

# Large population scalings of stochastic population dynamics in ecology and evolution

## Lecture 3: large population scaling of adaptive dynamics

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# Adaptive dynamics

**Darwinian evolution:** Three main ingredients

- **Heredity:** transmissions of individual characteristics from a generation to the next one.
- **Mutation:** cause of the variability in individual characteristics.
- **Selection:** consequence of the interactions between individuals and their environment, including the rest of the population (**ecology**).

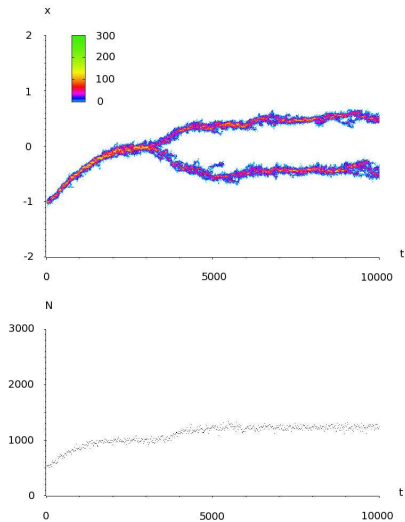
**Adaptive dynamics** (since the 90s): Hofbauer and Sigmund (1990), Metz, Geritz et al. (1992,1996), Dieckmann and Law (1996)...

- Focus on the **interplay between ecology and evolution**
- **Ecological interactions** modeled in detail
- Heredity is simplified as much as possible: **asexual (clonal) reproduction**

# Adaptive dynamics

- ↪ Density-dependent individual-based models where **no fitness is given**. The fitness landscape has to be constructed from the parameters of the model.
- ↪ New phenomenon of **evolutionary branching** (Metz et al., 1996)
  - Transition from a population concentrated around a single phenotype to a population concentrated around several distinct phenotypes, still under ecological interaction
  - Mechanism of **diversification**
  - Can lead to **sympatric speciation** (Dieckmann and Doebeli, 1999)
- ↪ Three biological main assumptions (Metz et al., 1996):
  - **large populations**
  - **rare mutations**
  - **small mutation steps**

# Evolutionary branching



# Individual-based model

**Birth-death-competition-mutation process** (Metz et al. 1996, Bolker-Pacala 97, Kisdi 99, Dieckmann-Law 00, Doebeli-Dieckmann 01, Fournier-Méléard 04, C.-Ferrière-Méléard 06...).

- Each individual characterized by a **continuous phenotypic trait**  $x \in \mathcal{X} \subset \mathbb{R}$  (individual size, age at maturity, rate of food intake...).
- $K$  scales the size of the population
- $\mu$  scales the probability of mutation
- $\sigma$  scales the size of mutation steps
- At time  $t$ , the population is composed of  $N_K(t)$  individuals with weights  $\frac{1}{K}$  and traits  $x_1, \dots, x_{N_K(t)} \in \mathcal{X}$ :

$$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N_K(t)} \delta_{x_i}.$$

# Transition rates for an individual with trait $x$

- Reproduction at rate  $b(x)$ :
    - With probability  $1 - \mu$ , **clonal reproduction** (offspring with trait  $x$ ).
    - With probability  $\mu$ , **mutation**, and the mutant trait is  $x + \sigma H$ , where  $H \sim m(h)dh$ , symmetric w.r.t. 0 (e.g. Gaussian distribution).
  - Death without competition at rate  $d(x)$ .
  - Death from competition with any other individual of trait  $y$  at rate  $\frac{1}{K} c(x, y)$ .
- ↪ an individual with trait  $x$  dies at density dependent rate

$$\begin{aligned}
 d(x) + \frac{1}{K} \sum_{i=1}^{N_K(t)} c(x, x_i) - c(x, x) \\
 = d(x) + \int_{\mathcal{X}} c(x, y) \left( \nu_t^K(dy) - \frac{1}{K} \delta_x(dy) \right).
 \end{aligned}$$

# On the limit $K \rightarrow +\infty$

Assume  $b(x) \equiv b$ ,  $d(x) \equiv d$  and  $c(x, y) \equiv c$  (**neutral case**).

Then the total number of individuals  $N_t^K$  is a Markov birth and death process with

- birth rate  $bn$
- death rate  $dn + cn \frac{n-1}{K}$  when  $N_t^K = n$ .

In this case,  $N_t^K/K$  converges when  $K \rightarrow +\infty$  to the solution of the logistic equation

$$\dot{n} = n(b - d - cn).$$

**Remark:** also true if  $\nu_0^K \rightarrow n_0 \delta_x$  and  $\mu = 0$ , with  $b = b(x)$ ,  $d = d(x)$  and  $c = c(x, y)$  (**monomorphic case**). We will use the notation

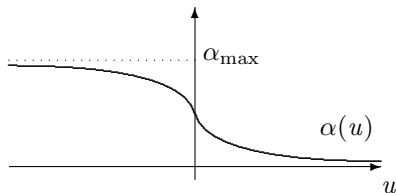
$$\bar{n}(x) = \frac{b(x) - d(x)}{c(x, x)}$$

the equilibrium of the logistic equation.

# Example 1

Arm-race competition (Kisdi 1999, Kisdi and Geritz 2000)

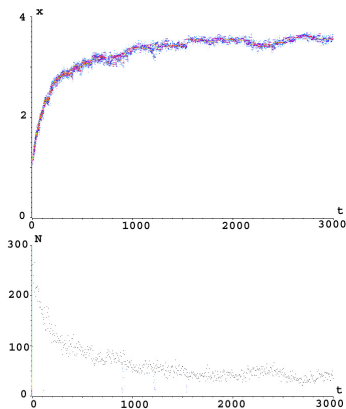
- $\mathcal{X} = [0, 4]$ ,  $d(x) \equiv 0$ ,  $p(x) \equiv p$
- $M(x, h)dh = \mathcal{N}(0, \sigma^2)$  (conditioned on  $x + h \in \mathcal{X}$ )
- $b(x) = 4 - x$  decreasing
- $\alpha(x, y) = \alpha(x - y)$  with



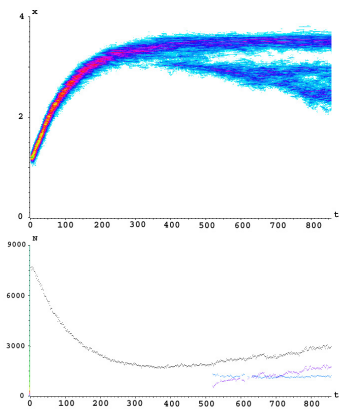
Asymmetric competition



# Simulations 1



$$\mu = 0.1 \quad \sigma = 0.03 \quad K = 50$$



$$\mu = 0.1 \quad \sigma = 0.03 \quad K = 1000$$

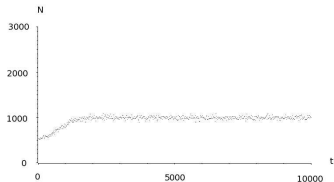
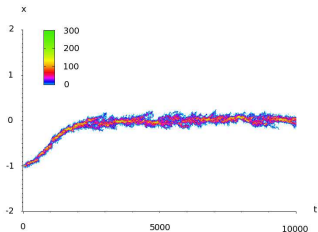
## Example 2

Roughgarden (1976,1979), Dieckmann-Doebeli (1999): symmetric competition.

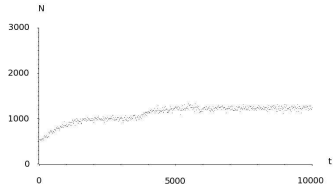
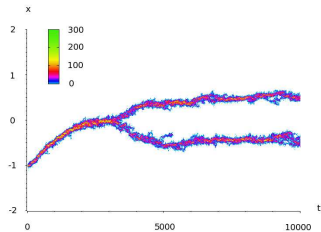
- $\mathcal{X} = [-2, 2]$     $d(x) \equiv 0$     $u_K = 1$     $p(x) = p$ .
- $m(h)dh = \mathcal{N}(0, 1)$    (conditioned on  $x + h \in \mathcal{X}$ ).
- $b(x) = \exp\left(-\frac{x^2}{2\sigma_b^2}\right)$ , maximum at 0.
- Symmetric competition for resources:

$$\alpha(x, y) = \alpha(x - y) = \exp\left(-\frac{(x - y)^2}{2\sigma_\alpha^2}\right).$$

# Simulations 2



$$\mu = 0.1, K = 1000, \sigma = 0.01, \\ \sigma_b = 0.9, \sigma_\alpha = 1.0.$$



$$\mu = 0.1, K = 1000, \sigma = 0.01, \\ \sigma_b = 0.9, \sigma_\alpha = 0.7.$$

# Comments

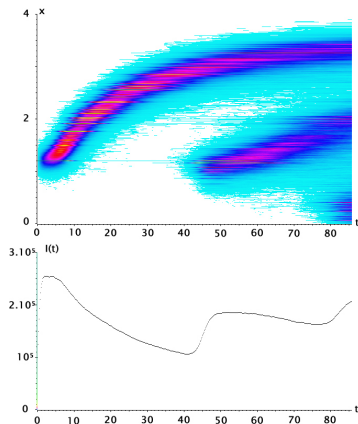
We observe quite complex phenomena (directional evolution, diversification...).

Our goals:

- use mathematical approaches to analyse these phenomena
- using “unrealistic” assumptions
- but enlightening about the phenomena, the building blocks, the effects of small mutations...

↪ Mathematical modeling and analysis to give a qualitative understanding of the biological phenomenon

# Example 1: large $K$ limit



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

$$K = 100000$$

# Large population limit

**Fournier and Méléard, 2004:** assuming that  $\nu_0^K$  converges in law to the measure  $u_0(x)dx$  for the weak topology when  $K \rightarrow +\infty$ , then  $(\nu_t^K, t \geq 0)$  converges in law to  $(u(t, x)dx, t \geq 0)$ , where  $u(t, x)$  is solution to the PDE

$$\partial_t u(t, x) = u(t, x) \left( (1 - \mu)b(x) - d(x) - \int_{\mathcal{X}} c(x, y)u(t, y) dy \right) + \int_{\mathcal{X}} b(y)\mu u(t, y)m\left(\frac{x - y}{\sigma}\right) \frac{dy}{\sigma}.$$

Assuming  $\mu = 1$  and  $\sigma = \varepsilon$ , this PDE can be written as

$$\partial_t u(t, x) = u(t, x) \left( r(x) - \int_{\mathbb{R}^\ell} c(x, y)u(t, y) dy \right) + \int_{\mathbb{R}^\ell} m(h)(u(t, x + \varepsilon h) - u(t, x)) dh,$$

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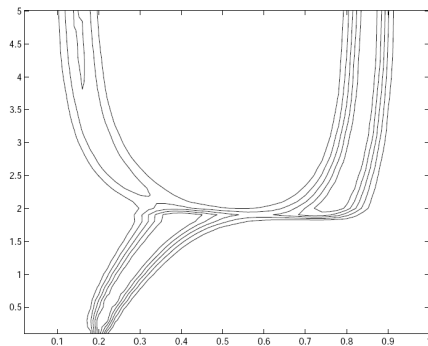
$$\partial_t u(t, x) = u(t, x) \left( (1 - \mu)b(x) - d(x) - \int_{\mathcal{X}} c(x, y)u(t, y) dy \right) + \int_{\mathcal{X}} b(y)\mu u(t, y)m\left(\frac{x - y}{\sigma}\right) \frac{dy}{\sigma}.$$

Assuming  $\mu = 1$  and  $\sigma = \varepsilon$ , this PDE can be written as

$$\partial_t u(t, x) = \frac{1}{\varepsilon} u(t, x) \left( r(x) - \int_{\mathbb{R}^\ell} c(x, y)u(t, y) dy \right) + \frac{1}{\varepsilon} \int_{\mathbb{R}^\ell} m(h)(u(t, x + \varepsilon h) - u(t, x)) dh,$$

scaling time as  $t/\varepsilon$  (large time, small mutations)

# Simulation



Competition for two resources  
(Diekmann, Jabin, Mischler, Perthame, 2005)



# Limit Hamilton-Jacobi equation (1)

Diekmann et al., 2005: defining (WKB ansatz)

$$u_\varepsilon(t, x) = \exp\left(\frac{\varphi_\varepsilon(t, x)}{\varepsilon}\right), \quad \partial_t u_\varepsilon = \frac{u_\varepsilon}{\varepsilon} \partial_t \varphi_\varepsilon,$$

the PDE becomes

$$\begin{aligned} \partial_t \varphi_\varepsilon(t, x) = & r(x) - \int_{\mathbb{R}^\ell} c(x, y) u_\varepsilon(t, y) dy \\ & + \int_{\mathbb{R}^\ell} m(h) \left[ \exp\left(\frac{\varphi_\varepsilon(t, x + \varepsilon h) - \varphi_\varepsilon(t, x)}{\varepsilon}\right) - 1 \right] dh. \end{aligned}$$

This suggests the convergence of  $\varphi_\varepsilon$  to the solution of

$$\partial_t \varphi(t, x) = r(x) - \int_{\mathbb{R}^\ell} c(x, y) \mu_t(dy) + \beta H(\nabla_x \varphi(t, x)),$$

where

$$H(p) = \int_{\mathbb{R}^\ell} \overline{m}(h) (e^{p \cdot h} - 1) dh$$

and  $\mu_t$  is (in some sense) the limit of  $u_\varepsilon(t, \cdot)$ .

## Limit Hamilton-Jacobi equation (2)

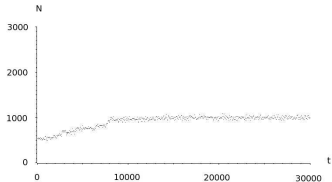
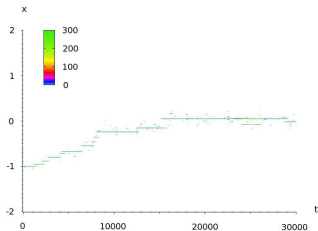
- The total population mass remains bounded  
 $\rightsquigarrow \max_x \varphi(t, x) = 0$  for all  $t \geq 0$ .
- The limit population density at time  $t$  is 0 except at the points  $x$  where  $\varphi(t, x) = 0$   $\rightsquigarrow \mu_t$  has support in  $\{\varphi(t, \cdot) = 0\}$ .
- The measure  $\mu_t$  has to be **metastable**, i.e.
  - $r(x) - \int c(x, y)\mu_t(dy) \leq 0$  for all  $x$  such that  $\varphi(t, x) = 0$ ,
  - $r(x) - \int c(x, y)\mu_t(dy) = 0$  for all  $x$  in the support of  $\mu_t$ .
- Under the assumption that **the kernel  $c(x, y)$  is positive**, these two conditions are satisfied for a unique measure  $\mu_t$ , and

$$\mu_t = \mu(\{\varphi(t, \cdot) = 0\}),$$

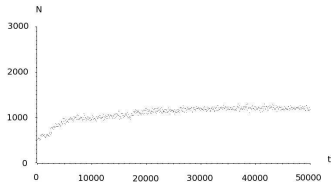
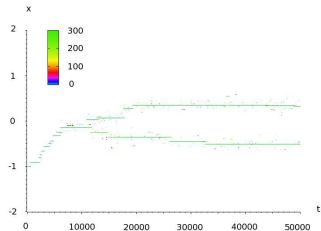
for some well-defined function  $\mu$

$\rightsquigarrow$  **closed Hamilton-Jacobi equation** (C., Jabin, 2011).

# Example 2: rare mutations



$$\mu = 0.0001, K = 1000, \\ \sigma = 0.08, \sigma_b = 0.9, \sigma_\alpha = 1.0.$$



$$\mu = 0.0001, K = 1000, \\ \sigma = 0.08, \sigma_b = 0.9, \sigma_\alpha = 0.7.$$

## Limit of rare mutations: Metz et al. 1996

- The selection process has sufficient time between two mutations to eliminate disadvantaged traits.
- **Large population assumption:** (nearly) deterministic population dynamics between mutations, so that one can **predict the outcome of competition** between the traits.

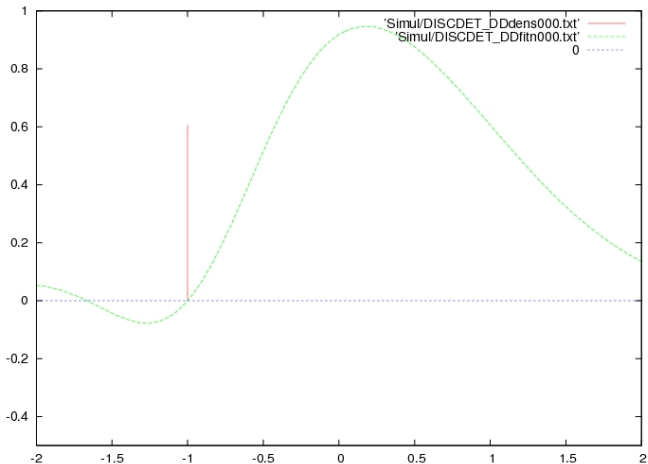
↪ Succession of phases of (random) **mutant invasion**, and phases of (fast, deterministic) **competition** between traits.

**Adaptive walk** in a fitness landscape that depends on the current state of the population: fitness of a mutant trait  $y$  in a population  $x$  at equilibrium

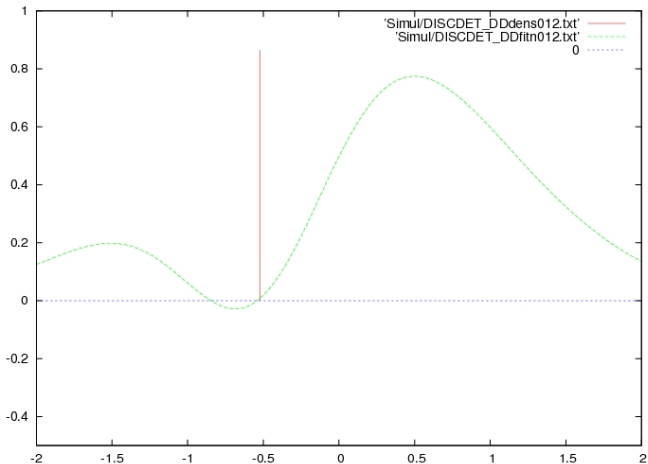
$$f(y, x) = b(y) - d(y) - c(y, x)\bar{n}(x)$$

(C., 2006, C. and Méléard 2011)

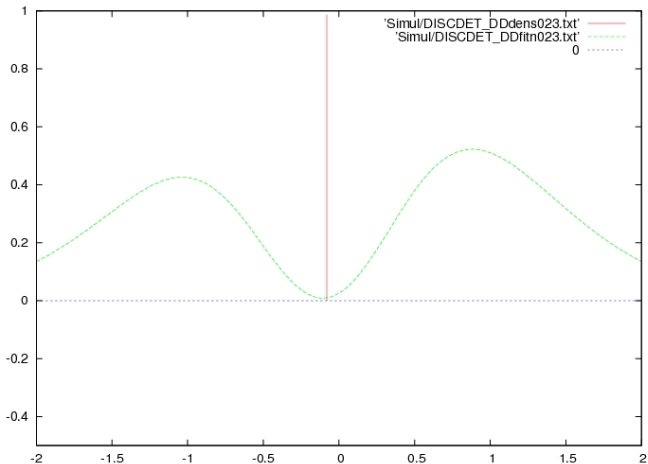
# Coevolution with the fitness landscape



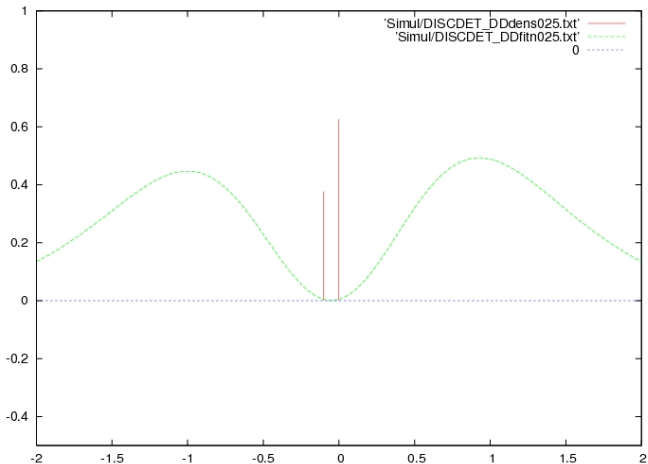
# Coevolution with the fitness landscape



# Coevolution with the fitness landscape

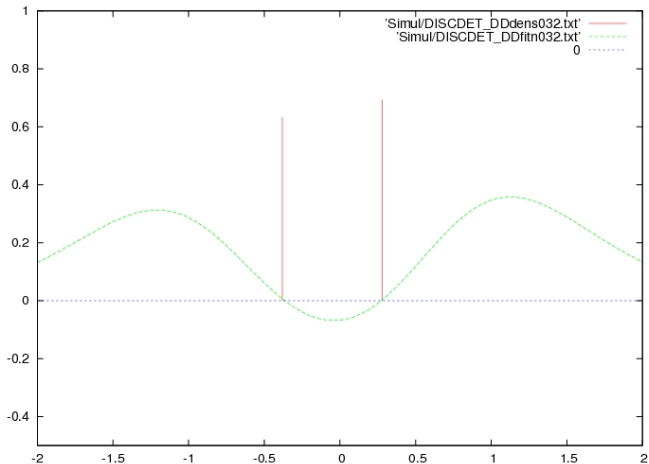


# Coevolution with the fitness landscape





# Coevolution with the fitness landscape



# Large population limit without mutation

- **Monomorphic case**

If  $p \equiv 0$  and  $\nu_0^K = n_0^K \delta_x$  with  $n_0^K \rightarrow n_0$ , then  $\nu_t^K \rightarrow n(t) \delta_x$ , with  $n(0) = n_0$  and

$$\dot{n} = (b(x) - d(x) - \alpha(x, x)n)n.$$

Logistic equation: one stable equilibrium

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

## Large population limit: dimorphic case

- If  $\nu_0^K = n_x^K(0)\delta_x + n_y^K(0)\delta_y$ , then  $\nu_t^K \rightarrow n_x(t)\delta_x + n_y(t)\delta_y$ , with

$$\dot{n}_x = (b(x) - d(x) - \alpha(x, x)n_x - \alpha(x, y)n_y)n_x$$

$$\dot{n}_y = (b(y) - d(y) - \alpha(y, x)n_x - \alpha(y, y)n_y)n_y.$$

- Equilibria:  $(0, 0)$  (unstable),  $(\bar{n}(x), 0)$ ,  $(0, \bar{n}(y))$  and possibly  $(\bar{n}_1(x, y), \bar{n}_2(x, y))$  in  $(0, \infty)^2$ .
- The stability of the equilibria is governed by the **invasion fitness** of the mutant trait  $y$  in a resident population of trait  $x$ :

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

- $(\bar{n}(x), 0)$  is unstable iff  $f(y; x) > 0$ .
- If  $f(y; x) > 0$  and  $f(x; y) > 0$ , there is a non-trivial equilibrium, globally asymptotically stable (**coexistence**).
- Note that  $f(x; x) = 0$ .

# Lotka-Volterra system $LV(d, x_1, \dots, x_d)$

For  $d$ -morphic initial conditions  $(x_1, \dots, x_d) \in \mathcal{X}^d$  we define the  $d$ -dimensional competitive Lotka-Volterra system  $LV(d, x_1, \dots, x_d)$

$$\dot{n}_i(t) = n_i(t) \left( r(x_i) - \sum_{j=1}^d \alpha(x_i, x_j) n_j(t) \right), \quad \forall 1 \leq i \leq d.$$

## Definition

- The traits  $x_1, \dots, x_d$  *coexist* if  $LV(d, x_1, \dots, x_d)$  has a unique equilibrium  $\bar{\mathbf{n}}(\mathbf{x})$  in  $(\mathbb{R}_+^*)^d$  locally strongly stable.
- Given  $x_1, \dots, x_d$  which coexist, the *fitness* of trait  $y$  is defined as

$$f(y; \mathbf{x}) = f(y; x_1, \dots, x_d) = r(y) - \sum_{i=1}^d \alpha(y, x_i) \bar{n}_i(\mathbf{x}).$$

Its sign governs the *possibility of invasion of the mutant trait  $y$* , i.e. the *stability* of the eq.  $(\bar{\mathbf{n}}(\mathbf{x}), 0)$  of  $LV(d+1, x_1, \dots, x_d, y)$ .

# Main assumption (A)

For all  $x_1, \dots, x_d$  which coexist,

- (A1) for a.e.  $y$  s.t.  $f(y; x_1, \dots, x_d) > 0$ , there exists a neighborhood  $\mathcal{N}$  of  $(\bar{\mathbf{n}}(\mathbf{x}), 0)$  s.t. all solutions of  $LV(d+1, x_1, \dots, x_d, y)$  starting from  $\mathcal{N} \cap (\mathbb{R}_+^*)^{d+1}$  converges to a **unique equilibrium  $\mathbf{n}^*$** .
- (A2)  **$\mathbf{n}^*$  is locally strongly stable** (the eigenvalues of the Jacobian matrix all have negative real part).

Not so restrictive:

- (A) is satisfied until the first time where there is **coexistence of 3 traits** (see below).
- (A) is satisfied if **the competition kernel is symmetric and positive** (C., Jabin, Raoul, 2010).

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$$\text{Let } \mathcal{M}_{\text{eq}}(\mathcal{X}) = \left\{ \sum_{i=1}^d \bar{n}_i \delta_{x_i}, \quad d \geq 1, \quad (x_1, \dots, x_d) \in \mathcal{X}^d \text{ coexist} \right\}.$$

# The Polymorphic Evolution Sequence (PES)

## Theorem

Assume (A) and that  $\nu_0^K = n_K \delta_x$  for  $x \in \mathcal{X}$ , with  $n_K \rightarrow \bar{n}(x)$  in probability when  $K \rightarrow +\infty$ . If

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

then, the process  $(\nu_{t/Ku_K}^K, t \geq 0)$  converges for f.d.d. to a process  $(\Lambda_t, t \geq 0)$  which is a Markov jump process on the set  $\mathcal{M}_{eq}(\mathcal{X})$ , with jumps

$$\text{from } \sum_{i=1}^d \bar{n}_i \delta_{x_i} \text{ to } \sum_{i=1}^d n_i^*(x_1, \dots, x_d, x_j + h) \delta_{x_i} + n_{d+1}^* \delta_{x_j+h}$$

with infinitesimal rate

$$p(x_j) b(x_j) \bar{n}_j(\mathbf{x}) \frac{[f(x_j + h; \mathbf{x})]_+}{b(x_j + h)} m(x_j, h) dh, \quad \forall 1 \leq j \leq d.$$

## Idea of the proof: (1) Mutation phase

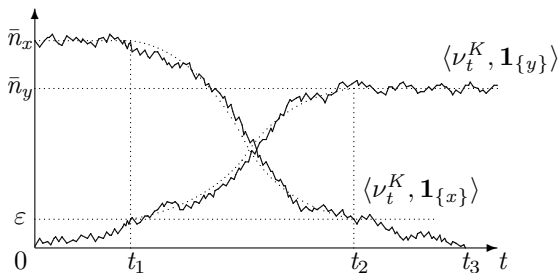
Before the first mutation in a monomorphic population of trait  $x$ :

- the population size is close to the solution of  $\dot{n} = (b(x) - d(x) - \alpha(x, x)n)n$ .
- the population size reaches any neighborhood of  $\bar{n}(x)$  in finite time.
- **Large deviations:** the exit time from  $[\bar{n}(x) - \varepsilon, \bar{n}(x) + \varepsilon]$  behaves as  $\exp(KC)$ , with  $C > 0$ .
- therefore, the rate of mutation is (close to)  $u_K p(x) b(x) K \bar{n}(x)$ .



## (2) Competition phase

- **Between 0 and  $t_1$** : the number of mutant individuals is close to a **branching process** with birth rate  $b(y)$  and death rate  $d(y) + \alpha(y, x)\bar{n}(x)$ .
- Survival probability :  $[f(y; x)]_+ / b(y)$ .
- **Between  $t_1$  and  $t_2$** : close to the 2-dim Lotka-Volterra system.
- **After  $t_2$** : the number of resident is close to a **sub-critical** branching process.



# Monomorphic case: Trait Substitution Sequence

Until the first coexistence time

$$\Lambda_t = \bar{n}(X_t)\delta_{X_t}$$

where the Markov jump process  $(X_t, t \geq 0)$  on  $\mathcal{X}$  satisfies  $X_0 = x$  and has infinitesimal generator

$$A\varphi(x) = \int (\varphi(x+h) - \varphi(x)) p(x) b(x) \bar{n}(x) \frac{[f(x+h; x)]_+}{b(x+h)} m(x, h) dh$$

The **first coexistence time** is the first time where  $f(X_t, X_{t-}) > 0$  and  $f(X_{t-}, X_t) > 0$ .

# Canonical Equation of Adaptive Dynamics (first form)

## Adaptive walk with small mutations:

When  $\sigma \rightarrow 0$ , on the time scale  $\frac{t}{\sigma^2}$ , the TSS converges to  $x(t)$  solution to

$$\frac{dx}{dt} = \int h^2 m(h) dh \bar{n}(x) \partial_1 f(x; x).$$

- “hill-climbing” process in the fitness landscape (Dieckmann and Law, 1996).
- evolutionary branching can also be described with this approach (C., Méléard, 2011)
- Criticism (Waxman, Gavrillets, 2005)
  - mutations are too rare (real populations are never monomorphic)
  - evolution on a too long time-scale  $t/\mu K \sigma^2$

↪ PDE analysts proposed a second approach.

# Conclusion

- Alternative approach to study limits of “concentration” in evolution
- The concentration limits provide simpler tools to study the long term evolution of the population
- Two main phenomena: directional evolution following the fitness gradient (canonical equation) and evolutionary branching
- It is possible to obtain a criterion for evolutionary branching following the stochastic approach (C., Méléard, 2011)
- The deterministic approach suffers from well-posedness problems for the limiting Hamilton-Jacobi equation
- Both approaches suffer from biologically unrealistic assumptions  
↔ many open problems