

Dynamic Random Environments

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Survival of the misfit: Live in times of change

Based on collaborations with:
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1. Adaptive dynamics and the role of mutations
2. A microscopic model of adaptive dynamics
3. Time scales and the grand picture
4. A two state toy model in a dynamic environment
5. Perspectives

Adaptive dynamics is a biological theory that describes the evolution of biological populations:

- ▷ in space of phenotypes and/or geographic locations
- ▷ with locally varying fitness
- ▷ interacting through ecological competition
- ▷ subject to mutation/migration

Adaptive dynamics explains how an initial populations distributes and diversifies to create a structured population invading the available geographic- resp. type space. Key mechanisms are

- ▷ drift towards higher fitness (canonical equation)
- ▷ ecological branching (splitting of populations to reduce competition)

Individual based models

Good way to understand adaptive dynamics in a mathematical way is by looking at populations as Markov processes on the space of positive measures.

- ▷ Trait-space: \mathcal{X} some Polish space (e.g. $\mathbb{R}^d, \mathbb{Z}^d$);
- ▷ Configuration space: Point measures on \mathcal{X} :

$$\nu_t \equiv \sum_{i=1}^{N_t} \delta_{x_i(t)}$$

represents a population of N_t individuals, i , with traits $x_i(t)$.

- ▷ Generator acting on a suitable core of functions $f : \mathcal{M}_p(\mathcal{X}) \rightarrow \mathbb{R}$ by

$$\begin{aligned} Lf(\nu) &= \int_{\mathcal{X}} [f(\nu + \delta_x) - f(\nu)] b(x)(1 - p(x)) \nu(dx) \\ &+ \int_{\mathcal{X}} [f(\nu - \delta_x) - f(\nu)] \left[d(x) + \int_{\mathcal{X}} c(x, y) \nu(dy) \right] \nu(dx) \\ &+ \int_{\mathcal{X}} \int_{\mathcal{X}} [f(\nu + \delta_{x+y}) - f(\nu)] p(x) m(x, dy) \nu(dx). \end{aligned}$$

Here the functions d, b, c, p, m have the following meaning:

- ▷ $b(x)$: the natural **birth rate** of an individual with trait x ;
- ▷ $d(x) + c(x, x)$: the natural **death rate** of a (lonely) individual with trait x ;
- ▷ $c(x, y)$ the increment of the death rate of an individual with trait x due to the presence of an individual with trait y (**competition kernel**);
 $\int c(x, y)\nu(dy)$ is the extra death rate of an individual of trait x due to the presence of the population ν .
- ▷ $p(x)$ rate of **mutation** of an individual x when giving birth;
- ▷ $m(x, dy)$ is the **probability distribution** of the type of a **mutant** child of an individual of type x .

Scaling and parametrization

We want to parametrize our processes by three key parameters:

- ▷ **large** typical population size K ;
- ▷ **small** total mutation rate μ ;
- ▷ **small** single mutations steps σ ;

This can be achieved by performing the following re-scaling:

- ▷ $\nu \rightarrow \frac{1}{K}\nu \equiv \nu^{K,\mu,\sigma}$;
- ▷ $c(x, y) \rightarrow \frac{1}{K}c(x, y)$;
- ▷ $p(x) \rightarrow \mu p(x)$;
- ▷ $m(x, dy) \rightarrow m(x, \sigma dy) \equiv m^\sigma(x, dy)$.

The generator $L^{K,\mu,\sigma}$ then takes the form

$$\begin{aligned} L^{K,\mu,\sigma} f(\nu) &= K \int_{\mathcal{X}} [f(\nu + K^{-1}\delta_x) - f(\nu)] (1 - \mu p(x)) b(x) \nu(dx) \\ &+ K \int_{\mathcal{X}} [f(\nu - K^{-1}\delta_x) - f(\nu)] \left[d(x) + \int_{\mathcal{X}} c(x, y) \nu(dy) \right] \nu(dx) \\ &+ K \int_{\mathcal{X}} \int_{\mathcal{X}} [f(\nu + K^{-1}\delta_y) - f(\nu)] \mu p(x) m^\sigma(x, dy) \nu(dx). \end{aligned}$$

Scaling limits

Assume first that $M \equiv 0$ (no mutations), and assume that $\nu_0^K = \sum_{i=1}^n z_i(0)\delta_{x_i}$. Then ν^K converges, as $K \uparrow \infty$, to ν_t^∞ given by

$$\nu_t^\infty \equiv \sum_{i=1}^n z_i(t)\delta_{x_i}$$

where $z_i(t)$ are non-negative solutions of the Lotka-Volterra systems

$$\frac{d}{dt}z_i(t) = z_i(t) \left(b(x_i) - d(x_i) - \sum_{j=1}^n c(x_i, x_j)z_j \right).$$

Note: This assume presence of macroscopic $\sim K$ number of individuals in initial state! Initial conditions with single individuals require a different (branching process) treatment.

Take initial conditions such that at some trait x_0 , $z_0(0) = 1/K$, otherwise initial conditions as in the previous slide: Then:

- ▷ In time of order 1, $z_i(t) \sim z_i^*$, where z^* is an equilibrium of the n -dim LV-system;
- ▷ **IF**

$$f(x_0, \underline{x}) \equiv b(x_0) - d(x_0) - \sum_{i=1}^n c(x_0, x_i) z_i^* > 0,$$

with probability $0 < q < 1$, $z_0(t)$ will reach a level $\eta > 0$ before reaching zero, in time of order $\ln K$, and will die out with probability $1 - q$.

- ▷ If 0 was successful, then the system $(z_0(t), \dots, z_n(t))$ will stay close to the solution of the LV-Eq. and approach an equilibrium in finite time;
- ▷ If for some trait, i , there is no positive equilibrium value, then this trait will die out in time of order $\ln K$.

The function $f(x)$ is called **invasion fitness**.

In Champagnat/Méléard '09 and Champagnat/B '10 the evolution of populations is studied in the presence of **small mutations**:

$$\mu \ll \frac{\sigma}{K \ln K}$$

This condition ensures that the systems can reach its LV-equilibrium in the time interval between two mutations.

The basic building blocks of the ensuing dynamics are the following:

- ▷ drift towards optimal fitness
- ▷ fast evolutionary branching
- ▷ slow evolutionary branching

We consider a system with a single occupied trait ($n = 1$) and trait space \mathbb{R} .

Theorem 1. Let $\nu_0 = \gamma\delta_x$. Assume that $(\mu, \sigma, K) \rightarrow (0, 0, \infty)$ such that

$$K^{-1/3} \ll \sigma \ll 1 \quad \text{and} \quad \exp(-CK) \ll \mu \ll \frac{\sigma}{K \ln K}$$

Then

$$\nu_{t\sigma^{-2}(\mu K)^{-1}} \rightarrow \bar{z}(x(t))\delta_{x(t)} \quad (*)$$

where

$$\frac{dx}{dt} = \frac{1}{2} \int h^2 m(x, dh) p(x) z^*(x) \partial_1 f(x, x)$$

Evolutionary branching

A point with $\partial_1 f(x, x)$ is a fixed point of the evolution described above. If this is a local **minimum** of the invasion fitness, the population will tend to split into two:

Theorem 1. Assume that the solution of Eq. (*) converges to a fix-point, x^* , as $t \uparrow \infty$ (i.e. $\partial_1 f(x^*, x^*) = 0$).

Assume that $(\mu, \sigma, K) \rightarrow (0, 0, \infty)$ satisfy

$$K^{-1/6} \ll \sigma \ll 1 \quad \text{and} \quad \exp(-CK) \ll \mu \ll \frac{\sigma}{K \ln K}$$

▷ $x(t)$ reaches an ϵ -neighborhood of x^* in time

$$T_\epsilon \ll \frac{\mu K \sigma^2}{\ln \sigma^{-1}}$$

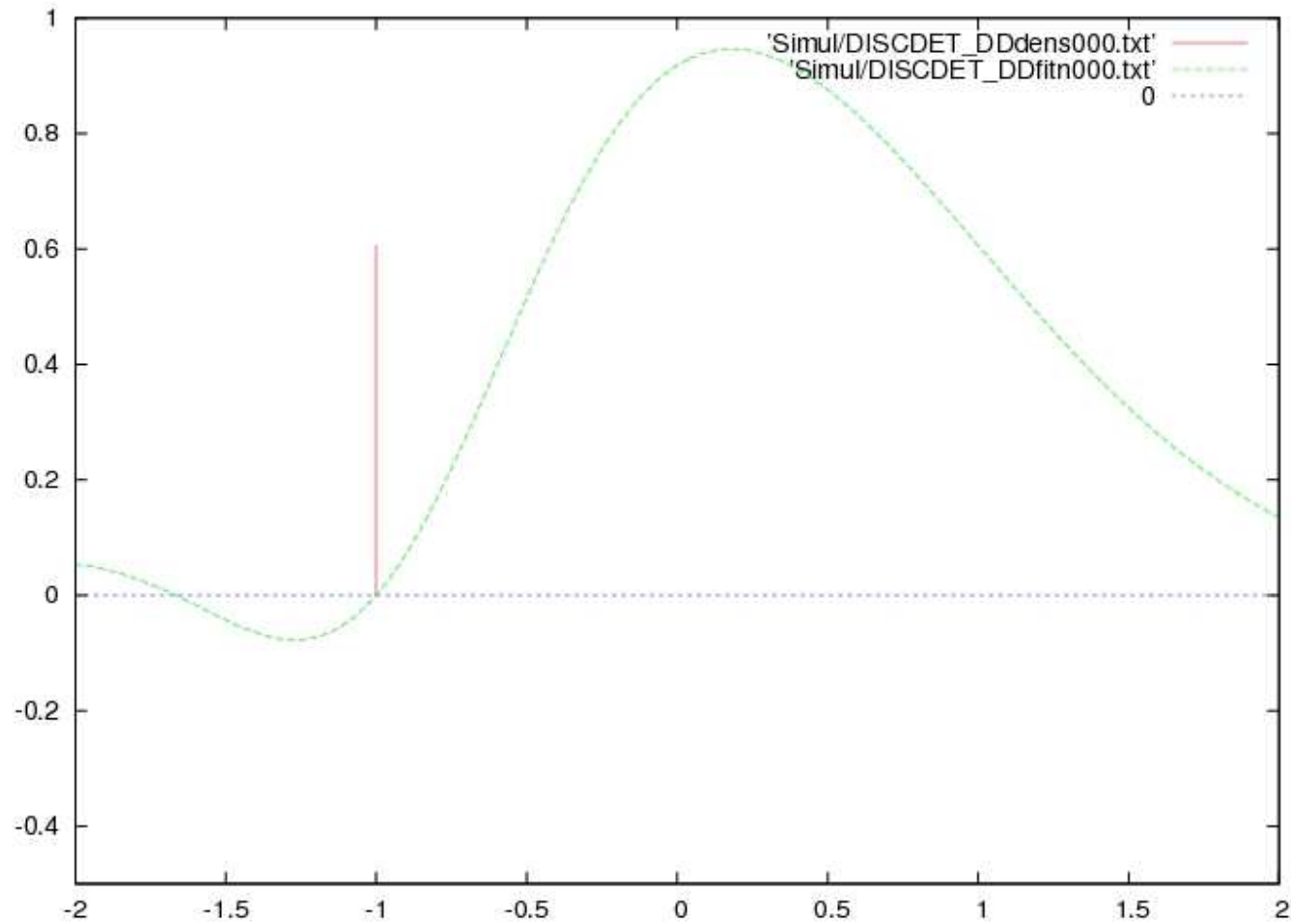
▷ If $\delta_1^2 f(x^*, x^*) > 0$, then after time

$$S_\epsilon = C \frac{\mu K \sigma^2}{\ln \sigma^{-1}}$$

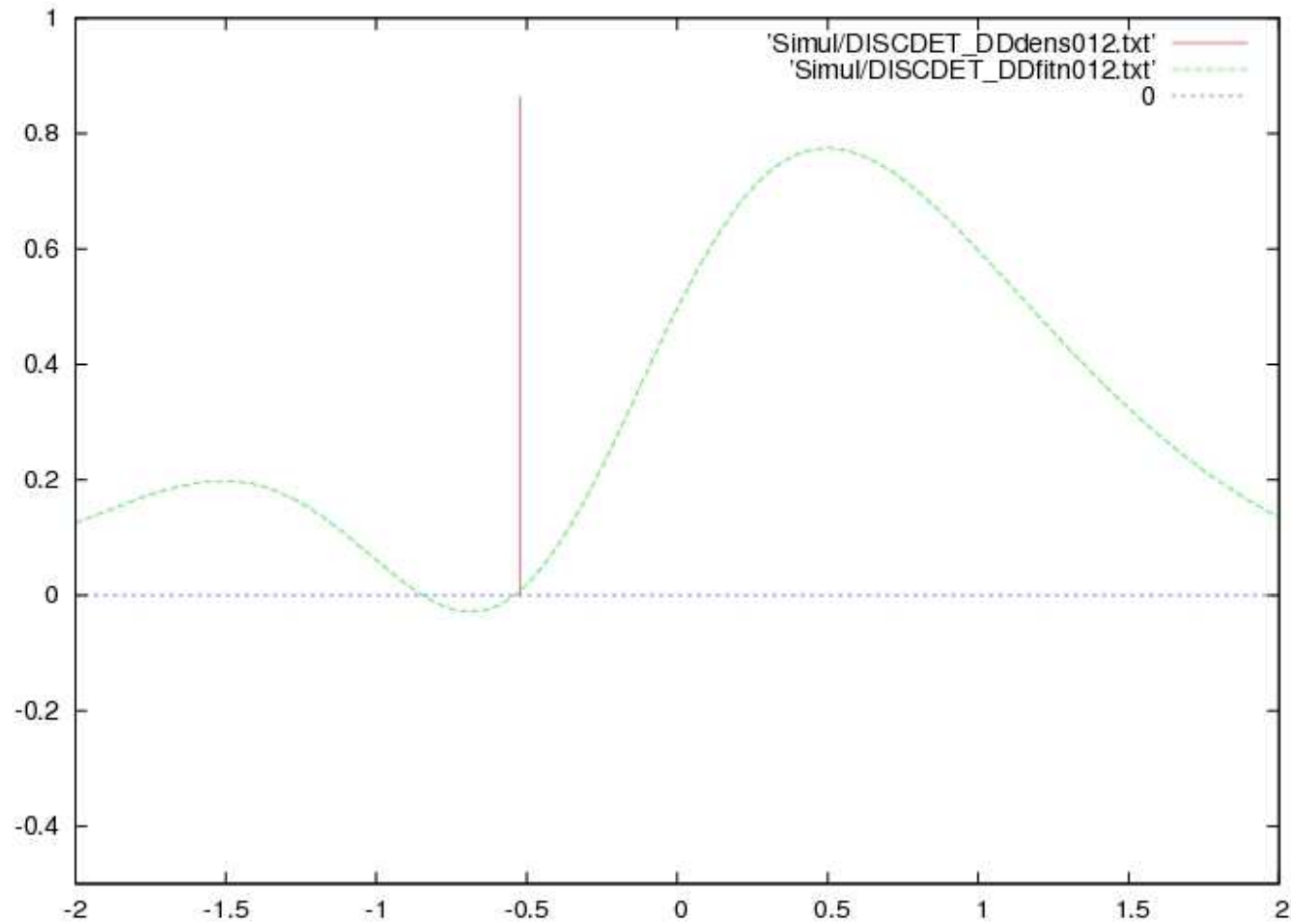
$$\nu_{S_\epsilon} = z_1 \delta_{x_1} + z_2 \delta_{x_2}, \quad \text{with} \quad |x_1 - x_2| \geq \epsilon$$

...and so on.....

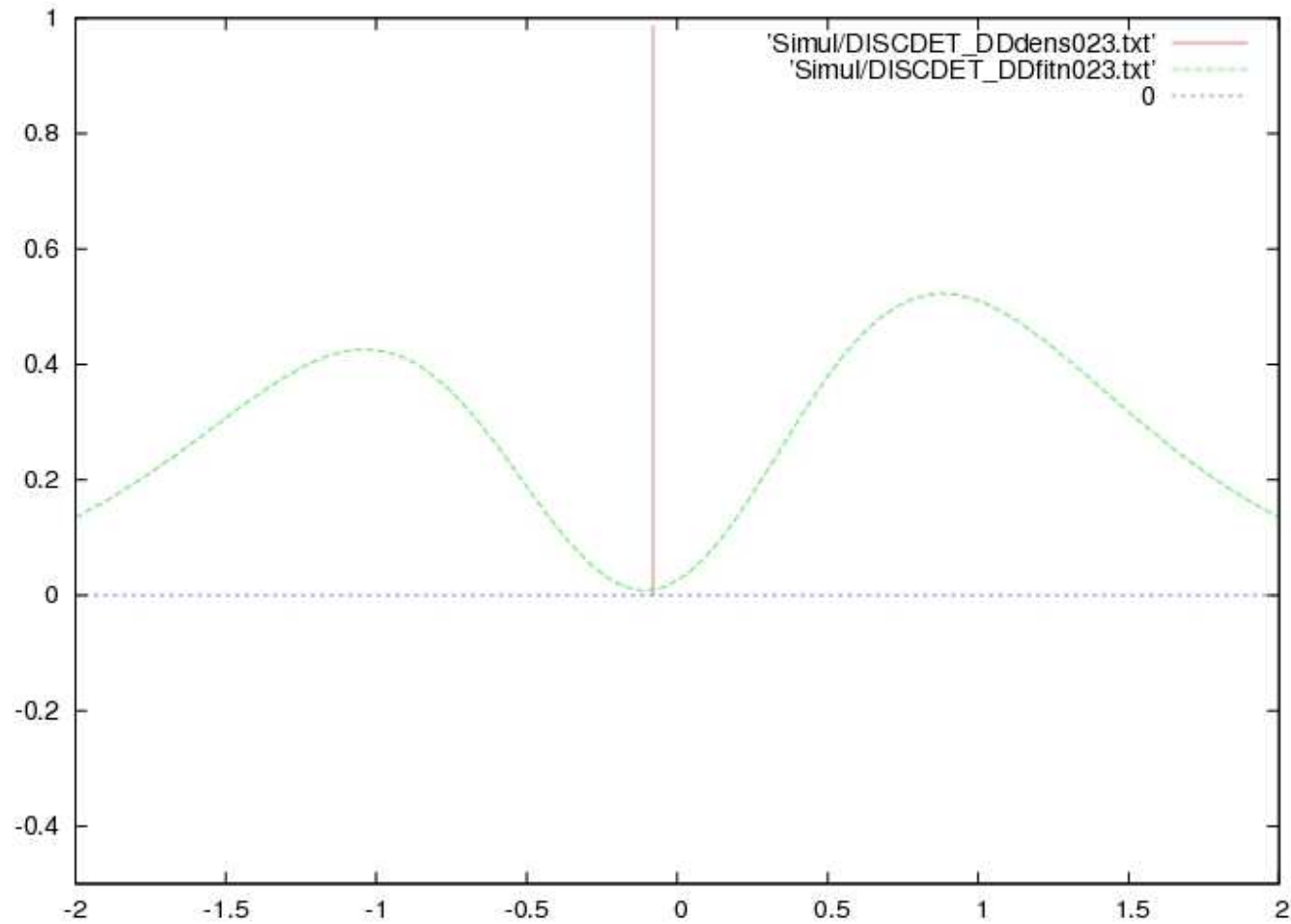
Evolutionary branching



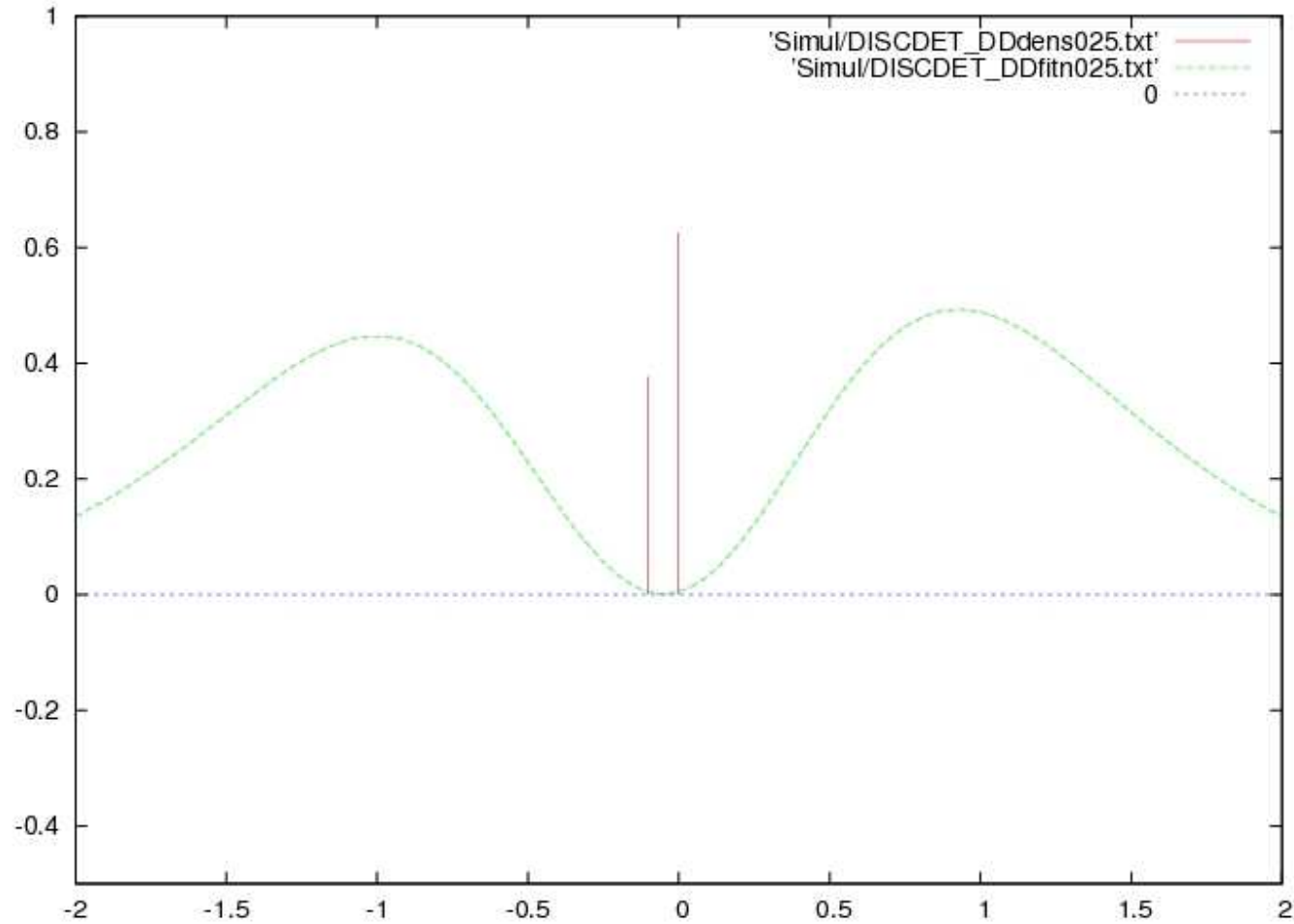
Evolutionary branching



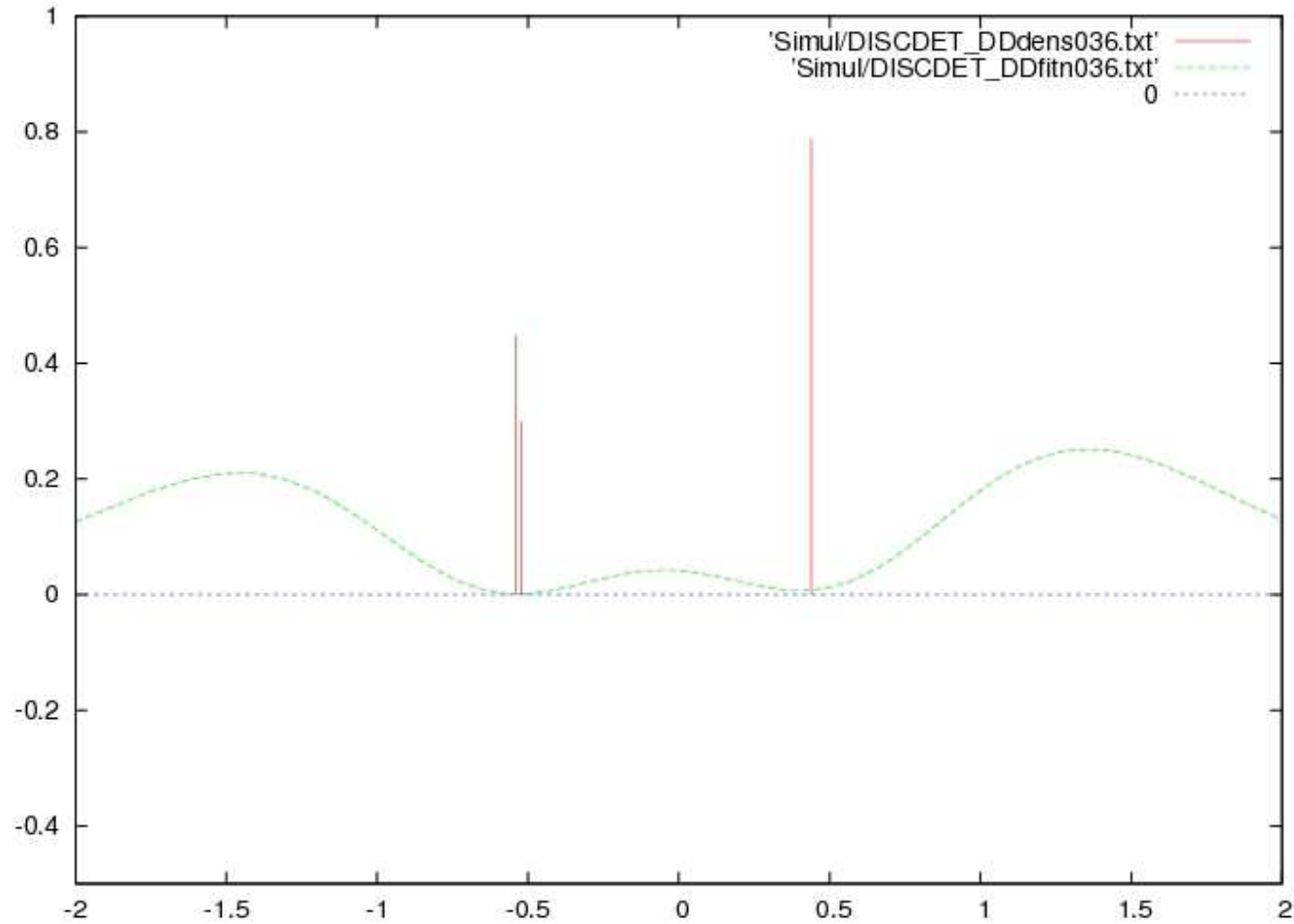
Evolutionary branching



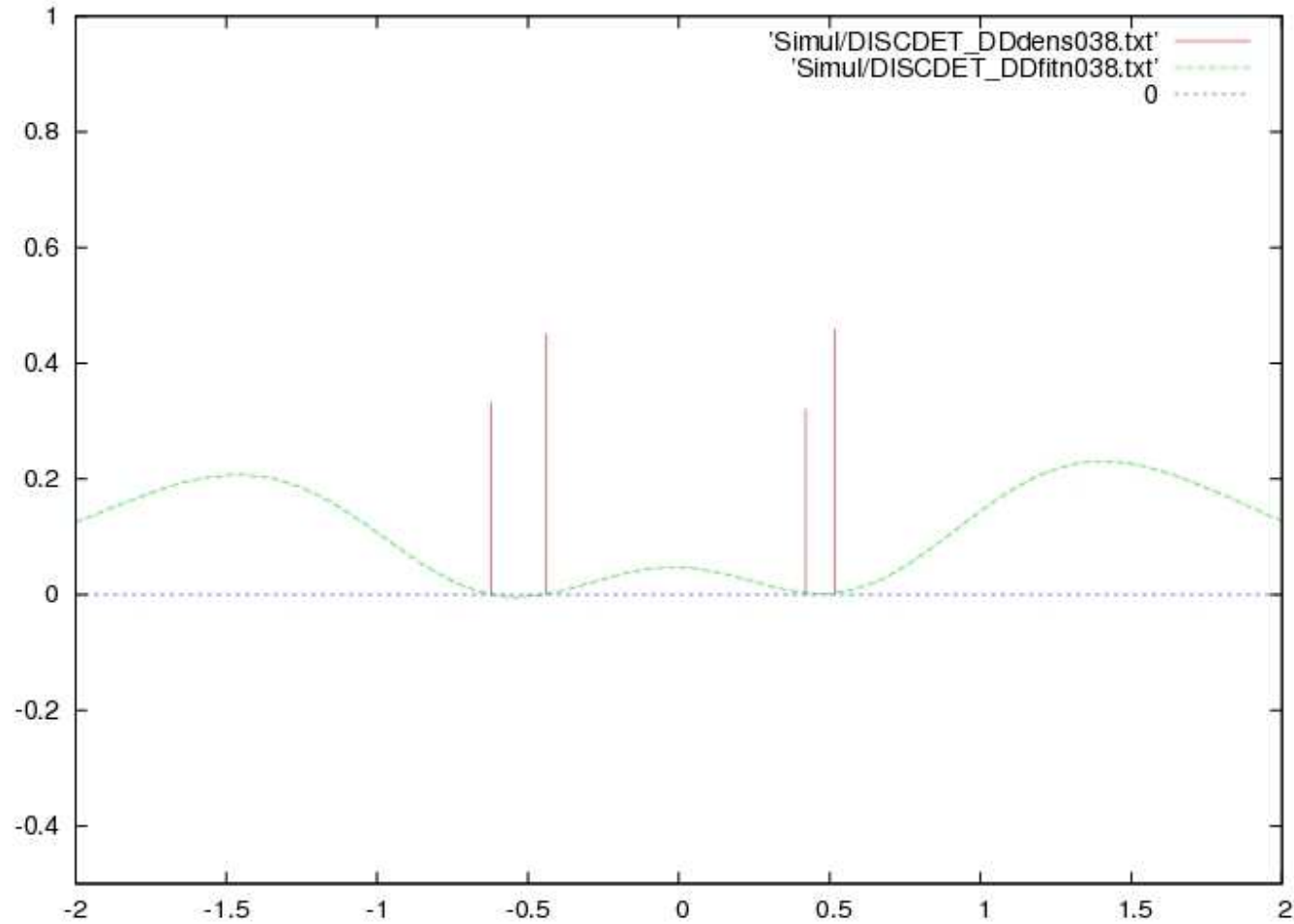
Evolutionary branching



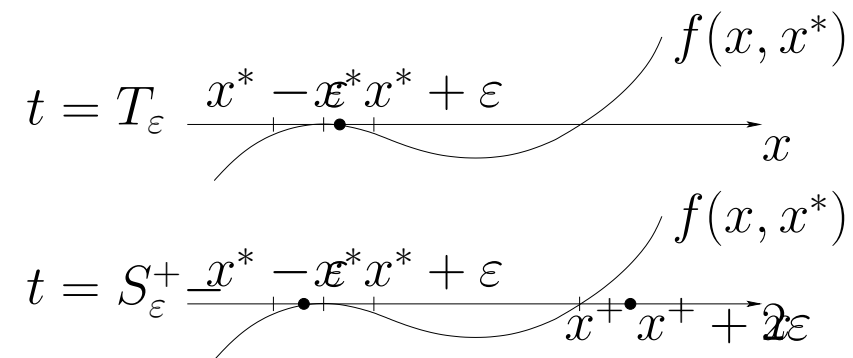
Evolutionary branching



Evolutionary branching



Once the system reaches equilibria with $\partial_{11}f(x^*, x^*) < 0$, further branching can occur on much longer time-scales through mutation towards far-away habitats:



Time dependence and the need of mutations

The entire construction can be done with **time dependent** parameters.

A simple interesting example is a situations where a monomorphic population is exposed to a time dependent environment such that, e.g.

$$\begin{aligned} b(x_1, t) - d(x_1, t) &> 0, & \text{for } t < T & \quad \text{and} \\ b(x_1, t) - d(x_1, t) &< 0, & \text{for } t \geq T \end{aligned}$$

while for some other trait x_2 ,

$$\begin{aligned} b(x_2, t) - d(x_2, t) &< 0, & \text{for } t < T & \quad \text{and} \\ b(x_2, t) - d(x_2, t) &> 0, & \text{for } t \geq T \end{aligned}$$

In this case, in the absence of mutation, a population will die out by time $T + C \ln K$.

Assume that in the above case $m(x_1, x_2 - x_1) = 1$, and $p(x_1) = 1$.

Then one can prove the following facts (A. Pohrt, Dipl.Thesis):

If p_K denotes the probability of survival up to time $T + \exp(K)$, then

- ▷ If $\mu \leq \frac{1}{K \ln K}$, then $p_K \downarrow 0$;
- ▷ If $\mu = \frac{C}{K}$, then $\lim_{K \uparrow \infty} p_K \in (0, 1)$;
- ▷ If $\mu \ll 1$, $\mu K \rightarrow \infty$, then $\lim_{K \uparrow \infty} p_K = 1$.

Note that the regime $\mu 1/(K \ln K)$ cannot secure survival. Proof in the other regimes requires considerable extension of the existing methods.

The analysis of microscopic models for adaptive dynamics in time dependent environments poses a great challenge and may provide interesting insights into the mechanisms of evolution.

Already our simple examples highlights that an appropriate rate of mutation is crucial not only for the exploration of evolutionary options but also for survival in a changing world.

An intriguing question is to understand whether mutation rates themselves can emerge through selection.

So far, we have only been scratching the surface....

Thank you for your attention!