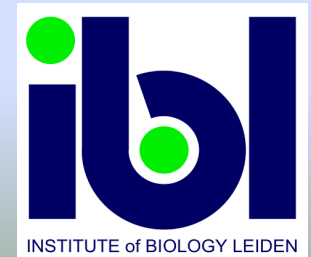


**On the  
Canonical Equation  
of  
(directional) Adaptive Dynamics  
for  
Physiologically Structured Populations**

**Hans Metz  
Michel Durinx**

**ADN, IIASA**



**a few words about**

- **adaptive dynamics**
- **(physiologically) structured populations**

**the canonical equation**

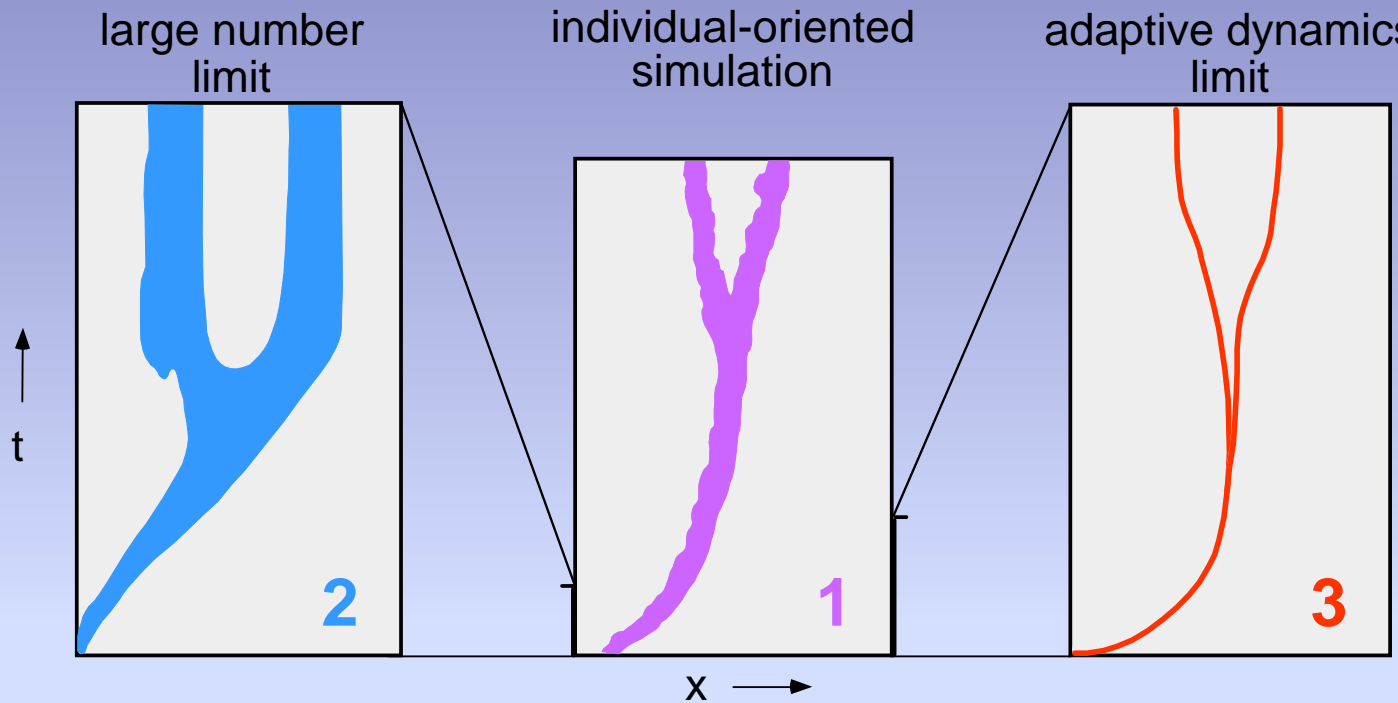
- **derivation for structured populations**
  - ~ **a single birth state**
  - ~ **more birth states**

**a final comment**

# Adaptive Dynamics

- **Example illustrating the individual-based justification.**
- **The fitness landscape picture of evolution: it is a seascape!**

# On the individual-based justification of Adaptive Dynamics

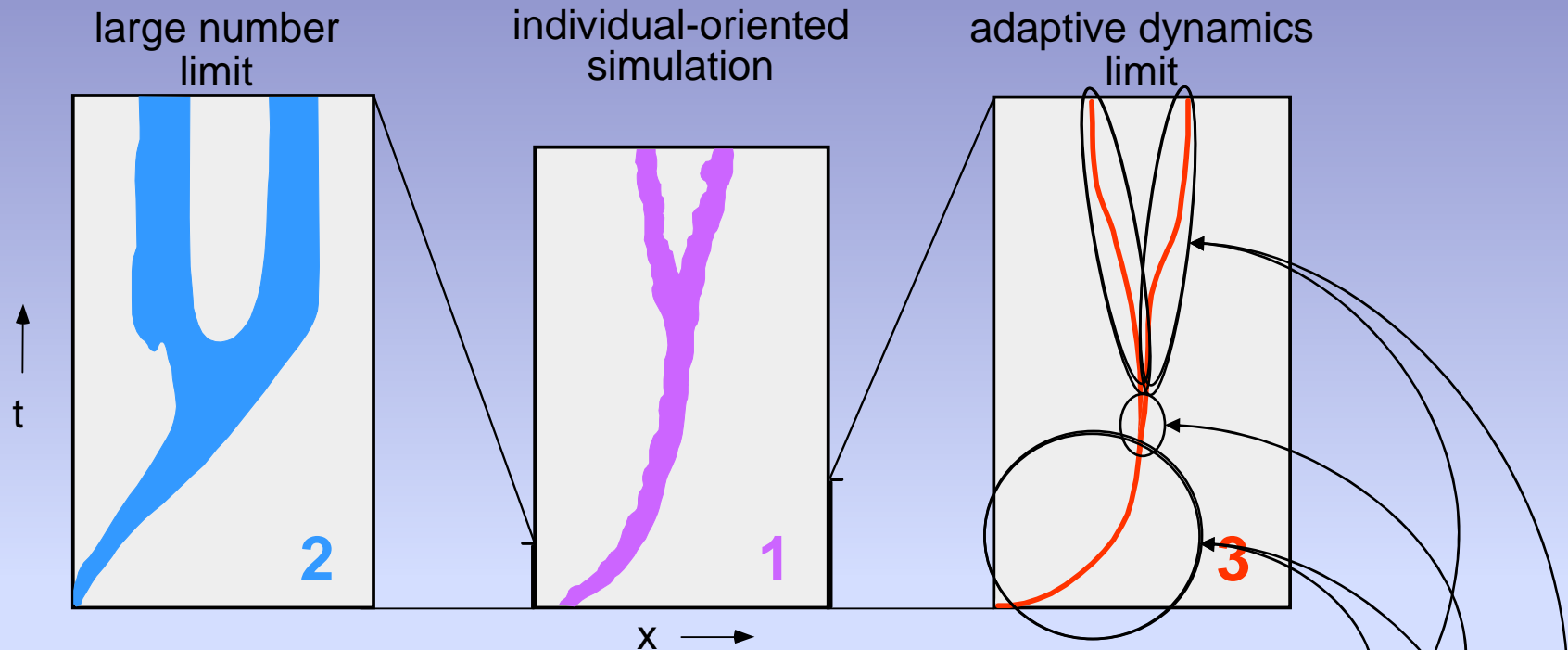


## 1 Individual-oriented model ("the ecological basis"):

$X_i \rightarrow X_i + Y, Y = X_i$	at rate	$1 - \epsilon$	} reproduction	faithful mutated
$X_i \rightarrow X_i + Y, Y \in (y, y + dy)$	at rate	$\epsilon \rho(y - X) dy$		
$X_i \rightarrow \text{ , }$	at rate	$\sum_j a(X_j, X_i) / [\Omega k(X_i)]$	death	

(Individual-based version of a so-called Lotka-Volterra model, with mutation added.)

# On the individual-based justification of Adaptive Dynamics



**3 adaptive dynamics: let  $\Omega \rightarrow \infty$ ,  $\Omega \varepsilon \rightarrow 0$ , and rescale time to on average one mutated birth per time unit**

$X \rightarrow Y, Y \in (y, y+dy)$  at rate  $\Omega \bar{n}(X) \varepsilon p(y-X) dy R_X(y) [1 - H(s_y(x))]$

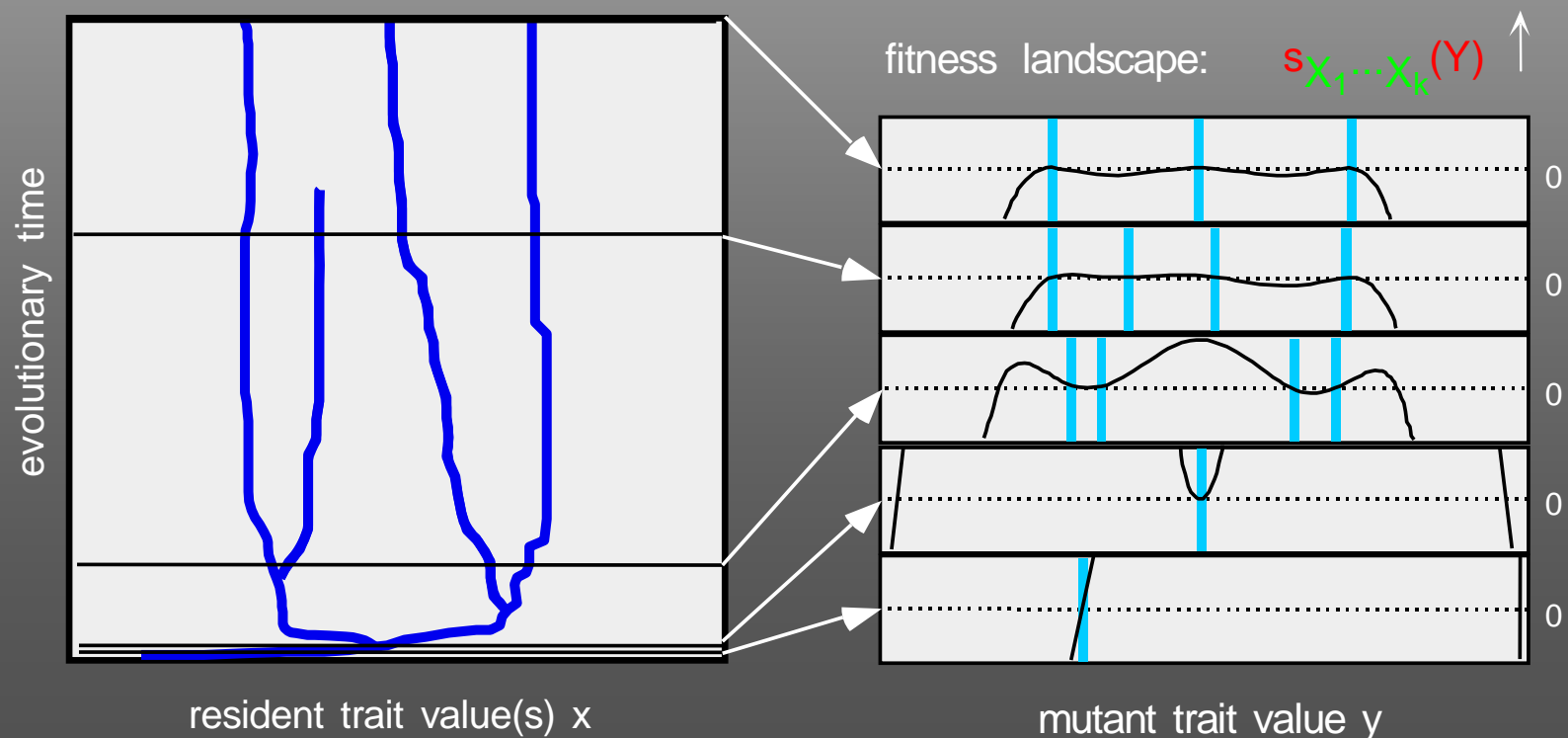
$X \rightarrow (X, Y), Y \in (y, y+dy)$  at rate  $\Omega \bar{n}(X) \varepsilon p(y-X) dy P_X(y) H(s_y(x))$

**3a canonical equation: subsequently let  $\text{Var}_p \rightarrow 0$ , and rescale time to keep the directional movement in view**

$$\frac{dX}{dt} = \frac{1}{2} \alpha \varepsilon \Omega \bar{n}(X) \mathbf{C} \left( \frac{\partial s_X(Y)}{\partial Y} \Big|_{Y=X} \right)^T \quad \text{with } \alpha = 2 T_f / (T_s \sigma^2)$$

# The fitness landscape picture of evolution:

Evolution crawls uphill in a fitness landscape that keeps changing so as to keep the fitness of the resident types at exactly zero.

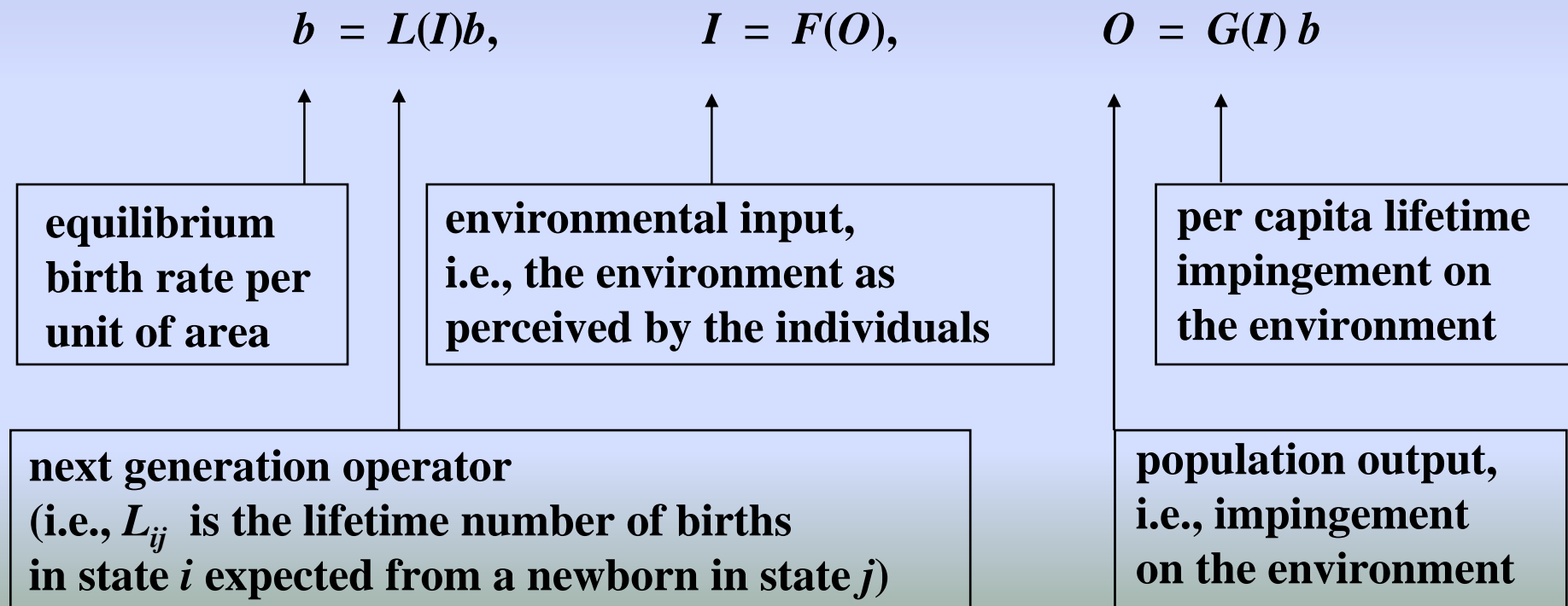


# Physiologically Structured Populations

- **Population equilibria: density dependent demography**
- **Invasion by mutants: classical linear demography**

# Calculating equilibria for physiologically structured populations

After Diekmann, Gyllenberg & Metz (2003) Theor Pop Biol 63: 309-338 :





**Start with the case where  $b$  is a scalar**

**i.e., everybody is born equal, but for the inherited traits.**

**Individuals do not inherit state variables  
like fat reserves, or social status**

# Calculating mutant invasion rates for physiologically structured populations

Invasion fitness:

$$s_X(Y) = r_Y(I_X)$$

with  $r_Y(I_X)$  the (unique) solution of

$$\tilde{\Lambda}_Y(I_X, r) = 1$$

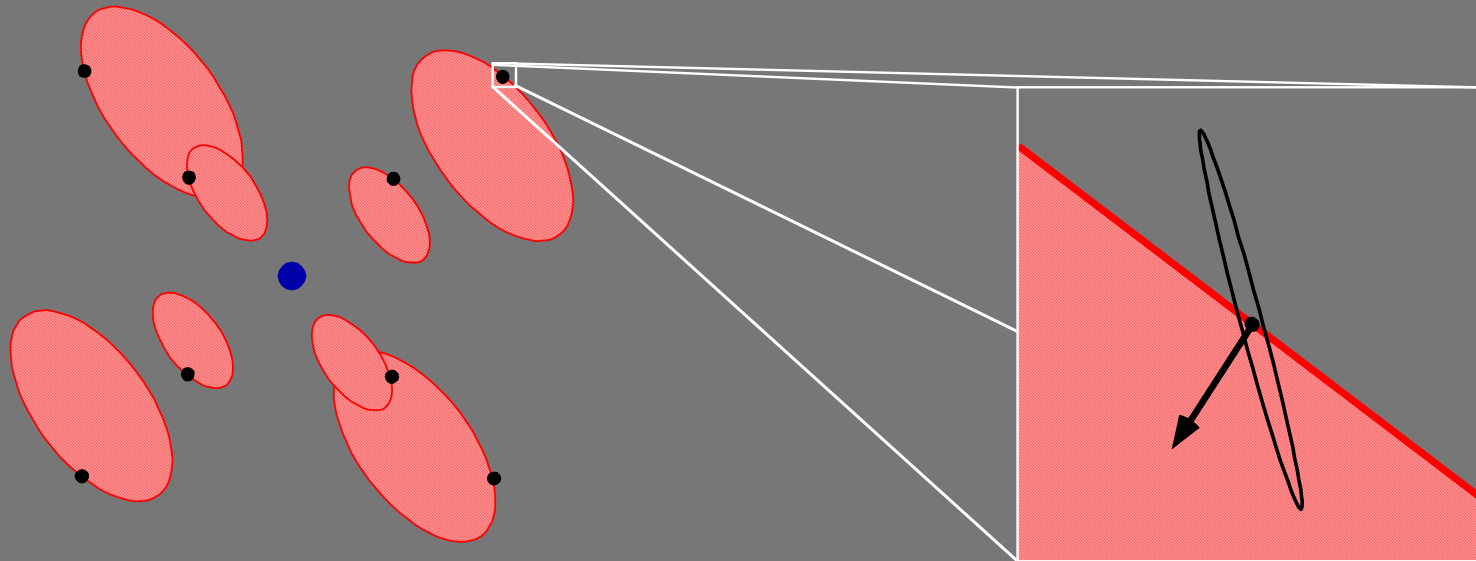
Laplace transform  
of birth kernel  
(Lotka's equation,  
scalar version)

with

$$\tilde{\Lambda}_Y(I_X, r) = \int_0^{\infty} e^{-ra} \Lambda_Y(I_X, da)$$

$\Lambda$  the so-called birth kernel of the invader  $Y$  in environment  $I_X$  [i.e.,  $\Lambda_Y(I_X, a)$  is the expected number of invaders produced up to age  $a$  by a newborn invader].  $L_Y(I_X) = \Lambda_Y(I_X, \infty)$

**the**  
**Canonical Equation**



To first order of approximation for small mutational steps:

$$\frac{dX}{dt} = \frac{1}{2} \alpha \varepsilon \bar{N}(X) \mathbf{C} \left( \frac{\partial s_X(Y)}{\partial Y} \Big|_{Y=X} \right)^T$$

where  $\varepsilon$  is the probability of a mutation per birth event,

$\mathbf{C}$  is the mutational covariance matrix,

and  $\alpha$  depends i.a. on the reproductive variability.

When the community attractor is just a point:

$$\alpha = 2 T_f / (T_s \sigma^2)$$

$T_f$  = average age of giving birth,  $T_s$  = average lifetime

$\sigma^2$  = Var[lifetime offspring number] .

(of resident)

**For ODE population models:**

**Dieckmann & Law (1996) J Math Biol 34: 579-612**

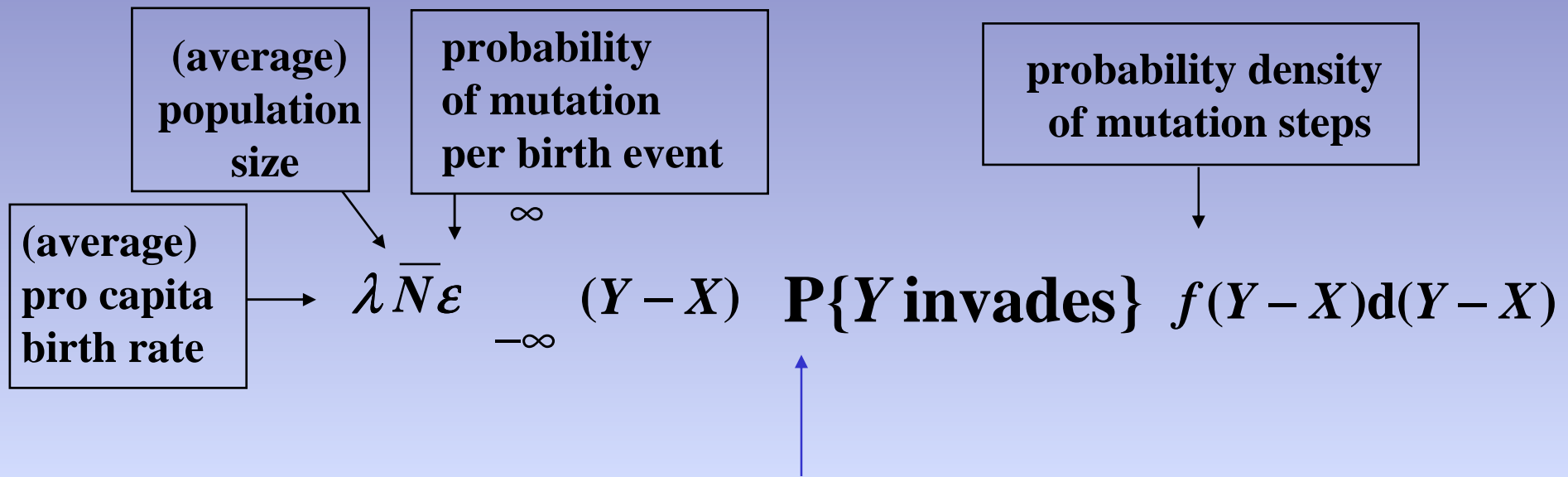
**Champagnat, Ferrière & Ben Arrous (2001) Selection 2**

## **heuristic derivation for general Physiologically Structured Populations**

**If we scale the mutational steps with  $\delta$ , and time with  $\delta^{-1}$ ,  $\delta$  small, so that any relevant part of the path consists of many small steps, a “law of large number” result comes into play.**

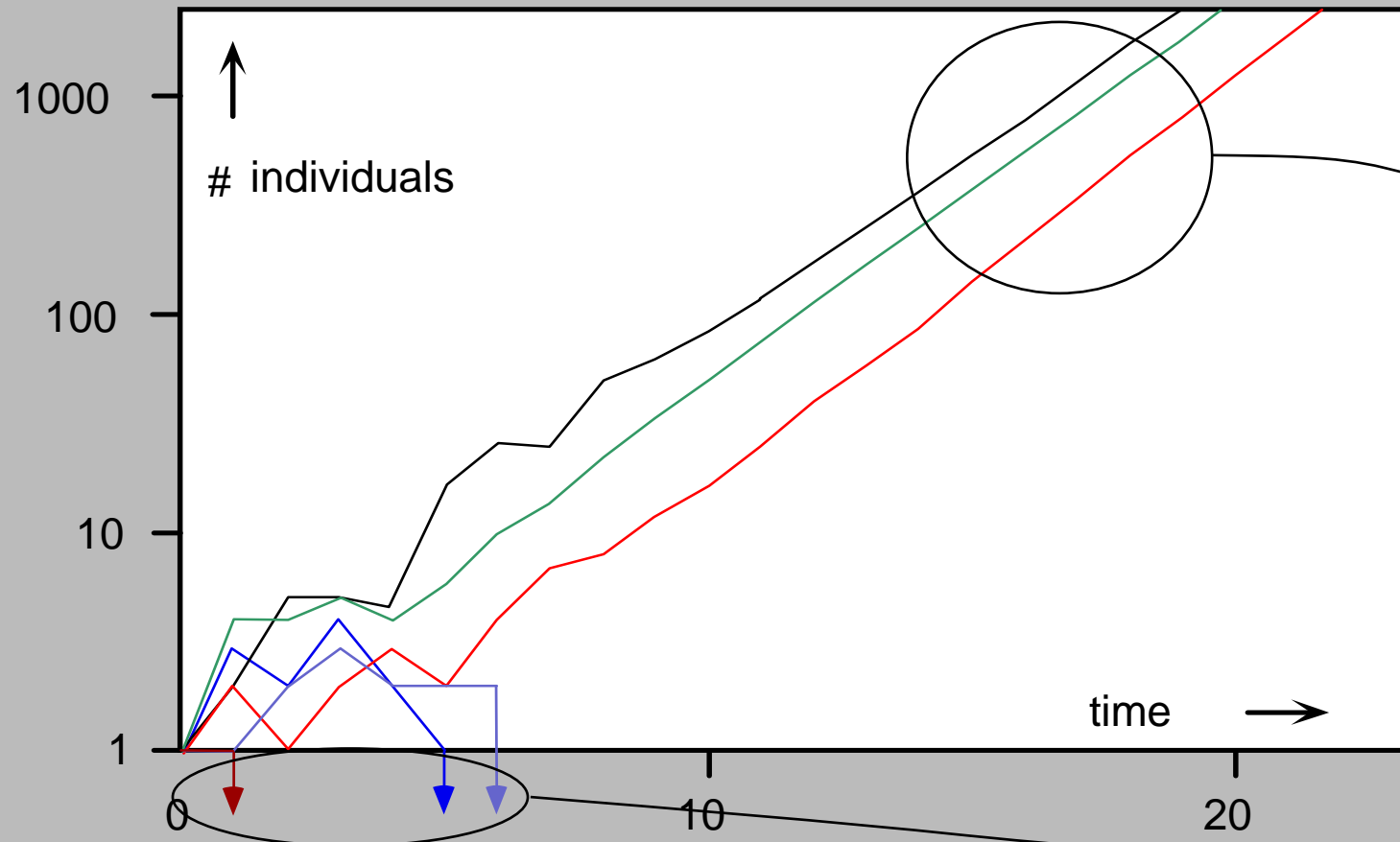
**(Proofs in Ethier & Kurtz, 1986)**

mean evolutionary step per time unit:



Mutants arrive singly. Therefore we have to account for the intrinsic stochasticity of the invasion process.

# From the theory of branching processes:



In an ergodic environment:

a population starting from a single individual either goes extinct, with probability  $Q$ , or "grows exponentially" at a relative rate  $r(y, I_x)$ .

# From the theory of branching processes II:

Let  $P$  be probability of invading:  $P = 1 - Q$ .

\* Under very general conditions

$$P > 0 \quad \text{if and only if} \quad r(I) > 0.$$

\* For constant  $I$  and small  $r(I) > 0$

$$(i) \quad P \approx 2 \ln [R_0(I)] / \sigma^2$$

with  $\sigma^2$  a measure for the variability in the life-time offspring production; when everybody is born equal

$$\sigma^2 = \text{Variance [life-time offspring production]}$$

$$(ii) \quad r(I) \approx \ln [R_0(I)] / T_f$$

with  $T_f$  the mean age at offspring production.

$$P \approx [2 T_f / \sigma^2] r(I)$$



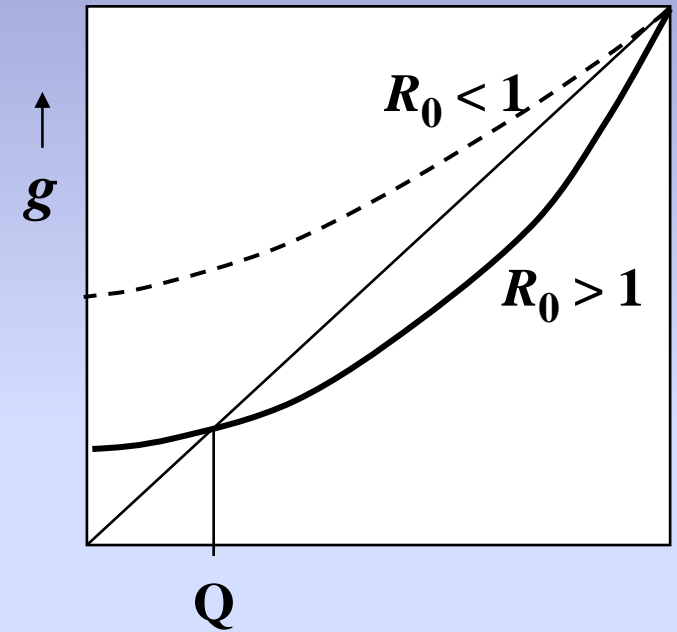
lifetime number of kids

$$Q = \sum_{m=0}^{\infty} p_m Q^m = g(Q) \quad \text{with } g(x) := \sum_{m=0}^{\infty} p_m x^m$$

$$g(0) = p_0, \quad g(1) = 1,$$

$$g'(1) = \mathbf{E} \underline{m} = R_0,$$

$$g''(1) = \mathbf{E} \underline{m}(\underline{m} - 1) = \text{Var } \underline{m} + R_0^2 - R_0$$



with  $\varepsilon := R_0 - 1 \approx \ln(R_0)$  :

$$1 - P = 1 - (1 + \varepsilon)P + \frac{1}{2}(\text{Var } \underline{m} + \varepsilon + \varepsilon^2)P^2 + [\text{h.o.t.} (< 0)]$$

$$P = \frac{2\varepsilon}{\text{Var } \underline{m}} + \text{h.o.t.}$$

characteristic equation:

$$\tilde{\Lambda}(r) := \int_0^{\infty} e^{-ra} \Lambda(da) = 1$$

take logarithms:

$$\phi(r) := \ln \tilde{\Lambda}(r) = 0$$

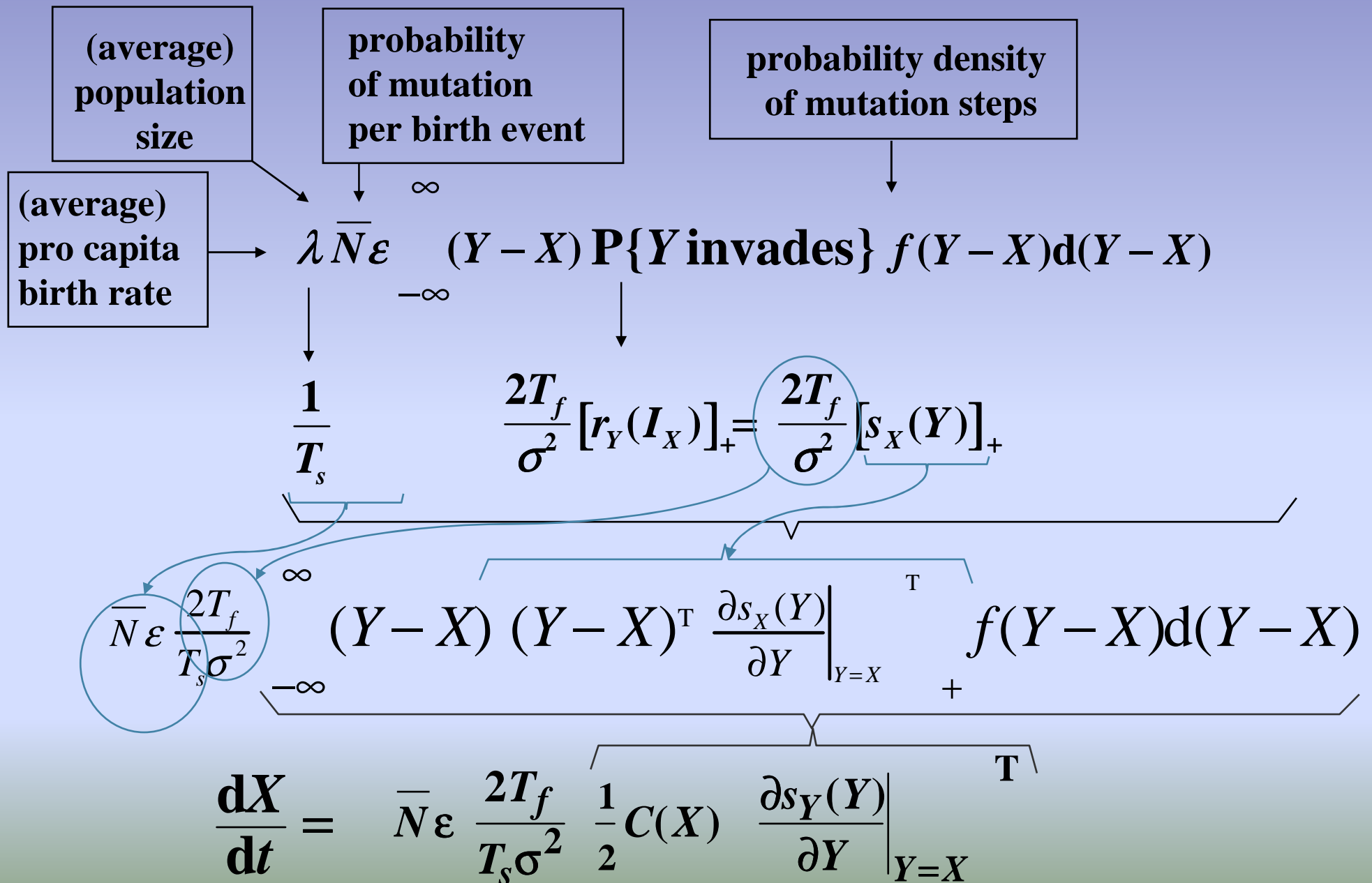
$$\phi'(r) = \frac{1}{\int_0^{\infty} e^{-ra} \Lambda(da)} \int_0^{\infty} -ae^{-ra} \Lambda(da)$$

$$\phi(0) = \ln R_0, \quad \phi'(0) = -T_f, \quad \text{with } T_f := \int_0^{\infty} a \Lambda(da) / R_0$$

to first order of approximation:

$$\ln R_0 - r T_f + \text{h.o.t} = 0 \quad r = \frac{\ln R_0}{T_f} + \text{h.o.t}$$

mean evolutionary step per time unit:



**For ODE population models:**

$$\sigma^2 = 2 \qquad T_f = T_s$$

$$\frac{2T_f}{T_s \sigma^2} = 1$$

**Finitely many different birth states:**

**(e.g. multiregional models)**

**The previous results immediately extend to this case  
with appropriate definitions for  
 $\sigma^2$ ,  $T_f$ , and  $T_s$**

(although it was a bit of a hassle to get the formulas right!).

**For the case of infinitely many birth states the required  
branching process results have not yet been proven.**

## Finely many different birth states:

$s_X(Y)$  is now the (generally unique) solution of

dominant eigenvalue of  $\tilde{\Lambda}_Y(I_X, r) = 1$

Laplace transform  
of birth kernel  
(Lotka's equation  
matrix version)

with

$$\tilde{\Lambda}_Y(I_X, r) = \int_0^{\infty} e^{-ra} \Lambda_Y(I_X, da)$$

with  $\Lambda$  now the birth kernel matrix of the invader  $Y$  in environment  $I_X$

$\Lambda_{Y,ij}(I_X, a)$  is the expected number of invaders born in state  $i$  produced up to age  $a$  by a newborn invader in state  $j$ .

As before  $L_Y(I_X) = \Lambda_Y(I_X, \infty)$ .

## Finely many different birth states:

Take for

- \*  $R_0$  the dominant eigenvalue of the next generation operator  $L_Y(I_X) = \Lambda_Y(I_X, \infty)$  of the mutant,

- \* for  $T_f$  the quantity 
$$T_f := \sum_{i,j} v_i \int_0^\infty a \Lambda_{Y,ij}(I_X, da) u_j$$

with  $u$  the right eigenvector normalised to sum to 1 of the next generation operator  $L_Y(I_X)$  of the resident (its stable birth distribution),

$v$  the corresponding left eigenvector, normalised so that  $v^T u = 1$  (the “reproductive values” associated with the different birth states),

## Finely many different birth states:

\* for  $T_s$  the quantity

$$T_s := \sum_j \int_0^{\infty} -a F_j(da) u_j$$

with  $F_j$  the probability that a resident individual born in state  $j$  survives till age  $a$ ,

\* for  $\sigma^2$  the quantity

$$\sigma^2 := \sum_j \text{Var}_j \sum_i v_i \underline{m}_{ij} u_j$$

with  $\underline{m}_{ij}$  the lifetime number of offspring of type  $i$  begotten by a resident individual born in state  $j$ .



## **Finitely many different birth states:**

**A second application is to periodic environments:**

**Take the phase (of the oscillation) at which an individual is born as its birth state.**

**(The proof still has to be worked out in all its gory technical detail.)**

**NB The idea of a proof works only for discrete time models due to the lack of hard results for continua of birth states.**

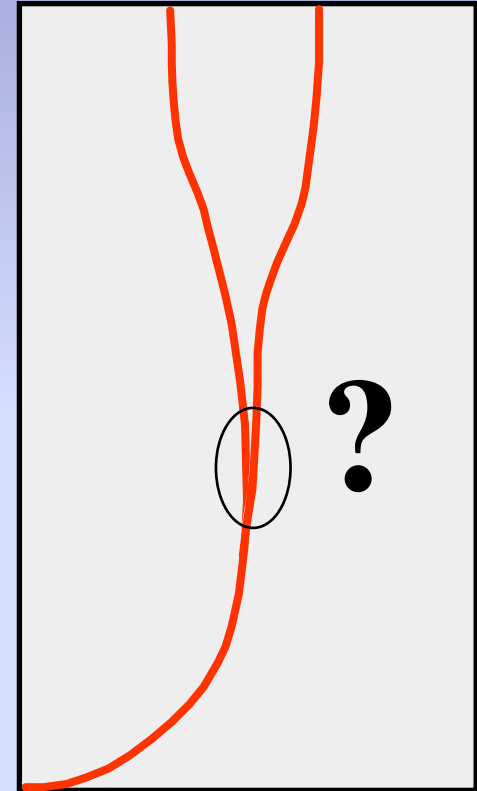
**(Ulf Dieckmann has additional heuristic results for simple ODE community models that apply to mutant invasion in any type of ergodic attractor.)**

## To round of: What happens near branching points?

This depends on the local geometrical structure of the function  $s_{\mathbf{x}}(\mathbf{Y})$ .

For one-dimensional trait spaces we have a full classification of what happens around any type of “singular point”, like Evolutionarily Stable Strategies or branching points.

For higher dimensional trait spaces we have so far only proved that: Any model in the class treated in this talk locally around a singular point has the same evolutionary properties as some appropriately chosen so-called (simple!) Lotka-Volterra model.





**The End**

**(for today)**