Adaptive evolution : dynamics of Dirac concentrations and Turing patterns

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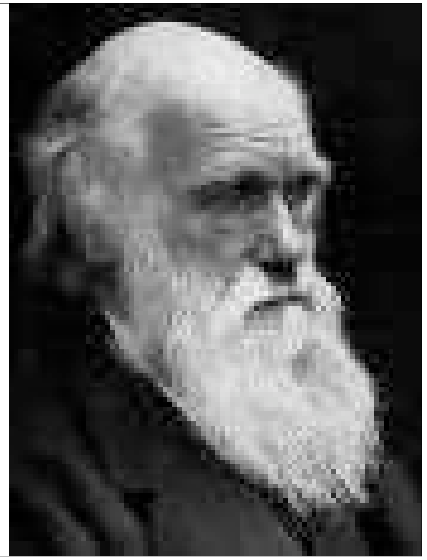
 

Motivation : adaptive evolution

Motivation. Mathematical formalism for Darwin's theory of evolution of living species, taking into account

(i) their interactions with an **environment** (nutrient for expansion) that these species consume,

(ii) individuals are characterized by a **trait** which characterizes their ability to use the environment. Because of competition, the individuals that are the most preforment in using the environment are **selected**,

(iii) the trait can be modified by **mutations** from mother to off-springs.

Motivation : adaptive evolution

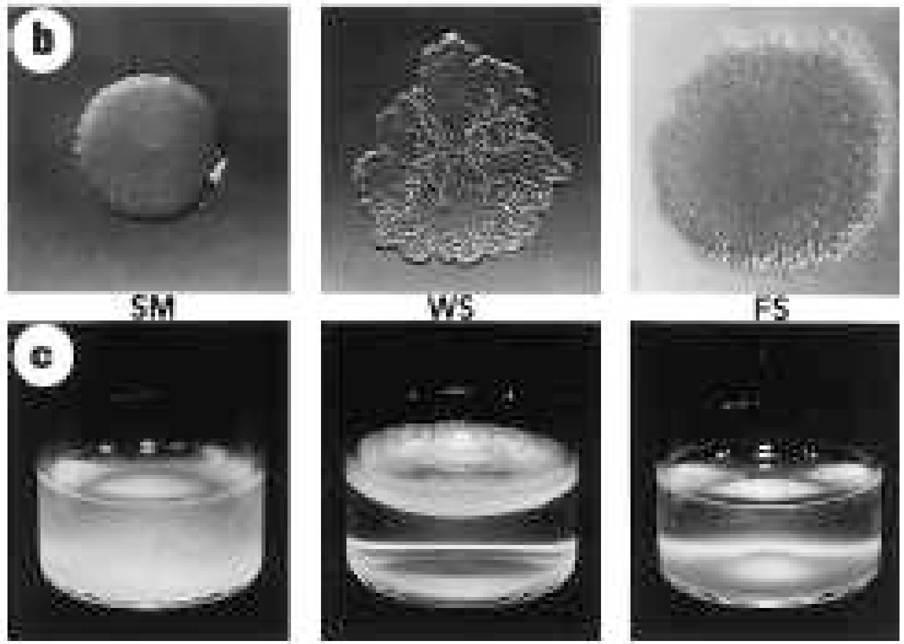
Several examples are wellknown

-) 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 : adaptive evolution

Various mathematical approaches

differential systems : U. Dieckmann and R. Law ; J. Metz, S. Geritz and O. Diekmann

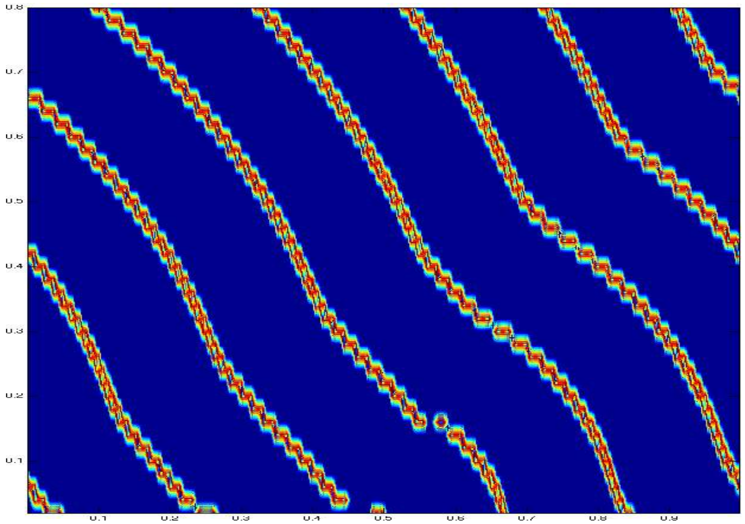
game theory : Maynard-Smith, J. Hofbauer and K. Sygmund

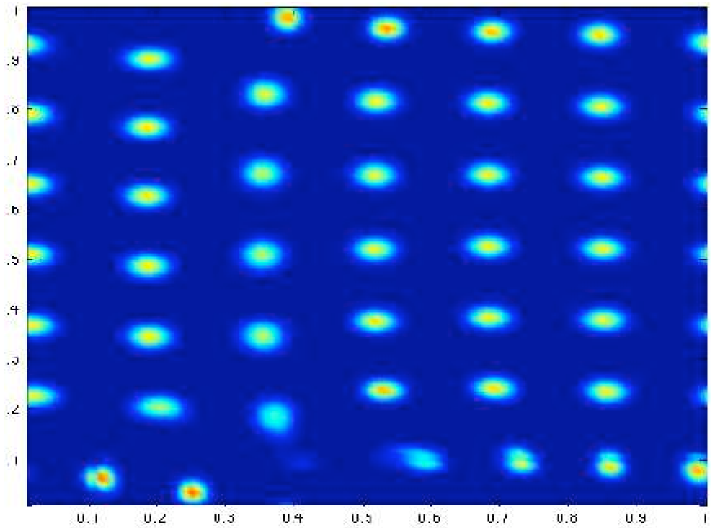
probabilities : N. Champagnat, R. Ferrière, N. Fournier, S. Méléard and L. Desvillettes

and Partial Differential Equations...

Motivation : adaptive evolution

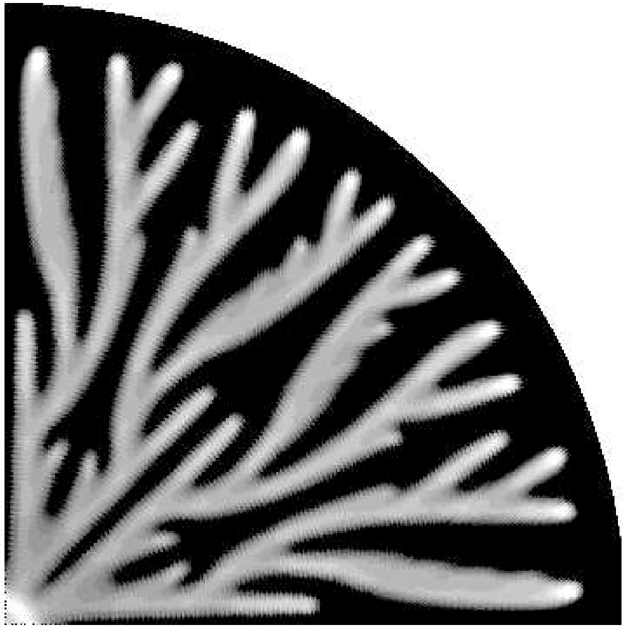
And Partial Differential Eq. Parabolic equations (systems) can exhibit amazing solutions, including Dirac concentrations.

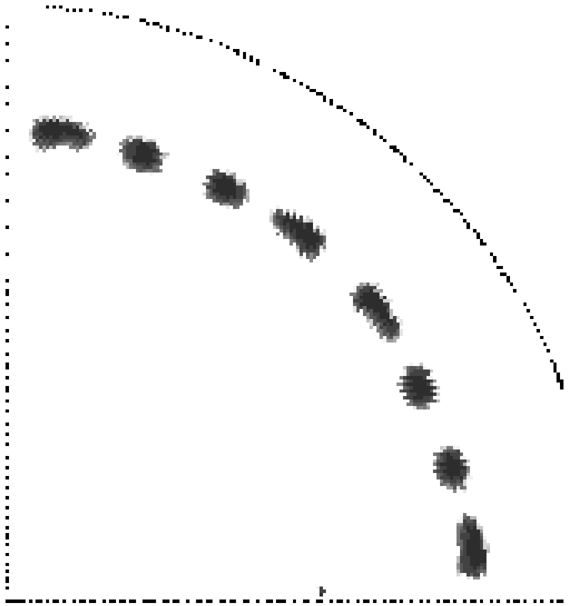




Examples of concentrations in Nonlocal Fisher equation ; a model by S. Genieys, V. Volpert and P. Auger

Motivation : Turing instability





Bacterial colony growth computed by A. Marrocco- INRIA Bang- using a parabolic system proposed by M. Mimura.

OUTLINE OF THE LECTURE

I. Adaptive dynamic model

II. Asymptotic method (monomorphic)

III. Canonical equation, polymorphism

IV. Turing instability on a toy model

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COLLABORATORS

O. Diekmann, P.-E. Jabin, St. Mischler,
G. Barles, S. Genieys, M. Gauduchon
S. Cuadrado and J. Carillo

Adaptive dynamic : selection principle

Suppose a population is structured with a trait (physiological parameter) x. The nutrient is used according to an uptake coef. $\eta(x)$

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

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

$$n(t,x) \xrightarrow[t \to \infty]{} \bar{\varrho}\, \delta(x = \bar{x}), \qquad \varrho(t) \to \bar{\varrho}, \quad \bar{\varrho} = \eta(\bar{x}),$$

with $\max_{[x_0,x_1]} \eta(x) = \eta(\bar{x})$ (supposed unique)

Adaptive dynamic : selection principle

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

Indeed, we have the a priori estimate

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

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

This implies

$$\min(\varrho(0), \min \eta) \leq \varrho(t) \leq \max(\varrho(0), \max \eta).$$

Adaptive dynamic : selection principle

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

Finally, use the explicit solution

$$n(t,x) = n^0(x)\ e^{\int_0^t [\eta(x) - \varrho(s)] ds},$$

then Laplace formula shows the result.

Adaptive dynamic : mutations

But off-springs undergo small mutations that change slightly the trait.

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

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We encounter a situation where the trait "slides" following the "time scale separation" assumption, (for increasing η)

$$[x_0, x_1] \xrightarrow[\text{selection}]{} x_1 \xrightarrow[\text{mutation}]{} [x_1 - \varepsilon, x_1 + \varepsilon] \xrightarrow[\text{selection}]{} x_1 + \varepsilon := x_2$$

$$\xrightarrow[\text{mutation}]{} [x_2 - \varepsilon, x_2 + \varepsilon] \xrightarrow[\text{selection}]{} x_2 + \varepsilon := x_3 \xrightarrow[\text{mutation}]{} [x_3 - \varepsilon, x_3 + \varepsilon] \xrightarrow[\text{selection}]{}$$

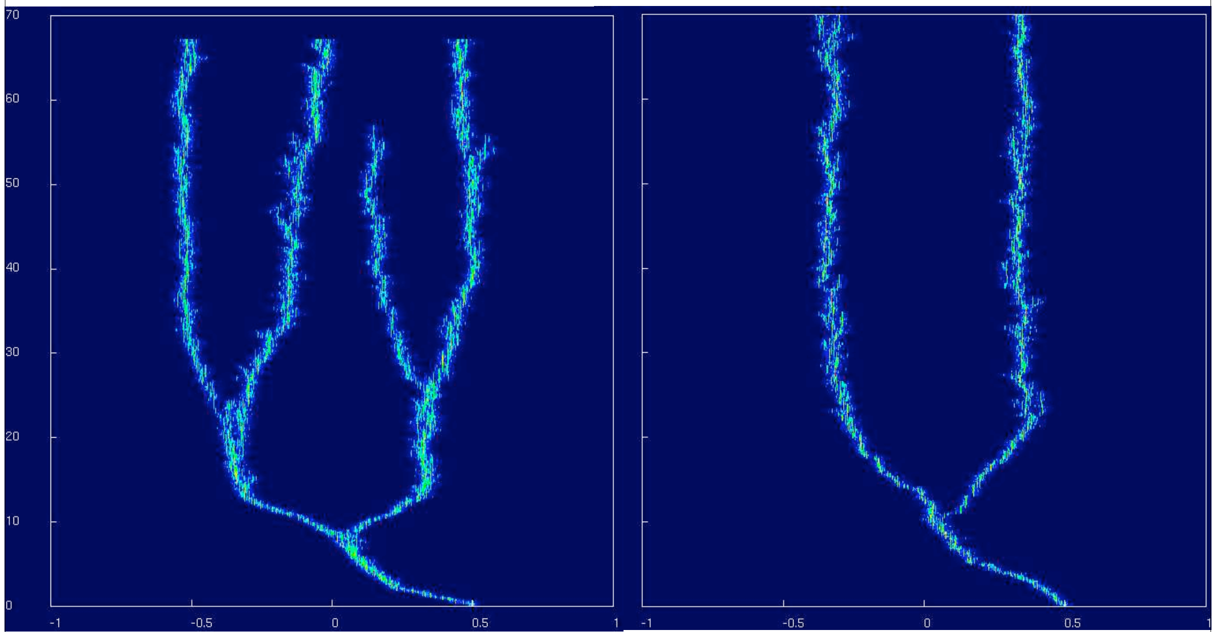
Adaptive dynamic : mutations

Population genetics derives macroscopic models from stochastic individual based models

R. Bürger 'The mathematical theory of selection...' (2000), Wiley
N. Champagnat, R. Ferrière, S. Méléard
Crow and Kimira (1964) : Another example of possible limit is

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

Adaptive dynamic : mutations



Monte-Carlo simulations by M. Gauduchon (individual based model)

Asymptotic method

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

$$\begin{cases} \frac{d}{dt} n(t,x) - \varepsilon^2 \Delta n = n(t,x)\Big(\eta(x) - \varrho(t)\Big), \\ \\ \varrho(t) = \int_{\mathbb{R}} n(t,x)dx. \end{cases}$$

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Then, we are led to consider large times and one changes also the time scale

$$\begin{cases} \frac{d}{dt}n(t,x) - \varepsilon \Delta n = \frac{1}{\varepsilon}n(t,x)\Big(\eta(x) - \varrho(t)\Big), \\ \\ \varrho(t) = \int_{\mathbb{R}} n(t,x)dx. \end{cases}$$

Asymptotic method

Theorem Suppose η is increasing, n^0 concentrates as a Dirac mass. 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 dominating trait $\bar{x}(t)$ is characterised by the H.-J. Eq. with constraints (viscosity solution)

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

$$\max_x \varphi(t,x) = 0 \qquad \Big(= \varphi(t,\bar{x}(t))\ \Big).$$

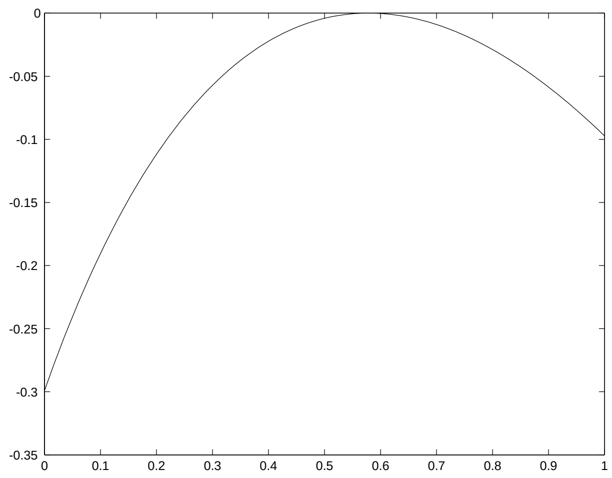
Asymptotic method

This problem should be understood as follows

$$\max_x \varphi(t,x) = 0,\ \forall t \qquad \text{is a constraint,}$$

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

This is not an obstacle problem !



Asymptotic method

Eikonal equation arises for oscillations (WKB method)

$$u_\varepsilon(x) \approx a(x)e^{i\,\varphi(x)/\varepsilon},$$

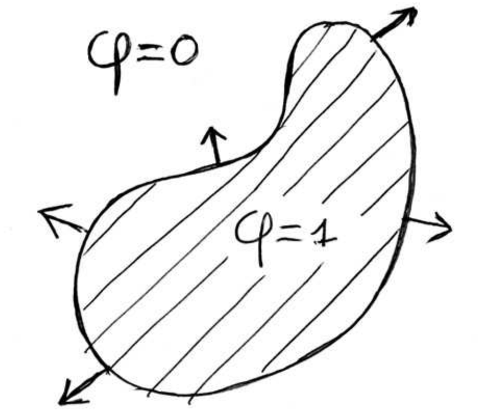
and other singularities (P. Gérard)

But this has to be understood in the phase space not with the viscosity solutions of Crandall-Lions

Asymptotic method

Our formalism is more related to geometric front propagation, (Freidlin, Evans-Souganidis, Barles, level set method).

Example : Fisher eq., $\begin{cases} \frac{\partial}{\partial t}u - \varepsilon \Delta u = \frac{1}{\varepsilon} u(1-u), \\ u^0(x) = 0 \quad \text{ou} \quad 1. \end{cases}$



But the notion of 'level set' is at odd with pointwise concentrations

Asymptotic method

Derivation 1 (1) We set $n_\varepsilon(t,x) = e^{\varphi_\varepsilon(t,x)/\varepsilon}$,

$$\frac{\partial}{\partial t} n_\varepsilon = \frac{n_\varepsilon}{\varepsilon} \frac{\partial}{\partial t} \varphi_\varepsilon$$

$$\Delta n_\varepsilon = [\frac{1}{\varepsilon^2} |\nabla \varphi_\varepsilon|^2 + \frac{1}{\varepsilon} \Delta \varphi_\varepsilon] n_\varepsilon$$

The equation

$$\varepsilon \frac{d}{dt} n_\varepsilon(t,x) = n_\varepsilon(t,x) \Big(\eta(x) - \varrho(t) \Big) + \varepsilon^2 \Delta n$$

becomes

$$\frac{\partial}{\partial t} \varphi_\varepsilon(t,x) = \eta(x) - \varrho(t) + \underbrace{|\nabla \varphi_\varepsilon(t,x)|^2 + \varepsilon \ \Delta \varphi_\varepsilon(t,x)}_{\longrightarrow |\nabla \varphi_\varepsilon(t,x)|^2}$$

Asymptotic method

Derivation 2 Recall that we have a control on the total mass of the system

(2) Since n_ε is bounded in L^1, for ε small enough, we have $\varphi \leq 0$ (assuming $\varphi_\varepsilon \longrightarrow \varphi$ uniformly),

(3) Since the total mass does not vanish, φ cannot be (strictly) negative : $\max_{x \in R} \varphi(t,x) = 0$.

(See also M. Freidlin for a direct proof)

Asymptotic method

Theorem (G. Barles, BP) With reasonable assumptions there exist a unique lipschitz continuous solution (S, φ) to the constraint H.-J. equation

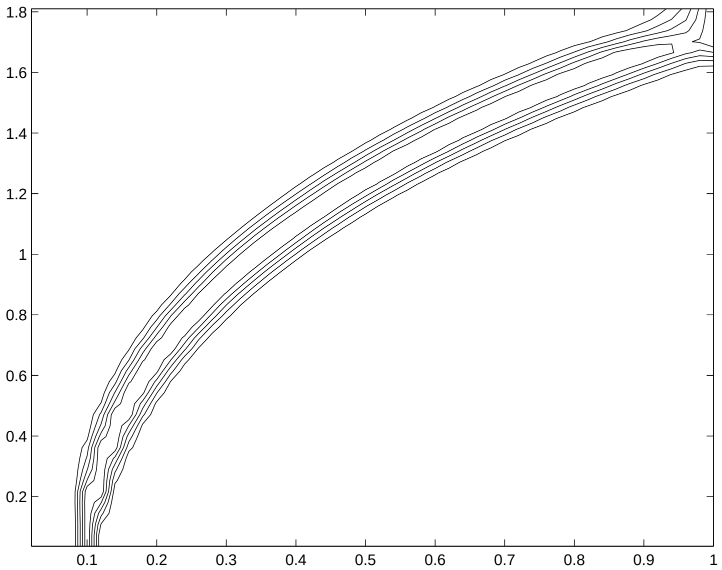
$$\begin{cases} \frac{\partial}{\partial t}\varphi(t,x) = \eta(x) - \varrho(t) + |\nabla \varphi|^2, \\ \max_x \varphi(t,x) = 0 \qquad \big(= \varphi(t, \bar{x}(t)) \big) \end{cases}$$

Question Extend the uniqueness to

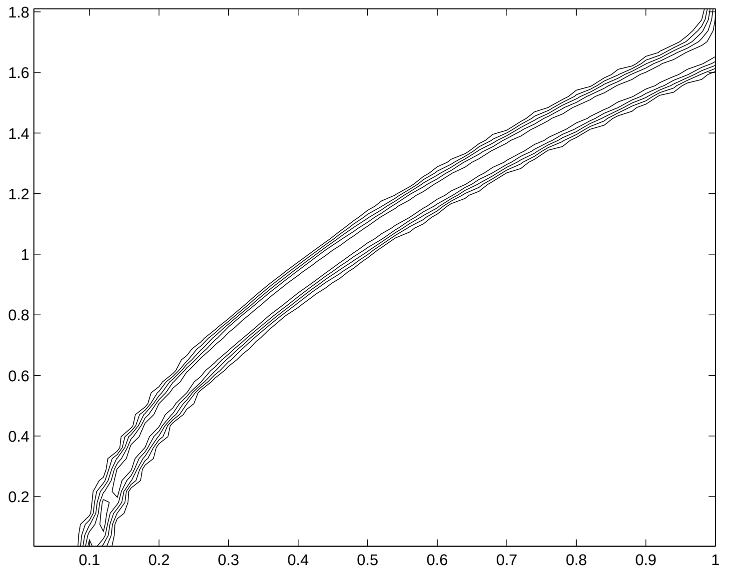
$$\frac{\partial}{\partial t}\varphi(t,x) = \frac{\eta(x)}{1+\varrho(t)} - \varrho(t) d(x) + |\nabla \varphi|^2.$$

Asymptotic method

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



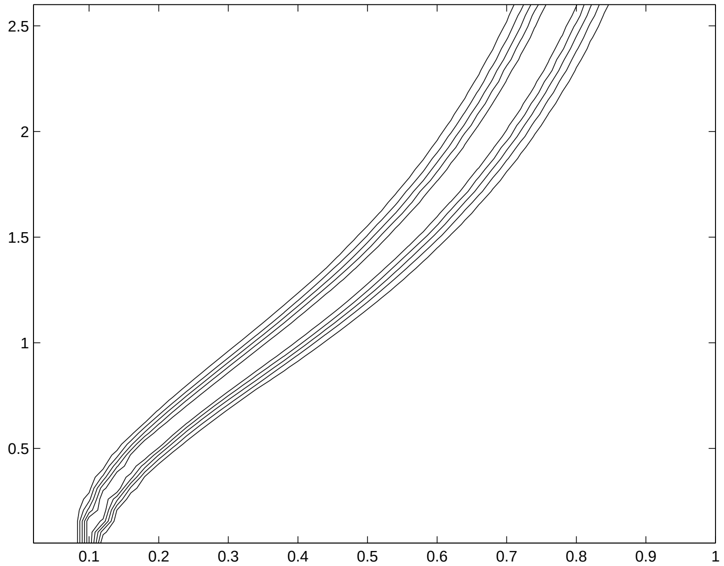
Direct simulation (1500 points)



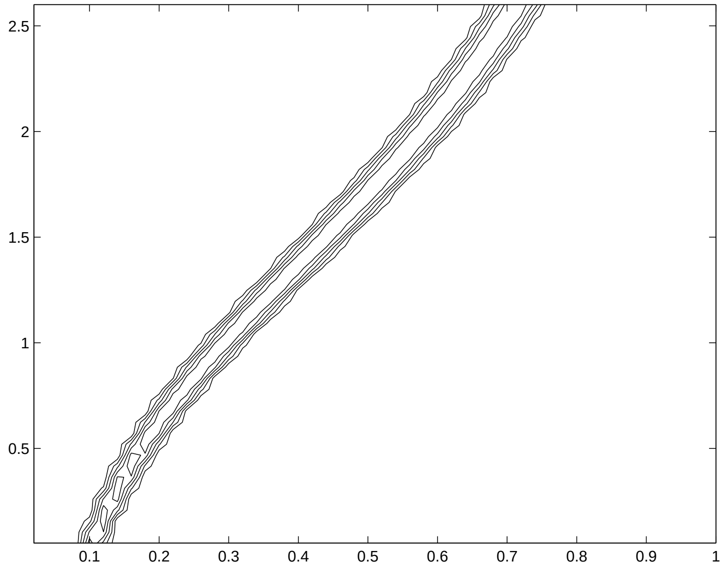
H.-J. solution (200 points)

Asymptotic method

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



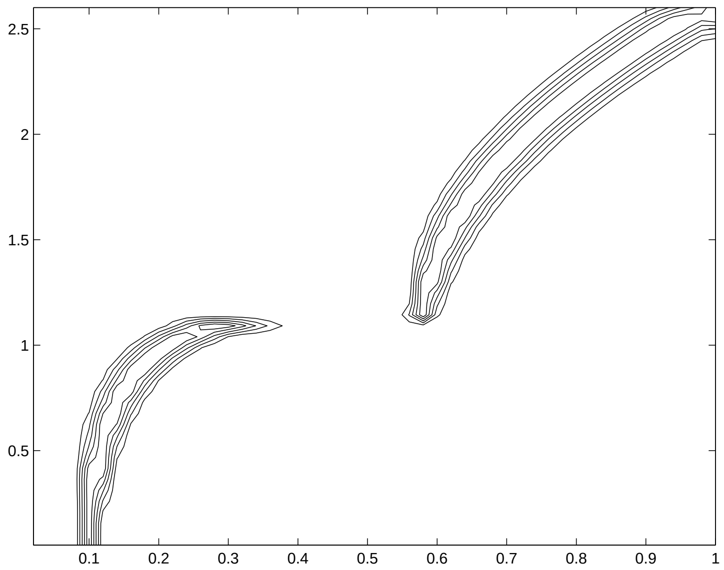
Direct simulation (1500 points)



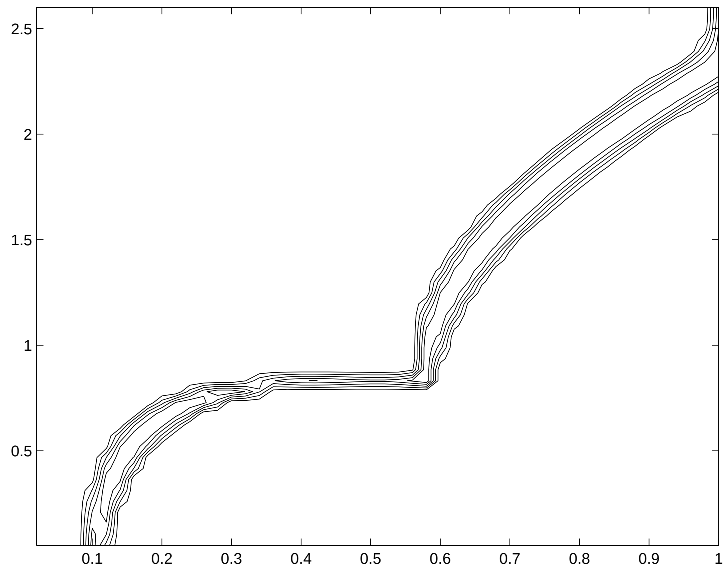
H.-J. solution (200 points)

Asymptotic method

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



Direct simulation (1500 points)



H.-J. solution (200 points)

Canonical equation

Can we derive canonical equations *à la* Dieckmann-Law.

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

Lemma We have $\frac{\partial}{\partial t}\varphi(t,\bar{x}(t)) = \nabla\varphi(t,\bar{x}(t)) = 0$ and the fundamental relation

$$\eta(\bar{x}(t)) = \varrho(t), \qquad a.e.$$

Monomorphism means there is a SINGLE solution $\bar{x}(t)$ (η is monotonic).

Canonical equation

Then one can go further and use $\frac{d}{dt}\nabla\varphi(t,\bar{x}(t)) = 0$. We obtain :

$$\begin{cases} \frac{d}{dt}\bar{x}(t) &= \left|\mathcal{K}_2(t)\right|^{-1} \left[\eta'(\bar{x}(t))\right], \\ \\ \frac{d}{dt}\mathcal{K}_2(t) &= \eta''(\bar{x}(t)) + H''(0) \left(\mathcal{K}_2(t)\right)^2 + ...\mathcal{K}_3(t), \end{cases}$$

with $\mathcal{K}_p(t) = \frac{\partial^p}{\partial x^p}\varphi(t,\bar{x}(t)) \leq 0$.

This system is not closed ! But the first equation gives the direction of the trait evolution and the Evolutionary Stable Strategies $(\bar{\varrho},\bar{x})$

$$\max_x \left[\eta(x) - \bar{\varrho}\right] = 0, \qquad \text{with} \;\; \eta(\bar{x}) = \bar{\varrho}$$

Polymorphism

Consider

$$\begin{cases} \frac{d}{dt} n_\varepsilon(t,x) = n_\varepsilon(t,x)\Big(\frac{\eta(x)}{1+\varrho_1(t)} - d(x)\varrho_2(t)\Big) + \varepsilon \Delta n_\varepsilon, \\ \\ \varrho_i(t) = \int_{\mathbb{R}} \psi_i(x)\, n(t,x) dx. \end{cases}$$

ESS $(\bar{x}, \bar{\varrho})$ are characterized by

$$\max_x \Big[\frac{\eta(x)}{1+\varrho_1} - d(x)\varrho_2\Big] = 0.$$

What happens if $\eta(x)/d(x)$ is NOT monotonic ?

Polymorphism

$$n_\varepsilon(t,x) \to \sum_j \alpha_j(t)\delta(x-\bar{x}_j(t)).$$

and the 'zero growth condition' gives

$$\Big[\frac{\eta(\bar{x}_j(t))}{1+\varrho_1(t)} - d(\bar{x}_j(t))\varrho_2(t)\Big] = 0 \qquad \forall j.$$

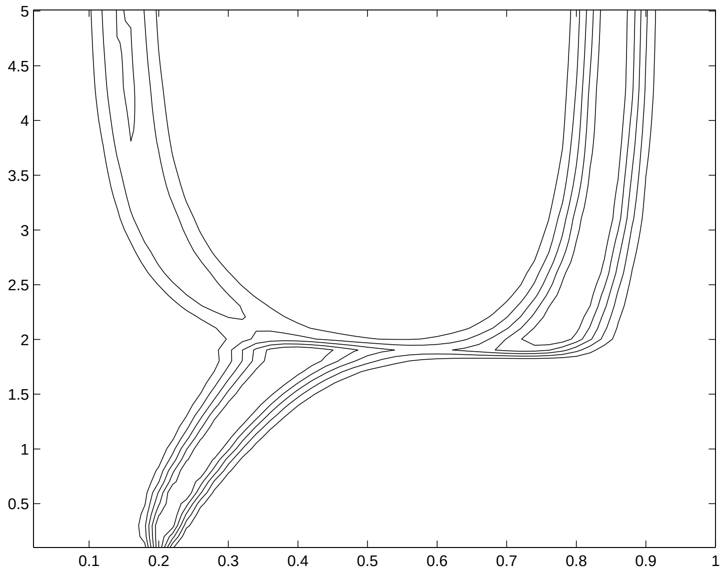
$$\varrho_i(t) = \sum_j \alpha_j(t)\ \psi_i(\bar{x}_j(t)).$$

Two Dirac masses are compatible with two values ϱ_1, ϱ_2.

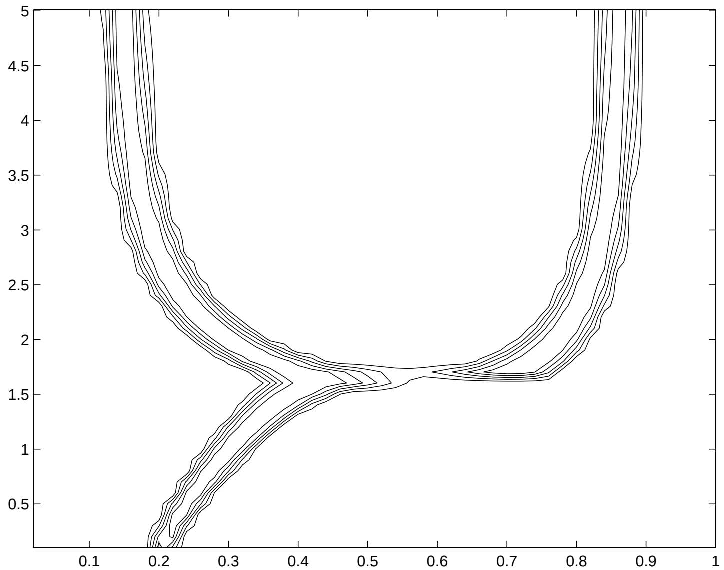
The constrained H.-J. equation looses uniqueness. Two Lagrange multipliers for a single constraint !

Polymorphism : Numerical results

$$\eta(x) = x - 1.8x(1-x)[x(1-x) - 6/25], \quad \xi(x) = 1 - x - 1.8....$$



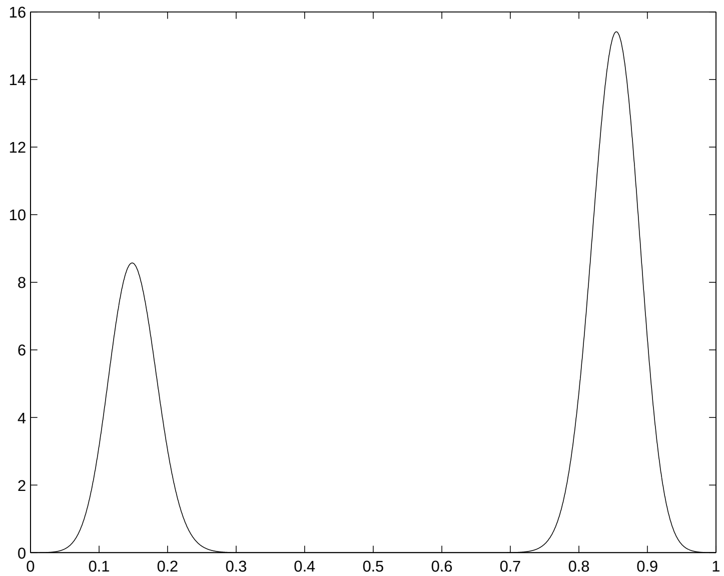
Direct simulation (1500 points)



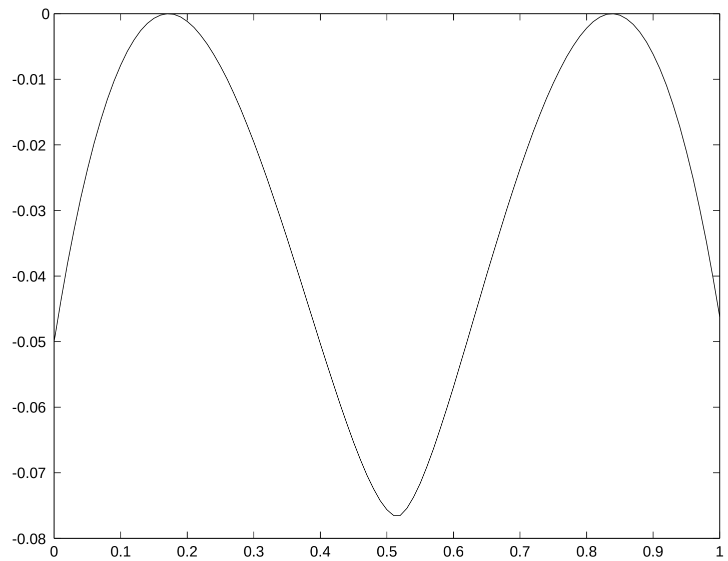
H.-J. solution (200 points)

Polymorphism : Numerical results

Computed objects



Direct simulation (1500 points)



H.-J. solution (200 points)

Turing instability

A simple model for Turing instability proposed by S. Genieys, V. Volpert, P. Auger,

$$\begin{cases} \frac{\partial n(t,x)}{\partial t} - \Delta n(t,x) = n(t,x)\Big(1 - K_b \star n(t)\Big), \\ \\ K_b(x) = \text{probability kernel}, \end{cases}$$

They use

$$K_b(x) = \frac{1}{2b} \mathbb{1}_{\{|z| \leq b\}}.$$

Interpretation Competition is higher between individuals that have similar traits.

Turing instability

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Theorem If $\exists \xi_0, \quad \widehat{K}(\xi_0) < 0$, then the steady state $n = 1$ is linearly unstable, i.e., some Fourier frequencies are growing exponentially.

Turing instability

A similar analysis can be carried out. First rescale equation

$$\begin{cases} \frac{\partial n(t,x)}{\partial t} - \varepsilon \Delta n(t,x) = \frac{n(t,x)}{\varepsilon}\Big(1 - K_b \star n(t)\Big), \\ \\ K_b(x) = \frac{1}{2b} \mathbb{I}_{\{|z| \leq b\}}. \end{cases}$$

As usual in Turing theory, if one sets
$b \longrightarrow 0$, ε $fixed$, (short range inhibitor, long range activitor), we recover Fisher front propagation,
$\varepsilon \longrightarrow 0$, b $fixed$, we recover Turing patterns... and Dirac concentrations which can be analyzed as before.

Turing instability

Turing instability : For $b = 0$ the system is STABLE. Convolution is regularizing. The outcome is UNSTABLE !

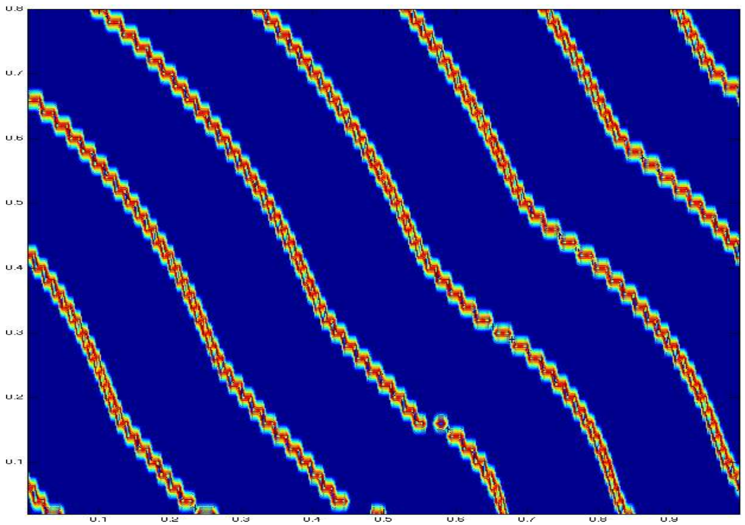
This is very counter-intuitive.

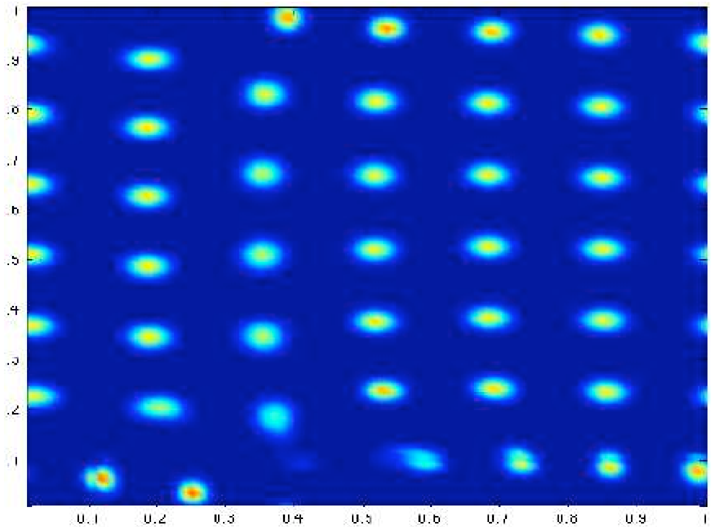
Turing instability

Turing instability : For $b = 0$ the system is STABLE. Convolution is regularizing. The outcome is UNSTABLE !

Motivation : adaptive evolution

TURING patterns In the nonlocal Fisher quation





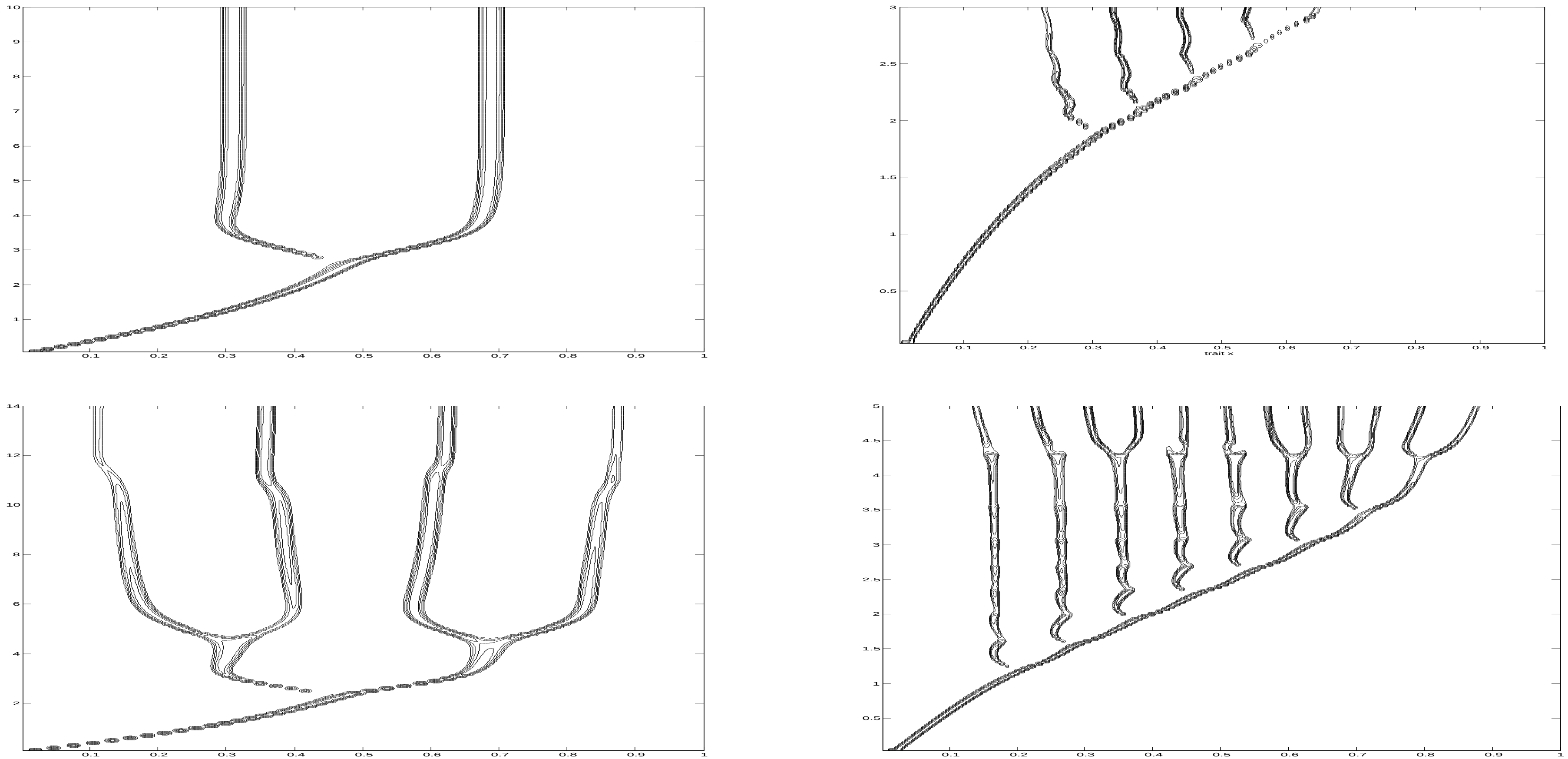
Turing instability

More general models of adaptative dynamics are

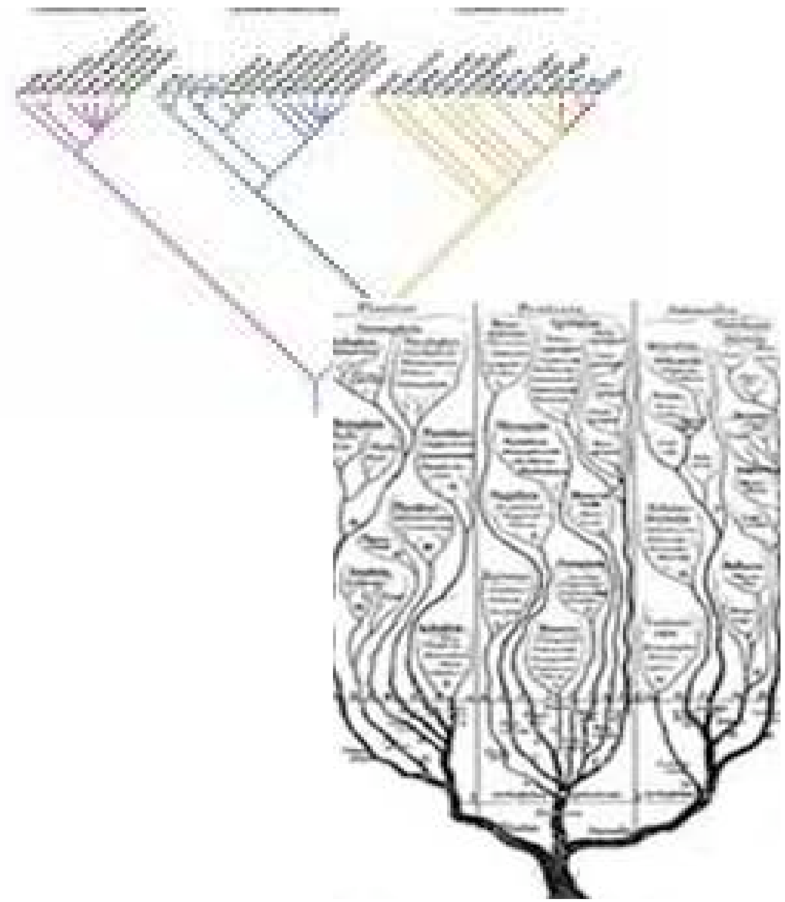
$$\frac{\partial n(t,x)}{\partial t} - \varepsilon \Delta n(t,x) = \frac{n(t,x)}{\varepsilon}\Big(b(x) - K_b \star n(t)\Big),$$

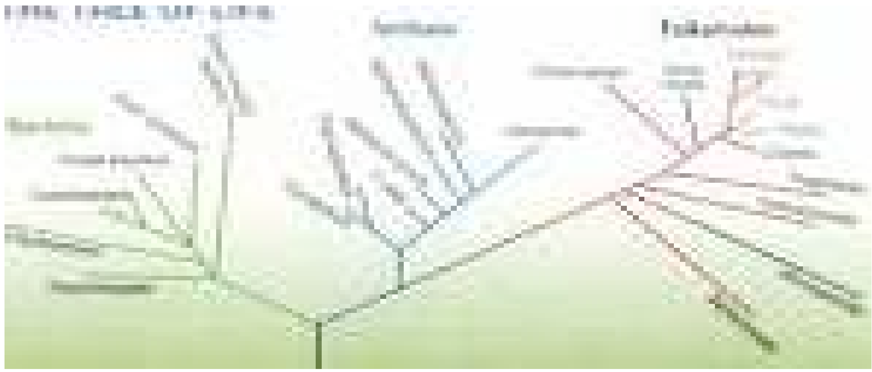
where $K_b(x)$ describes the local competition between individuals of 'similar traits'.

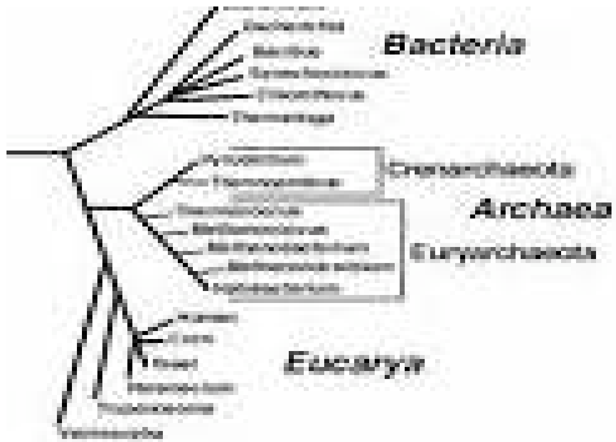
Motivation : adaptive evolution



Motivation : adaptive evolution







Motivation : adaptive evolution