Modèles de populations spatialis'ees et/ou soumise à sélection et approximations diverses évolutif

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Introduction

- Modèles individu-centrés stochastiques qui mettent l'accent sur les interactions écologiques (avec densité-dépendence) et reproduction clonale (asexuée)
- Suivant les objectifs, peut s'appliquer à l'étude de
  - l'évolution (mouvement spatial = mutations)
  - la dispersion spatiale (e.g. populations de plantes)
  - les deux
- A l'inverse de beaucoup de modèles de génétique des populations (Wright-Fisher, Moran, Flemming-Viot), la taille de la population n'est pas fixée, et il n'y a pas de fitness pré-définie

Dynamiques adaptatives

- A l'origine, ma motivation venait de l'étude de l'évolution des populations (dynamique adaptative, Hofbauer et Sigmund 1990, Metz et al. 1992, 1996, Dieckmann et Law 1996)
  - liens entre évolution et écologie
  - sélection résultant de lécologie
  - hérédité simplifiée dans un premier temps (asexuée)
- Hypothèses simplificatrices
  - Grande population
  - Mutations de petite amplitude et/ou rares
- Le même formalisme peut aussi s'appliquer à des populations spatialement structurées avec des hypothèses similaires sur le mouvement spatial.

Notations

A general birth-and-death process with competition and mutation (already studied in Bolker and Pacala 1997, Dieckmann and Law 2000, Fournier and Méléard 2004,...)

- Spatially structured population and/or evolution of a finite number of quantitative phenotypic traits (individual size, age at maturity,...)
- State space = physical space + trait space: $\mathcal{X} \subset \mathbb{R}^d$, closed
- A population composed of $I(t)$ individuals holding positions and/or traits $x_1, \dots, x_{I(t)} \in \mathcal{X}$ is represented by the counting measure $\nu_t = \sum_{i=1}^{I(t)} \delta_{x_i}$
- State space: $\mathcal{M} = \left\{ \sum_{i=1}^{n} \delta_{x_i} : n \geq 0, x_i \in \mathcal{X} \right\}$

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Population dynamics

For an individual with trait $x \in \mathcal{X}$ in the population ν_t:

- Reproduction with rate $b(x)$
- Mutation and/or dispersal with probability $\mu(x)$

- Death with rate $d(x) + \sum_{i=1}^{N_t} \alpha(x, x_i) = d(x) + \int_{\mathcal{X}} \alpha(x, y)\nu_t(dy)$

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Comments

- Logistic interaction = competition
  Easy generalization to more general interactions (N.C., R. Ferrière, S. Méléard, 2006)
  - birth rate $b(x, U * \nu_t(x))$
  - death rate $d(x, V * \nu_t(x))$
- Multispecific (prey-predator, host-parasite, ressource exploitation, mutulistic community,...) generalization
- Spatial interpretation: mutation = dispersion can also be replaced by other motions such as diffusions (Bolker, Pacala, 1997, Dieckmann, Law, 2000, Desvillette, Ferrière, Prévost, 2006, C., Méléard, JMB 2007)

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$\rightsquigarrow$ Existence et uniqueness in law of ν (Fournier and Méléard 2004)
Total jump rate per individual $\le \bar{C}(1 + \langle \nu_t, \mathbf{1} \rangle)$
Total population jump rate $\le \bar{C}\langle \nu_t, \mathbf{1} \rangle (1 + \langle \nu_t, \mathbf{1} \rangle)$

Algorithm: acceptance-rejection procedure

Initial state: N_0 individuals, with traits $\mathbf{X}_0 = (X_0^i)_{1 \leq i \leq N_0}$.
$\mathbf{X}_t$ = trait vector at time t.

- $(\tau_k)_k$ exponential r.v. with parameter 1 $\rightsquigarrow$ time steps
- $(\theta_k)_k$ uniform r.v. on $[0,1]$ $\rightsquigarrow$ to decide which kind of event happens
- $(\alpha_k)_k$ uniform r.v. on $[0, \bar{\alpha}]$ $\rightsquigarrow$ for the logistic competition
- $(Z_k)_k$ with law $\bar{M}(z)dz$ $\rightsquigarrow$ in the case of mutation

- $T_0 = 0$, N_0, $\mathbf{X}_0$
- Given $(T_{k-1}, N_{k-1}, \mathbf{X}_{T_{k-1}})$,
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Iteration on k

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At time T_k choose an individual i uniformly among the N_{k-1}.

- If $\theta_k < U_1 := \frac{(N_{k-1}-1)\bar{\alpha}}{\bar{b}+\bar{d}+\bar{\alpha}(N_{k-1}-1)}$, choose another individual $j \neq i$ at random. If $\alpha_k < \alpha(X^i_{T_{k-1}}, X^j_{T_{k-1}}) \rightsquigarrow j$ kills i
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- If $U_3 \leq \theta_k < U_4 := U_3 + \frac{d(X^i_{T_{k-1}})}{\bar{b}+\bar{d}+\bar{\alpha}(N_{k-1}-1)} \rightsquigarrow$ (natural) death of i
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- If $\theta_k < U_1 := \frac{(N_{k-1}-1)\bar{\alpha}}{\bar{b}+\bar{d}+\bar{\alpha}(N_{k-1}-1)}$, choose another individual $j \neq i$ at random. If $\alpha_k < \alpha(X^i_{T_{k-1}}, X^j_{T_{k-1}}) \rightsquigarrow j$ kills i
- If $U_1 \leq \theta_k < U_2 := U_1 + \frac{b(X^i_{T_{k-1}})(1-\mu(X^i_{T_{k-1}}))}{\bar{b}+\bar{d}+\bar{\alpha}(N_{k-1}-1)} \rightsquigarrow$ birth of a clone of i
- If $U_2 \leq \theta_k < U_3 := U_2 + \frac{b(X^i_{T_{k-1}})\mu(X^i_{T_{k-1}})M(X^i_{T_{k-1}},Z_k)}{\bar{M}(Z_k)(\bar{b}+\bar{d}+\bar{\alpha}(N_{k-1}-1))} \rightsquigarrow$ birth of a mutant with trait $X^i_{T_{k-1}} + Z_k$
- If $U_3 \leq \theta_k < U_4 := U_3 + \frac{d(X^i_{T_{k-1}})}{\bar{b}+\bar{d}+\bar{\alpha}(N_{k-1}-1)} \rightsquigarrow$ (natural) death of i
- If $\theta_k \geq U_4 \rightsquigarrow$ nothing happens

Example 1

Parameters from Kisdi (1999)

$$\mathcal{X} = [0,4] \quad d(x) \equiv 0 \quad \mu(x) \equiv \mu$$

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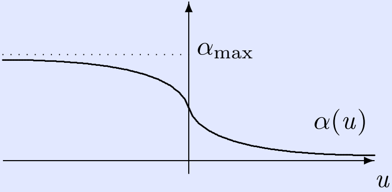

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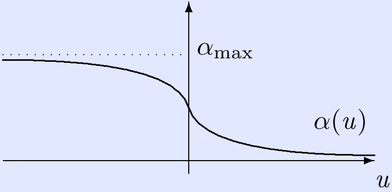
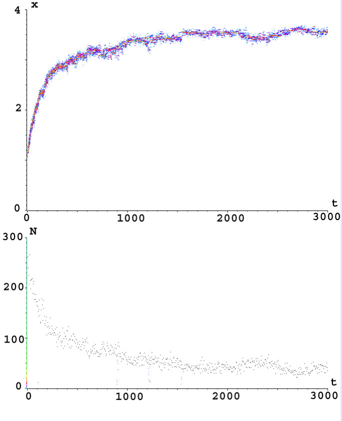


Asymetric competition

- arm-race competition
- evolution of the cell size at division

Simulations



$\mu = 0.1 \quad \sigma = 0.03$
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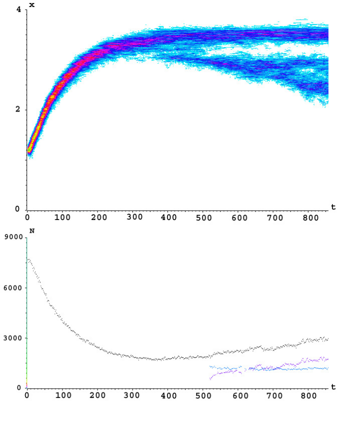

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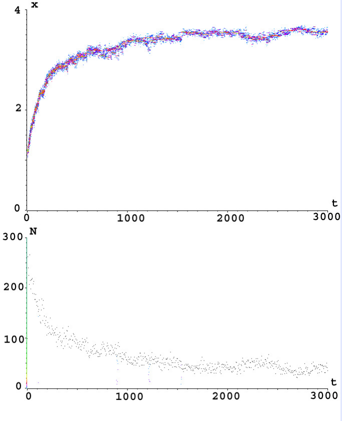

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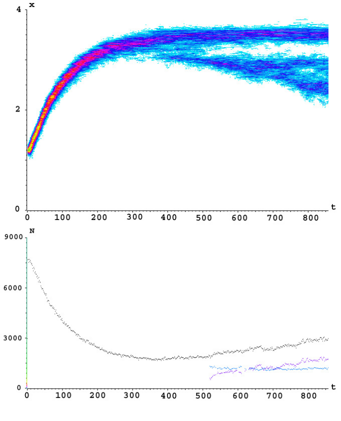

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Symetric competition (competition for ressources)

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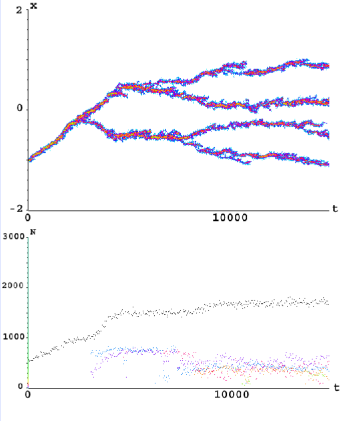
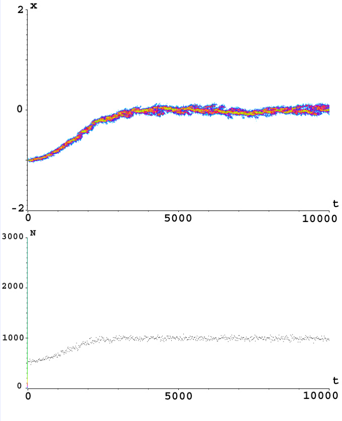


$\mu = 0.05,\ K = 1000,\ \sigma = 0.01,\ \sigma_\alpha = 0.5,\ \sigma_b = 0.9$



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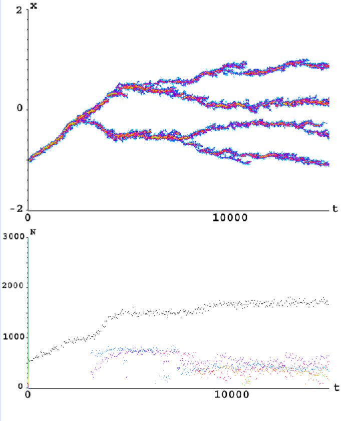

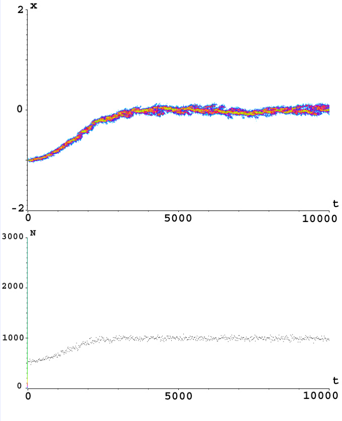

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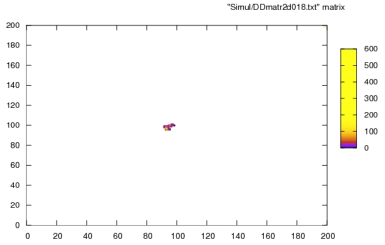

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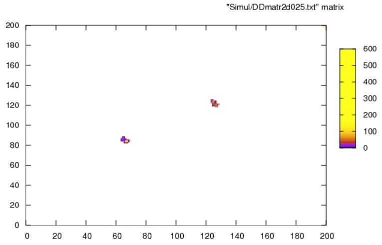

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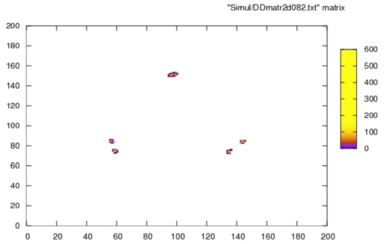

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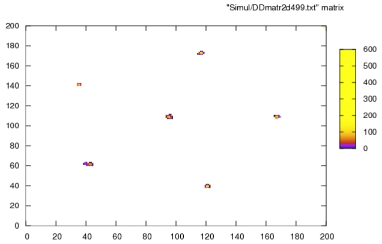

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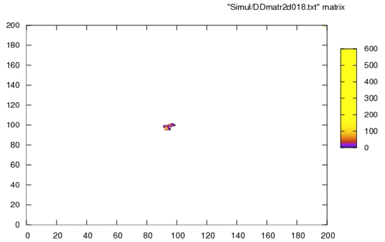

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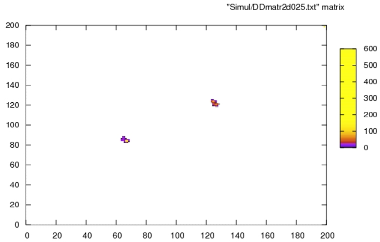

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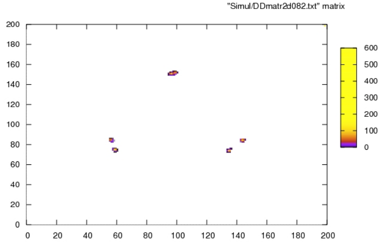

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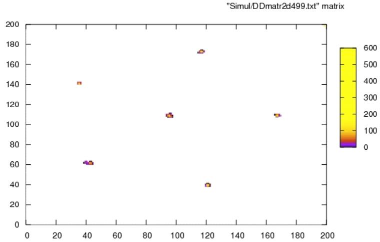

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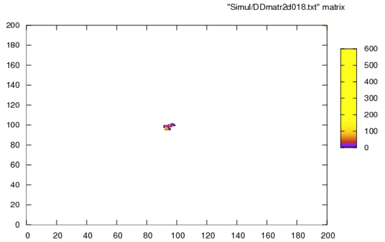

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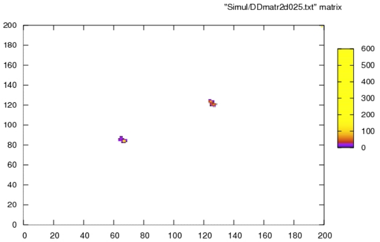

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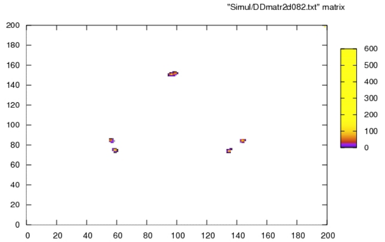

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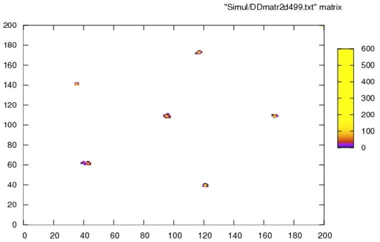

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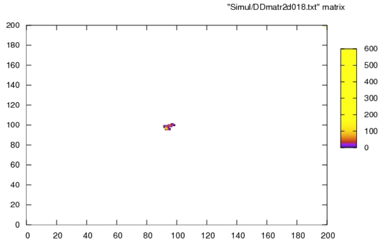

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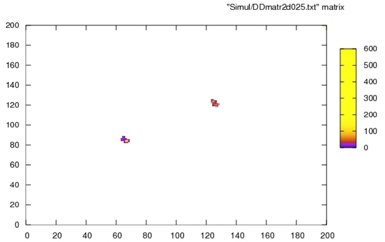

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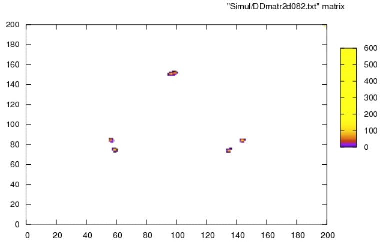

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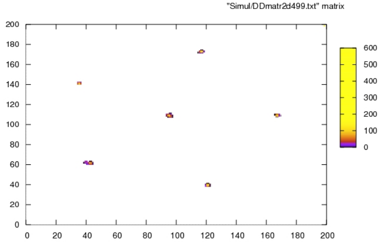

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Example: Clustering and Polymorphism:
Dieckmann and Doebeli 2000
Growth rate maximal for $u = x$: gradual spatial distribution of different resources (for some species of birds; seed size $\leftrightarrow$ beak size).

- $\mathcal{X} = \mathcal{U} = [0, 1]$
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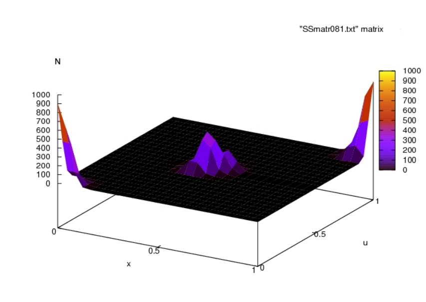

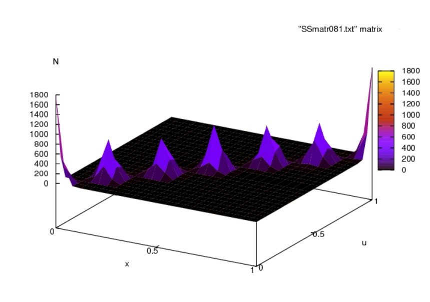

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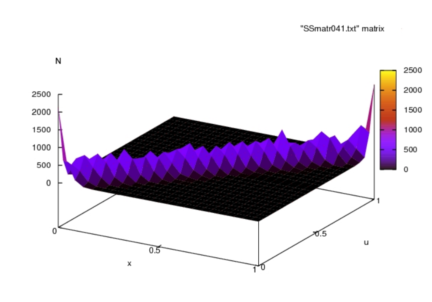

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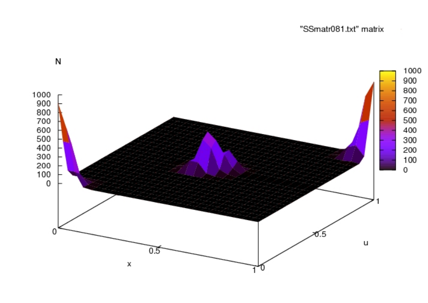

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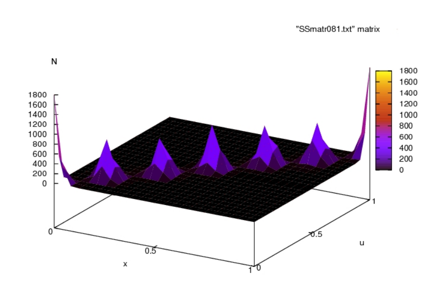

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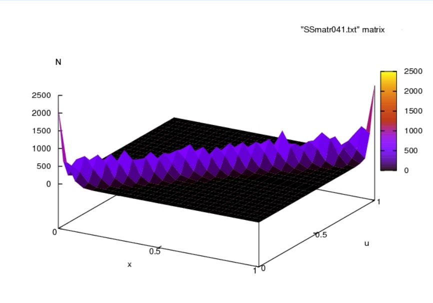

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Triangular invasion pattern: invasion front composed of faster individuals.

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- $I^\delta(y) = A_\delta 1_{\{|y| \leq \delta\}}$; $M(x, u, v)dv = 0.1N(u, s^2)$

Triangular invasion pattern: invasion front composed of faster individuals.

Example: Invasion and Evolution of Migration Speed Cane toads in

Australia (Nature 2006), Phillips et al.: the annual rate of progress of the toad invasion front has increased. The toads with longer legs are the first to arrive in new areas, but also those at the invasion front have longer legs than toads in older populations.

- $\mathcal{X} = [-1, 1], \mathcal{U} = [0, 3]$
- $m(x, u) = m(u + 0.1)$
- $b(x, u) = 1$
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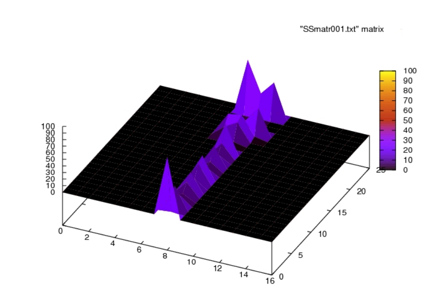
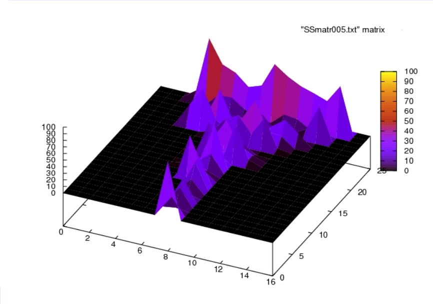
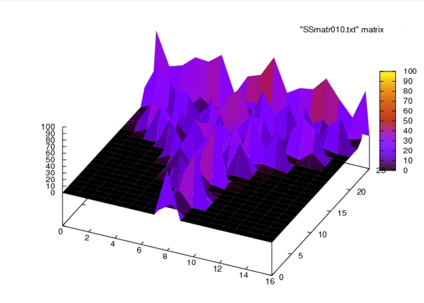
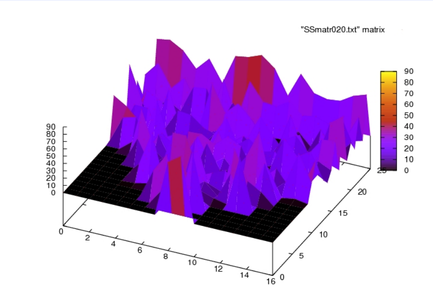




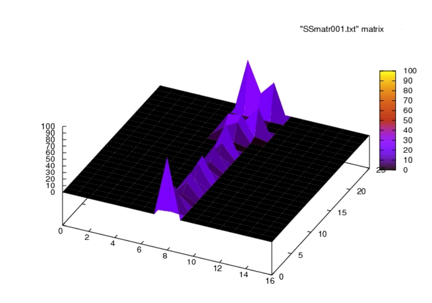
$K = 100, s = 0.03, m = 0.003, \delta = 0.1$ and $t = 25$

$t = 125$





Examples



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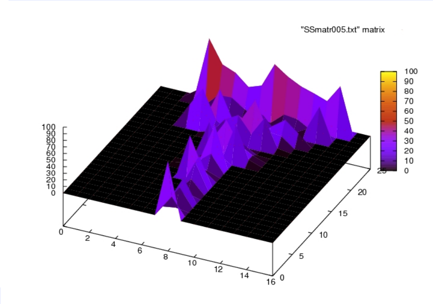
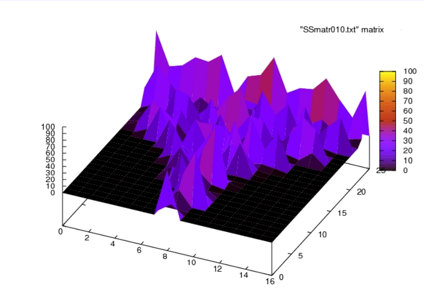
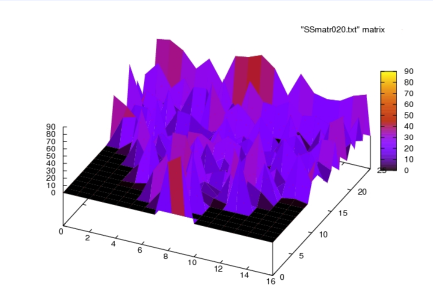


$t = 125$





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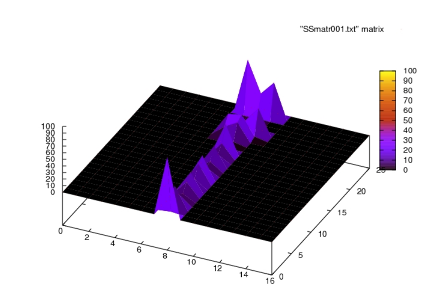

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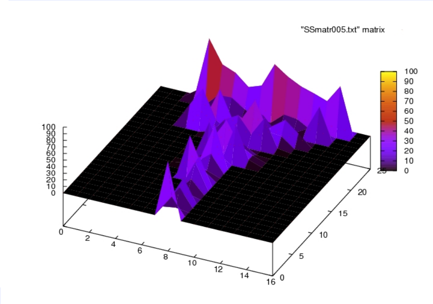
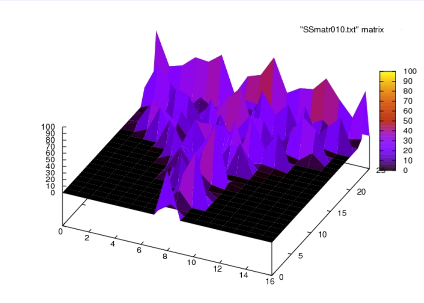
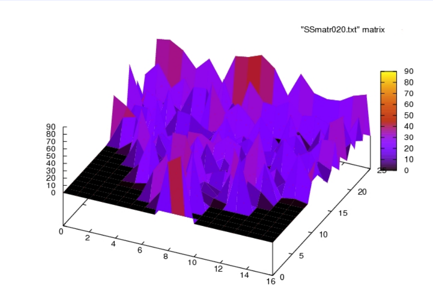


$t = 125$

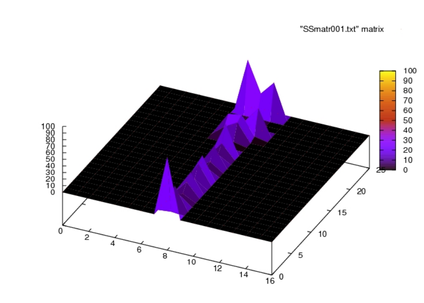


$t = 250$



$t = 500$

Examples



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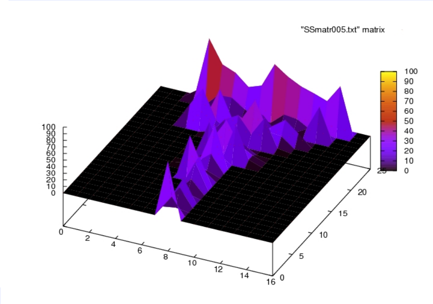

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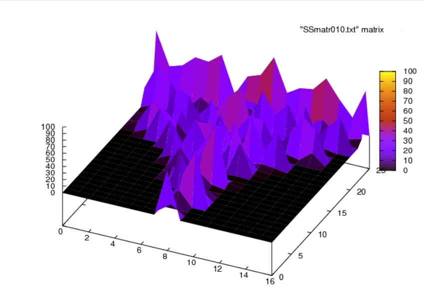
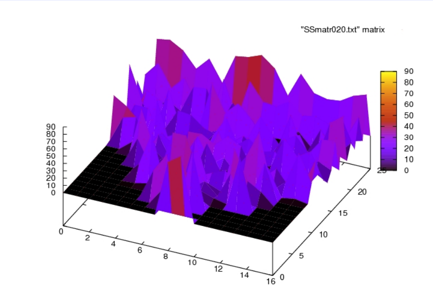


$t = 250$



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Large population scalings (C., Ferrière, Méléard, TPB 2006)

Parameter K: b_K, d_K, μ_K, M_K and

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$$\begin{aligned} L\ \phi(\nu) &= \int_{\mathcal{X}} [\phi(\nu+\delta_x) - \phi(\nu)](1-\mu\ (x))b\ (x)\nu(dx) \\ &+ \int_{\mathcal{X}} \int_{\mathbb{R}^d} [\phi(\nu+\delta_{x+z}) - \phi(\nu)]\mu\ (x)b\ (x)M\ (x,z)dz\nu(dx) \\ &+ \int_{\mathcal{X}} [\phi(\nu-\delta_x) - \phi(\nu)] \left(d\ (x) + \int_{\mathcal{X}} \alpha(x,y)(\nu(dy) - \delta_x(dy)) \right) \nu(dx) \end{aligned}$$

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First large population limit

$b_K = b$, $d_K = d$, $\mu_K = \mu$, $M_K = M$.
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Theorem

Assume that $X_0^K \Rightarrow \xi_0$, $\sup_K \mathbf{E}[\langle X_0^K, \mathbf{1}\rangle^3] < +\infty$ *and the regularity of the parameters.*

Then $X^K \Rightarrow \xi \in \mathcal{C}([0,T], M_F(\mathcal{X}))$ *deterministic, where*

$$\langle \xi_t, f\rangle = \langle \xi_0, f\rangle + \int_0^t \int_{\mathcal{X}} \Big\{ \Big[(1-\mu(x))b(x) - d(x) - \int_{\mathcal{X}} \alpha(x,y)\xi_s(dy)\Big] f(x) + b(x)\mu(x) \int f(x+z) M(x,z)\,dz \Big\} \xi_s(dx)\,ds. \tag{1}$$

Remarks

- If $\xi_0(dx) = u_0(x)dx$, then $\xi_t(dx) = u(t,x)dx$, $\forall t > 0$ and $u(t,x)$ is weak solution to

$$\partial_t u = [(1-\mu(x))b(x) - d(x) - \int \alpha(x,y)u(t,y)dy]u(t,x) + \int \mu(y)b(y)M(y,x-y)u(t,y)dy$$

- Monomorphic case: if $\mu \equiv 0$ and $X_0^K = n_0^K \delta_x$ with $n_0^K \to n_0$ when $K \to \infty$, then $X_t^K \to n(t)\delta_x$, with

$$\dot{n} = (b(x) - d(x) - \alpha(x,x)n)n, \quad n(0) = n_0$$

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$$\begin{cases} \dot{n} = (b(x) - d(x) - \alpha(x,x)n - \alpha(x,y)m)n \\ \dot{m} = (b(y) - d(y) - \alpha(y,x)n - \alpha(y,y)m)m \end{cases}$$

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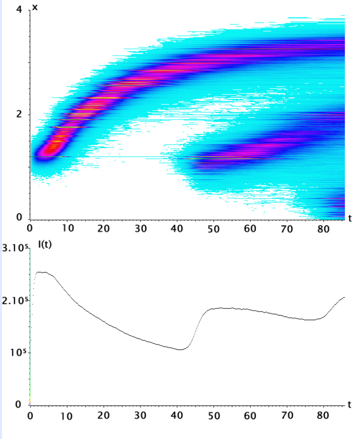
Simulation of example 1



$$\mu = 0.1 \quad \sigma = 0.03$$
$$K = 100000$$

Large population limit with accelerated births and deaths

Here, the limit of large system size is combined with an acceleration of births and deaths $\mathcal{X} = \mathbb{R}^d$, $\alpha_K(x, y) = \alpha(x, y)/K$,

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Biological interpretation: being slow and living fast but slow demography
$\rightsquigarrow$ relevant for microorganisms in colonies
Since births are accelerated, the effect of mutation (either the mutation probability or the mutation amplitude) must be rescaled accordingly: $\mu_K = \mu, \qquad M_K(x,z)dz \sim \mathcal{N}(0, \sigma^2(x)\mathrm{Id}/K^\eta).$

Small mutation step

Case $\eta < 1$

- $X^K \Rightarrow \xi \in \mathcal{C}([0,T], M_F)$ where

$$\begin{aligned}\langle \xi_t, f\rangle = \langle \xi_0, f\rangle &+ \int_0^t \int_{\mathcal{X}} \Big\{ (b(x) - d(x) - \int_{\mathcal{X}} \alpha(x,y)\xi_s(dy))f(x) \\ &+ \frac{1}{2} r(x)\mu(x)\sigma^2(x)\Delta f(x) \Big\} \xi_s(dx)ds.\end{aligned}$$

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$\rightsquigarrow$ Generalization of Fisher's models in ecology (reaction-diffusion equation)

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$X^K \Rightarrow Z \in \mathcal{C}([0,T], M_F)$ where Z is defined by the 3 conditions:

- $\sup_{t\leq T} \mathbf{E}[\langle Z_t, \mathbf{1}\rangle^3] < \infty$
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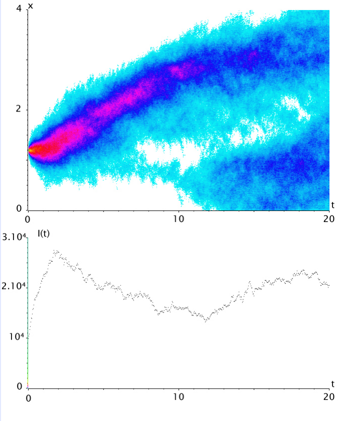
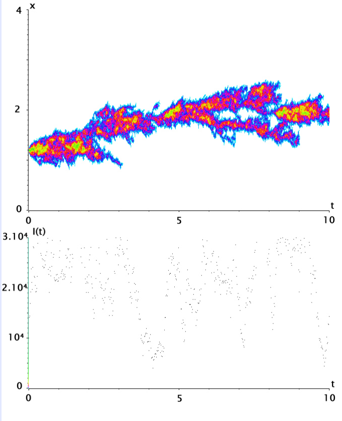
$\rightsquigarrow$ Microscopic justification of superprocesses with density-dependent interaction, recently proposed and studied in population genetics (Etheridge 04)

- birth and death stochasticity reflected on the demographic time-scale
- diversification vs extinction

Simulations of example 1

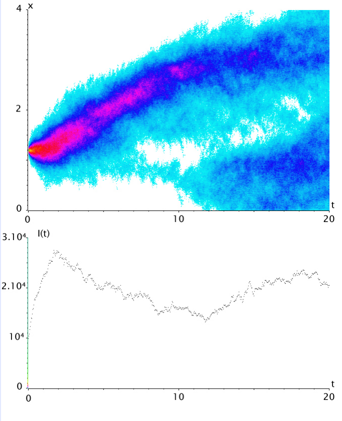


$\mu = 0.3 \quad \sigma = 0.3$
$K = 10000 \quad \eta = 0.5$

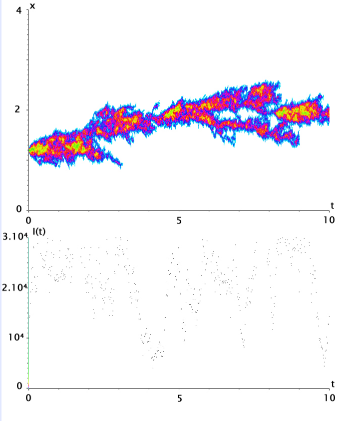


$\mu = 0.3 \quad \sigma = 0.3$
$K = 10000 \quad \eta = 1$

Simulations of example 1



$\mu = 0.3 \quad \sigma = 0.3$
$K = 10000 \quad \eta = 0.5$



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Discussion

- Mathematical justification of several (old and new) macroscopic evolutionary models
- Precising the biological assumptions and scales underlying each macroscopic model (large ressources, different scales for individual births and deaths and for demography,...)
- Unifying these models from the same microscopic model

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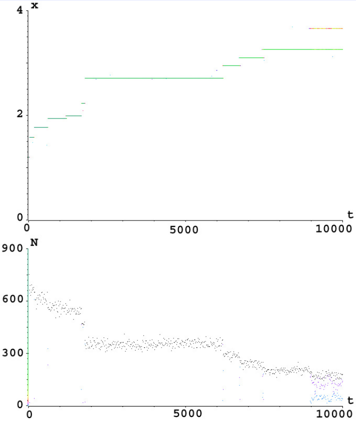
An interpretation of evolutionary branching

- The theory of adaptive dynamics (Metz et al. 1996) proposes an interpretation of evolutionary branching based on the assumptions of rare and small mutations, using an approximate model called the "trait substitution sequence".
- These assumptions are restrictive. However, the branching criterion obtained this way is very robust in simulations.

Large population and very rare mutations



$\mu = 0.00003 \quad \sigma = 0.2 \quad K = 3000$

Large population and very rare mutations: timescales separation

Biological heuristics

The selection process has sufficient time between two mutations to eliminate disadvantaged traits (time scale separation):

- Minimal number of coexisting traits
- Succession of phases of mutant invasion, and phases of competition between traits

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The assumption of large populations allows to assume a deterministic population dynamics, so that one can predict the outcome of competition between two traits (or more).

Renormalization

- Large population: $\alpha_K(x,y) = \alpha(x,y)/K$, $b_K = b$, $d_K = d$, $M_K = M$
- Rare mutations: $\mu_K(x) = u_K \mu(x)$ where $u_K \to 0$ when $K \to +\infty$

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Logistic equations ($\mu \equiv 0$)

- Monomorphic case: $\dot{n} = (b(x) - d(x) - \alpha(x,x)n)n$

- Dimorphic case: the logistic system

$$\begin{cases} \dot{n} = (b(x) - d(x) - \alpha(x,x)n - \alpha(x,y)m)n \\ \dot{m} = (b(y) - d(y) - \alpha(y,x)n - \alpha(y,y)m)m \end{cases}$$

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has a single stable steady state, $(\bar{n}_x, 0)$ or $(0, \bar{n}_y)$ under the assumption

(H') For any $x \neq y \in \mathcal{X}$, $f(x,y)f(y,x) < 0$, where

$$f(y,x) = b(y) - d(y) - \alpha(y,x)\bar{n}_x.$$

Theorem

Assume (H), (H') and

$$\forall C > 0, \quad \log K \ll \frac{1}{K u_K} \ll \exp(CK)$$

and $X_0^K = (\gamma_K/K)\delta_x$ *with* $\gamma_K/K \to \gamma > 0$,

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for finite dimensional distributions,
where the Markov process $(Y_t, t \geq 0)$ *satisfies* $Y_0 = x$ *and has as infinitesimal generator:*

$$A\varphi(x) = \int_{\mathbb{R}^d} (\varphi(x+z) - \varphi(x))\mu(x)b(x)\bar{n}_x \frac{[f(x+z,x)]_+}{b(x+z)} M(x,dz).$$

Some remarks

- t/Ku_K is the time scale of mutations.
- Because of the discontinuity of Z at $t = 0+$, we cannot hope to obtain a "functional" convergence.
- If assumption (H') is not satisfied, this result can be extended to polymorphic populations.
- $f(x, y)$ is a fitness function which depends on the resident and mutant trait, which is rigorously defined from the ecological parameters of the model.

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Consequences

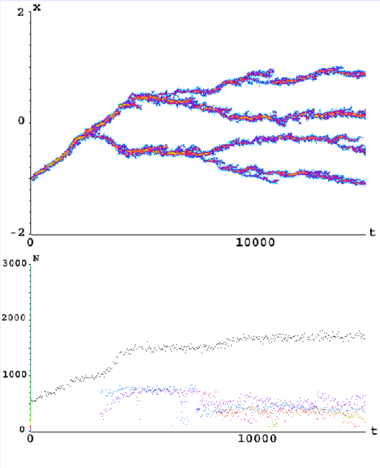
Under the additional assumption of small mutations

- the TSS can be approximated by an ODE called the "canonical equation of adaptive dynamics" (Dieckmann and Law 1996) driven by the fitness gradient
- when the evolution arrives at an equilibirum of this ODE, the analysis of the TSS at this points allows to determine if branching can occur. It is possible to mathematically justify (Bénaïm, C., Méléard, in prep.) the branching criterion:
    - if $\partial_1 f(x^*, x^*) = 0$, there is branching at x^* if and only if

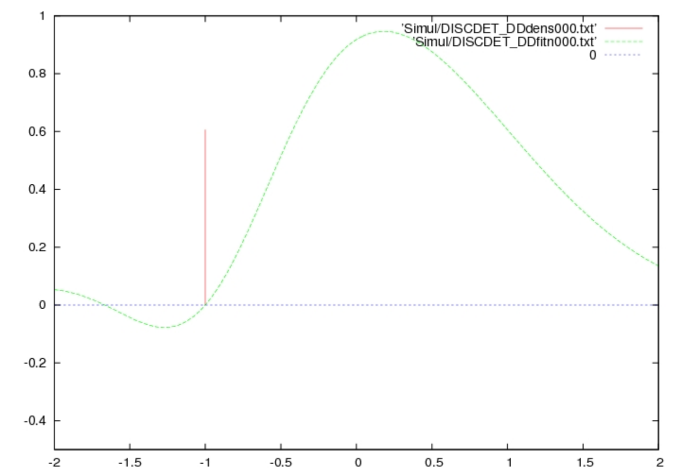
$$\partial_{22} f(x^*, x^*) < \partial_{11} f(x^*, x^*) \quad \text{and} \quad \partial_{11} f(x^*, x^*) > 0.$$

    - It is also possible to compute the (asymptotic) branching time

An example



Fitness landscape



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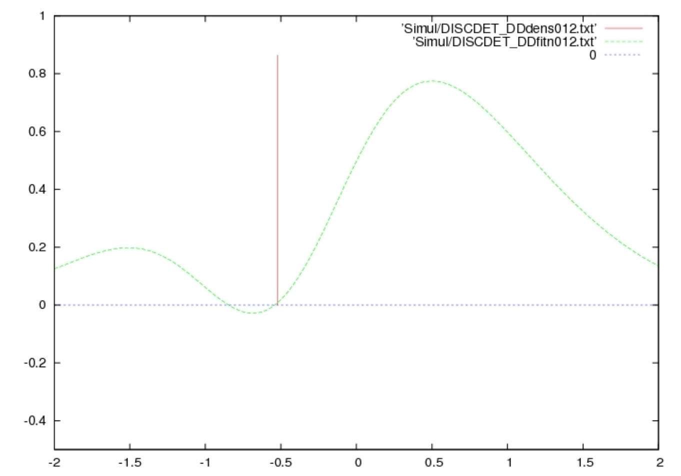

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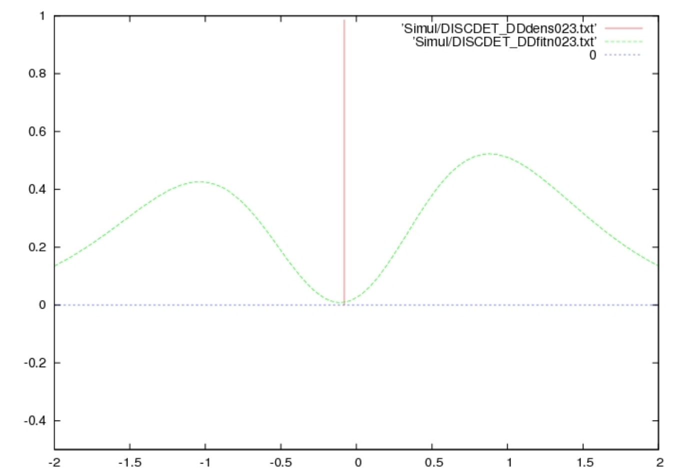

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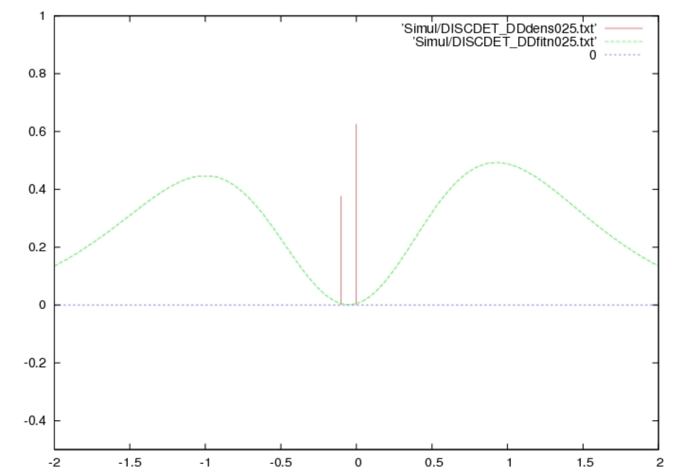

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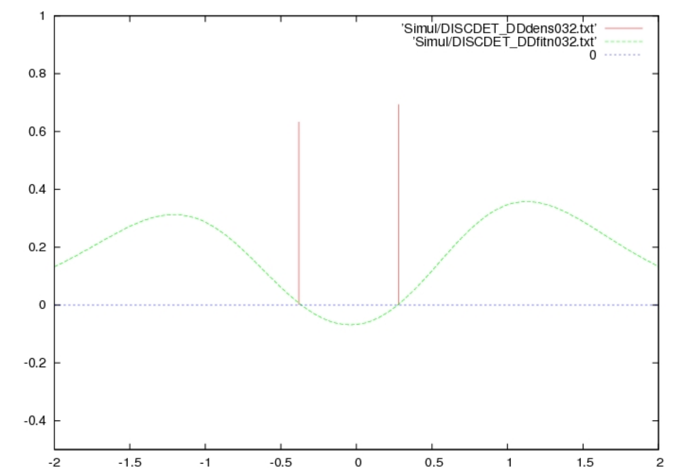

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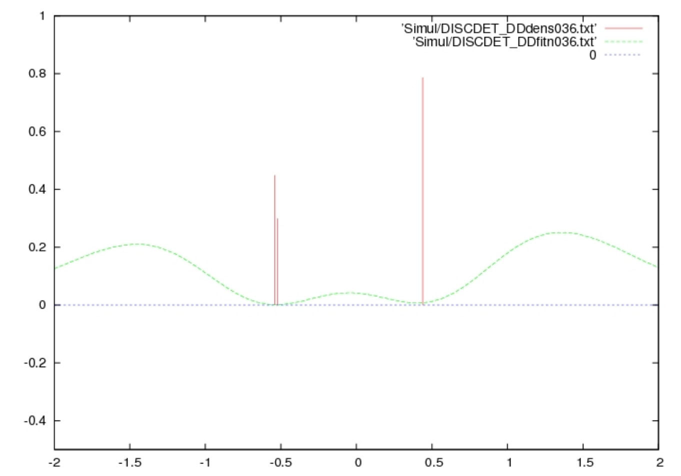

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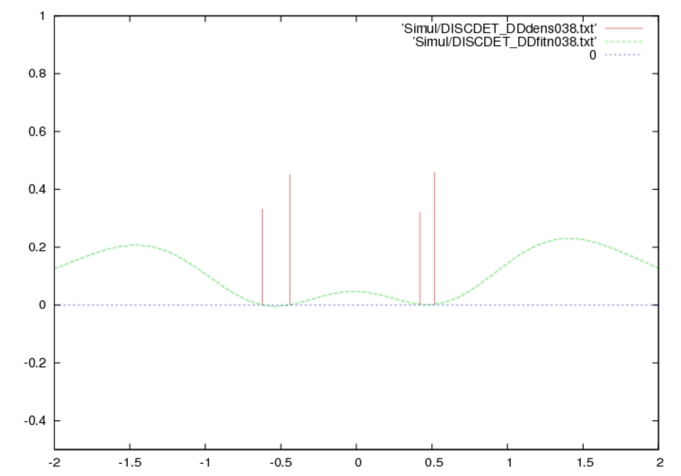

Conclusion

Nous avons

- présenté un modèle simple stochastique spatial avec interactions, facile à simuler, pouvant s'appliquer à de nombreuses situations
- expliqué ses liens avec d'autres modèles plus ou moins classiques, pouvant tous se déduire du même modèle microscopique
- expliqué le phénomène de branchement évolutif, qui peut aussi s'interpréter comme clustering spatial, ou invasions par colonies de populations (métapopulations) ; favorisé par
  - petite portée d'interaction spatiale (par rapport aux variations environementales)
  - petite portée moyenne de dispersion
  - peut également apparaître dans un milieu très homogène
  - le critère de branchement est obtenu dans une asymptotique particulière, mais est assez robuste d'après les simulations
- spécifié les hypothèses précises sur les paramètres nécessaires pour chacun de ces modèles