An Introduction to Adaptive Dynamics Theory

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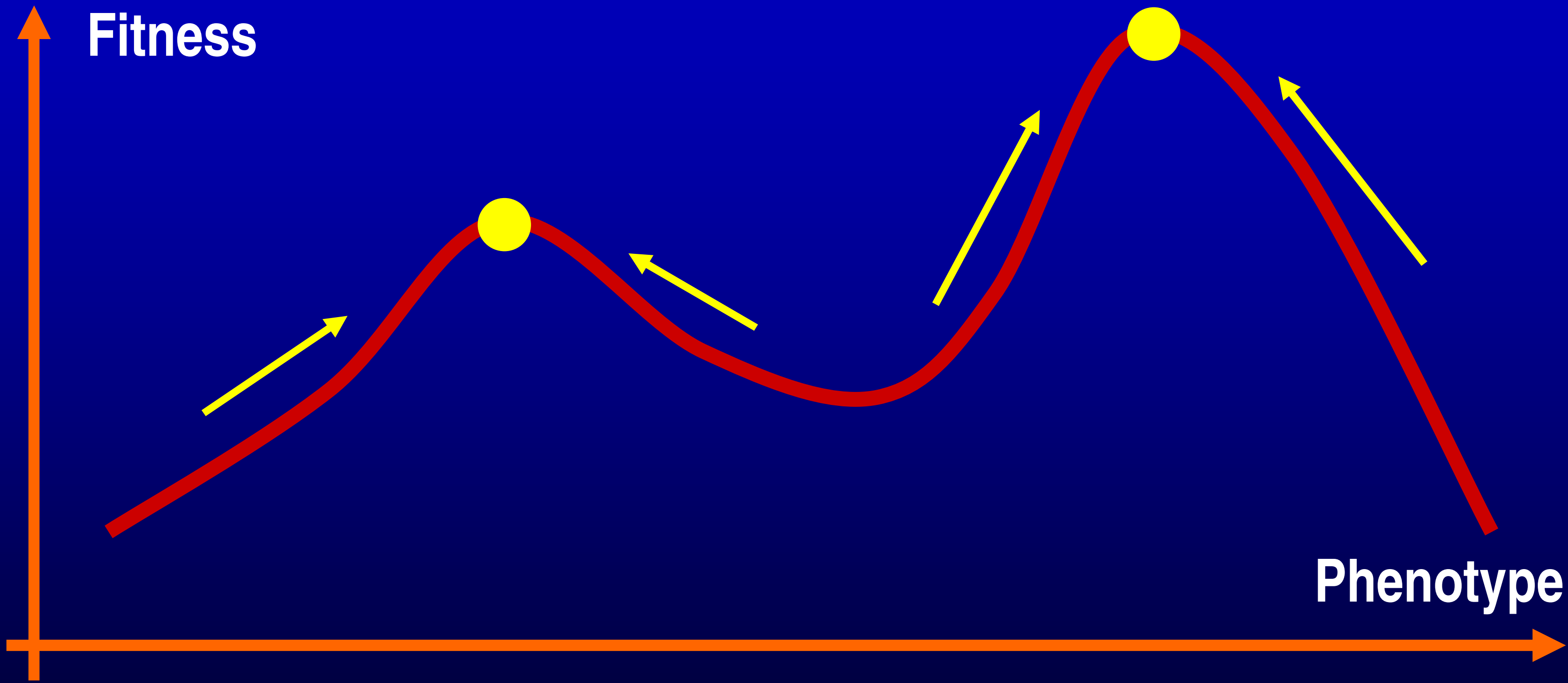
Overview

1. Background
2. Models of Adaptive Dynamics
3. Evolutionary Invasion Analysis
4. Example: Resource Competition

1 Background

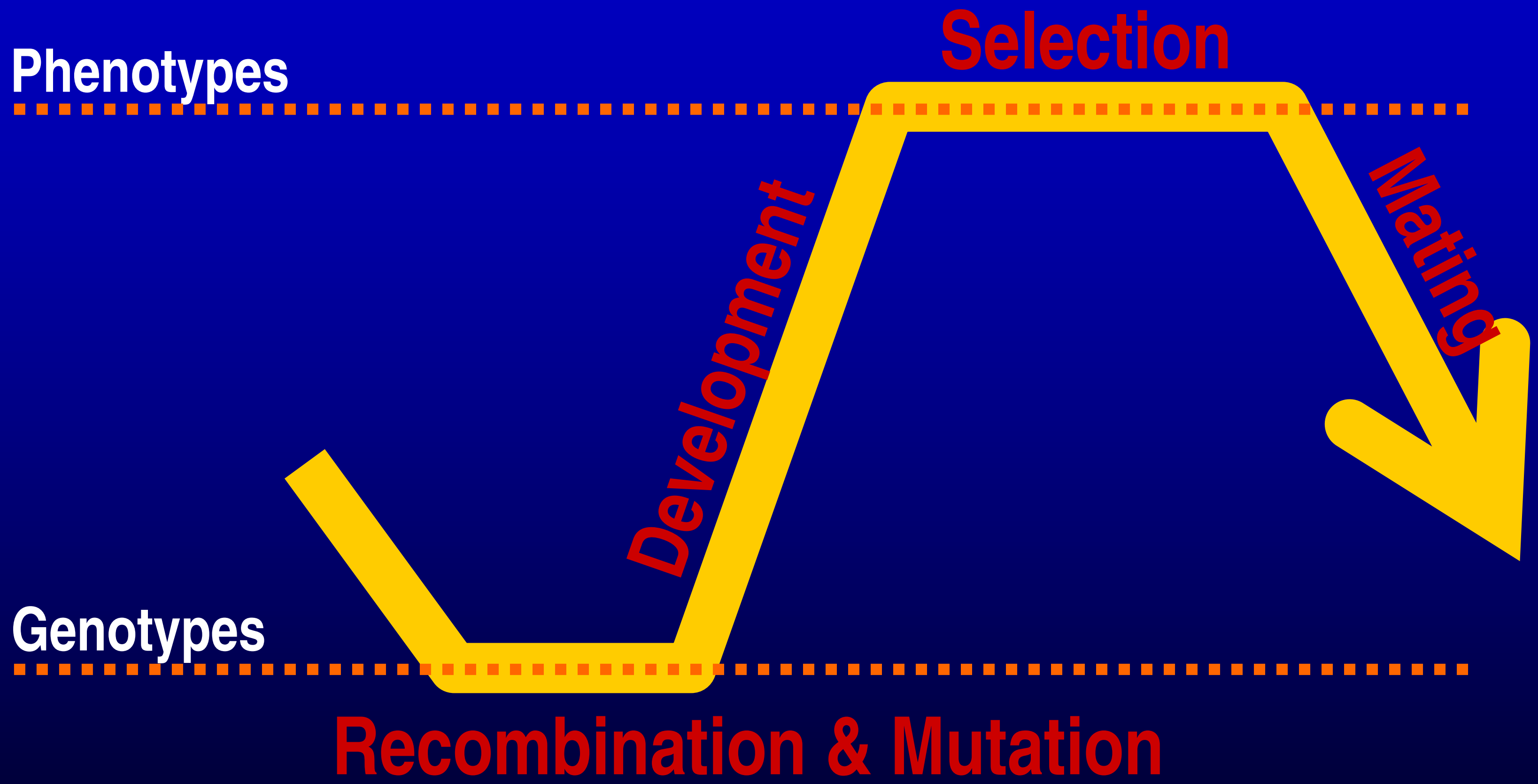
Evolutionary Optimization



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

Genetic Inheritance

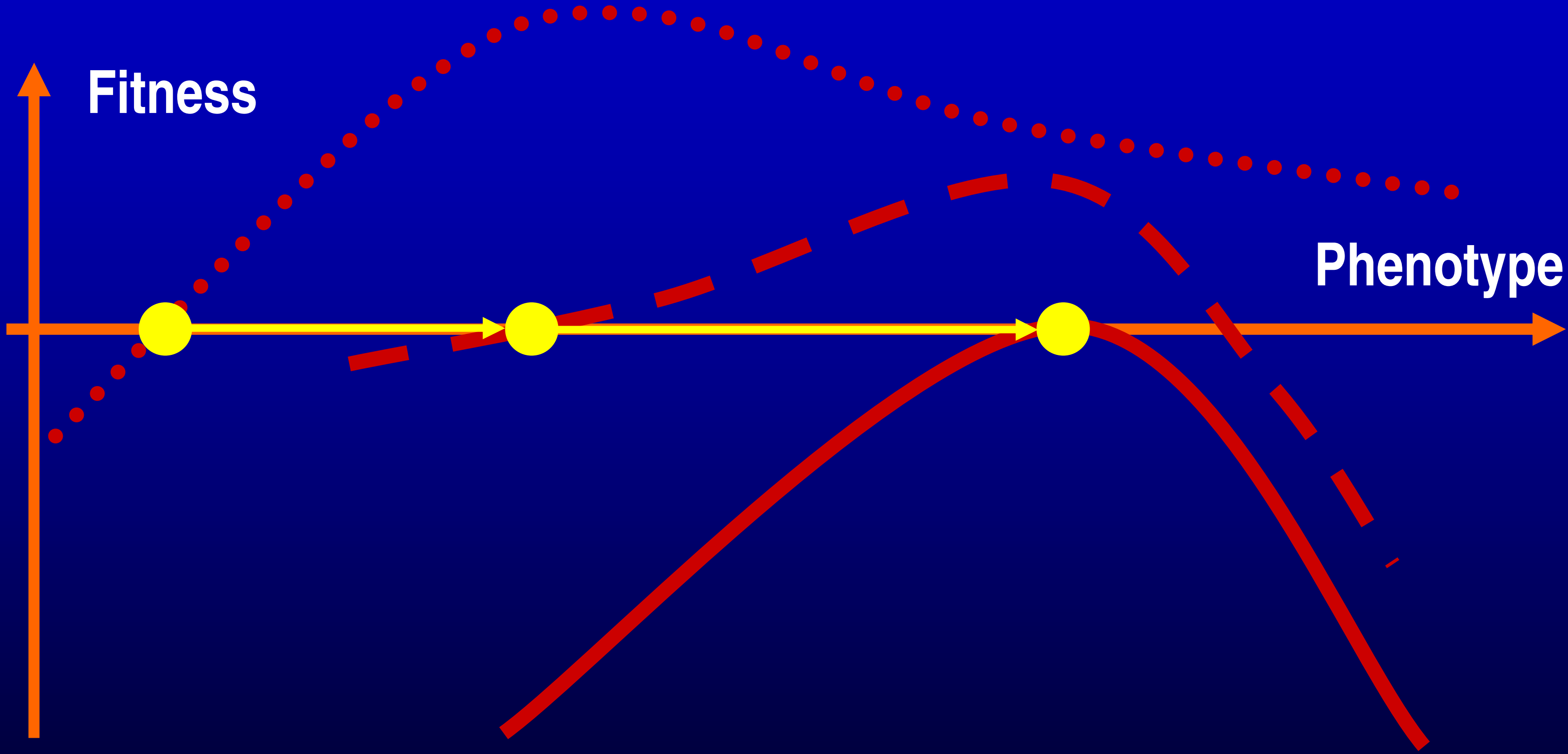
1



Describing evolution at the level of phenotypes alone is sometimes not possible.

Environmental Feedback

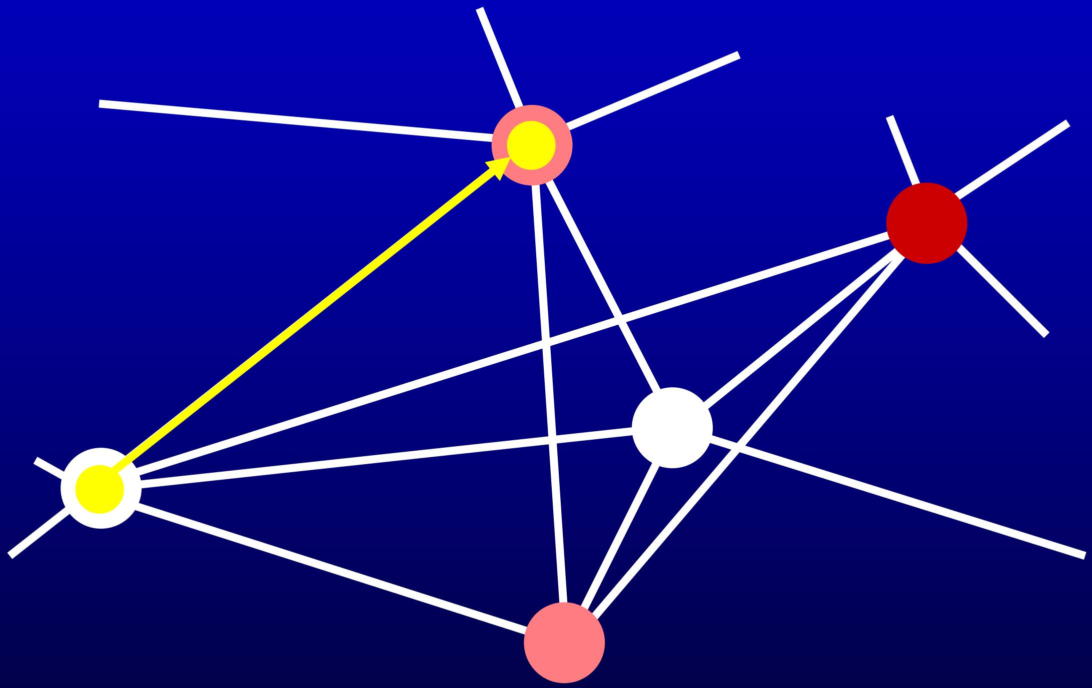
2



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

Search Space Dimension

3



Fitness landscapes can be very high dimensional, with topologies that greatly differ from those expected in two or three dimensions.

Historical Developments

1	2	3
Population Genetics (1930)	Evolutionary Game Theory (1970)	Evolutionary Algorithms (1985)
Quantitative Genetics (1940)	Adaptive Dynamics (1990) ✓	Theory of Fitness Landscapes (1995)

Adaptive Dynamics

… extends evolutionary game theory in a number of respects:

- Frequency- und density-dependent selection
- Stochastic and nonlinear population dynamics
- Continuous strategies or metric characters
- Evolutionary dynamics
- Derivation of fitness function

Density and Frequency Dependence

- **Phenotypes, Densities, and Fitness**
  x_1, n_1, f_1 and x_2, n_2, f_2
- **Assumption in Classical Genetics**
  f_1 is a function of x_1
- **Density-dependent Selection**
  f_1 is a function of x_1 and $n_1 + n_2$
- **Frequency-dependent Selection**
  f_1 is a function of x_1 and $n_1 / (n_1 + n_2)$ and x_2

} both are generic

The Context of Evolution is Ecology

The Ecological Theater and the Evolutionary Play

G. E. Hutchinson (1967)

2 Models of Adaptive Dynamics

Four Models of Adaptive Dynamics

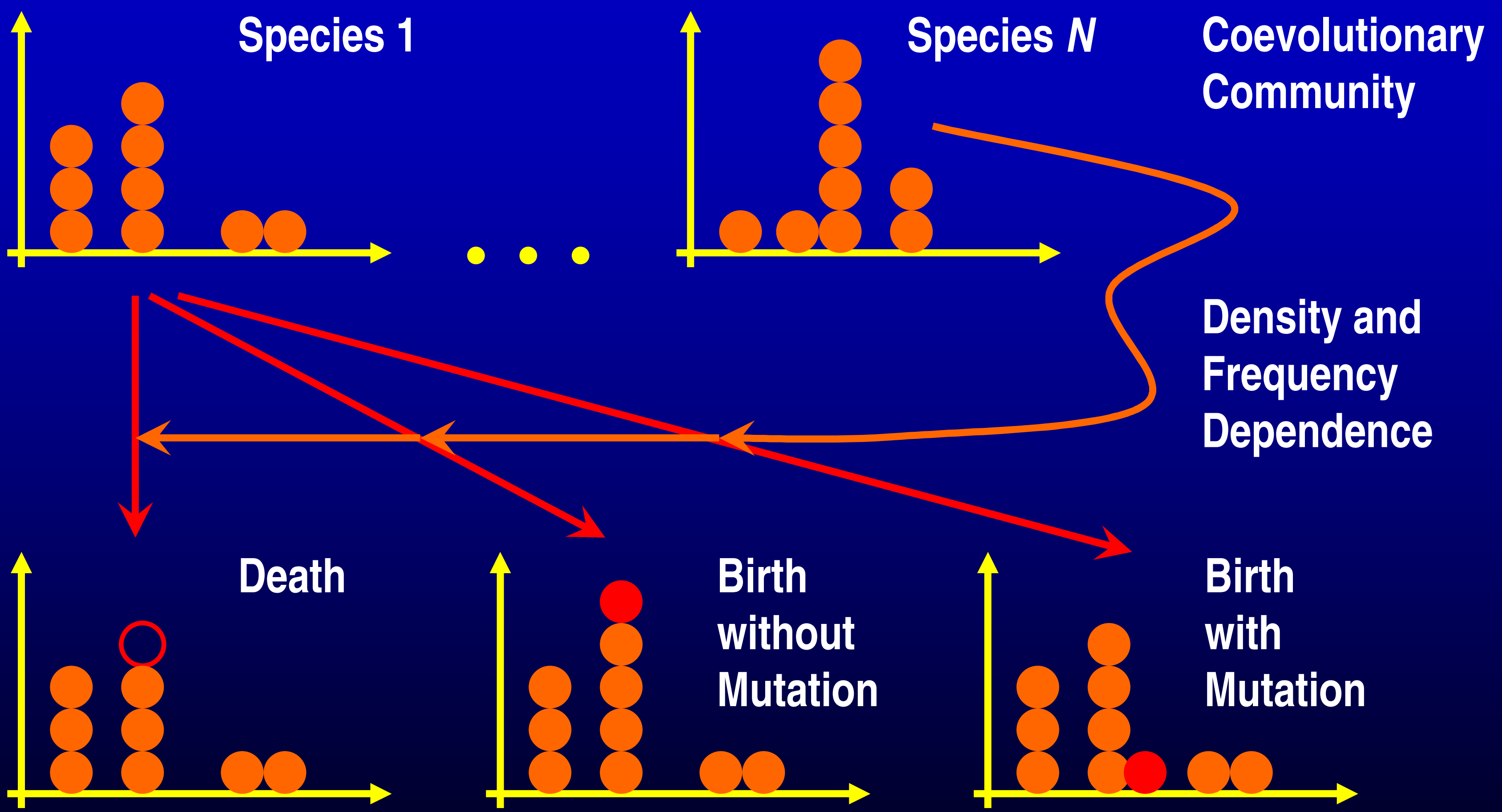
PS	MS	MD	PD

These models describe

- either polymorphic or monomorphic populations
- either stochastic or deterministic adaptive dynamics

Birth-Death-Mutation Processes

Polymorphic and Stochastic

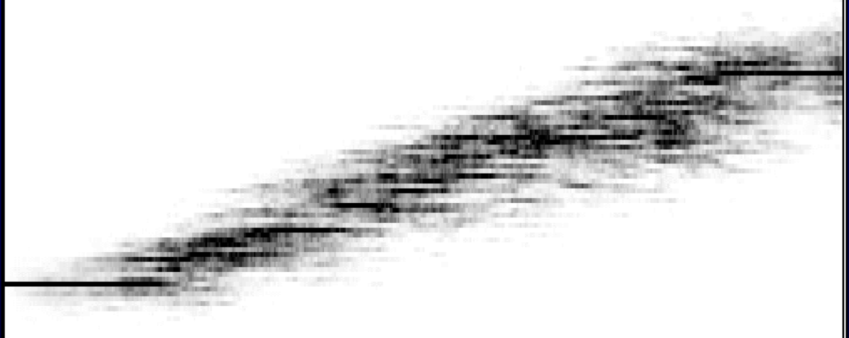


Minimal Process Method

- Determine the birth and death rates of all individuals.
- Add these to obtain the total birth rate and total death rate, and add the latter to obtain the total event rate.
- Choose the time until the next event from an exponential probability distribution with a mean given by the total event rate.
- Randomly choose an event type according to the contribution of total birth and death rates to the total event rate.
- Randomly choose an individual according to its contribution to the total rate of the chosen even type.
- If the event is a birth, potentially carry out a mutation.
- Implement chosen event on chosen individual at chosen time, and start over.

Effect of Mutation Probability

Large: 10%

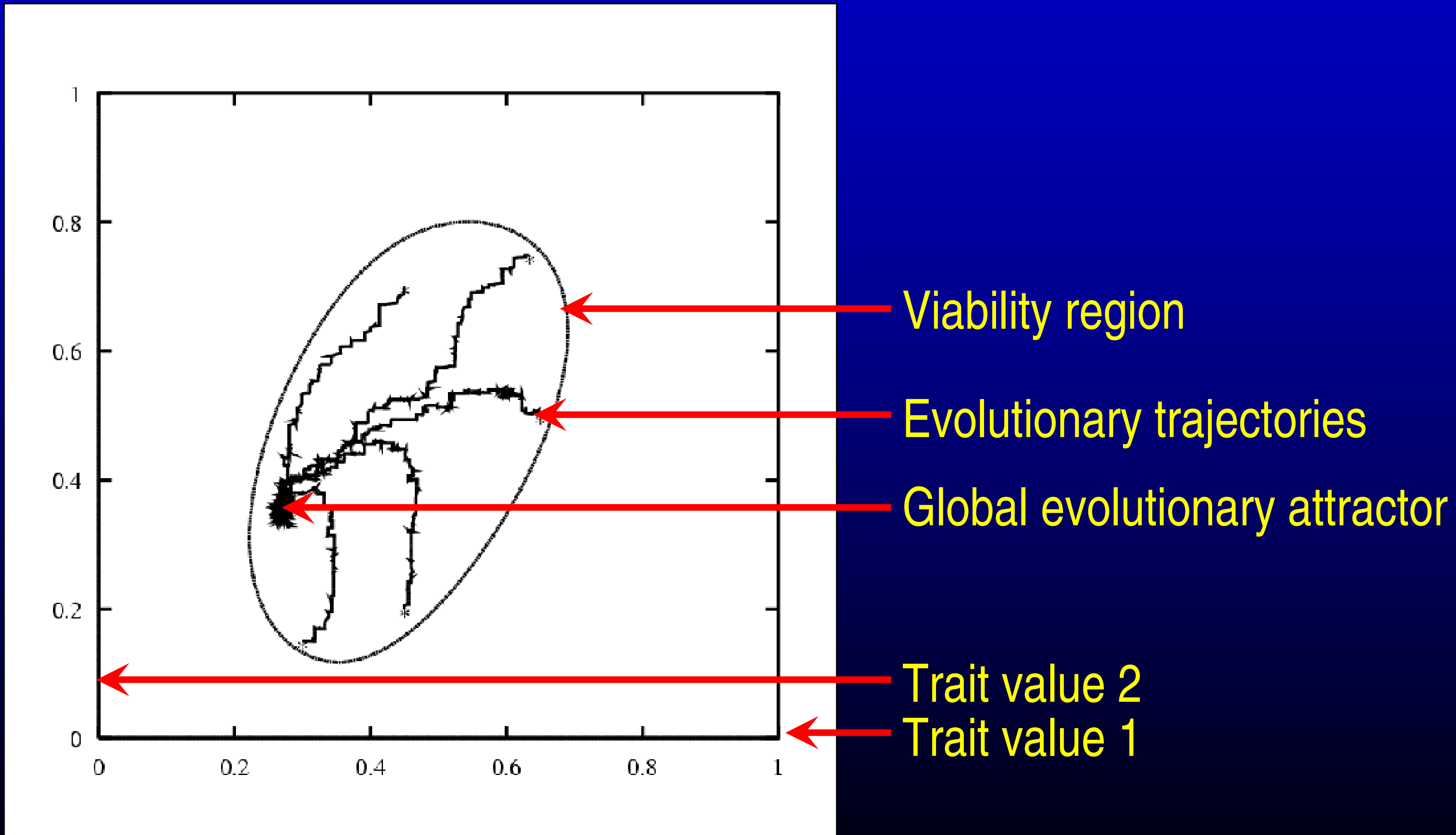


Mutation-Selection Equilibrium

Small: 0.1%

Mutation-limited Evolution

Illustration



Random Walk Models

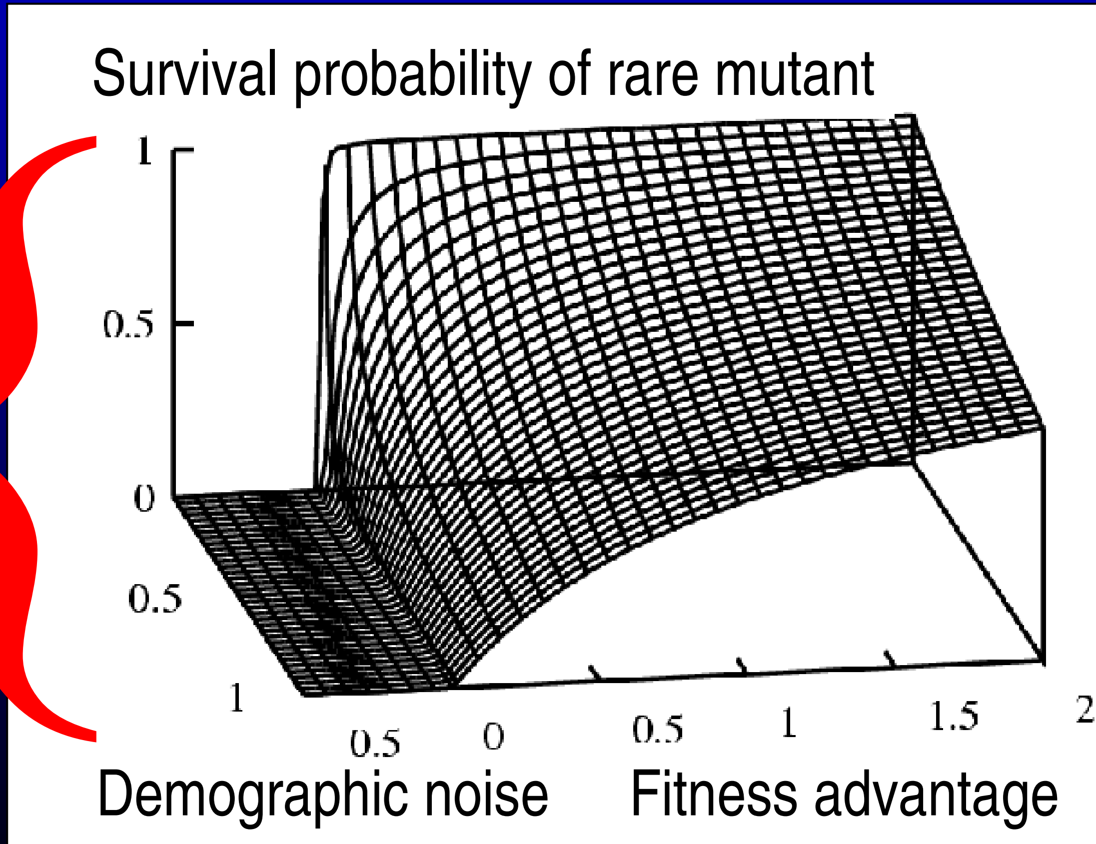
Monomorphic and Stochastic

- **Probability for a Trait Substitution**

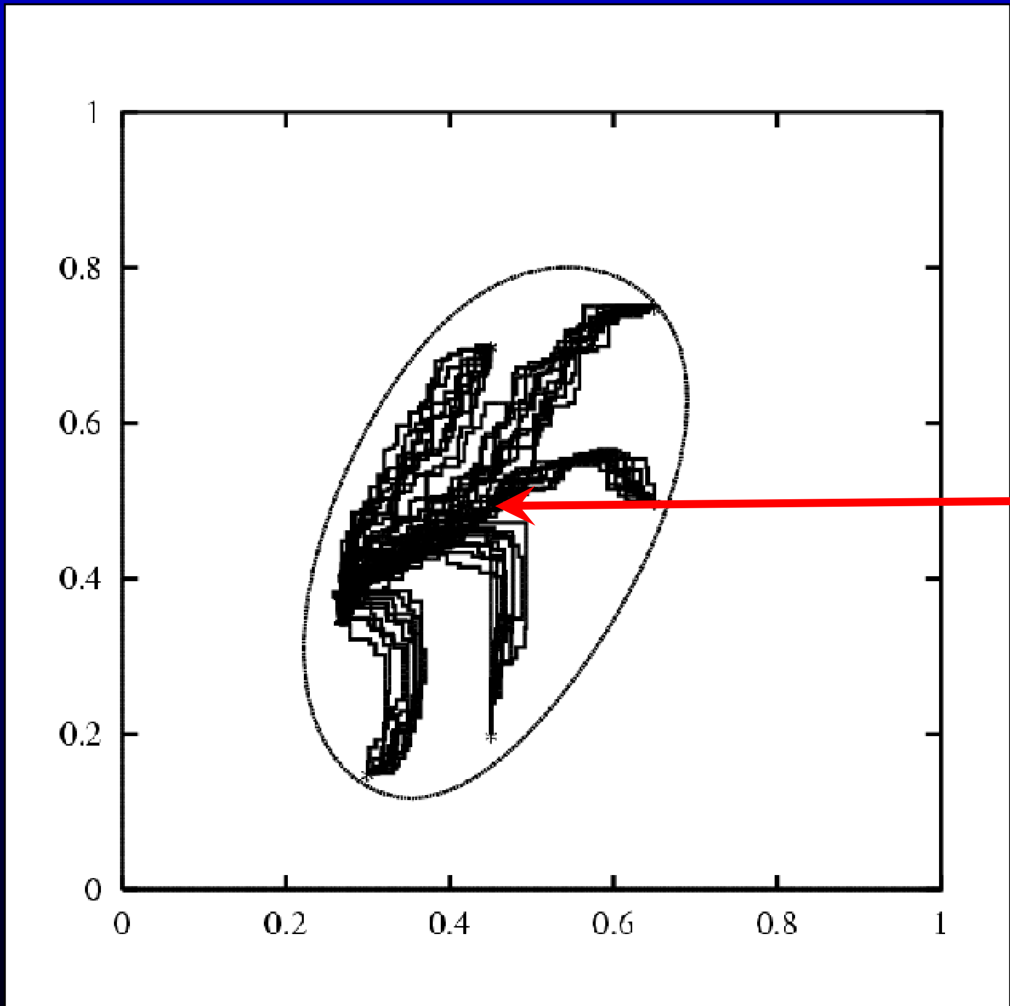
❶ **Mutation**
Population dynamics

❷ **Invasion**
Branching process theory

❸ **Fixation**
Invasion implies fixation

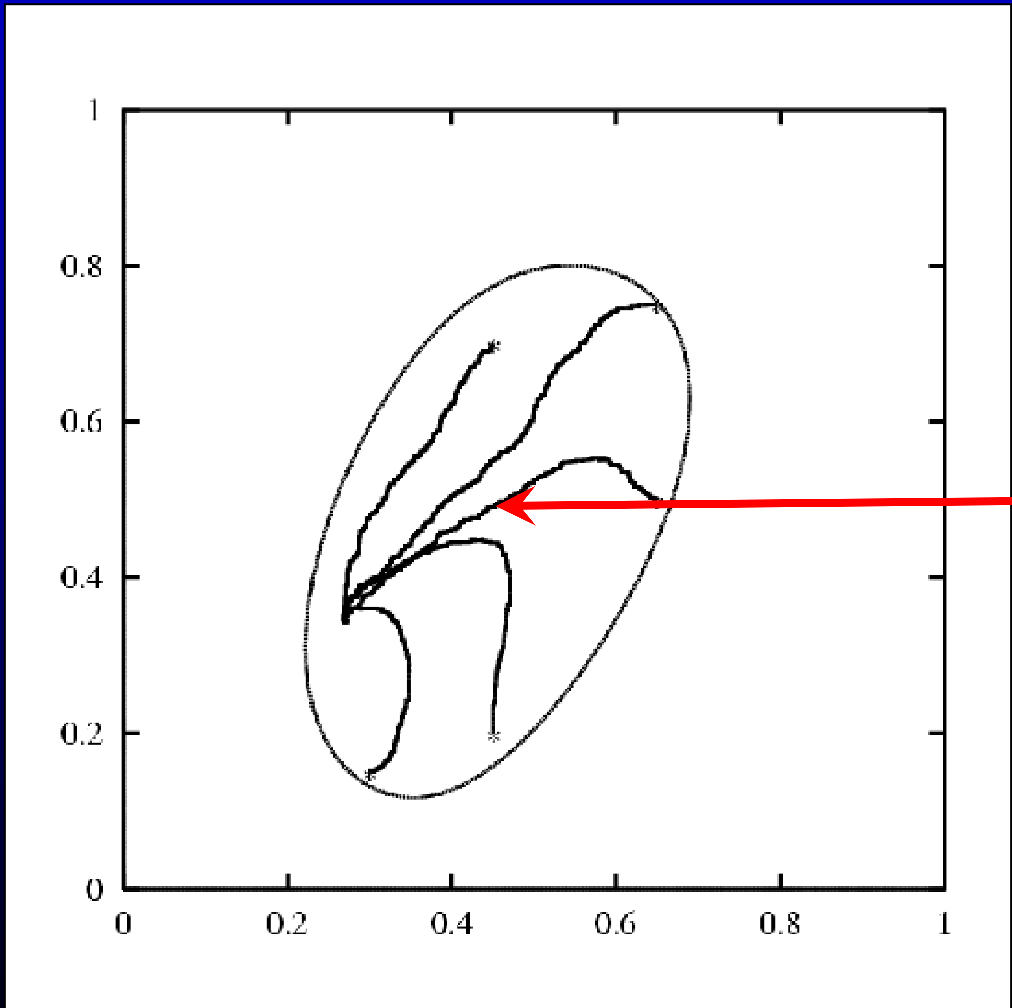


Illustration



Bundles of
evolutionary trajectories

Illustration



Mean
evolutionary trajectories

Hill-climbing on Adaptive Landscapes

Monomorphic and Deterministic

- **Canonical equation of adaptive dynamics**

$$\frac{d}{dt}x_i = \frac{1}{2}\mu_i n_i \sigma_i^2 \frac{\partial}{\partial x_i'} f_i(x_i', x)\Big|_{x_i' = x_i}$$

evolutionary rate in species *i*

mutation probability

population size

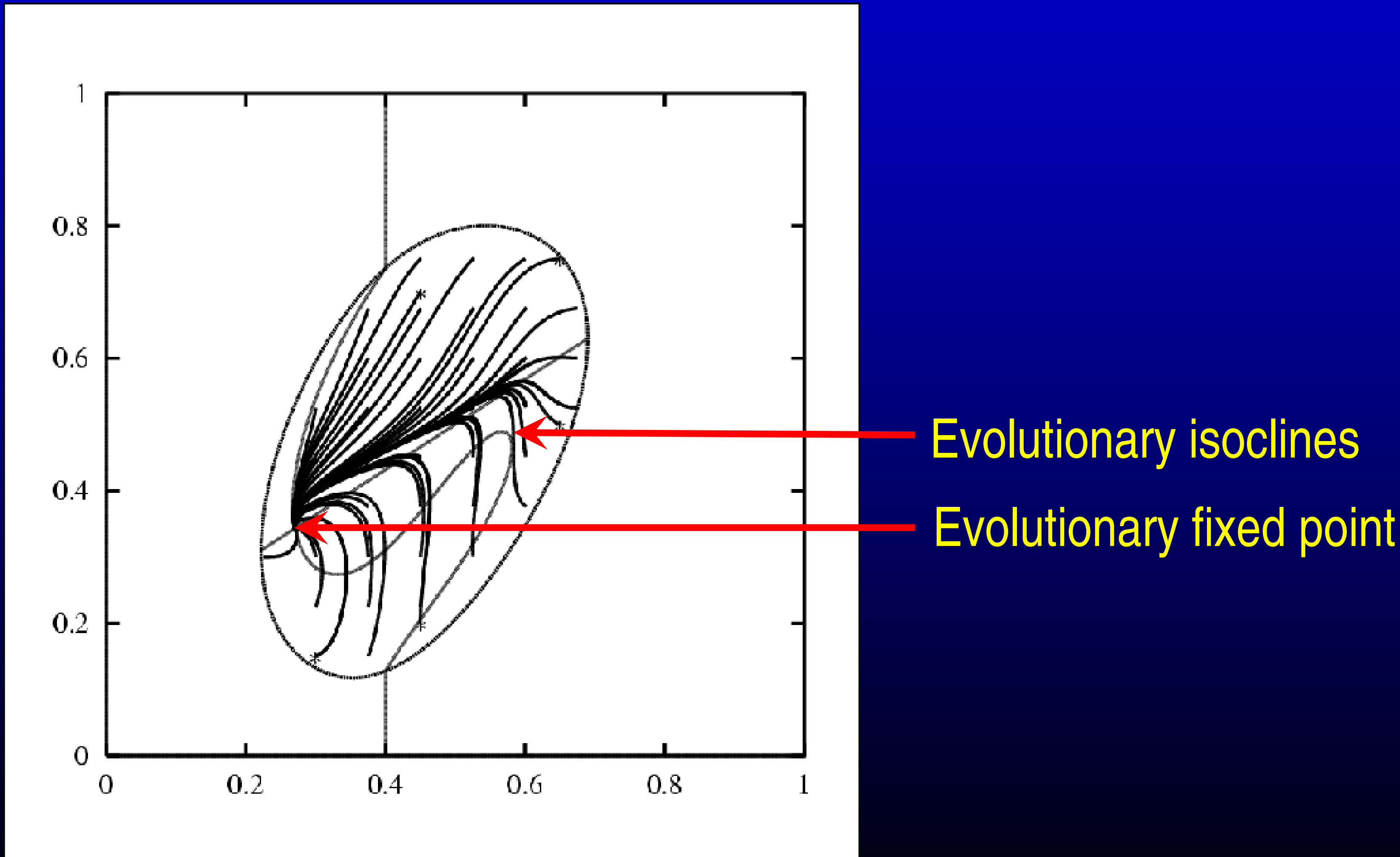
mutation variance-covariance

local selection gradient

invasion fitness

Dieckmann and Law (1996)

Illustration



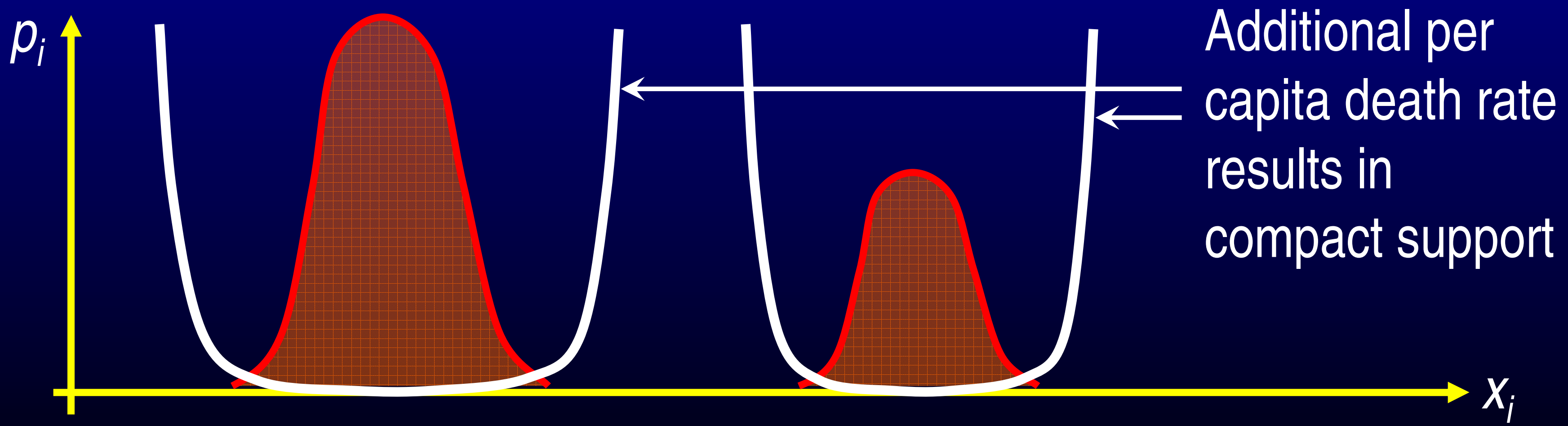
Reaction-Diffusion Models

Polymorphic and Deterministic

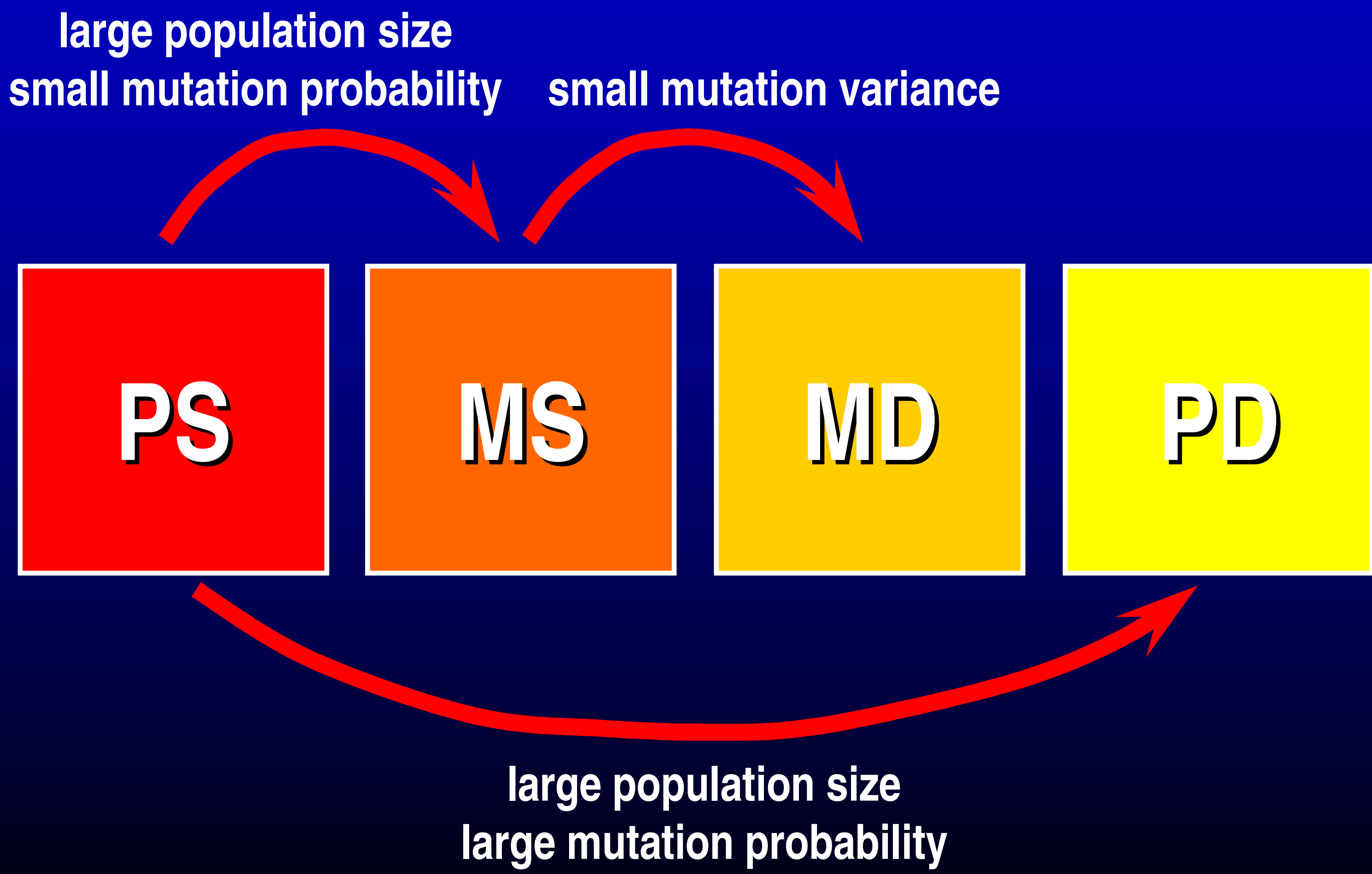
- **Kimura limit**

$$\frac{d}{dt} p_i(x_i) = f_i(x_i, p)\, p_i(x_i) + \frac{1}{2} \mu_i \sigma_i^2 \frac{\partial^2}{\partial x_i^2} b_i(x_i, p)\, p_i(x_i)$$

- **Finite-size correction**



Summary of Derivations

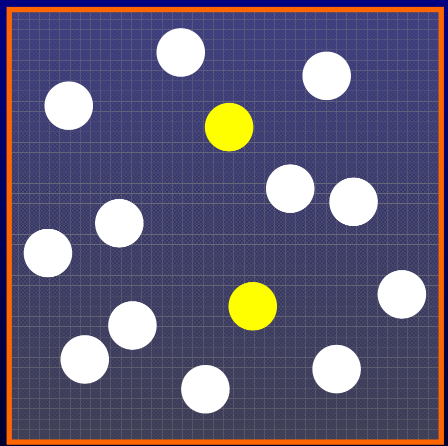


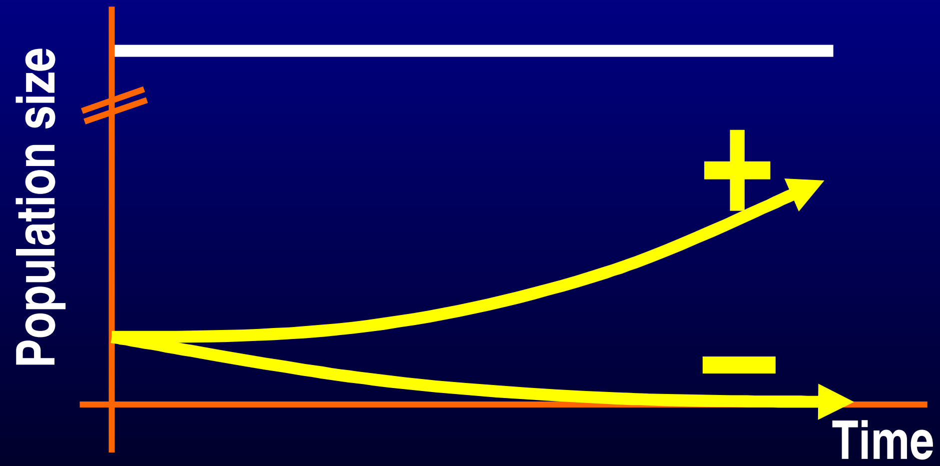
3 Evolutionary Invasion Analysis

Invasion Fitness

- **Definition**

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





Metz *et al.* (1992)

Invasion Fitness

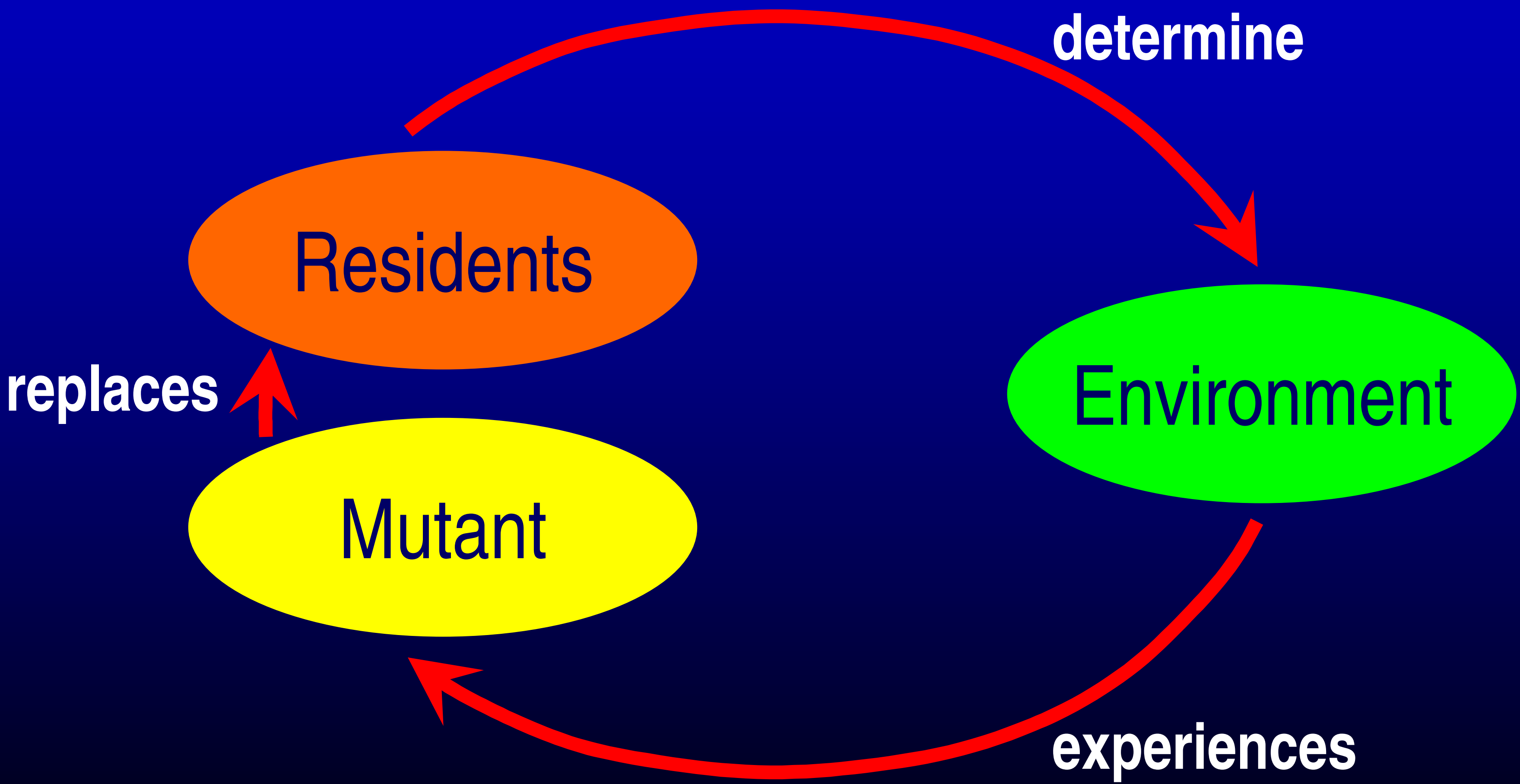
- Fitness is a function of two variables:

$$f(x', x)$$

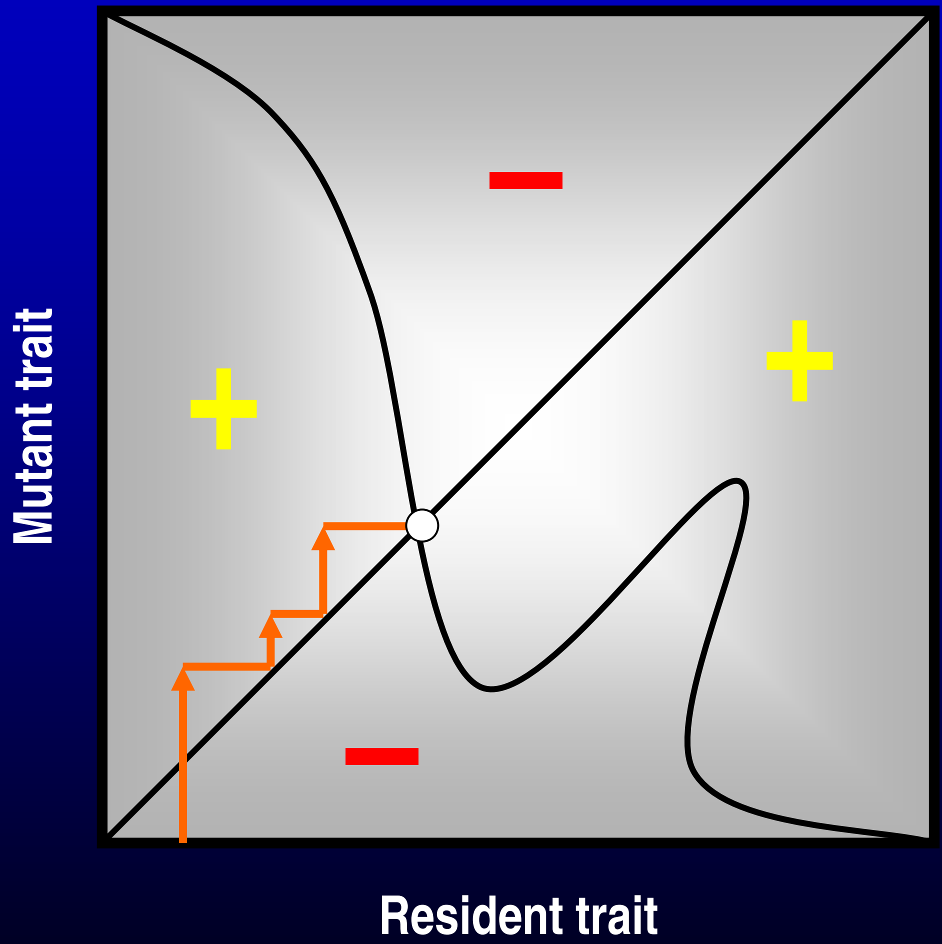
mutant trait — x'

resident trait: determines environment — x

Environmental Feedback



Pairwise Invasibility Plots (PIPs)

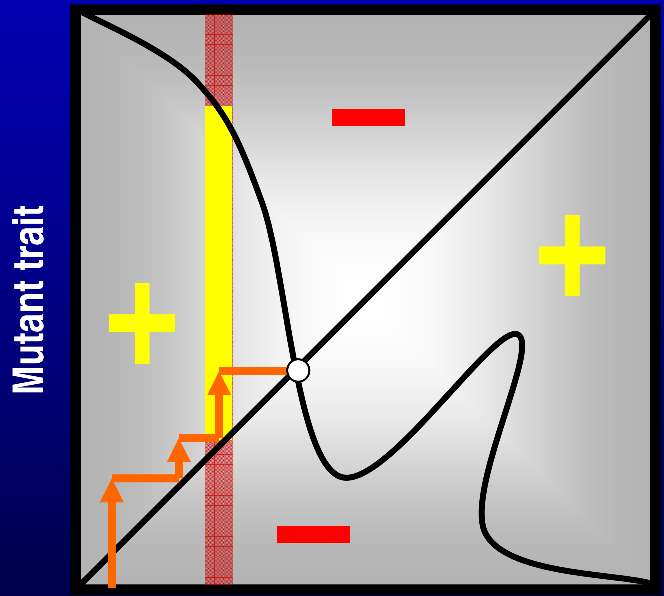


- **+** Invasion of the mutant into the resident population possible
- **–** Invasion impossible
- One trait substitution
- Singular phenotype

Geritz *et al.* (1997)

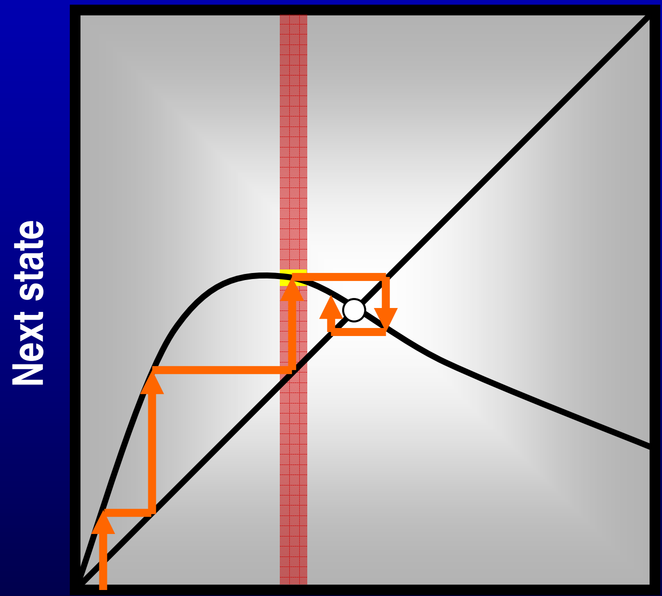
Reading PIPs: Comparison with Recursions

- **Trait substitutions**



Size of vertical steps stochastic

- **Recursion relations**

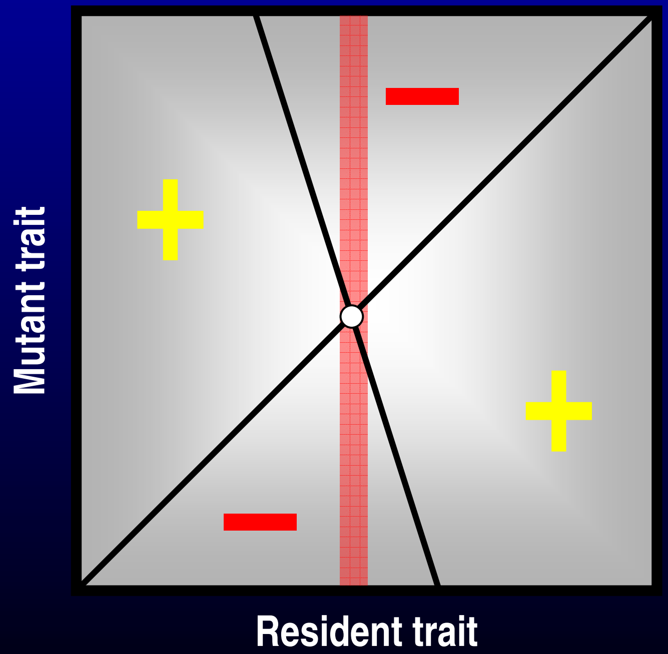


Size of vertical steps deterministic

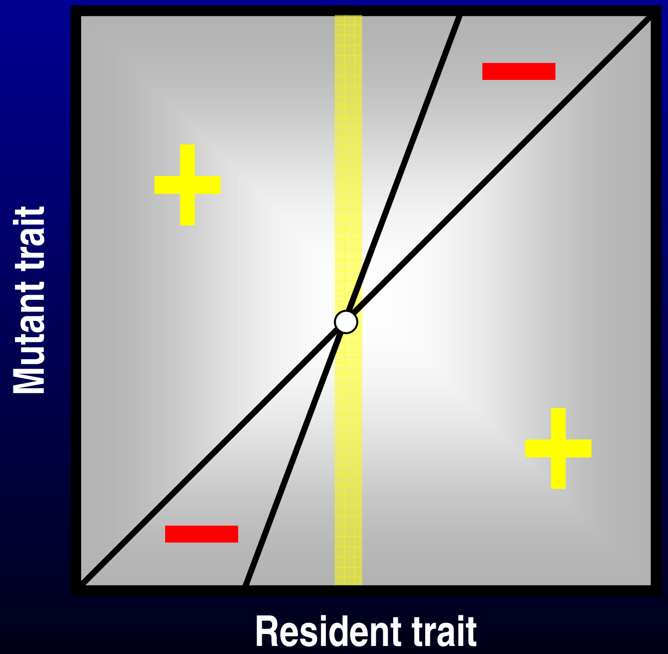
Reading PIPs: Evolutionary Stability

- Is a singular phenotype immune to invasions by neighboring phenotypes?

Yes:

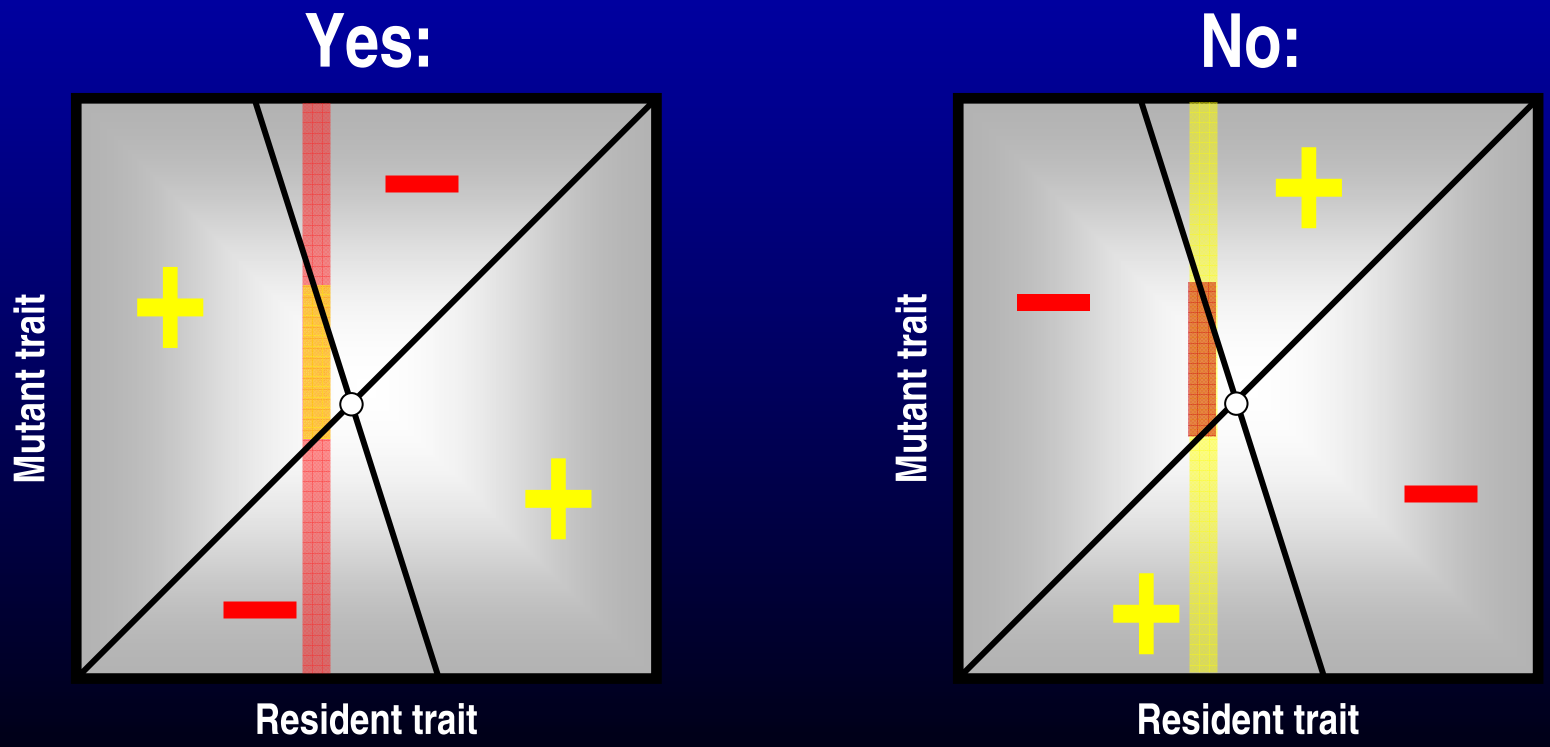


No:



Reading PIPs: Convergence Stability

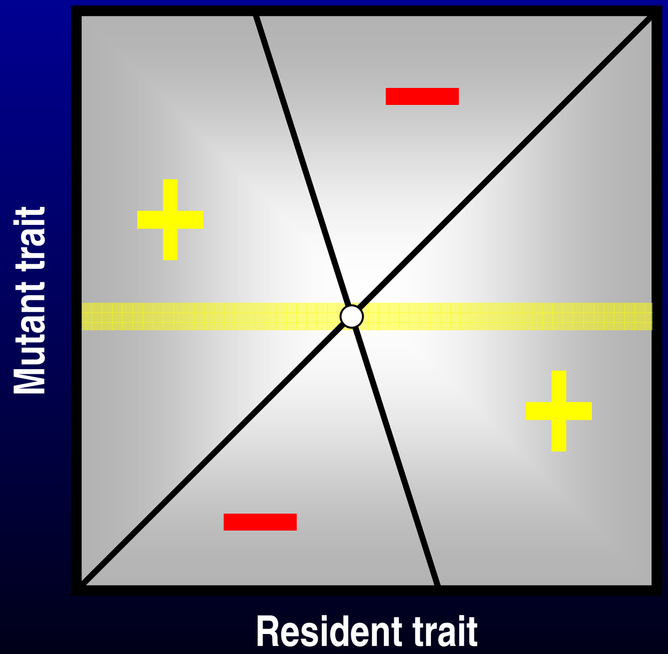
- When starting from neighboring phenotypes, do successful invaders lie closer to the singular one?



Reading PIPs: Invasion Potential

- Is the singular phenotype capable of invading into all its neighboring types?

Yes:



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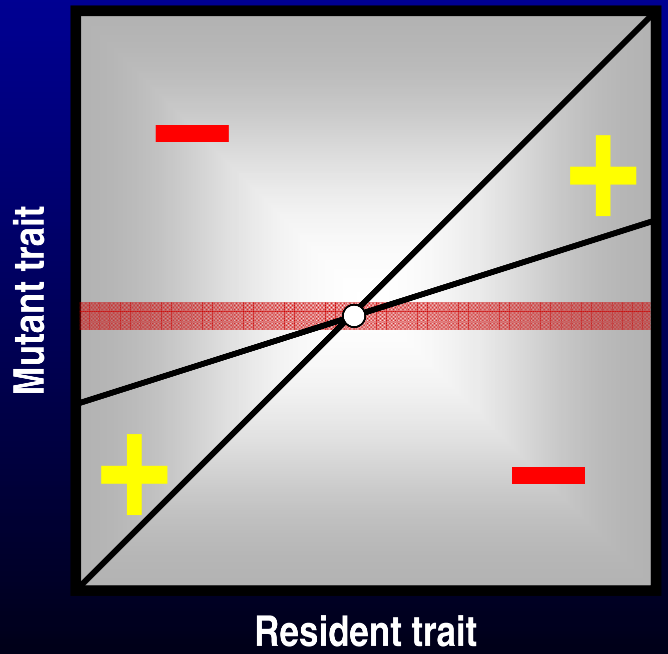
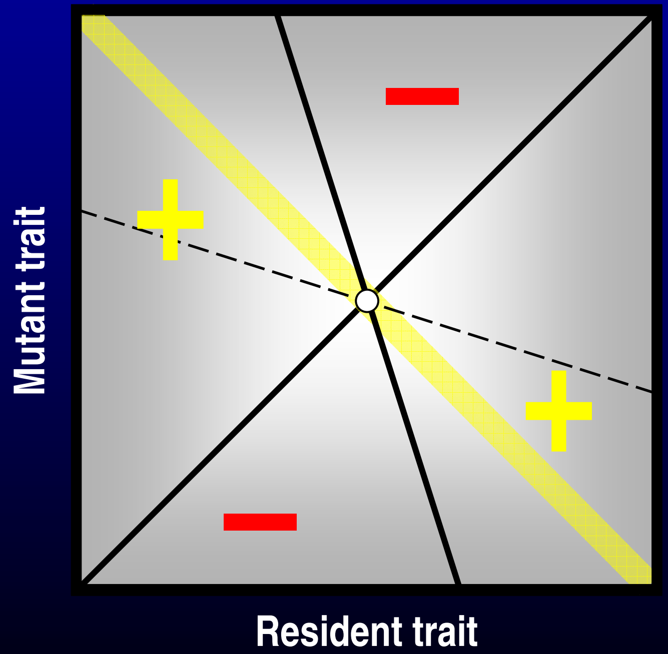


Reading PIPs: Mutual Invasibility

- Can a pair of neighboring phenotypes on either side of a singular one invade each other?

Yes:



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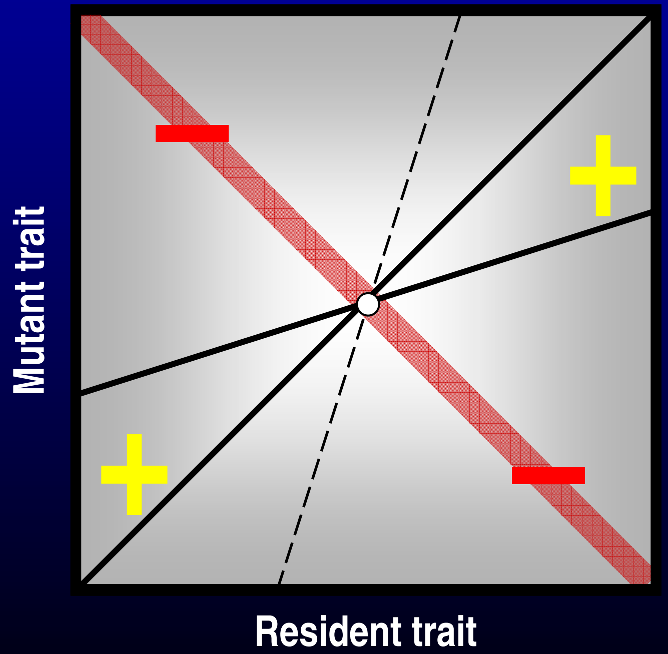
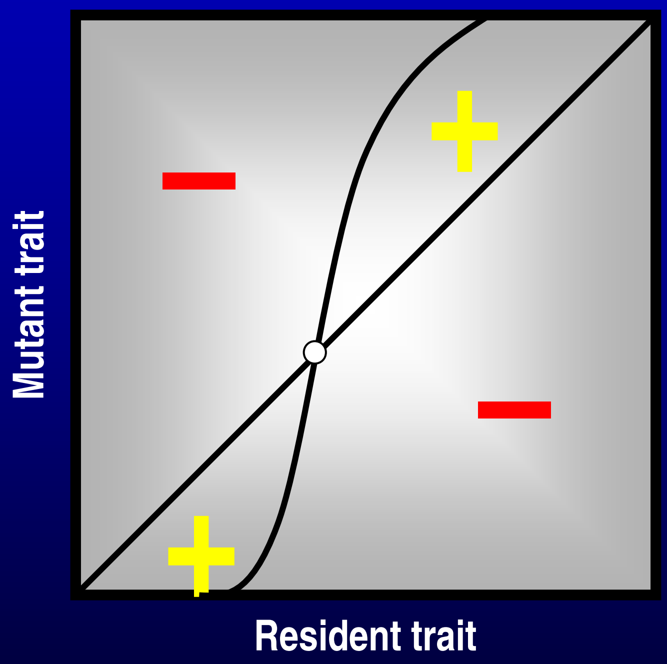


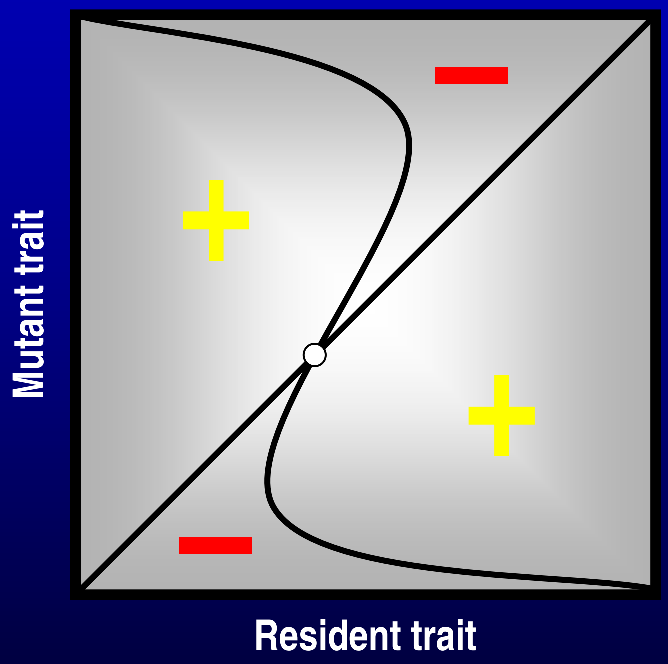
Two Especially Interesting Types of PIP

- **Garden of Eden**



Evolutionarily stable,
but not convergence stable

- **Branching Point**



Convergence stable,
but not evolutionarily stable

4

Example: Resource Competition

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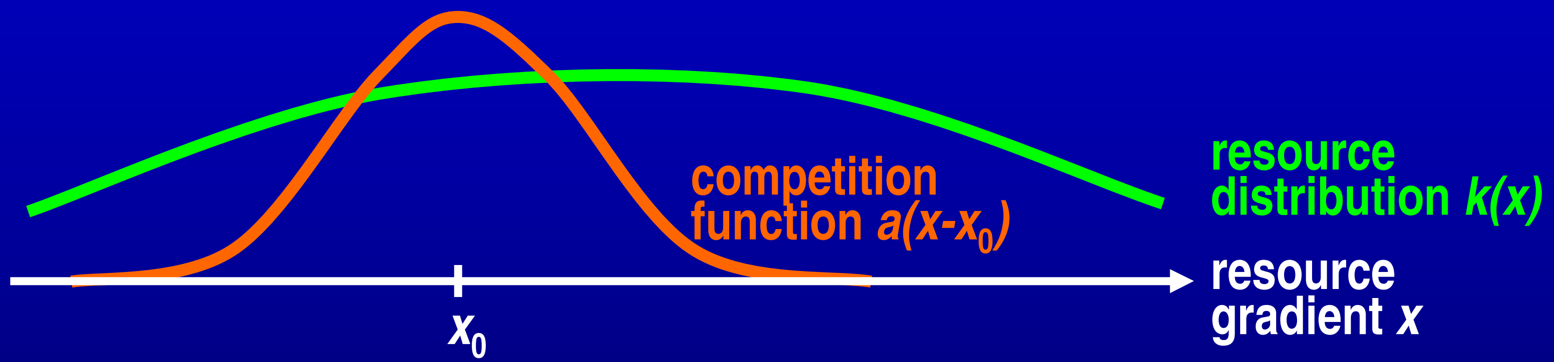


Dynamics of population sizes n_i of strategy x_i

$$\frac{d}{dt} n_i = r\, n_i \left[1 - \frac{1}{k(x_i)} \quad {}_j\, a(x_i - x_j)\, n_j \right]$$

Analysis of Example

■ **Step 1: Invasion Fitness**

$$f(x', x) = r[1 - \frac{1}{k(x')}(a(0)n' + a(x' - x)n)]$$

1 $n' \to 0$

2 $n \to n_{\mathrm{eq}} = k(x)$

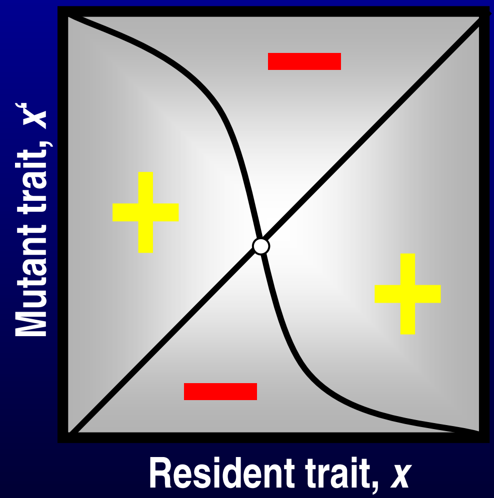
$$f(x', x) = r[1 - a(x' - x)\frac{k(x)}{k(x')}]$$

Analysis of Example

- **Step 2: Pairwise Invasibility Plots**

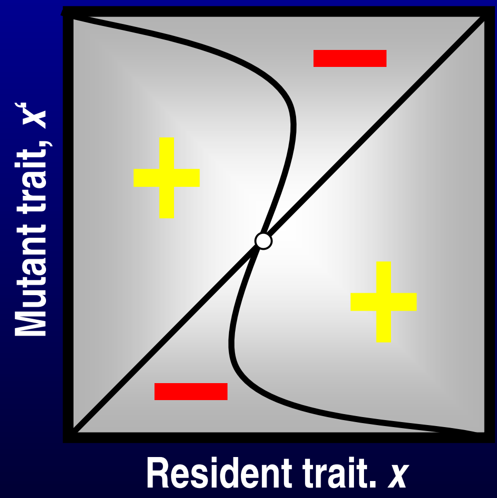
With $k = k_0\ N(0,\sigma_k)$ and $a = N(0,\sigma_a)$ we obtain

for $\sigma_a > \sigma_k$



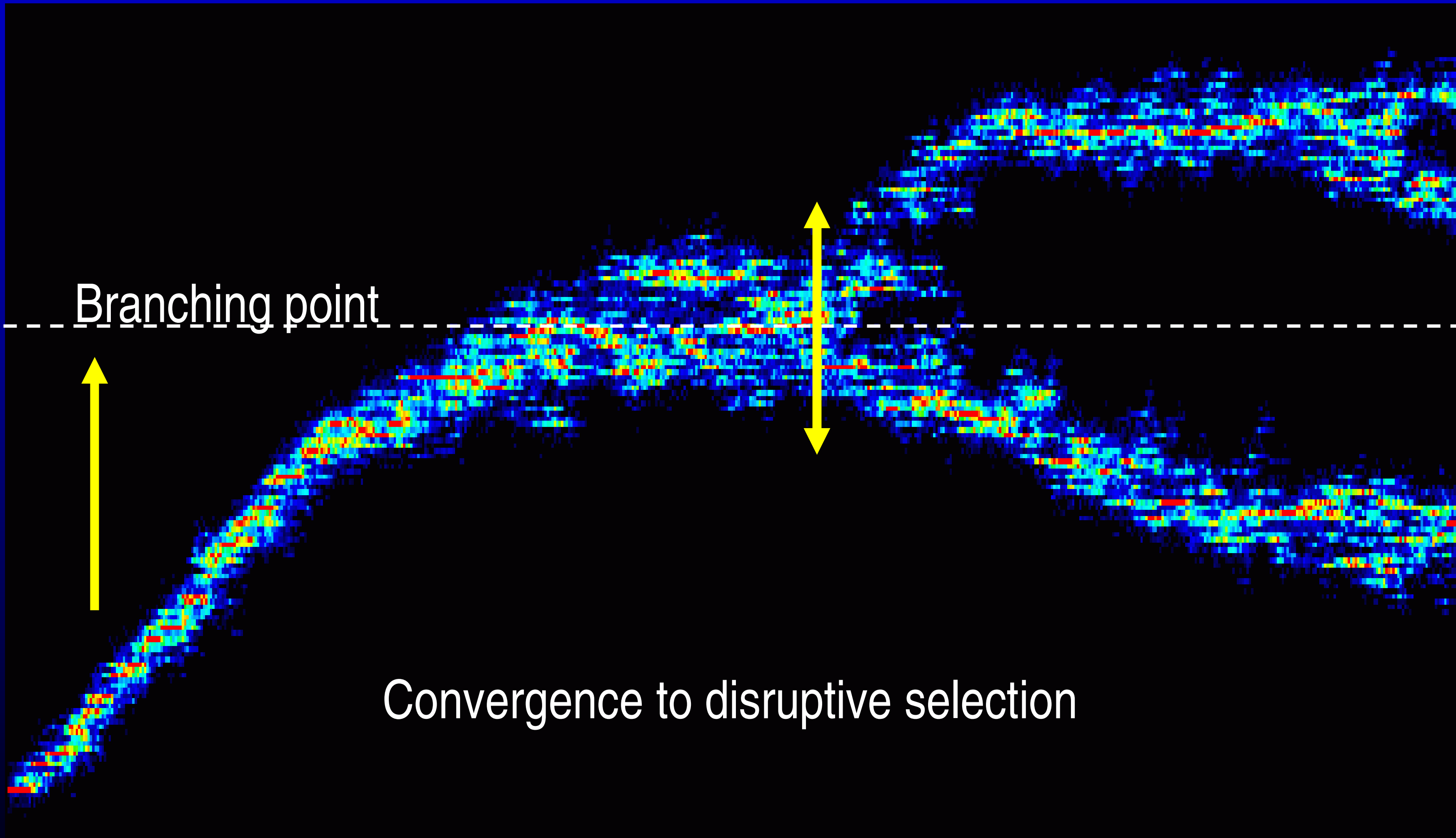
Evolutionary Stability

for $\sigma_a < \sigma_k$

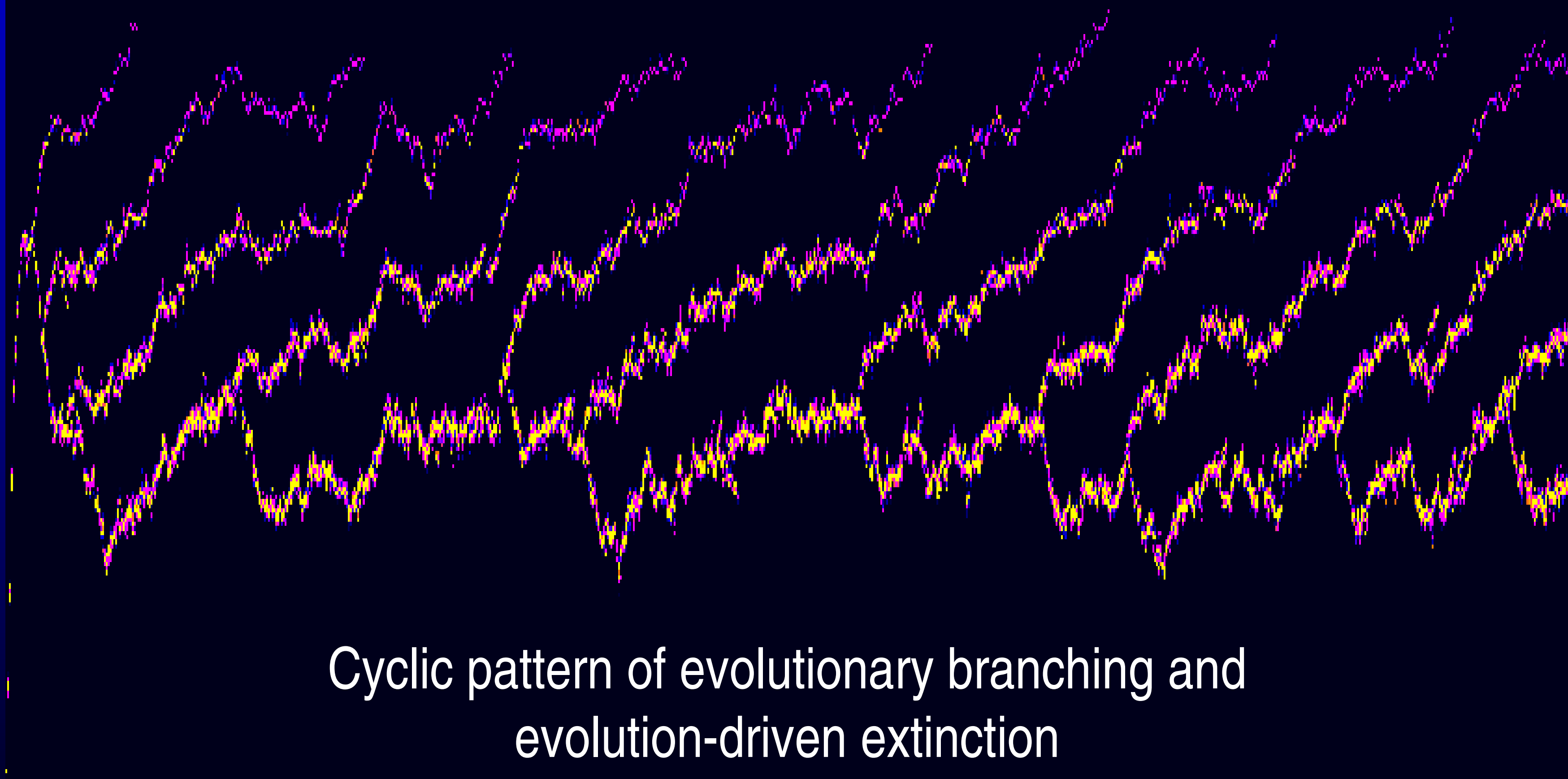


Evolutionary Branching

Evolutionary Branching



Asymmetric Competition: Taxon Cycles



Cyclic pattern of evolutionary branching and evolution-driven extinction