

Adaptive Dynamics and Evolving Biodiversity

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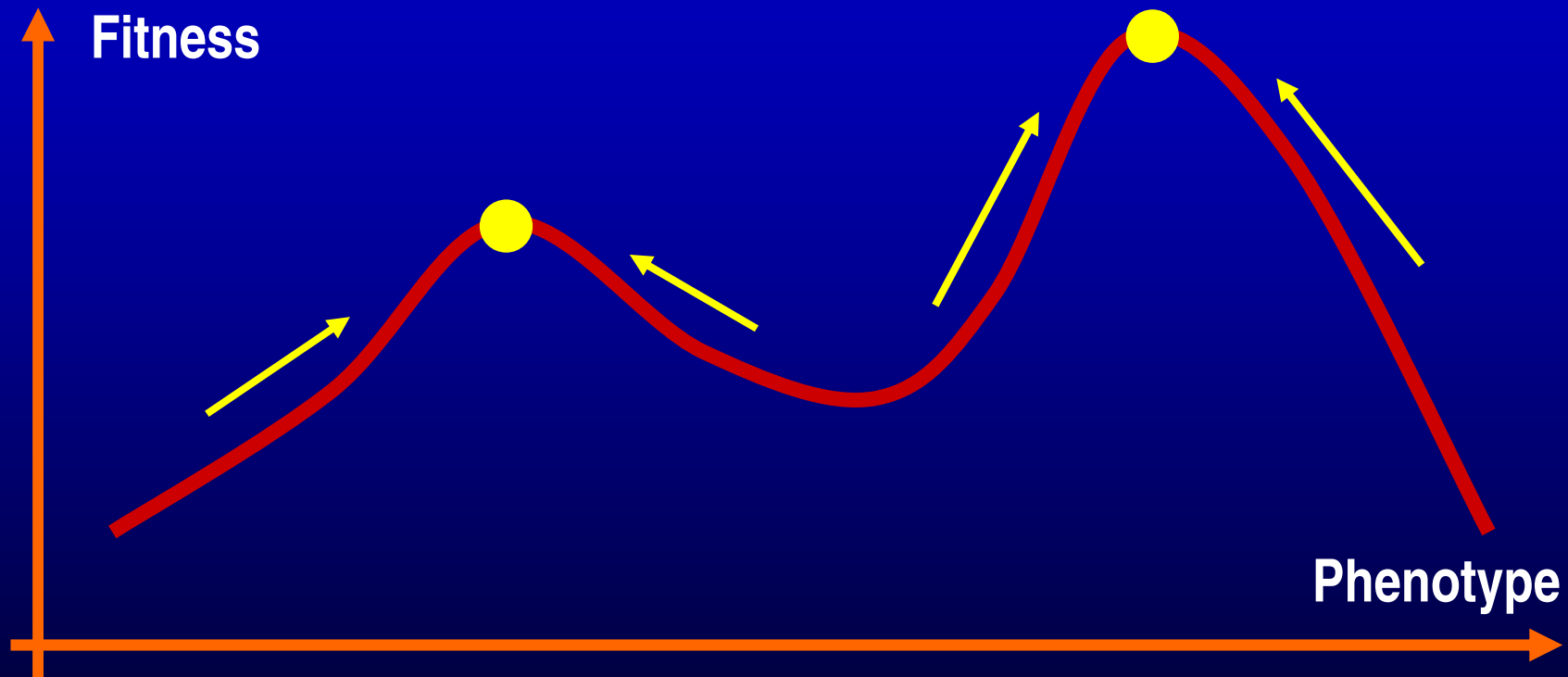
Laxenburg, Austria

In collaboration with:

Régis Ferrière, Laboratoire d'Ecologie, Ecole Normale

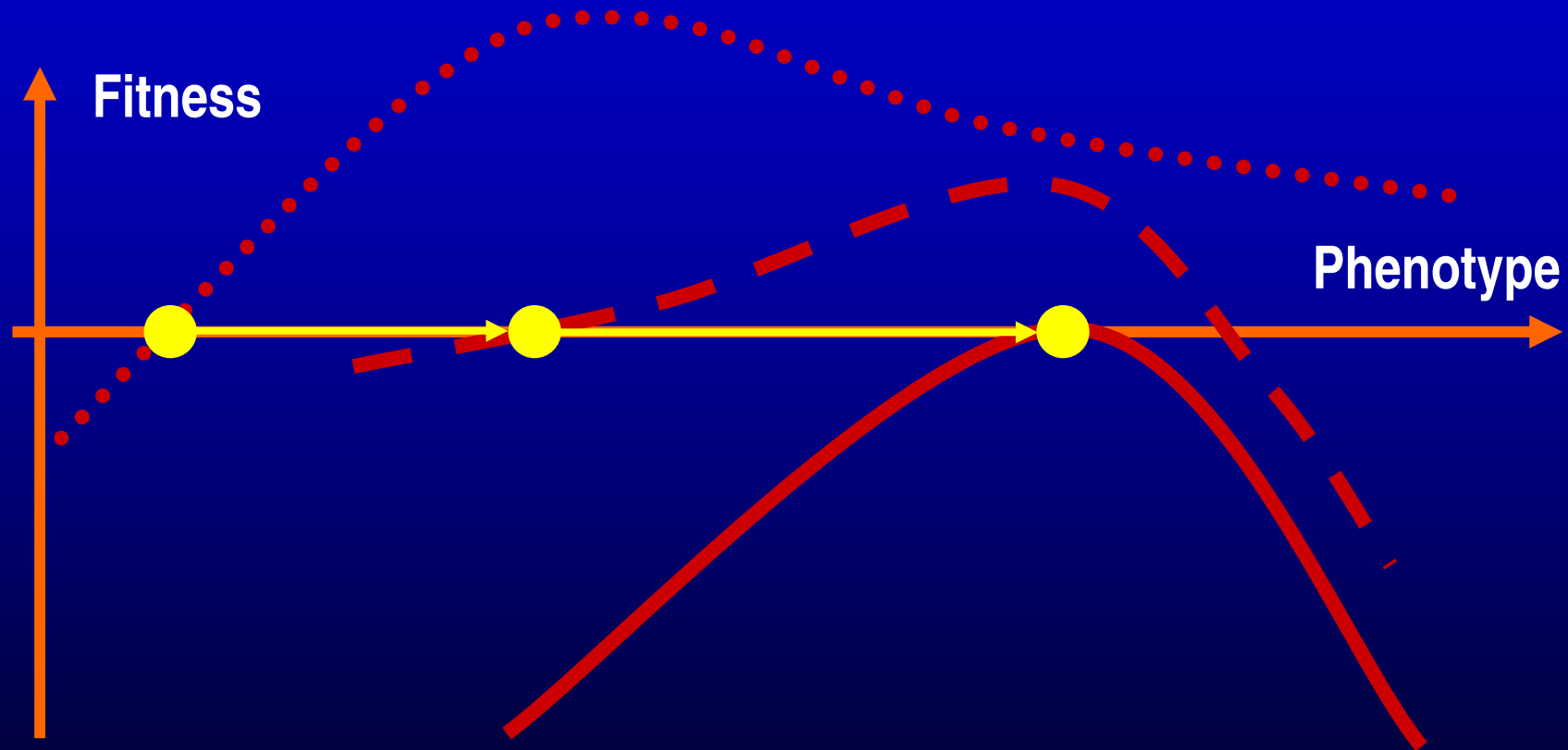
Supérieure, Paris, France

Evolutionary Optimization



Envisaging evolution as a hill-climbing process on a static fitness landscape is attractively simple, but essentially wrong for most systems.

Frequency-Dependent Selection

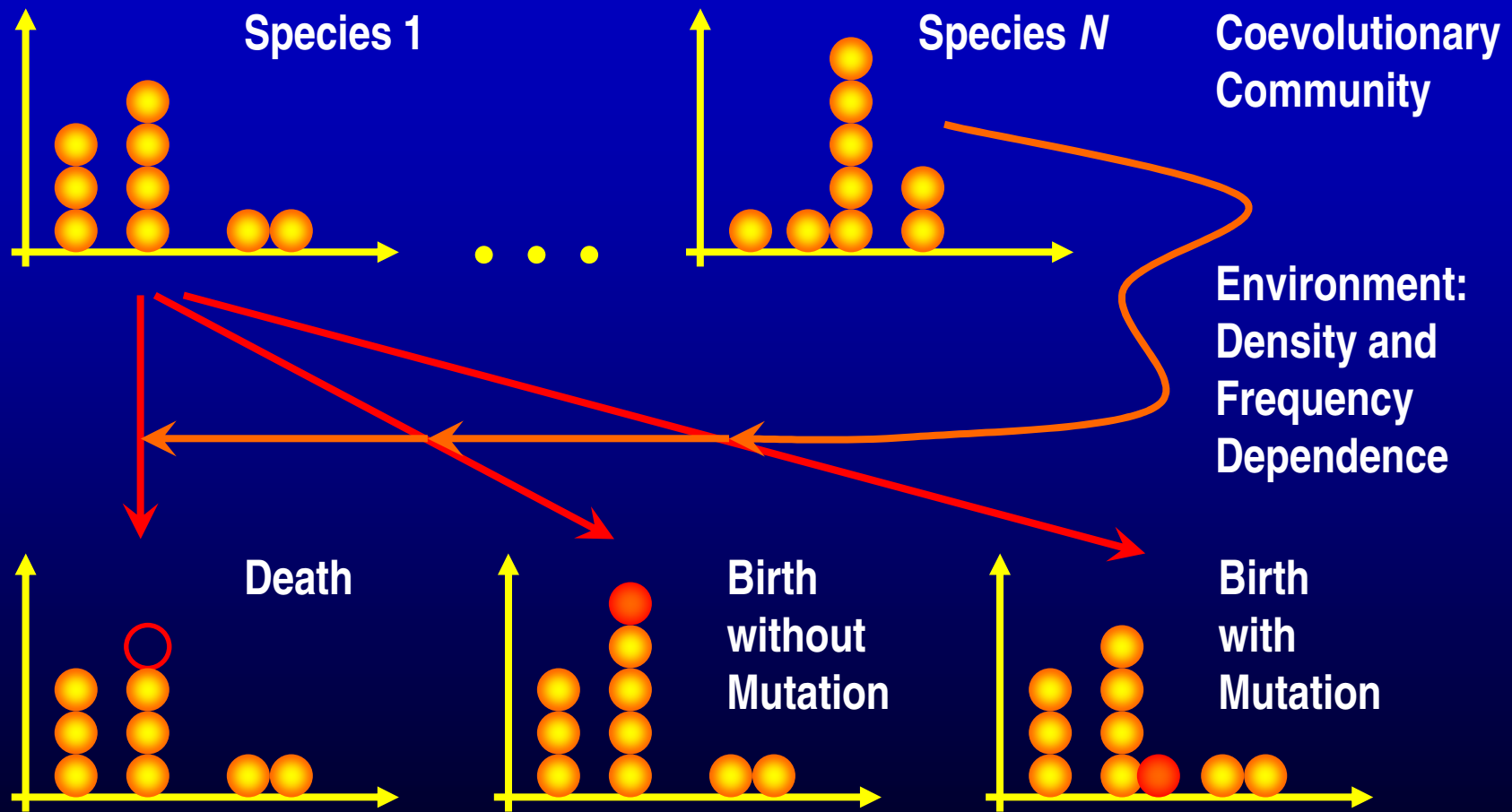


Fitness landscapes change in dependence on a population's current composition.



Models of Adaptive Dynamics

Birth-Death-Mutation Processes



Individual-based Evolutionary Dynamics

Polymorphic and Stochastic

Dieckmann (1994)

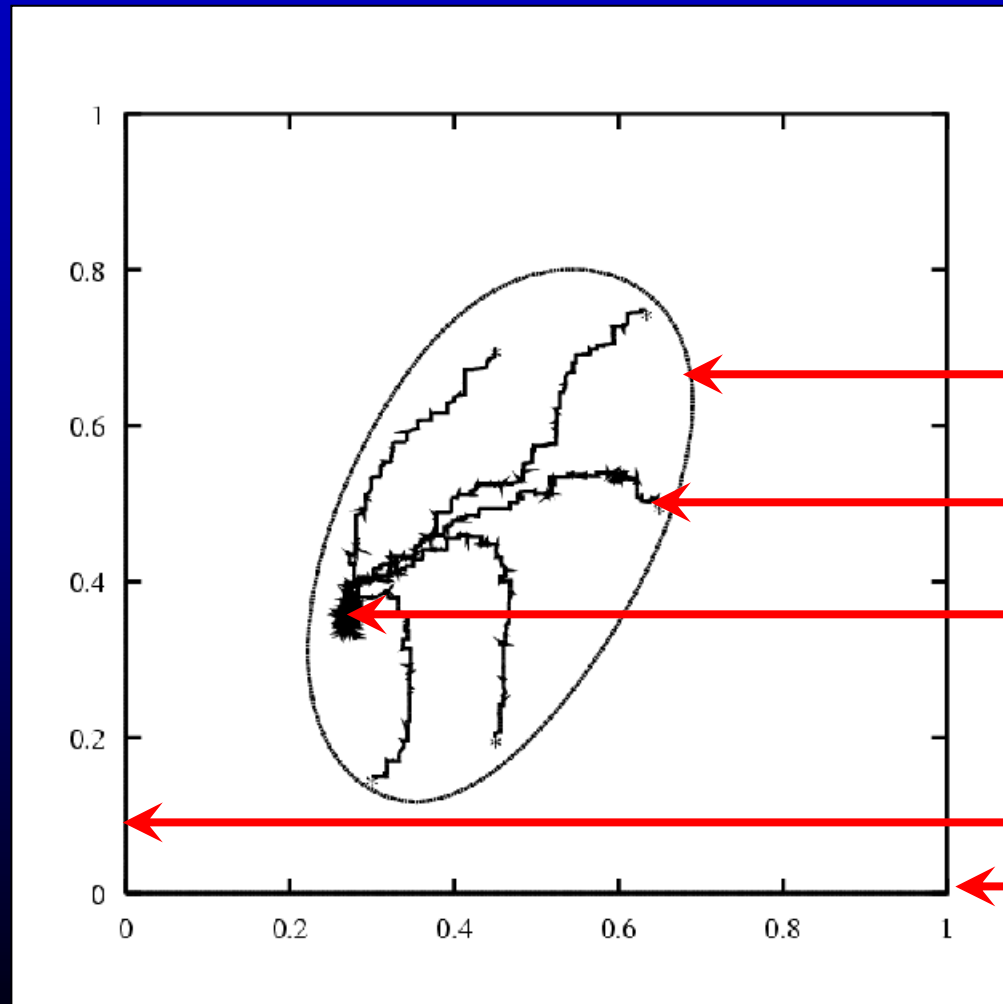
■ Generalized Replicator Equation

$$\frac{d}{dt} P(p) = \int [w(p | p') P(p') - w(p' | p) P(p)] dp'$$

$$w(p' | p) = \sum_{i=1}^N \int [d_i(s'_i, p) p_i(s'_i) \Delta(p_i - \delta_{s'_i} - p'_i) \prod_{j \neq i} \Delta(p'_j - p_j) \\ + \int b_i(s_i, p) p_i(s_i) B_i(s'_i, s_i) ds_i \Delta(p_i + \delta_{s'_i} - p'_i) \prod_{j \neq i} \Delta(p'_j - p_j)] ds'_i$$

Measure-valued stochastic process in a space of atomic distributions.

Individual-based Coevolution



Viability region

Coevolutionary trajectories

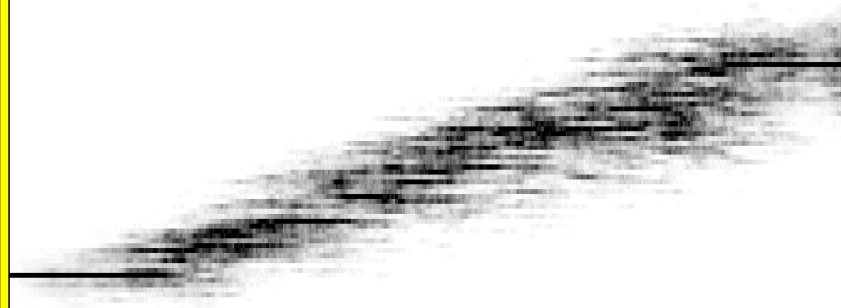
Global coevolutionary attractor

Trait value 2

Trait value 1

Effect of Mutation Rates

Large: 10%

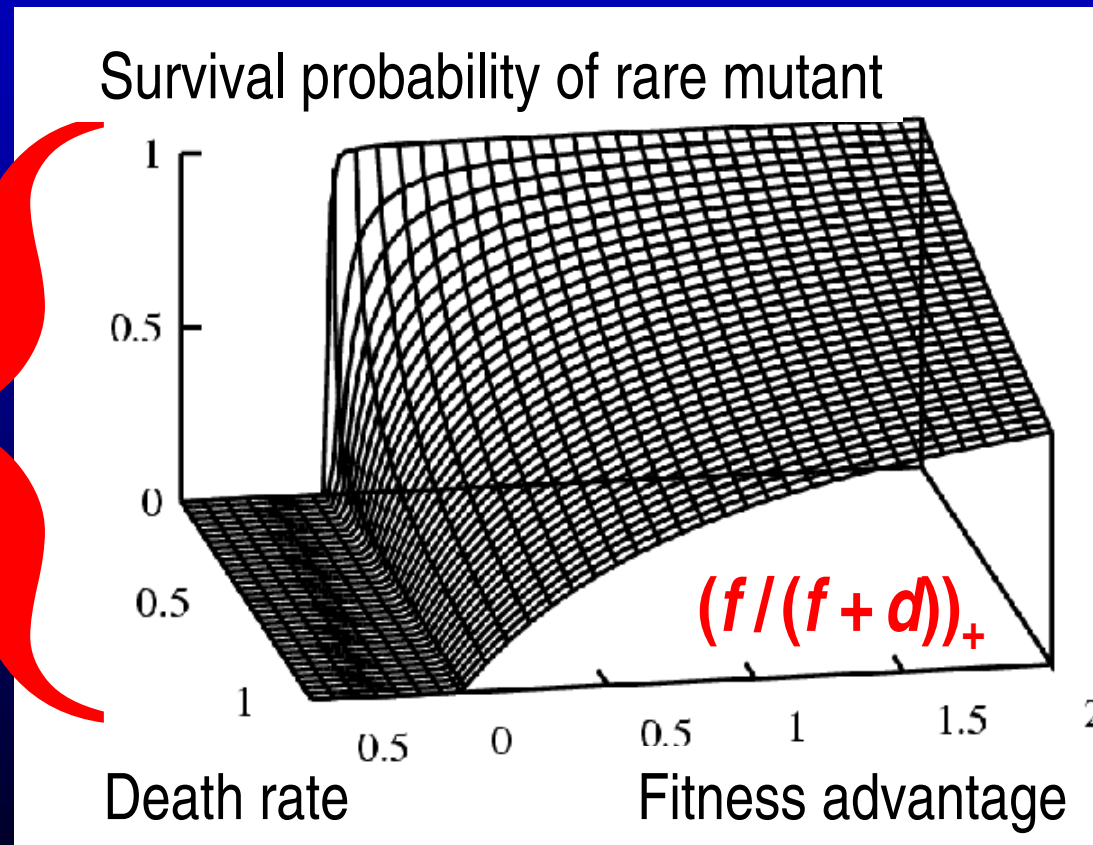


Small: 0.1%



Probability for a Trait Substitution

- 1 **Mutation**
population dynamics
- 2 **Invasion**
branching process theory
- 3 **Fixation**
invasion implies fixation



Random Walk Models

Monomorphic and Stochastic

Dieckmann & Law (1996)

■ Master Equation

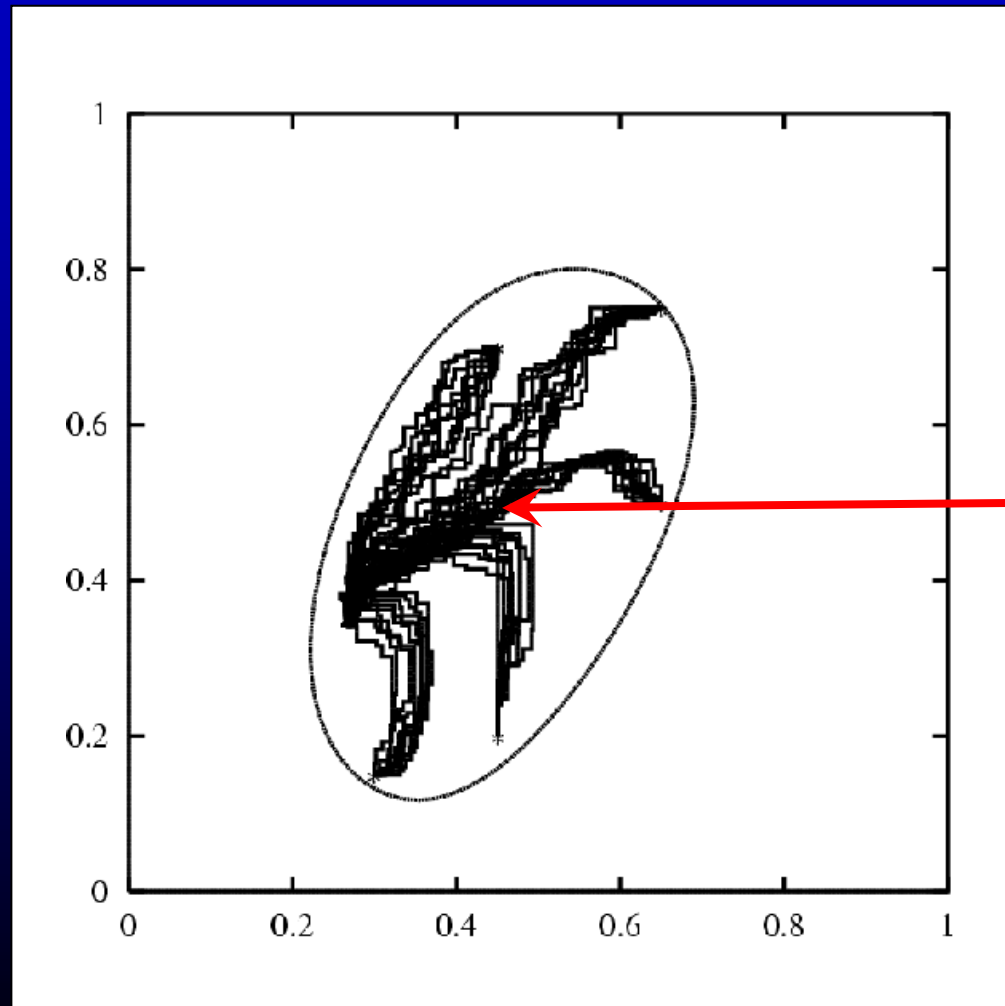
$$\frac{d}{dt}P(s) = \int [w(s | s')P(s') - w(s' | s)P(s)] ds'$$

$$w(s' | s) = \sum_{i=1}^N w_i(s'_i, s) \prod_{j \neq i} \delta(s'_j - s_j)$$

$$w_i(s'_i, s) = \mu_i b_i(s_i, s) n(s) M(s_i - s'_i) \cdot f_i(s'_i, s) / b_i(s'_i, s)$$

Real-valued stochastic process in trait space.

Random Walks in Trait Space



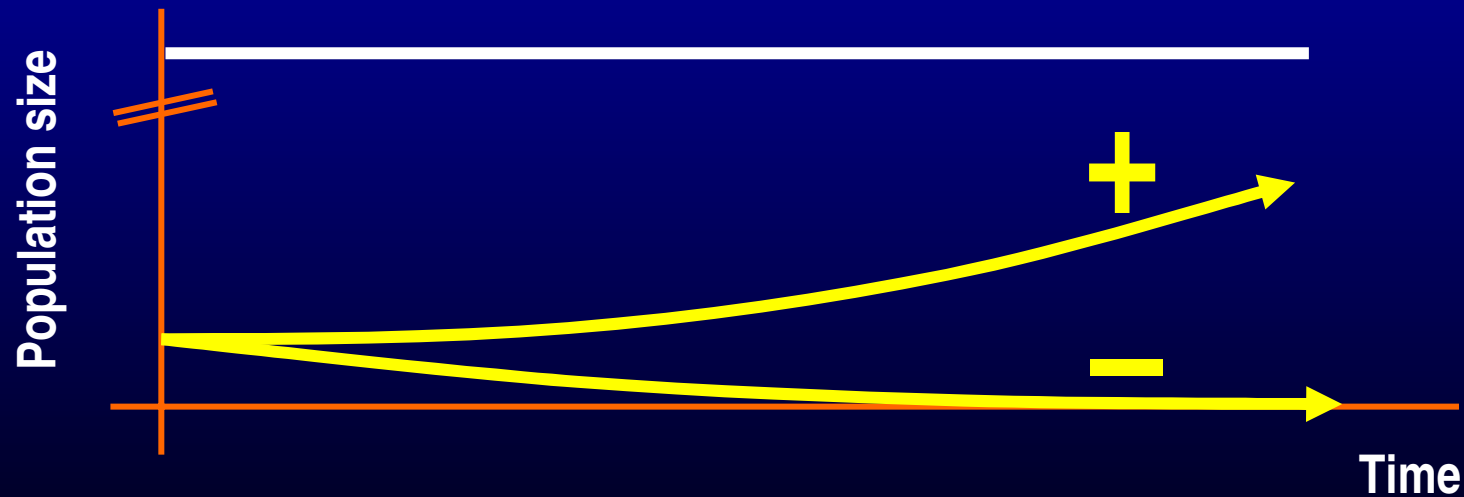
**Bundles of
coevolutionary trajectories**

Invasion Fitness

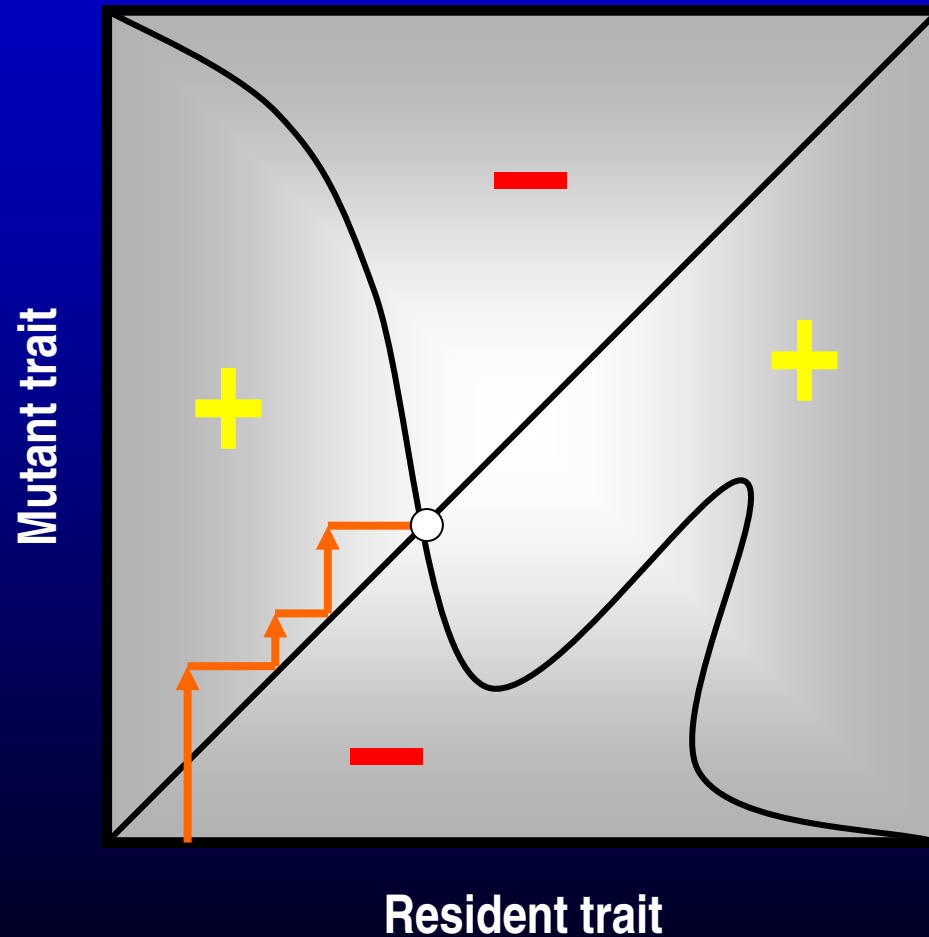
Metz *et al.* (1992)

■ Definition

Initial per capita growth rate of a small **mutant** population within a resident population at ecological equilibrium.

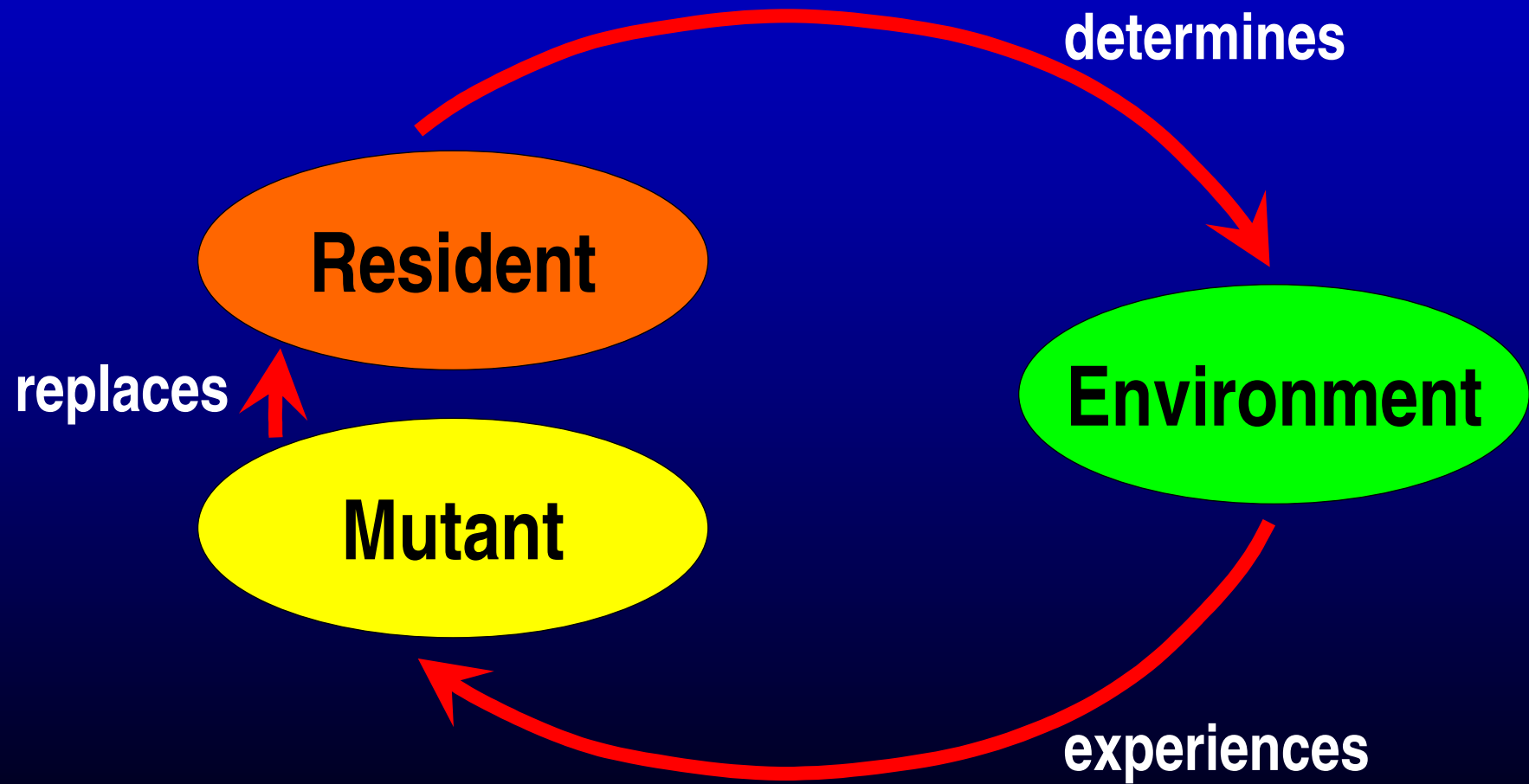


Pairwise Invasibility Plots (PIPs)

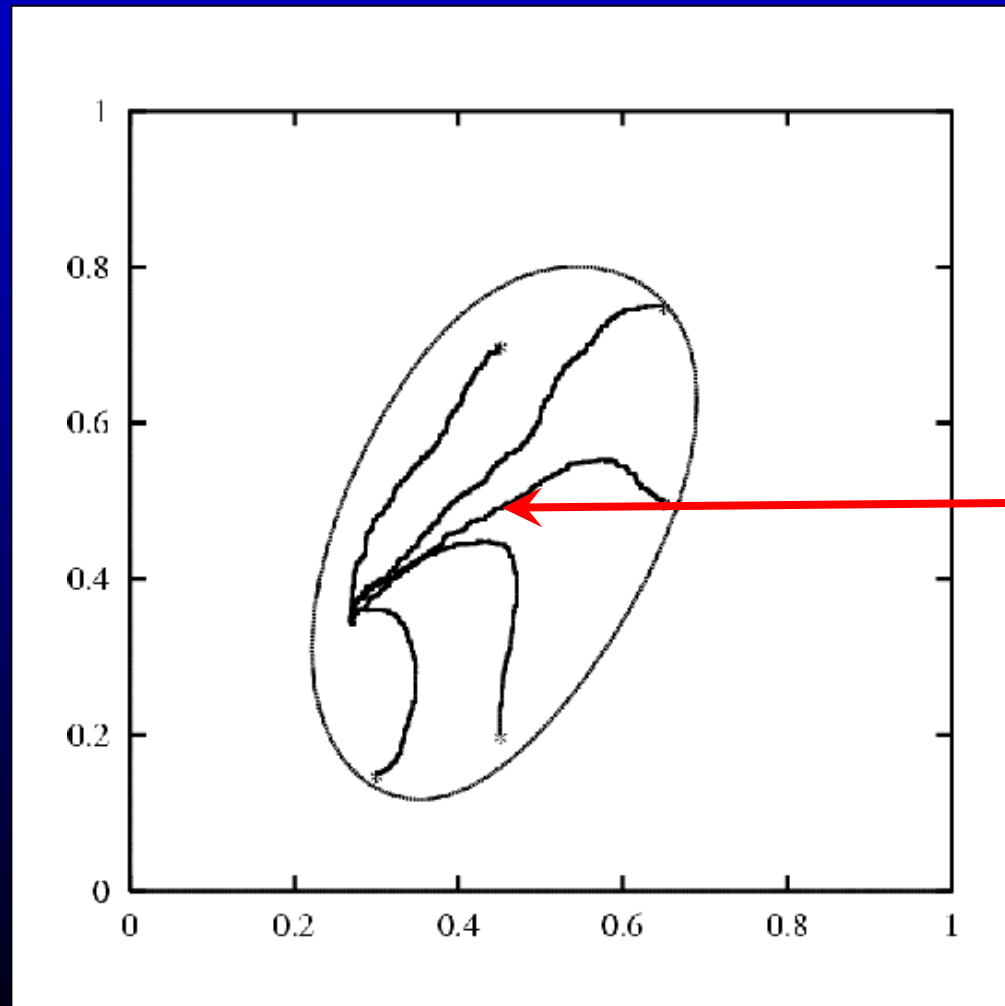


- +** Invasion of the mutant into the resident population possible
- Invasion impossible
- ↗** One trait substitution
- Singular phenotype

Environmental Feedback



Average of Random Walks



**Mean
coevolutionary trajectories**

Hill-climbing on Adaptive Landscapes

Monomorphic and Deterministic

Dieckmann & Law (1996)

■ Canonical equation of adaptive dynamics

$$\frac{d}{dt} s_i = \frac{1}{2} \mu_i \sigma_i^2 n_i \frac{\partial}{\partial s'_i} f(s'_i, s_i) \Big|_{s'_i = s_i}$$

evolutionary rates

mutation probability

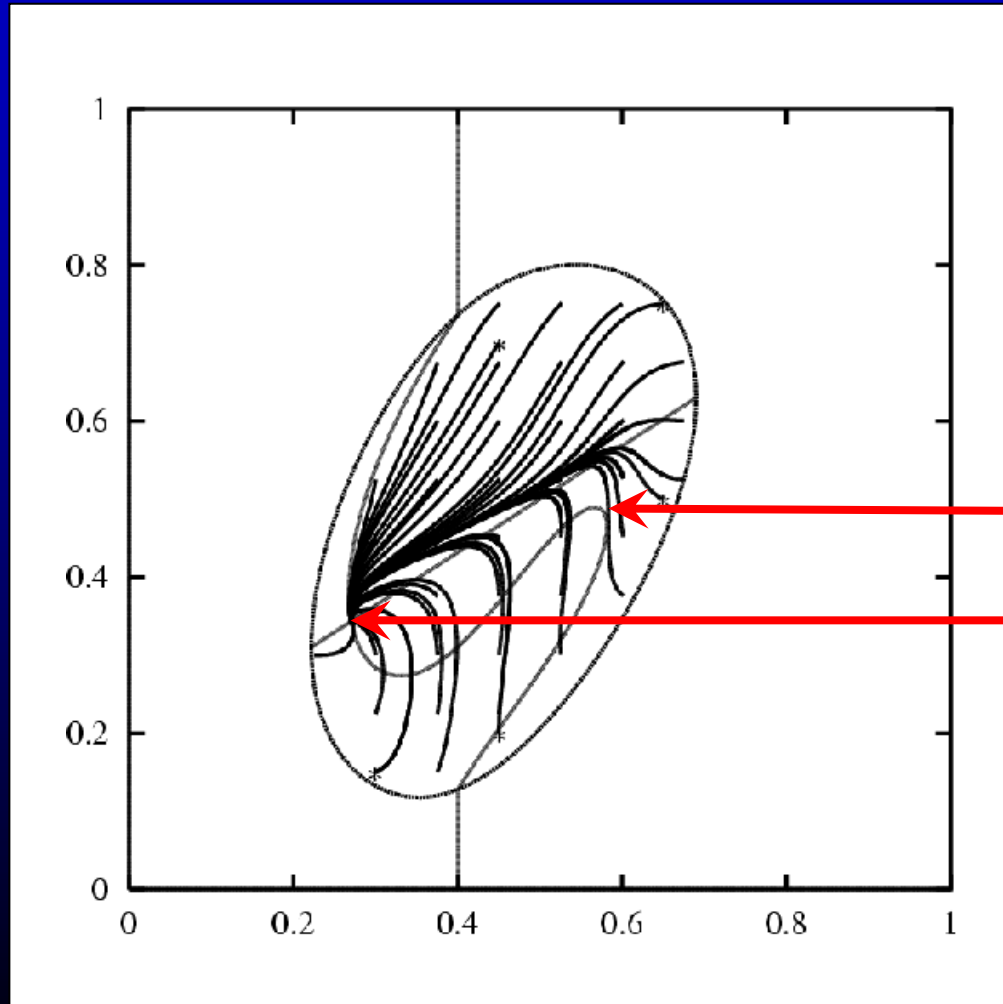
mutation variance

population size

invasion fitness

The diagram shows the canonical equation of adaptive dynamics. Red arrows point from labels below to terms in the equation: 'evolutionary rates' points to the derivative with respect to time (d/dt); 'mutation probability' points to the term mu_i; 'mutation variance' points to the term sigma_i^2; 'population size' points to the term n_i; and 'invasion fitness' points to the function f(s'_i, s_i).

ODE Approximation



Coevolutionary isoclines
Global coevolutionary attractor

Reaction-Diffusion Models

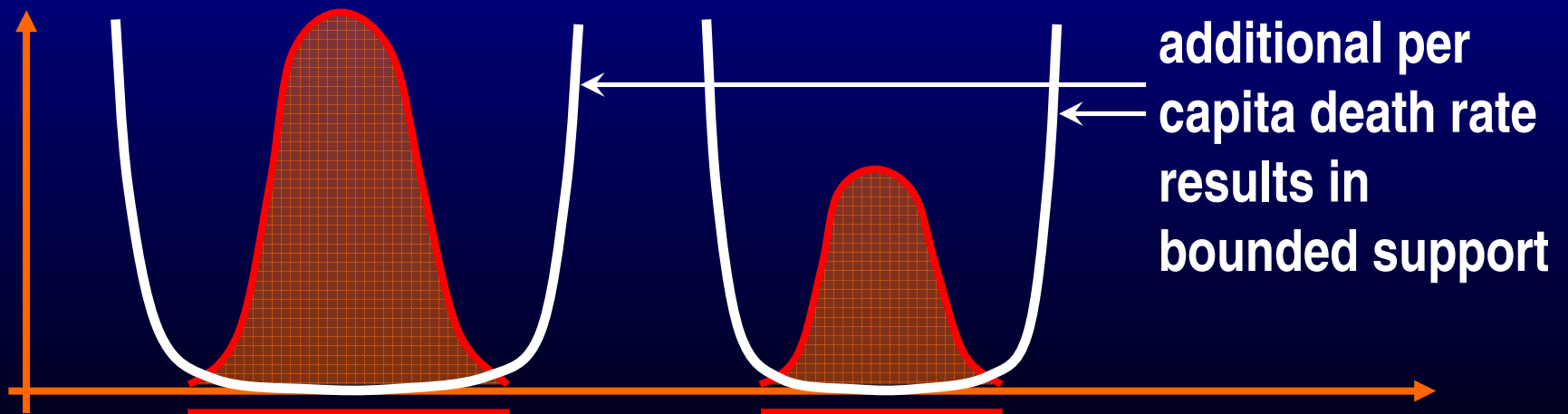
Polymorphic and Deterministic

Dieckmann (in preparation)

■ Kimura limit

$$\frac{d}{dt} p_i(s_i) = [b_i(s_i, p) - d_i(s_i, p)] p_i(s_i) + \frac{1}{2} \mu_i \sigma_i^2 \frac{\partial^2}{\partial s_i^2} b_i(s_i, p) p_i(s_i)$$

■ Finite-size correction



Summary of Derivations

large population size
small mutation probability small mutation variance



large population size
large mutation probability

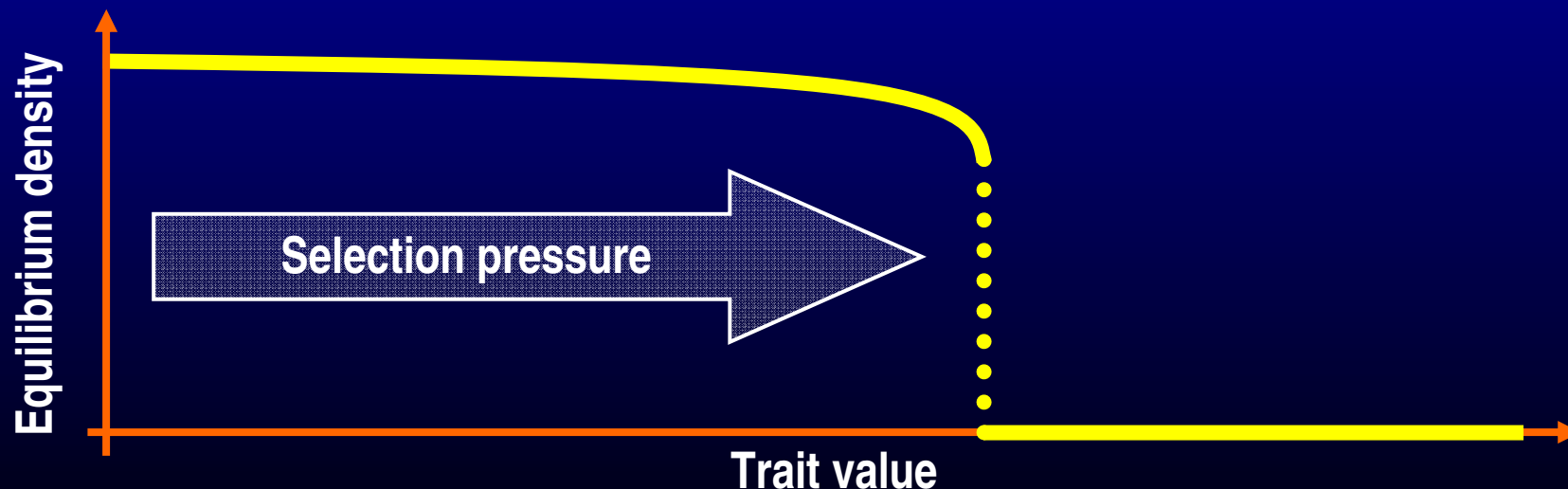
2a

Evolutionary Suicide

Evolutionary Suicide

Ferrière (2000)

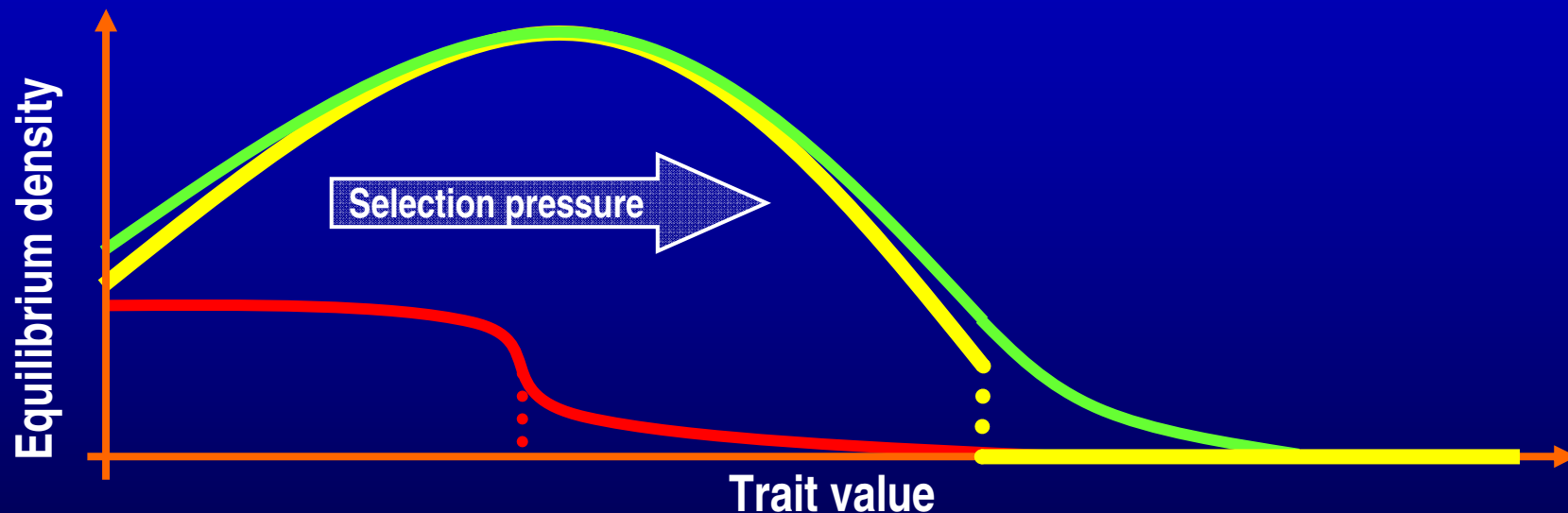
- Evolutionary suicide = selection-driven extinction
- Evolutionary suicide occurs when the evolution of an adaptive trait induces a bifurcation in the underlying population dynamics that involves a discontinuous transition to extinction:



Simplest Setting

Matsuda & Abrams (1994)

- Unimodal carrying capacity with asymmetric competition:

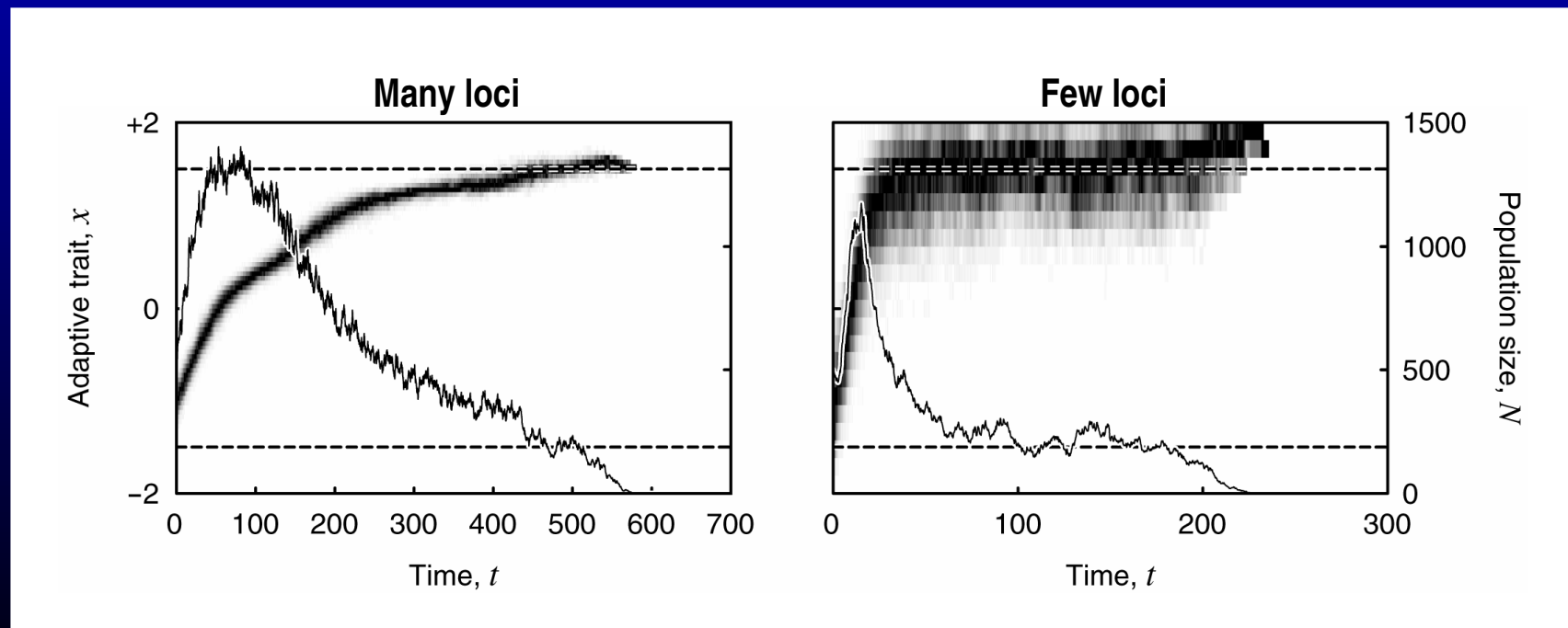


- Allee effects imply discontinuous transitions to extinction.
- Many other ecological settings also give rise to evolutionary suicide: a well-studied example is dispersal evolution in metapopulations.

Sexual Evolution

Dieckmann & Ferrière (2004)

- Evolutionary suicide is not an artifact of phenotypic evolutionary models; it can also occur in sexual populations:

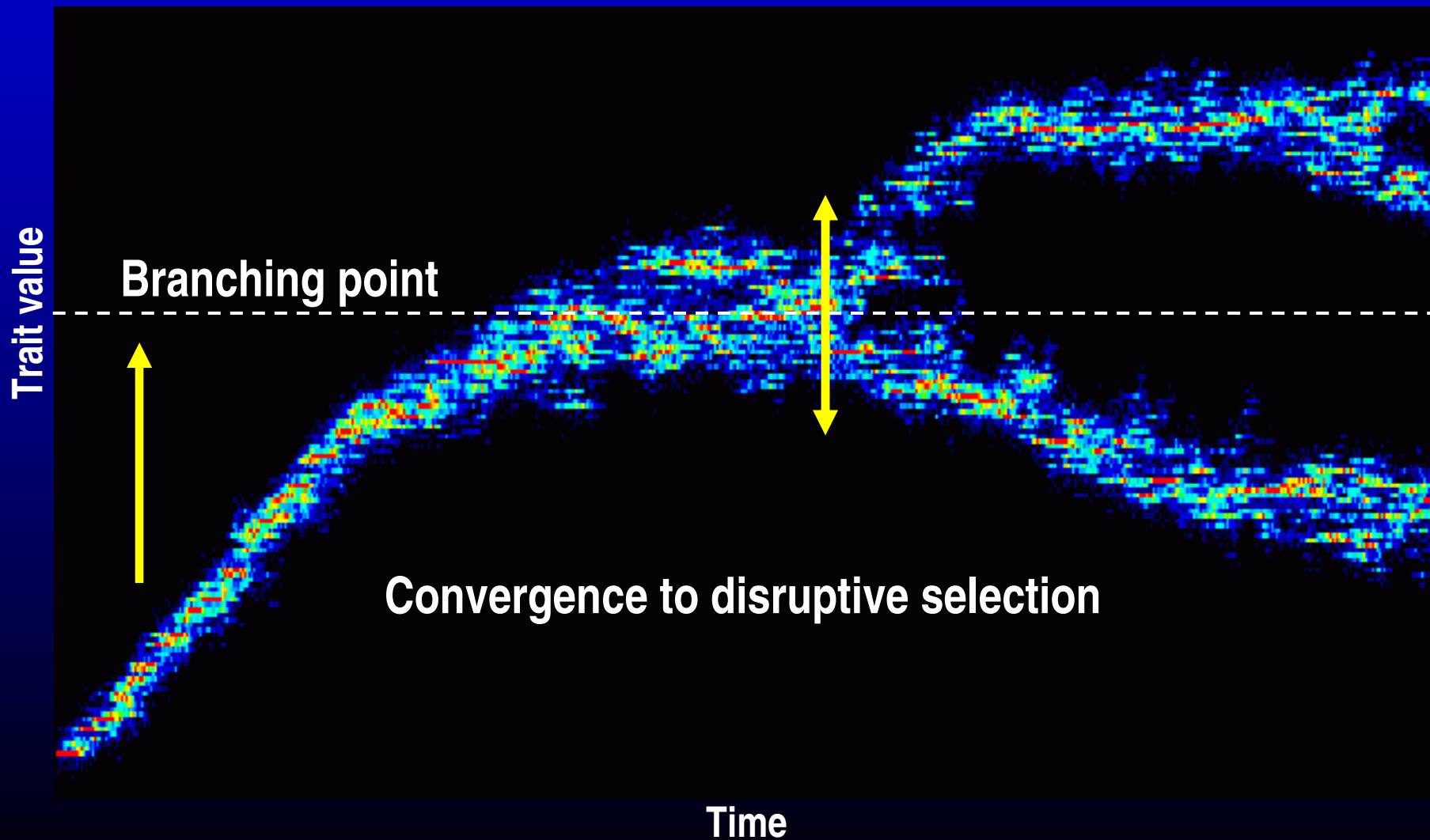


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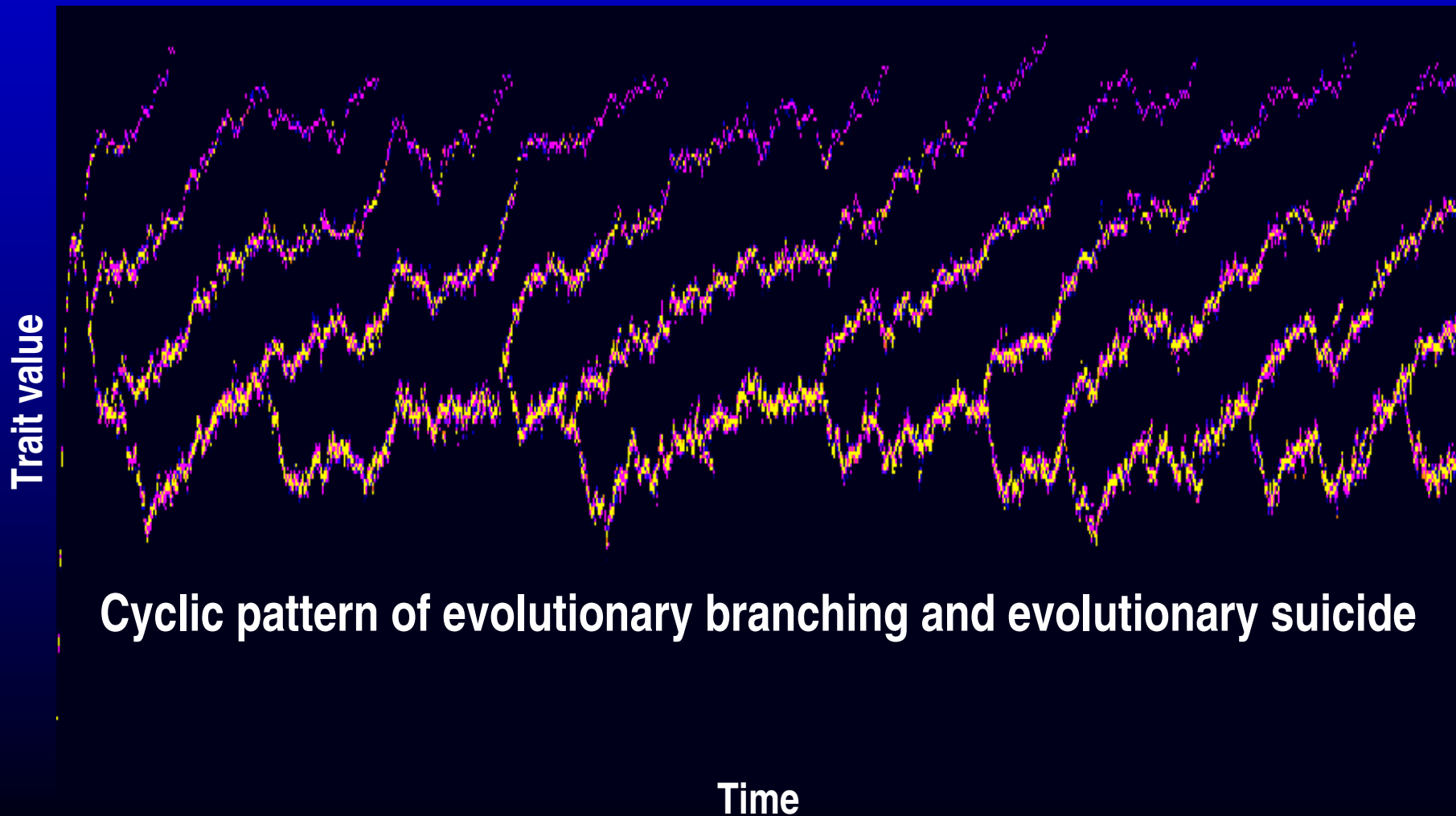
Adaptive Speciation

Evolutionary Branching

Metz *et al.* (1992)

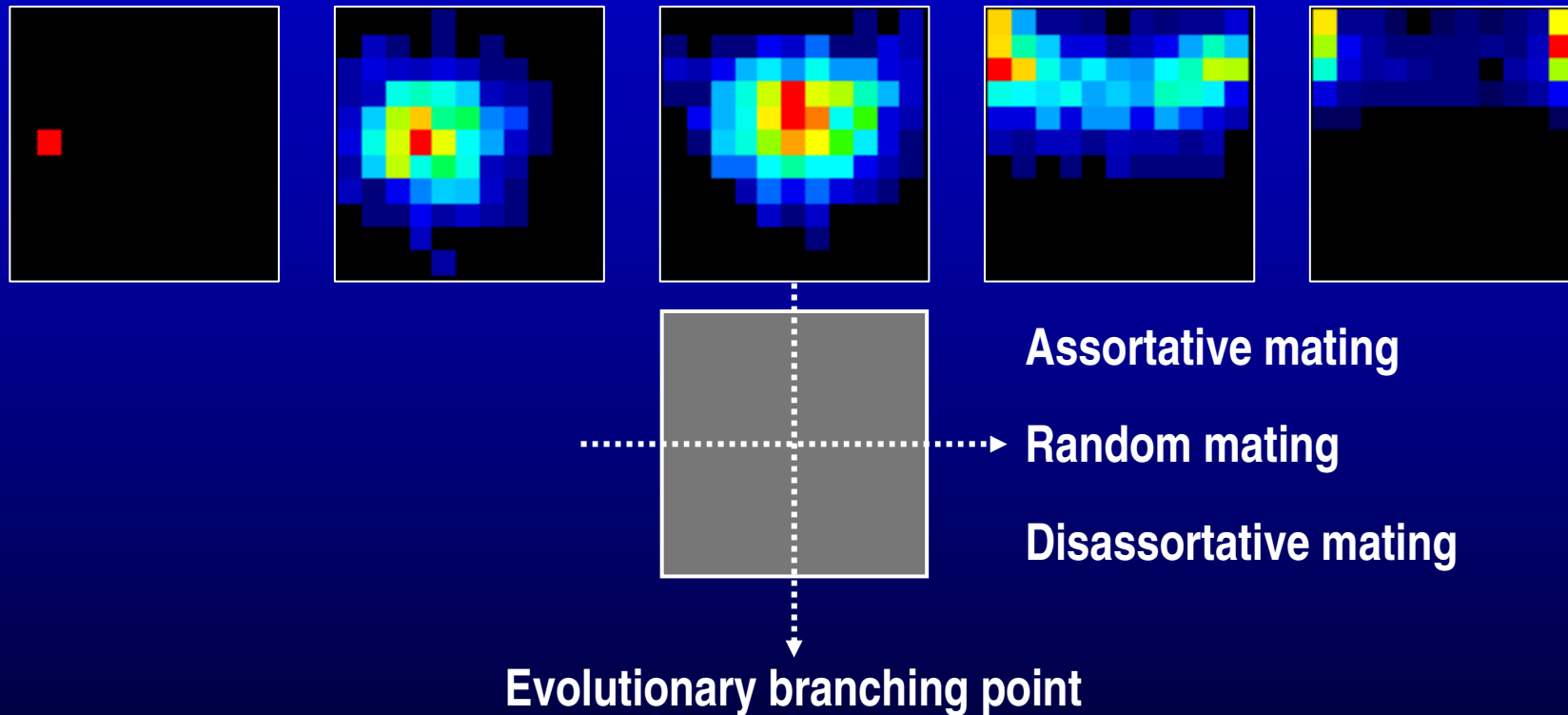


Multiple Evolutionary Branching



Sympatric Speciation

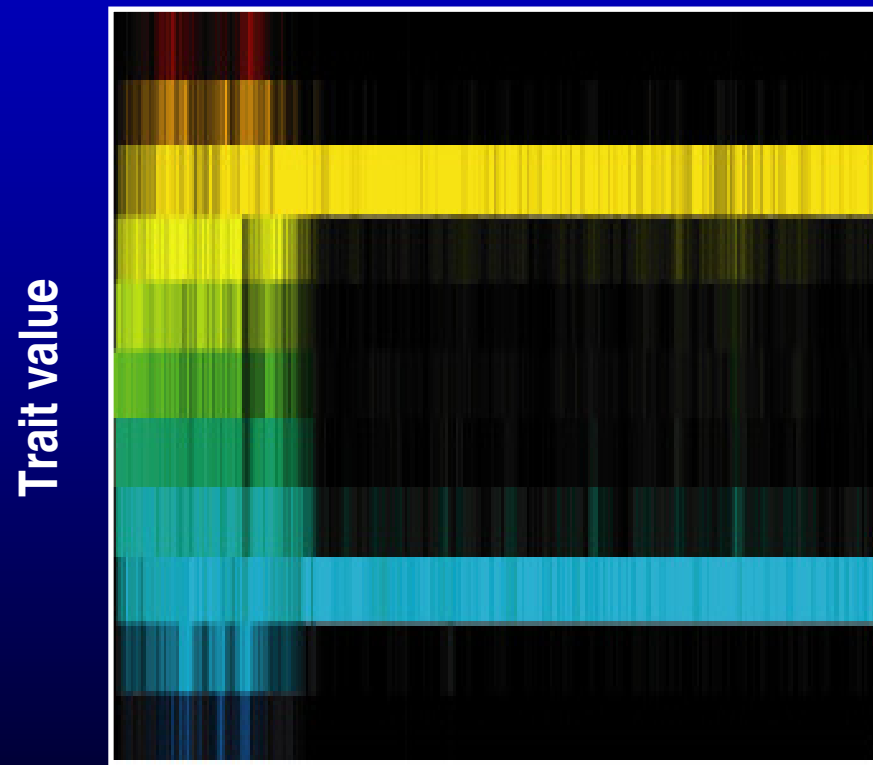
Dieckmann & Doebeli (1999)



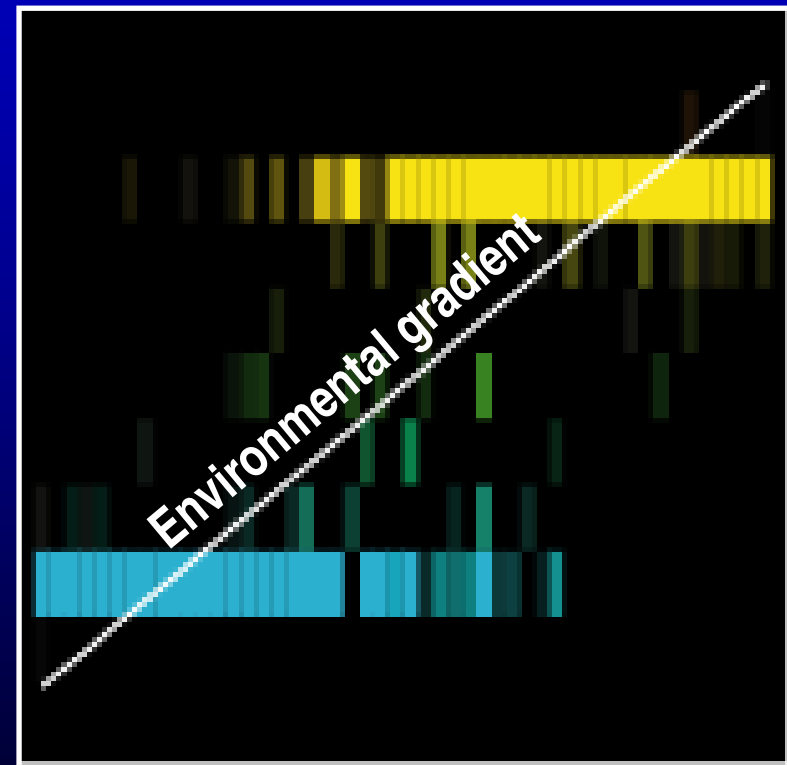
Disruptive selection at branching point favors assortative mating and thus enables the emergence of genetic isolation.

Parapatric Speciation

Doebeli & Dieckmann (2003)



Time



Spatial location

Summary

- The theory of adaptive dynamics offers a versatile toolbox for studying phenotypic evolution.
- Simplified models are deduced from a common individual-based underpinning.
- Adaptive dynamics are particularly helpful for investigating the evolutionary implications of complex ecological settings.
- Frequency-dependent selection, which lies at the heart of adaptive dynamics theory, is essential for understanding the evolutionary formation and loss of biological diversity.