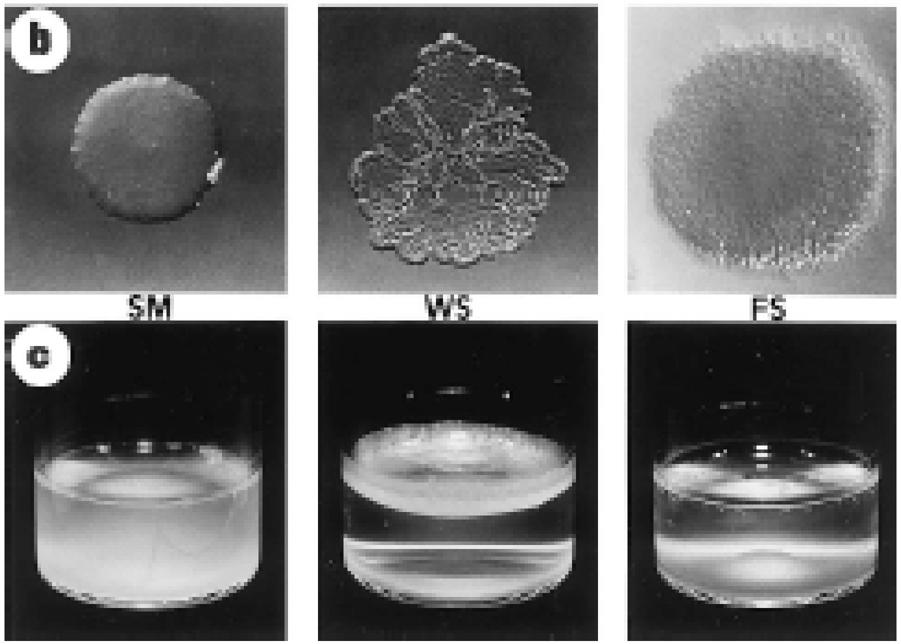


Motivation : adaptive evolution

But adaptation can be seen on shorter times scales

- Bacterial resistance to antibiotics
- Resistance of tumor cells to chemotherapy
- Lab experiments on bacteria...

Motivation : adaptive evolution



Phenotypic diversity for *Pseudomonas fluoresens*.

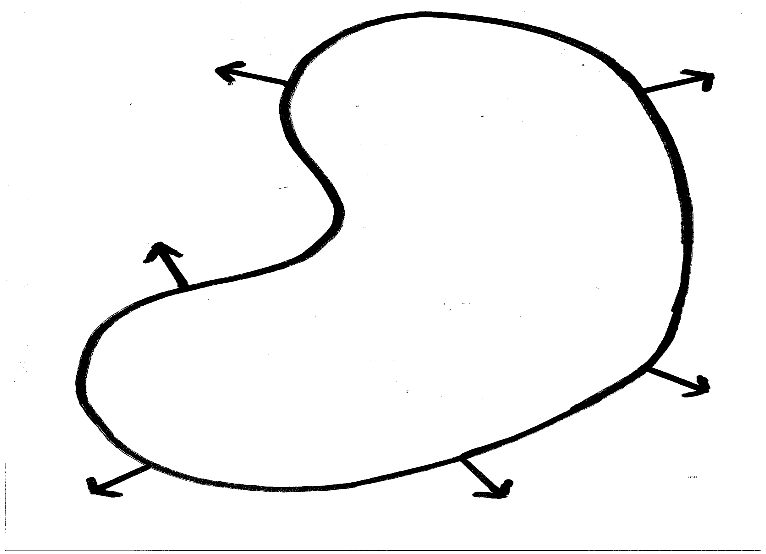
Populations were founded from single morph cells.

From Rainey and Travisano, Letters to Nature, 1998

Motivation 2 : geometric motion

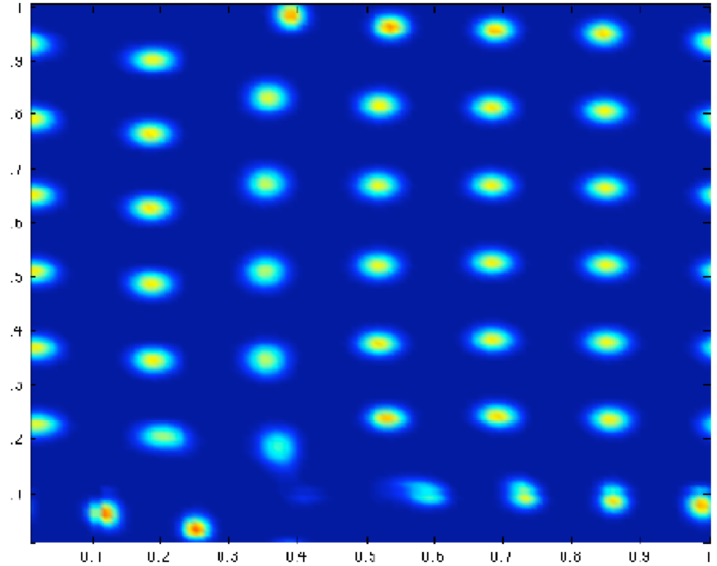
Combustion or invasion fronts lead to sharp moving interfaces described by geometric equations

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



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

Motivation 3 : Turing patterns



Dentritic patterns

OUTLINE OF THE LECTURE

I. Adaptive dynamic model
II. Asymptotic method (monomorphic)
III. Canonical equation
IV. Dimorphism
V. Polymorphism

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II. Asymptotic method (monomorphic)
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V. Polymorphism

COLLABORATORS

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Motivation : adaptive evolution

Motivation. Analyze a **self-contained** mathematical formalism for Darwin's theory at the population scale using only the

Ingredients.

(i) Population **multiplication**

(ii) **Natural selection :**
individuals own a **phenotypical trait** : ability to use the environment.
Because of competition, the individuals that are the most preforment are **selected**,

(iii) **Mutations** can modify the trait from parents to off-springs.

Adaptive dynamic : selection principle

Consider a structured population model

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

Examples type 1 :

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

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

Keep in mind : R changes sign : $\qquad R_\varrho < 0$

Adaptive dynamic : selection principle

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

with

$$\min_x R(x,\rho) < 0, \quad \max_x R(x,\rho) > 0, \quad \frac{\partial}{\partial \rho} R(x,\rho) < 0.$$

Theorem Suppose that supp $n^0(x) = [x_0, x_1]$ then

$$n(t,x) \underset{t \to \infty}{\longrightarrow} \bar{\varrho}\, \delta(x = \bar{x}), \qquad \varrho(t) \to \bar{\varrho} \qquad \text{(Competitive exclusion)}$$

with (assuming uniqueness)

$$\max_{[x_0,x_1]} R(x,\bar{\rho}) = 0 = R(\bar{x},\bar{\rho}) \text{ (pessimism principle)}$$

Adaptive dynamic : selection principle

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

Indeed, we have the a priori estimate

$$\frac{d}{dt}\varrho(t) = \int \eta(x) n(t,x) dx - d(x)\ \varrho(t)^2 \le \varrho(t)[\max \eta - \min d\ \varrho(t)],$$

$$\frac{d}{dt}\varrho(t) = \int \eta(x) n(t,x) dx - d(x) \varrho(t)^2 \ge \varrho(t)[\min \eta - \max d\ \varrho(t)],$$

This implies

$$\min(\varrho(0), \min \eta/d) \le \varrho(t) \le \max(\varrho(0), \max \eta/d).$$

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

Adaptive dynamic : selection principle

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

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

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

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

Adaptive dynamic : selection principle

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

• 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)... 2 ways to see this

Adaptive dynamic : selection principle

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

Replace $\bar{n}(x) = \bar{\varrho}\ \delta(x-\bar{x})$ by a concentrated gaussian

$$n_\varepsilon^0(x) = e^{\varphi_\varepsilon^0(x)/\varepsilon} \qquad \max \varphi_\varepsilon^0(x) \text{ gives the Dirac location}$$

Then, set

$$n_\varepsilon(t,x) = e^{\varphi_\varepsilon(t,x)/\varepsilon}$$

and with a rescaling in time

$$\frac{d}{dt}\varphi_\varepsilon(t,x) = R\Big(x, \varrho_\varepsilon(t)\Big), \qquad \max_{x\in\mathbb{R}} \varphi_\varepsilon(t,x) = o(1).$$

Adaptive dynamic : mutations

Off-springs undergo small mutations that change slightly the trait

$$\begin{cases} \frac{\partial}{\partial t} n(t,x) - \Delta n = n(t,x) R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}} n(t,x) dx. \end{cases}$$

Adaptive dynamic : mutations

Off-springs undergo small mutations that change slightly the trait

$$\begin{cases} \frac{\partial}{\partial t} n(t,x) - \Delta n = n(t,x) R\Big(x, \varrho(t)\Big), \\ \varrho(t) = \int_{\mathbb{R}} n(t,x)dx. \end{cases}$$

We assume that mutations are SMALL and introduce a scale ε for 'small' mutations

$$\begin{cases} \varepsilon \frac{\partial}{\partial t} n_\varepsilon(t,x) - \varepsilon^2 \Delta n_\varepsilon = n_\varepsilon(t,x) R\Big(x, \varrho_\varepsilon(t)\Big), \\ \\ \varrho_\varepsilon(t) = \int_{\mathbb{R}} n_\varepsilon(t,x)dx. \end{cases}$$

Asymptotic method

Theorem Suppose $R_x > 0$, $R_\rho < 0$. Then, as $\varepsilon \to 0$, we have

$$n_\varepsilon(t,x) \to \bar{\varrho}(t)\delta(x = \bar{x}(t)), \qquad \varrho_\varepsilon \to \bar{\varrho}(t) = \int n(t,x)dx,$$

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and the 'fittest' trait $\bar{x}(t)$ is characterised by the H.-J. Eq. with constraints

$$\begin{cases} \frac{\partial}{\partial t}\varphi(t,x) = R\Big(x, \bar{\varrho}(t)\Big) + |\nabla\varphi(t,x)\Big)|^2 \\ \max_x \varphi(t,x) = 0 \qquad \Big(= \varphi(t, \bar{x}(t)) \Big). \end{cases}$$

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Definition This situation is called monomorphism

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Definition This situation is called monomorphism

Difficulty Solutions are not smooth

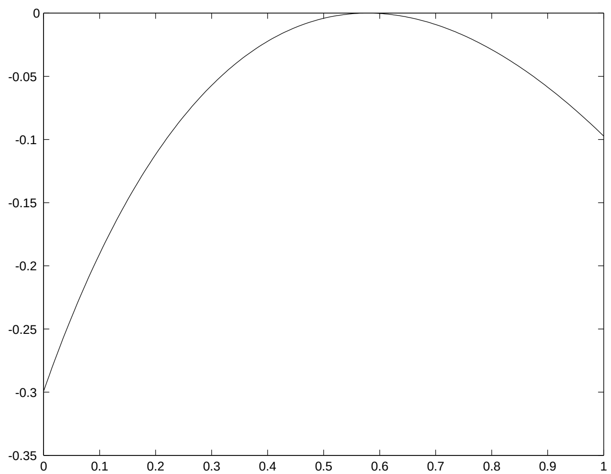
Asymptotic method

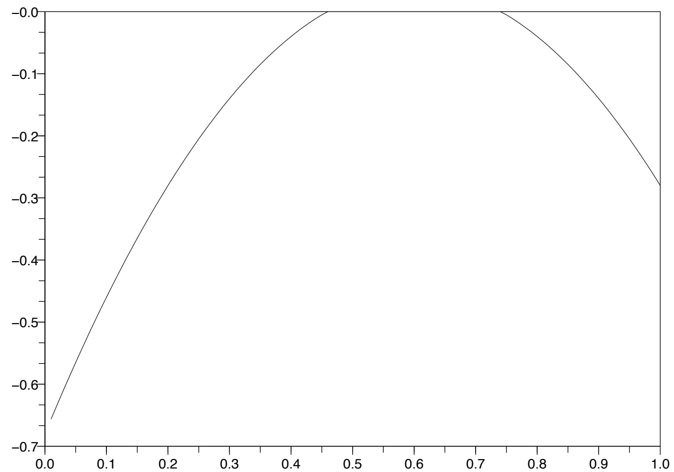
This problem should be understood as follows

$\max_x \varphi(t,x) = 0, \ \forall t$ is a constraint,

$\bar{\varrho}(t)$ is a Lagrange multiplier.

This is not an obstacle problem !





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$$n_\varepsilon(t,x) \longrightarrow \bar{\varrho}(t)\delta(x = \bar{x}(t)), \qquad \varrho_\varepsilon \longrightarrow \bar{\varrho}(t) = \int n(t,x)dx,$$

and the 'fittest' trait $\bar{x}(t)$ is characterised by the H.-J. Eq. with constraints

$$\begin{cases} \frac{\partial}{\partial t}\varphi(t,x) = R\Big(x, \bar{\varrho}(t)\Big) + |\nabla\varphi(t,x)\Big)|^2 \\ \max_x \varphi(t,x) = 0 \qquad \Big(= \varphi(t, \bar{x}(t)) \Big). \end{cases}$$

Proof Set

$$n_\varepsilon(t,x) = e^{\varphi_\varepsilon(t,x)/\varepsilon}$$

Asymptotic method

Theorem (G. Barles, BP) Uniqueness With reasonable assumptions there exist a unique lipschitz continuous solution $(\bar{\varrho}, \varphi)$ to the constraint H.-J. equation

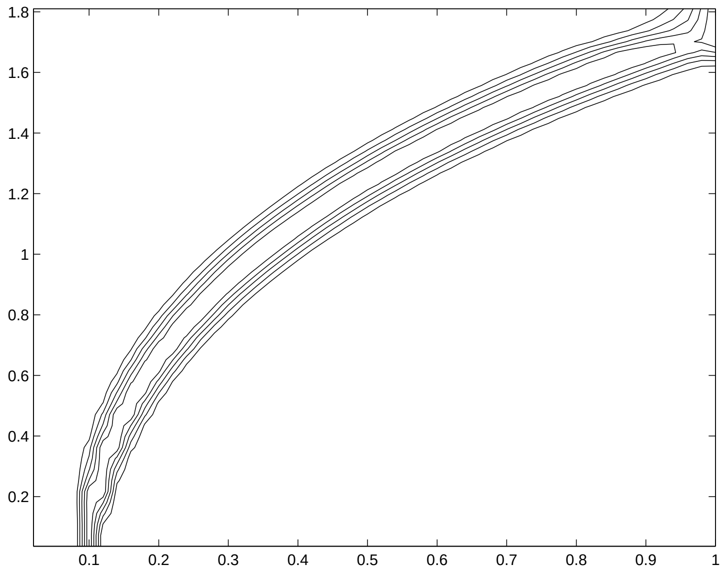
$$\begin{cases} \frac{\partial}{\partial t}\varphi(t,x) = \eta(x) - \bar{\varrho}(t)d(x) + |\nabla\varphi|^2, \\ \\ \max_x \varphi(t,x) = 0 \qquad \Big(= \varphi(t,\bar{x}(t)) \Big) \end{cases}$$

Open question Extend uniqueness to

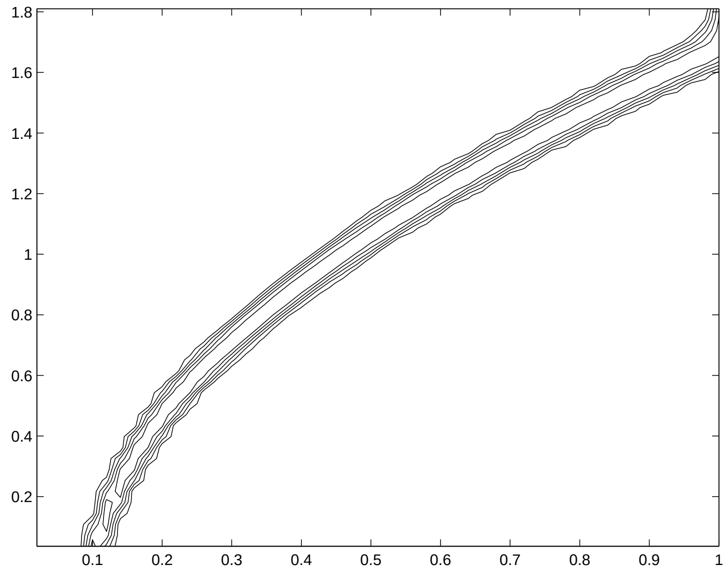
$$\frac{\partial}{\partial t}\varphi(t,x) = \frac{\eta(x)}{1+\bar{\varrho}(t)} - \bar{\varrho}(t)d(x) + |\nabla\varphi|^2.$$

Asymptotic method

Numerical tests : $\eta(x) = .5 + x$



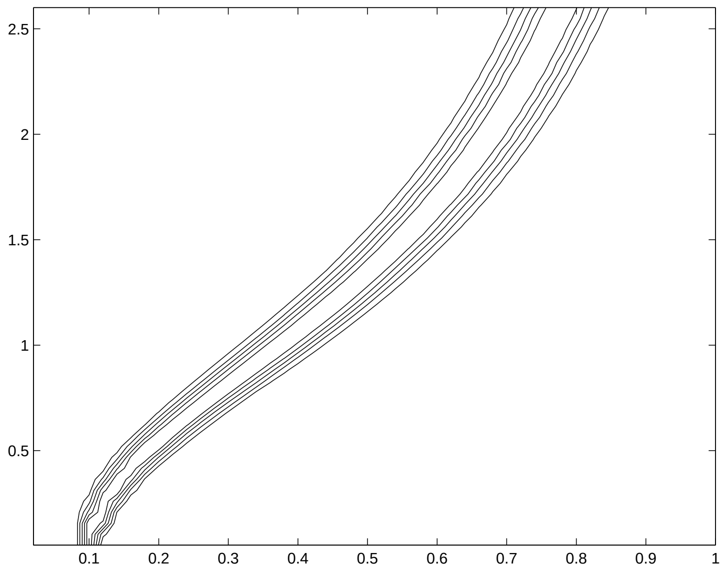
Direct simulation (1500 points)



H.-J. solution (200 points)

Asymptotic method

Numerical tests : $\eta(x) = .5 + x(2 - x)$



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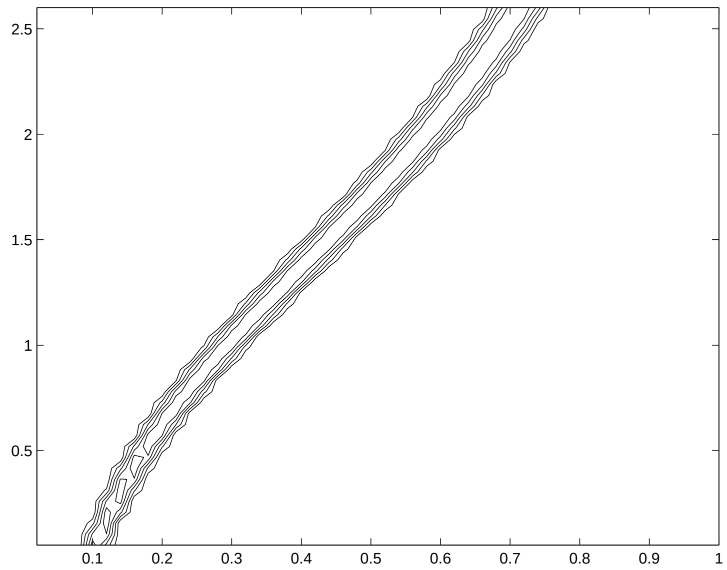
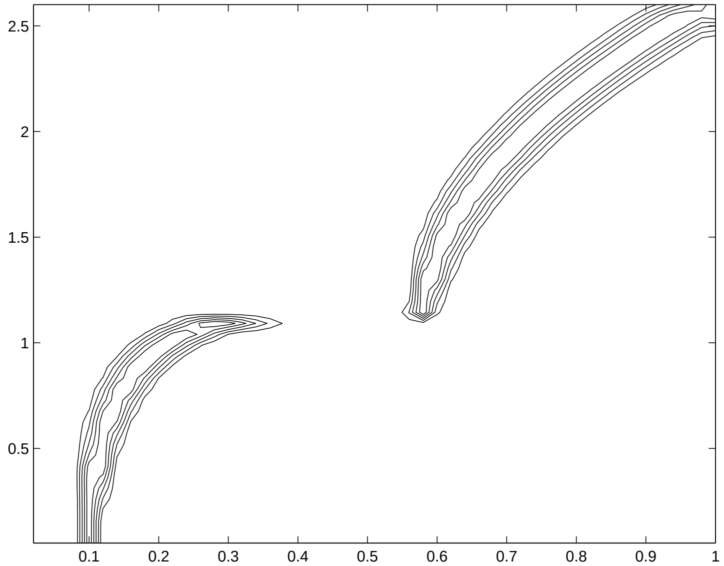


H.-J. solution (200 points)

Asymptotic method

Numerical tests : $min(.45 + x.^2, .55 + .4 * x)$



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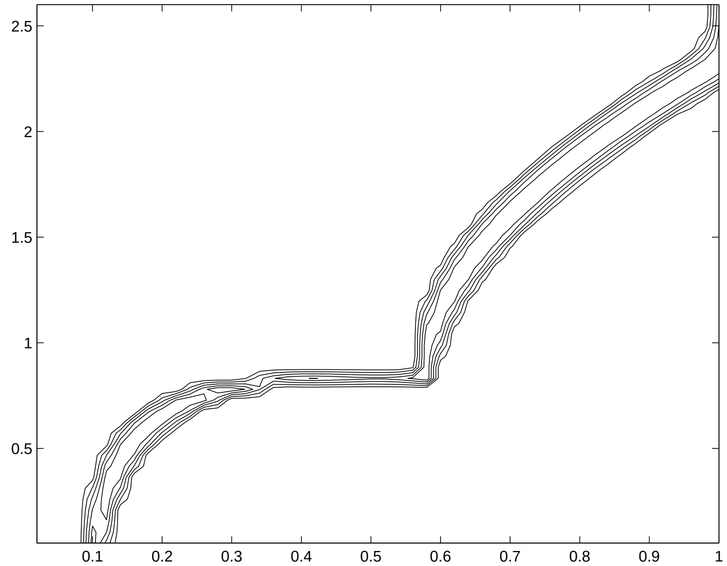


H.-J. solution (200 points)

Canonical equation

A smoothness regime exists under different assumptions, $x \in \mathbb{R}^d$

$$-C_1 I \leq D^2 R\Big(x, \varrho\Big) \leq -C_2 I \qquad \text{idendity matrix,}$$

$$-D_1 I \leq D^2 \varphi^0 \leq -D_2 I.$$

Then the Hamilton-Jacobi equation admits smooth solutions φ.

This implies n^0 is a single Dirac mass

This is generic : SHOW MOVIE

Canonical equation

Theorem (A. Lorz, S. Mirrahimi, BP)

(i) Then the solution to the Hamilton-Jacobi equation is smooth and

$$-D_1(t)I \leq D^2\varphi(t,x)) \leq -D_2(t)I.$$

(ii) $n_\varepsilon(t,x) \rightharpoonup \bar{\varrho}(t)\delta(x-\bar{x}(t)),$

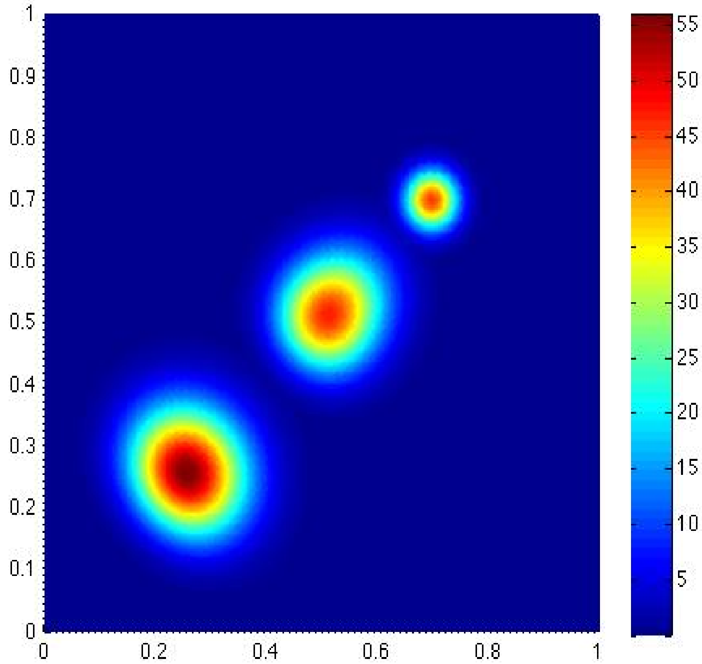
(iii) $\bar{x}(t)$, $\bar{\varrho}(t)$ are smooth

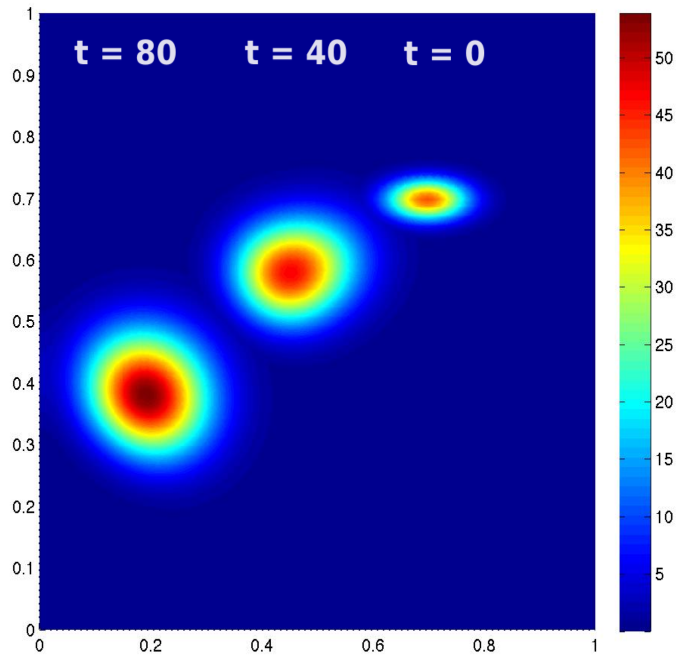
(iv) $R\Big(\bar{x}(t),\bar{\varrho}(t)\Big) = 0$

(v) $\frac{d}{dt}\bar{x}(t) = \Big(-D^2\varphi(\bar{x}(t),t)\Big)^{-1}.\nabla R\Big(\bar{x}(t),\bar{\varrho}(t)\Big)$

Canonical equation

Effect of the mutation matrix $\left(-D^2\varphi(\bar{x}(t),t)\right)^{-1}$





Other models

Other models are typically direct competiton with closer traits

$$\frac{d}{dt}n(t,x) = n(t,x)\Big[R(x) - K * n(t,x)\Big],$$

See Desvillettes, Jabin, Raoul, and Champagnat, Méléard,

Consider two examples

Other models

Other models are typically direct competiton with closer traits

$$\frac{d}{dt}n(t,x) - \varepsilon \Delta n = \frac{1}{\varepsilon} n(t,x)\Big[R(x) - K * n(t,x)\Big],$$

$$R(x) = \frac{1}{\sqrt{\sigma_1}} e^{-\frac{|x|^2}{2\sigma_1}}, \qquad K(x) = \frac{1}{\sqrt{\sigma_2}} e^{-\frac{|x|^2}{2\sigma_2}}$$

- $\sigma_1 > \sigma_2$, then $n(x) = \frac{1}{\sqrt{\sigma}} e^{-\frac{|x|^2}{2\sigma}}$, $\sigma = \sigma_1 - \sigma_2$ is a solution
- $\sigma_1 \leq \sigma_2$, then $n_\varepsilon(t,x)$ should have concentration .

Other models

Other models are typically direct competiton with closer traits

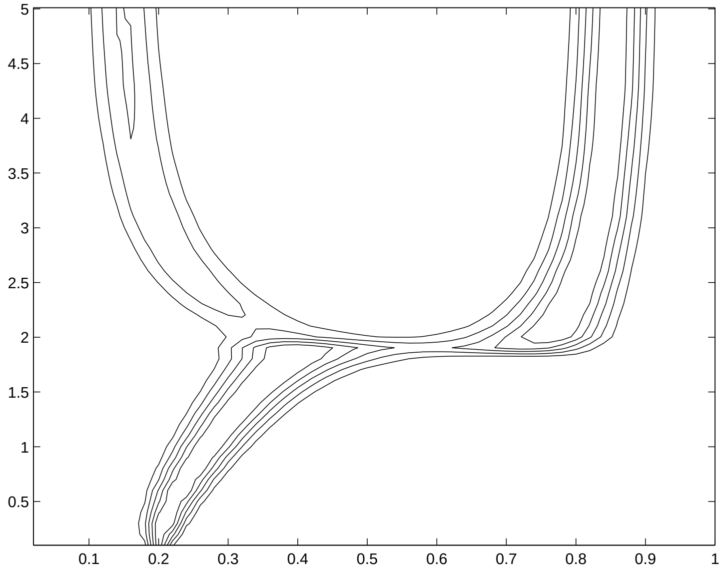
$$\frac{d}{dt}n(t,x) - \varepsilon \Delta n = \frac{1}{\varepsilon} n(t,x)\Big[R(x) - K * n(t,x)\Big],$$

$$R(x) \equiv 1, \qquad K \text{ a probabilty}$$

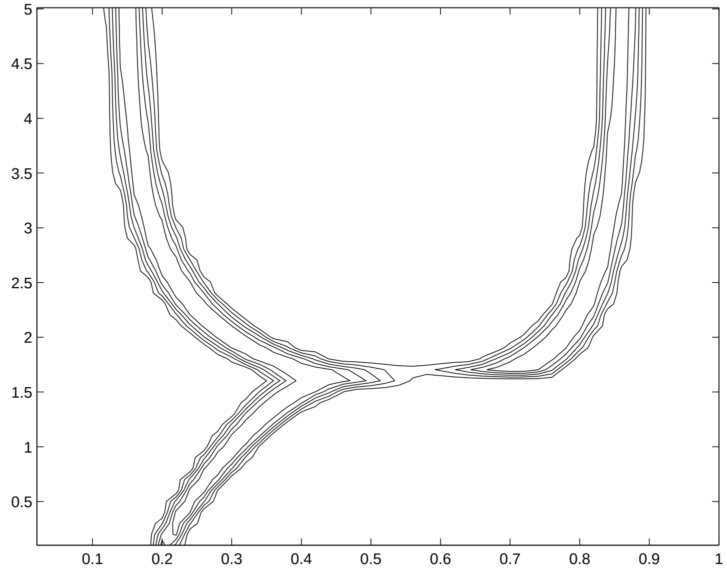
• $\widehat{K} \geq 0$, then $n(x) = 1$ is a stable steady state

• $\widehat{K}(\xi_0) < 0$, then $n(x) = 1$ is linearly unstable (Auger, Genieys, Volpert) and one observs concetrations.

Other models



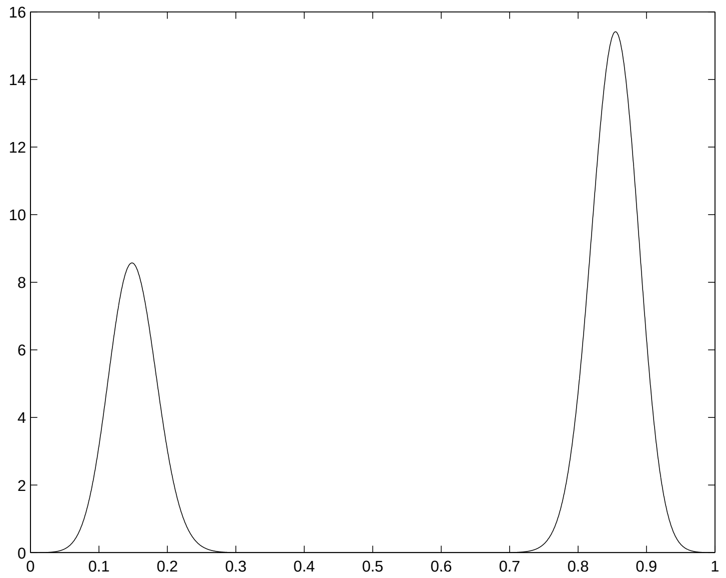
Direct simulation (1500 points)



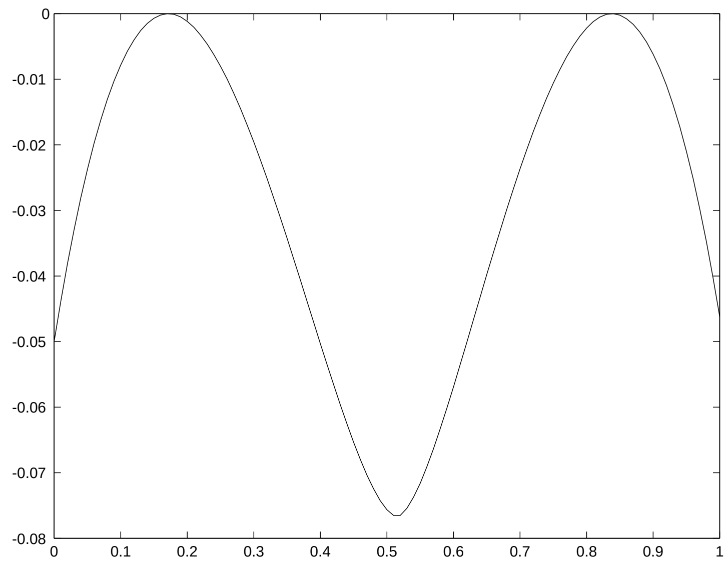
H.-J. solution (200 points)

Other models

Computed density n and phase φ



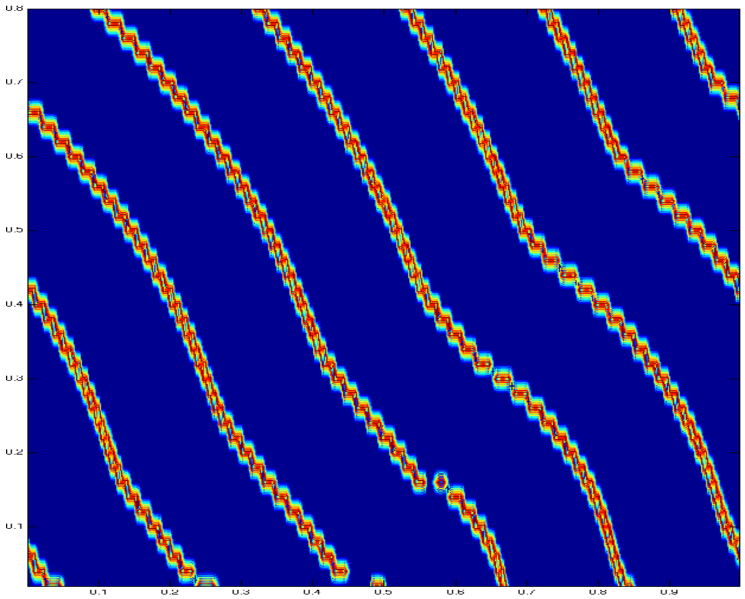
Direct simulation (1500 points)



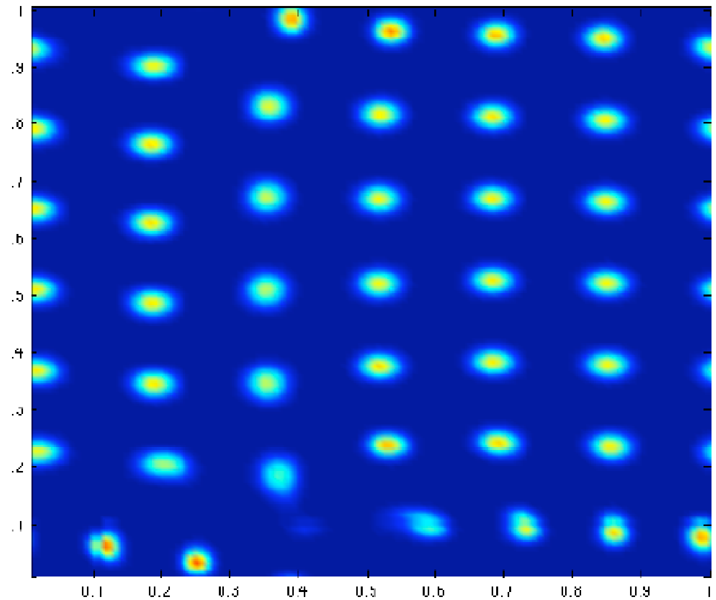
H.-J. solution (200 points)

Other models

These models can create TURING patterns



Asymmetric kernel



Nonlocal Fisher equation

Other models

Lotka-Volterra type of equations differ from reaction diffusion.

Typically is the Gray-Scott/Mimura type of systems

$$
\begin{cases}
\frac{\partial}{\partial t} u(x,t) - d_u \Delta u(x,t) = u[uv - \mu], \\
\frac{\partial}{\partial t} v(x,t) - d_v \Delta v(x,t) = -u^2 v, \\
\frac{\partial}{\partial t} w(x,t) = \mu u.
\end{cases}
$$

Polymorphism

Next ingredient is the notion of survival threshold.

$$\frac{\partial n(t,x)}{\partial t} - \varepsilon \Delta n(t,x) = \frac{n(t,x)}{\varepsilon}\Big(b(x) - K_b \star n(t)\Big) - \frac{\sqrt{\bar{n} n(t,x)}}{\varepsilon}$$

Motivated by

- Population really vanishes ; some traits are not represented
- The notion of 'individual' is somehow included in the parameter $\bar{n}$

Polymorphism

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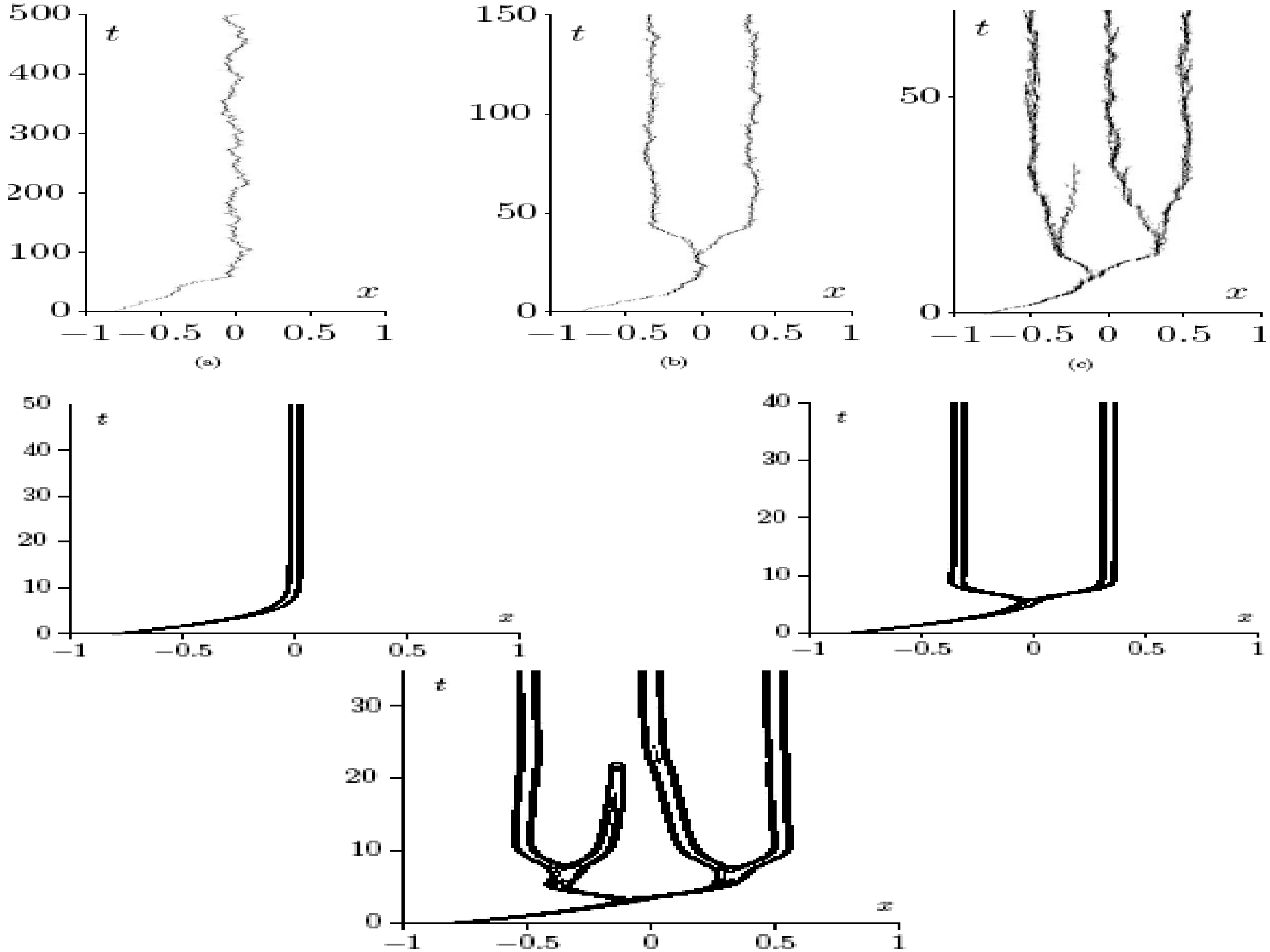
$$\frac{\partial n(t,x)}{\partial t} - \varepsilon \Delta n(t,x) = \frac{n(t,x)}{\varepsilon}\Big(b(x) - K_b \star n(t)\Big) - \frac{\sqrt{\bar{n} n(t,x)}}{\varepsilon}$$

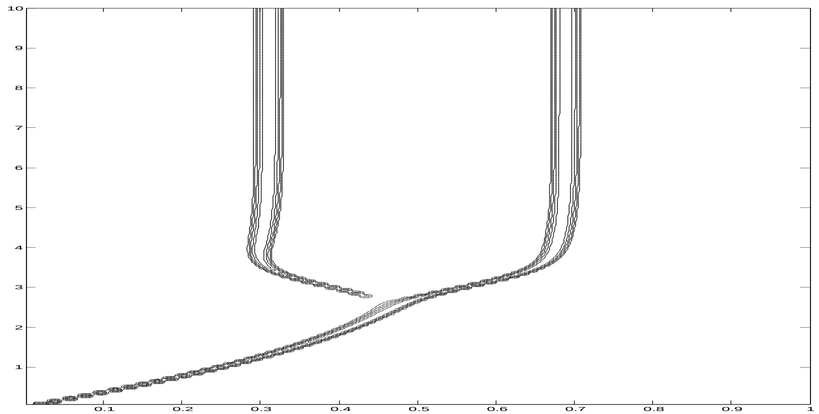
Motivated by

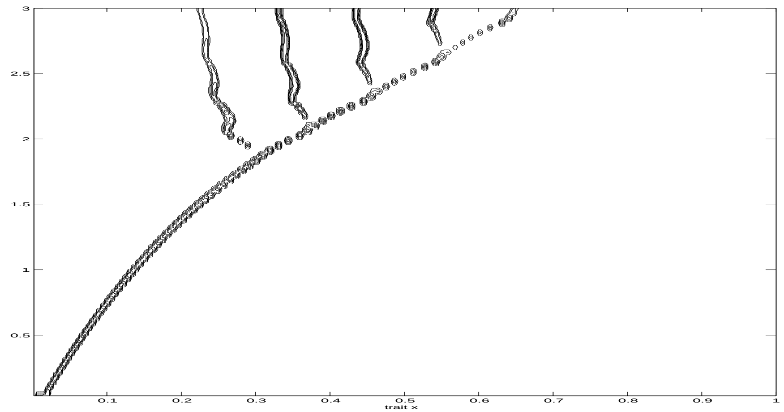
- Population really vanishes ; some traits are not represented
- The notion of 'individual' is somehow included in the parameter $\bar{n}$
- A similar notion represents 'demographic stochasticity'
- compatibility with Monte-Carlo simulations

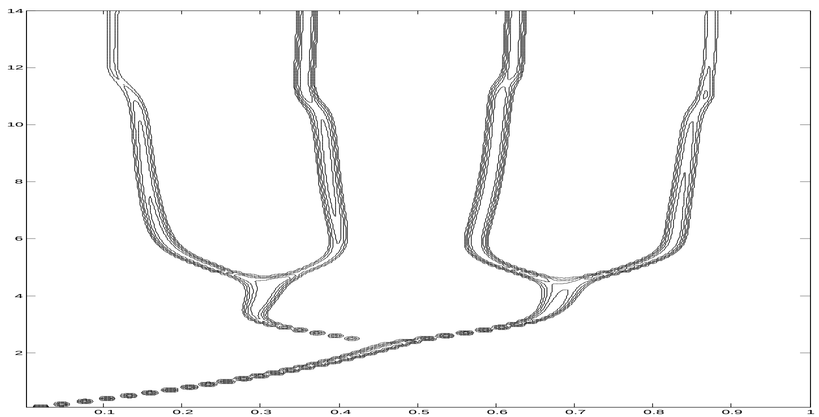


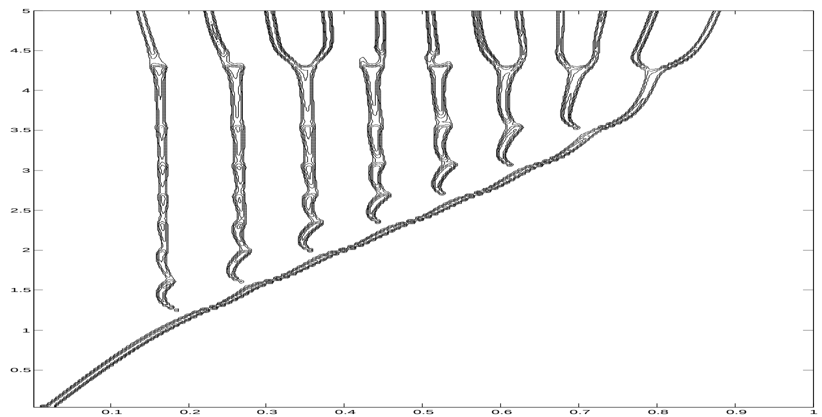
500
400
300
200
100
0
t
x
−1
−0.5
0
0.5
1
(a)
150
100
50
0
t
x
(b)
50
0
t
x
(c)
50
40
30
20
10
0
t
x
40
30
20
10
0
t
x
30
20
10
0
t
x

Polymorphism









Conclusion

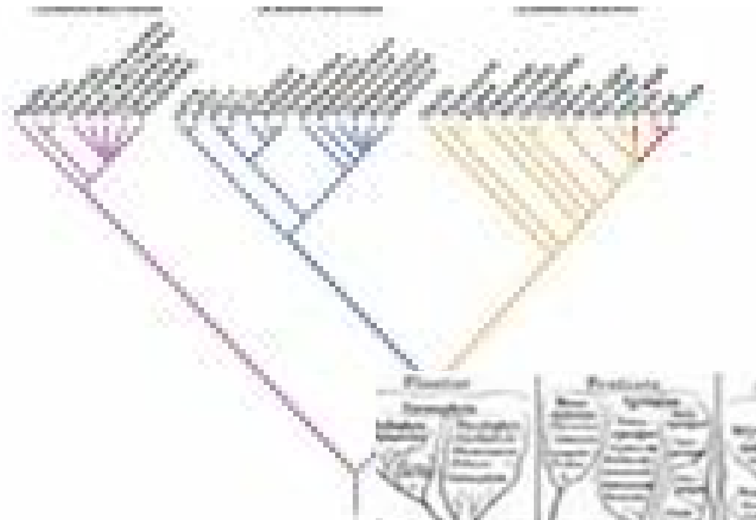
Population models with the two simple ingredients :

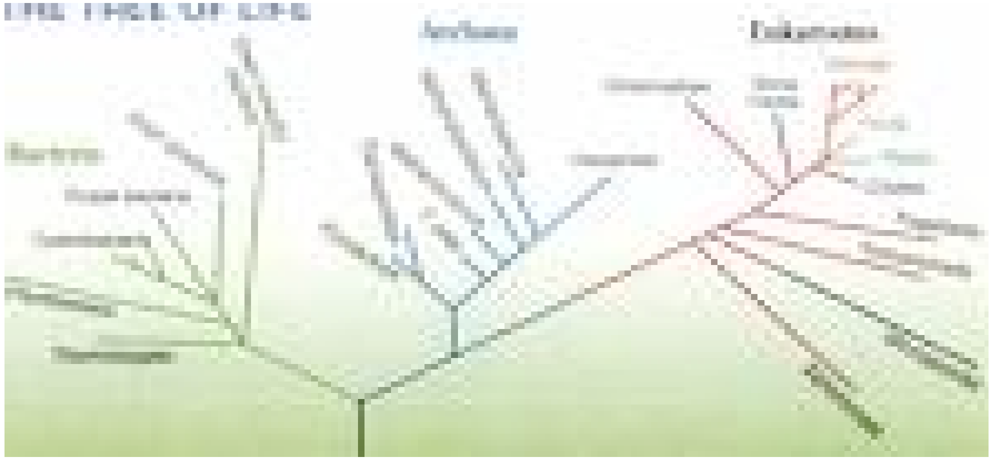
- local competiton between traits,
- mutations

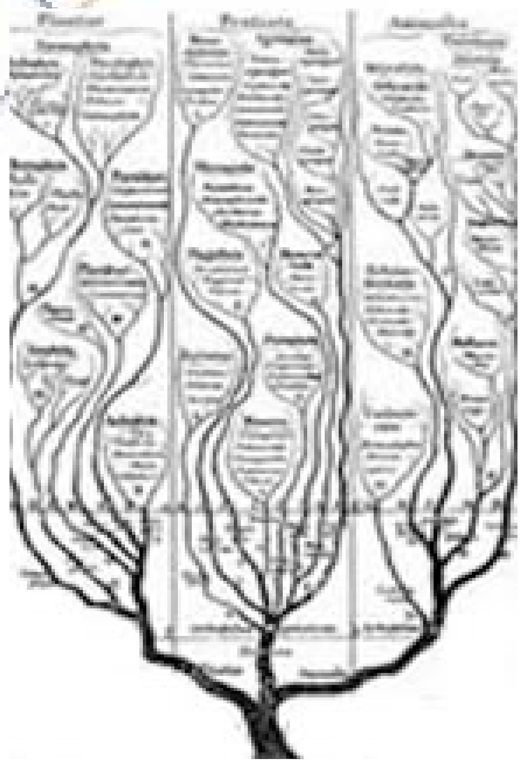
are able to express

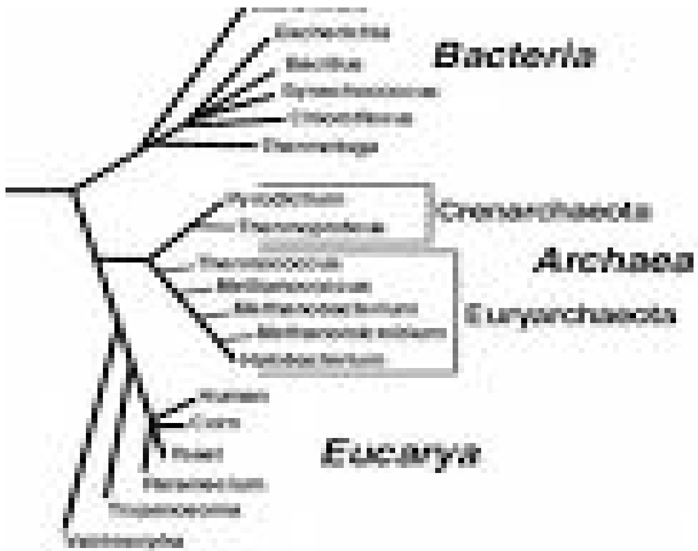
- highly concentrated solutions (speciation ?)
- branching

Many mathematical issues are still open in understanding these phenomena.




Archaea
Eukaryotes




Escherichia
Bacillus
Synechococcus
Chloroflexus
Thermotoga
Bacteria
Pyrodictium
Thermoproteus
Crenarchaeota
Archaea
Thermococcus
Methanococcus
Methanobacterium
Halobacterium
Euryarchaeota
Corn
Yeast
Paramecium
Trypanosoma
Vairimorpha
Eucarya