Introduction to Adaptive Dynamics Theory

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Overview

Part A Basic Theory

Part B Examples

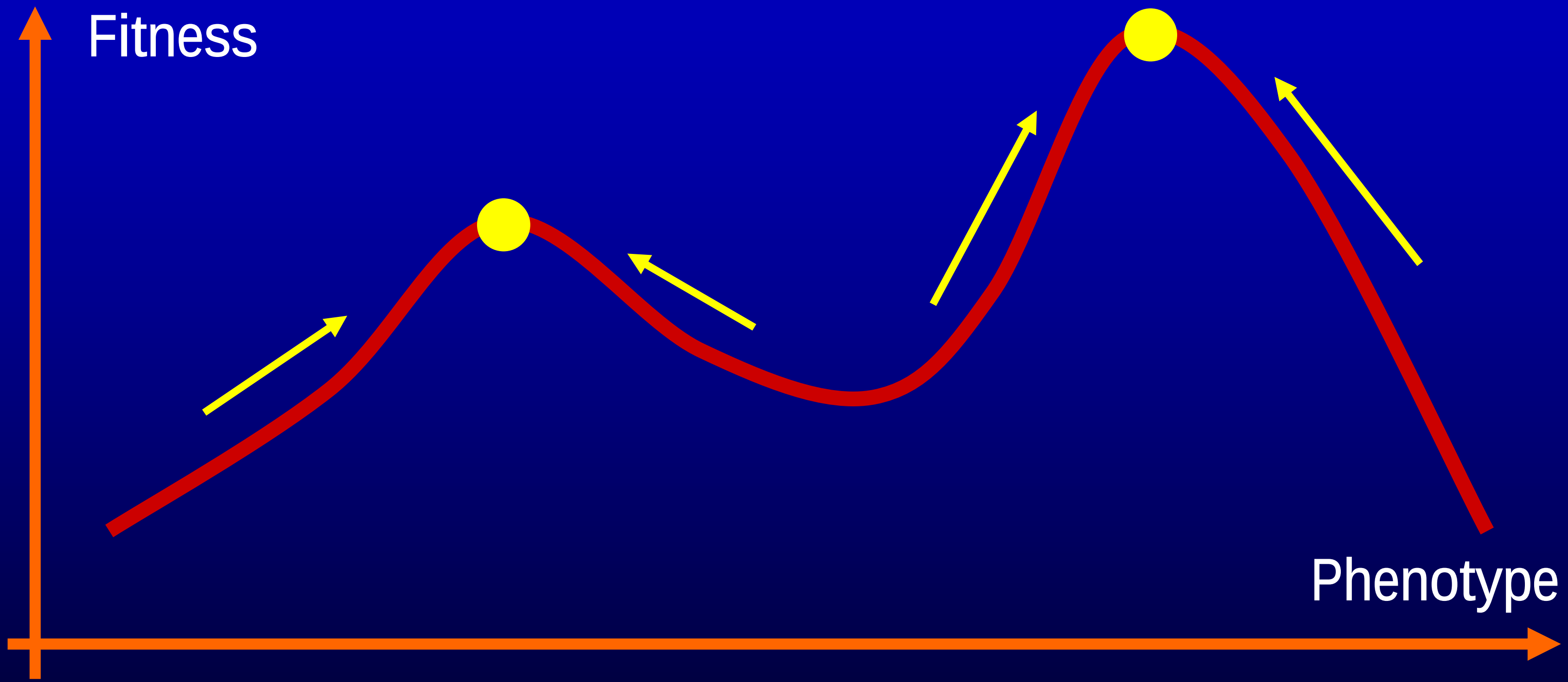
Part C Function-valued Traits

Part A: Overview

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

1 Evolutionary Complexity

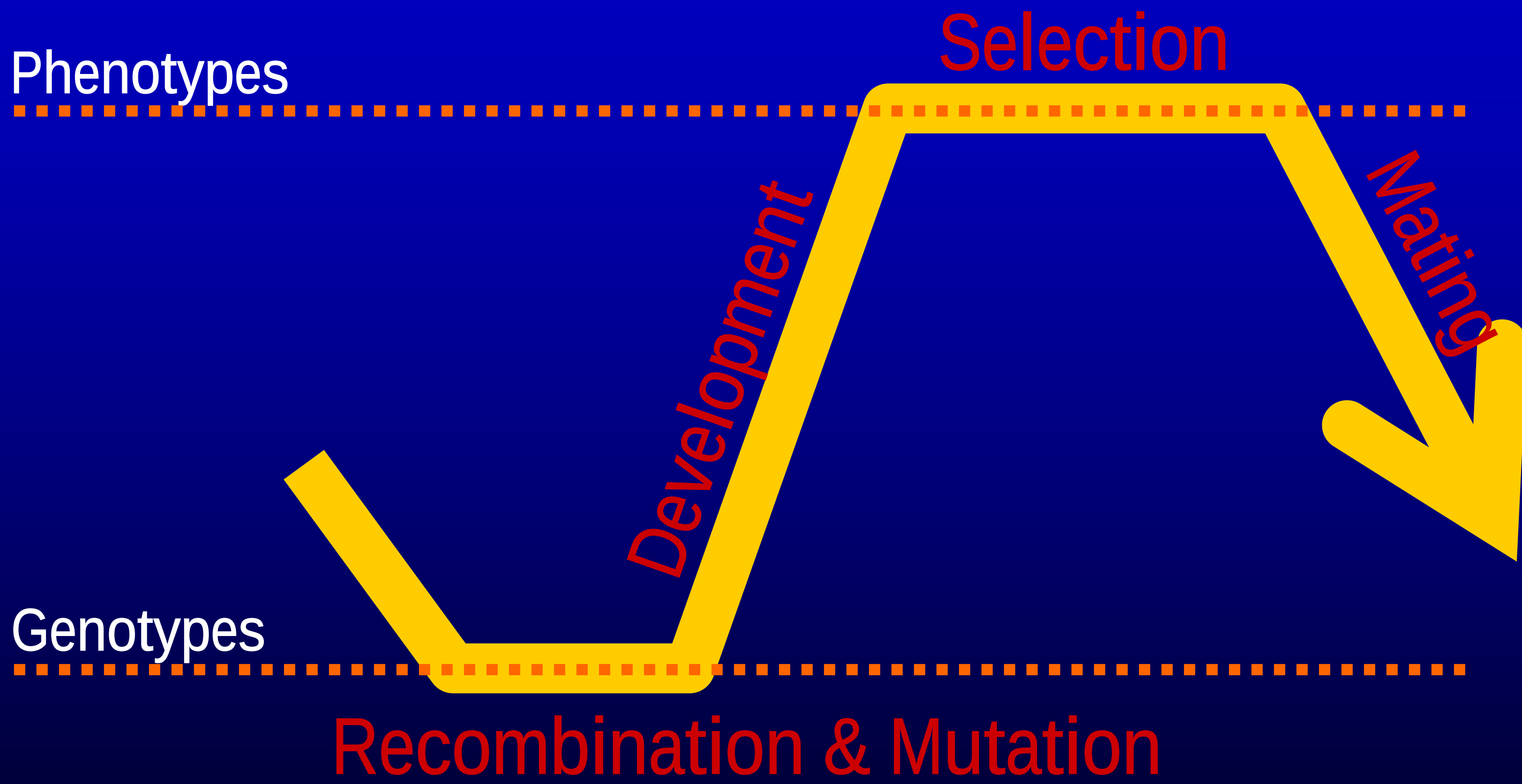
Evolutionary Optimization



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

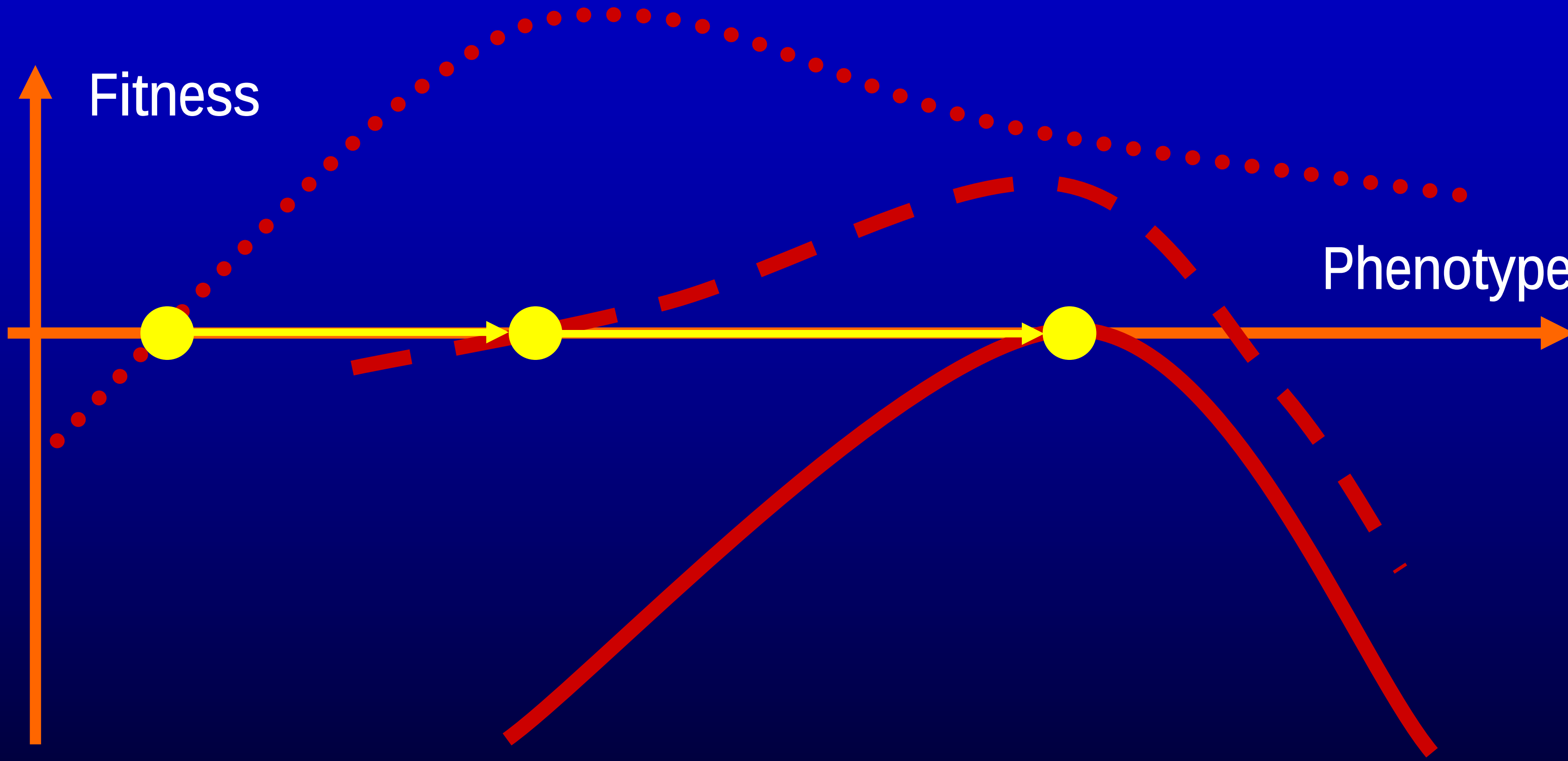
1



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

Frequency-Dependent Selection

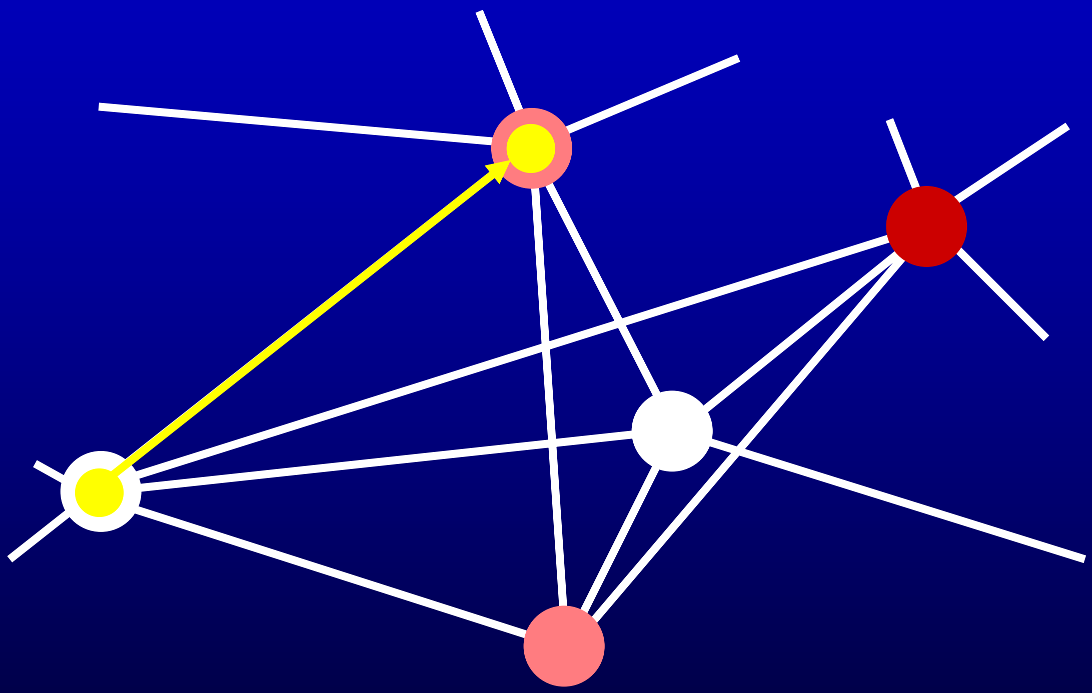
2



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

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

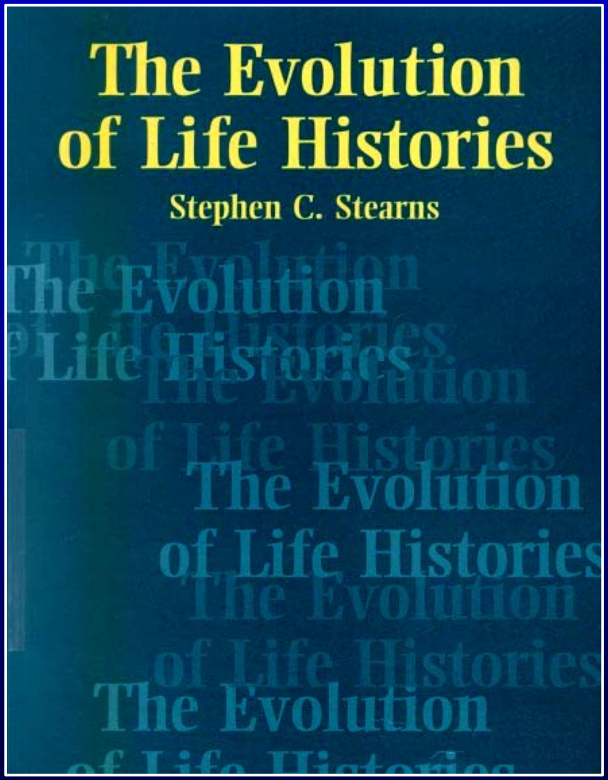
  f_1 is a function of x_1 and $n_1 / (n_1 + n_2)$ and x_2

Both are generic in nature

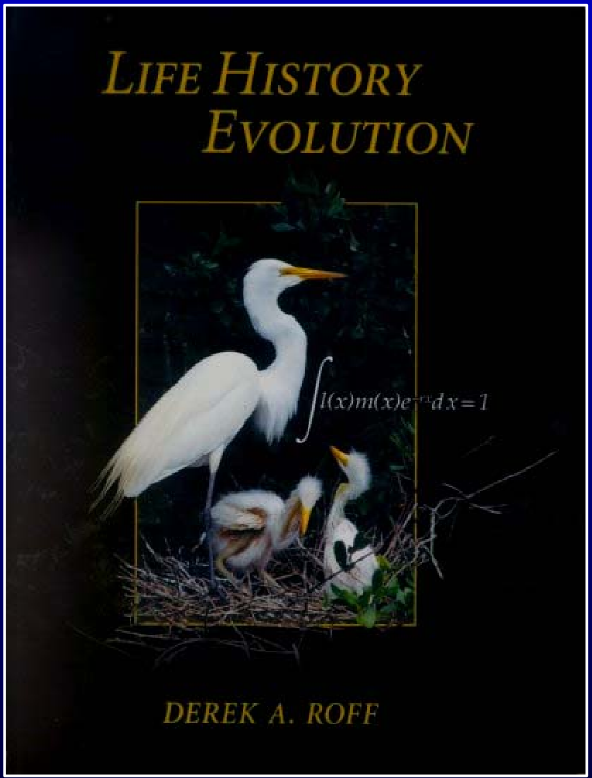
Frequency-dependent Selection

- Coping with frequency-dependent selection arguably is one of the biggest challenge for modern evolutionary theory.
- Frequency dependence arises whenever selection pressures in a population vary with its phenotypic composition.
- Virtually any ecologically serious consideration of life-history evolution implies frequency-dependent selection. Only carefully crafted (or ecologically unrealistic) models circumvent this complication.

Textbook Coverage: Roughly 1%



2 out of 249 pages



5 out of 465 pages

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

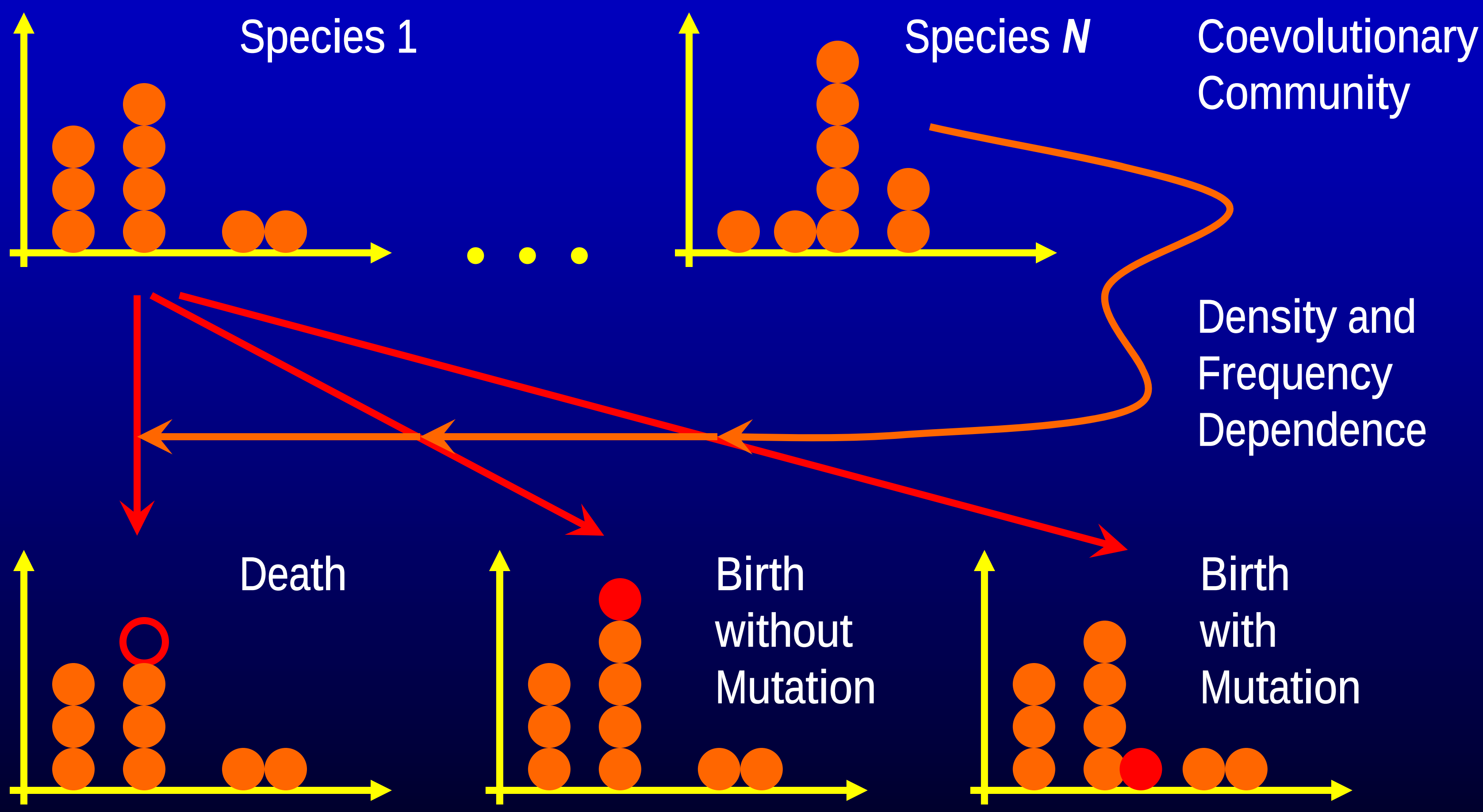
These models describe

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

Birth-Death-Mutation Processes

Polymorphic and Stochastic

Dieckmann (1994)



Minimal Process Method

Gillespie (1976)

- 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

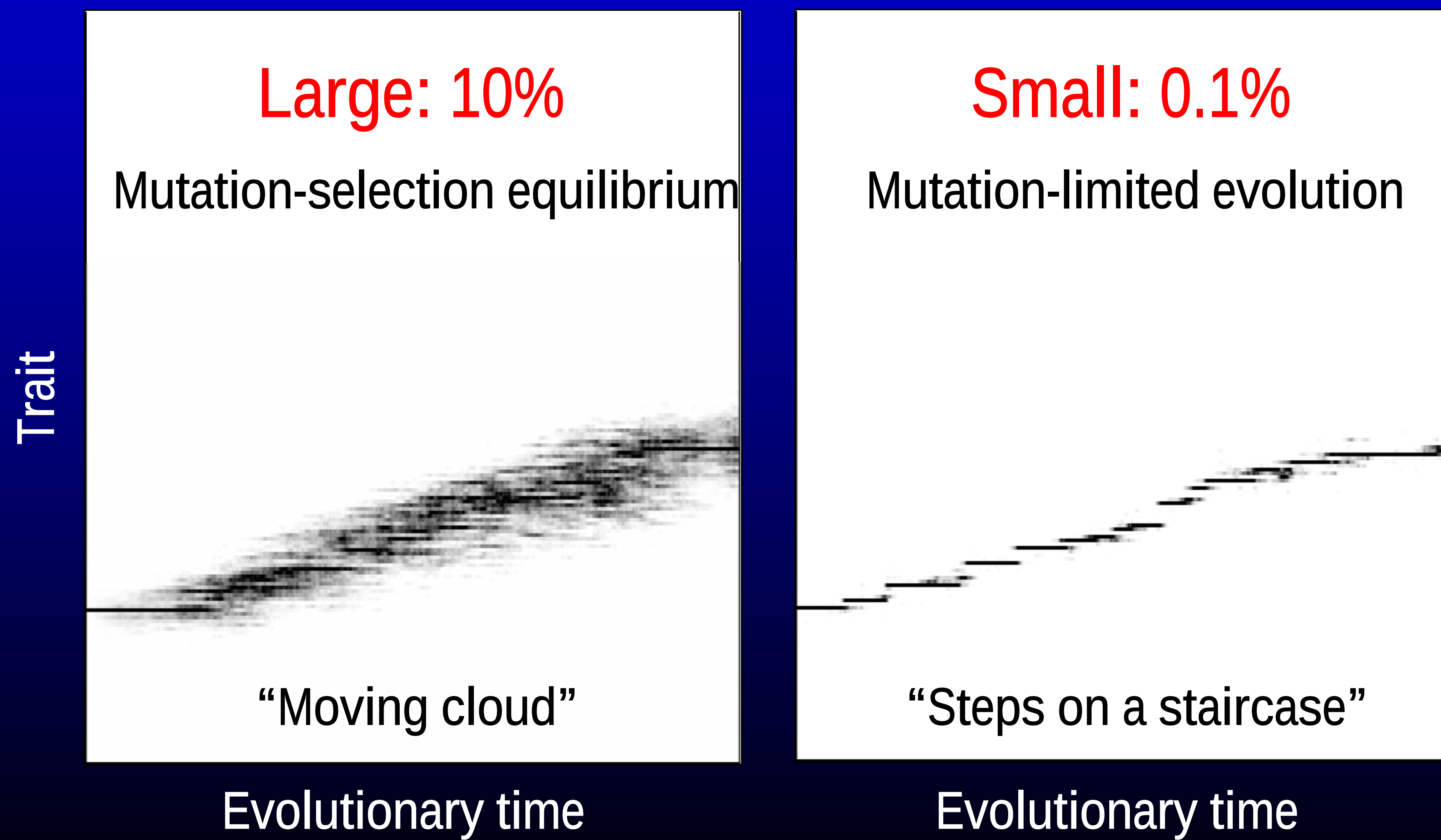
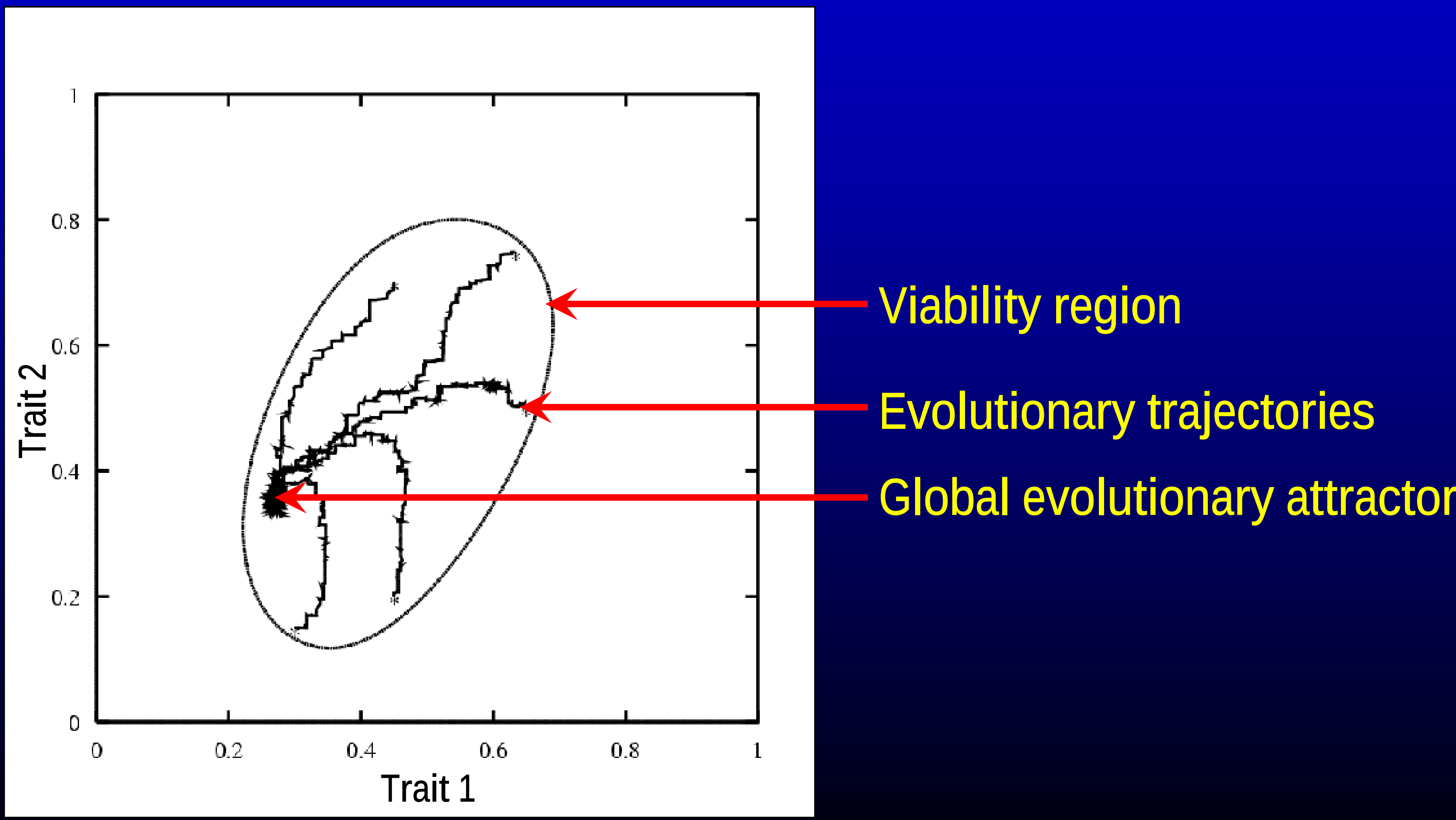


Illustration of Birth-Death-Mutation Processes



Random Walk Models

Monomorphic and Stochastic

Dieckmann & Law (1996)

- Probability for a Trait Substitution

❶ **Mutation**
Population dynamics

❷ **Invasion**
Branching process theory

❸ **Fixation**
Invasion implies fixation

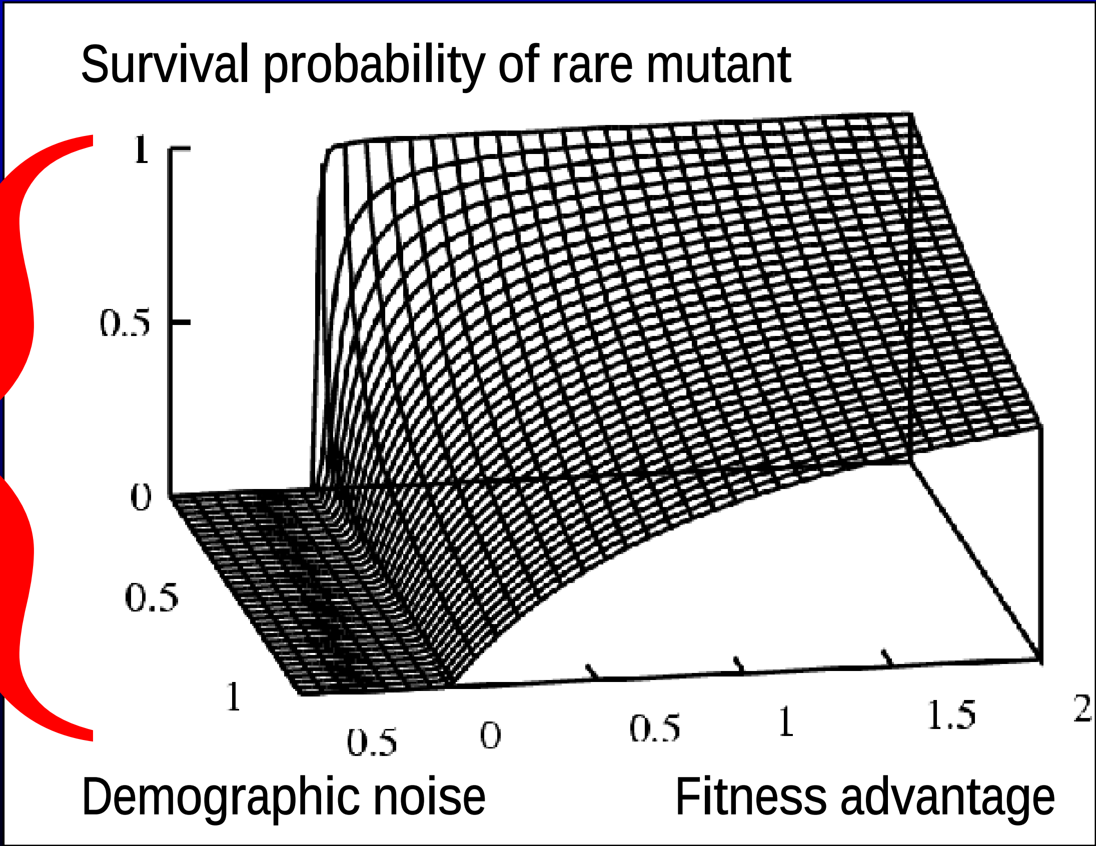
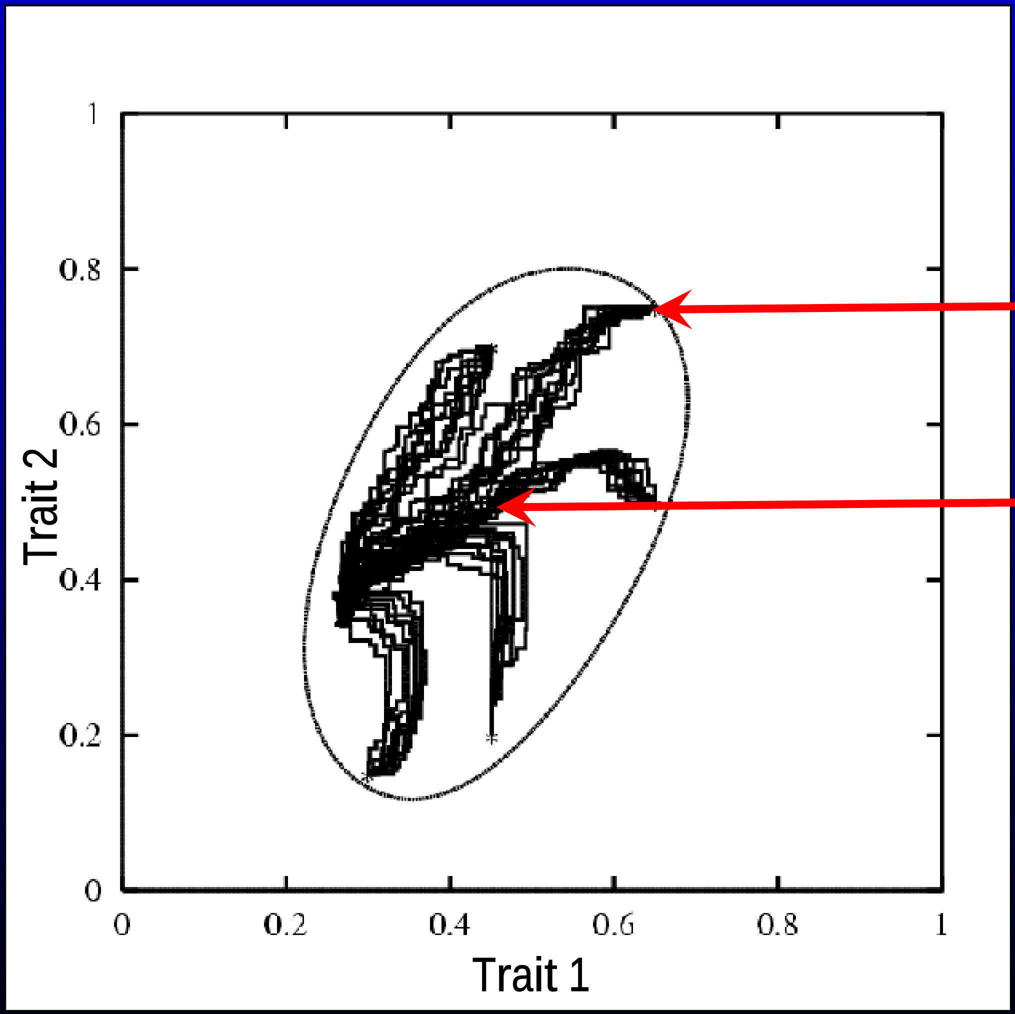


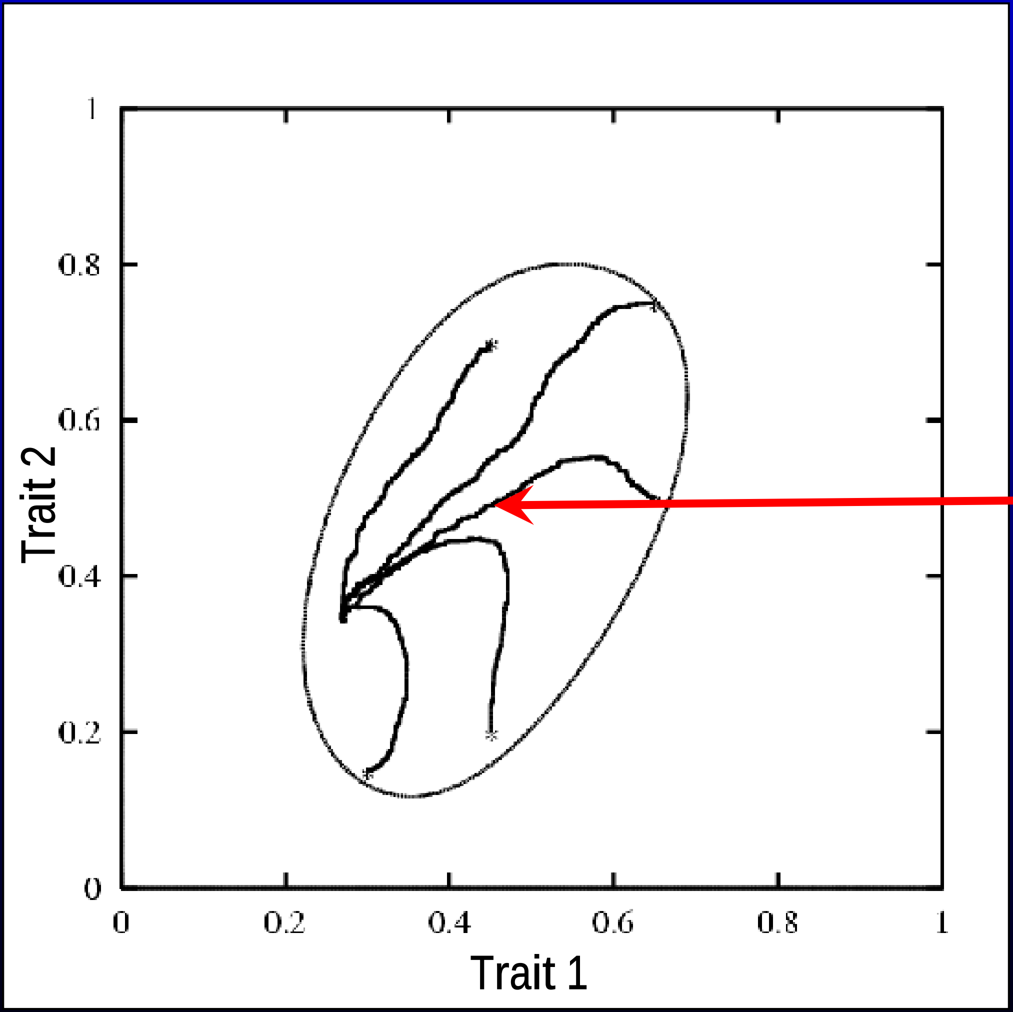
Illustration of Evolutionary Random Walks



Initial condition

Bundles of evolutionary trajectories

Illustration of Averaged of Random Walks



Mean
evolutionary trajectories

Hill-climbing on Adaptive Landscapes

Monomorphic and Deterministic

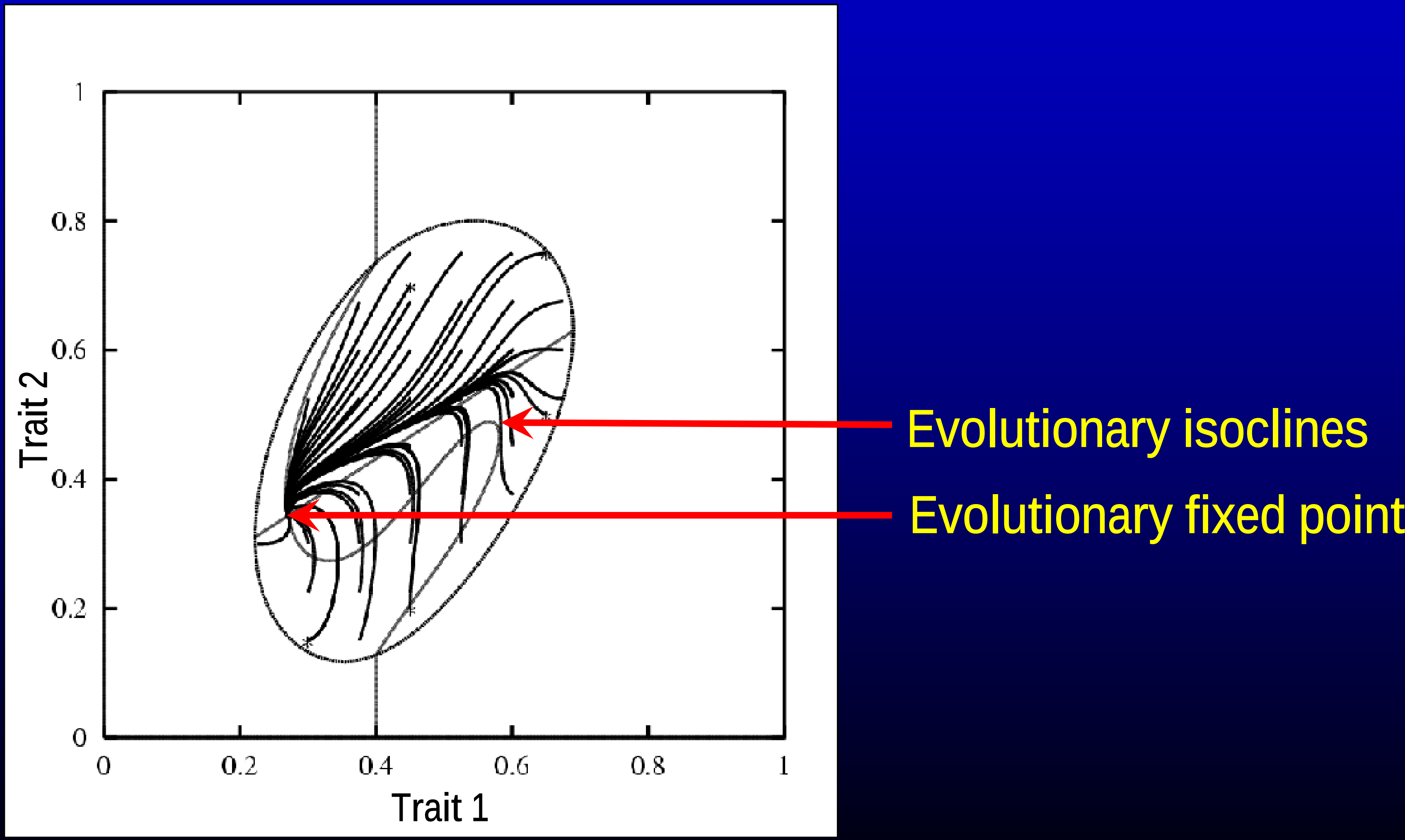
Dieckmann & Law (1996)

- Canonical equation of adaptive dynamics

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

- $\frac{d}{dt} x_i$: evolutionary rate in species *i*
- μ_i: mutation probability
- n_i: population size
- σ_i^2: mutation variance-covariance
- $\frac{\partial}{\partial x_i'}$: local selection gradient
- $f_i(x_i', x)$: invasion fitness

Illustration of Deterministic Evolution



Reaction-Diffusion Models

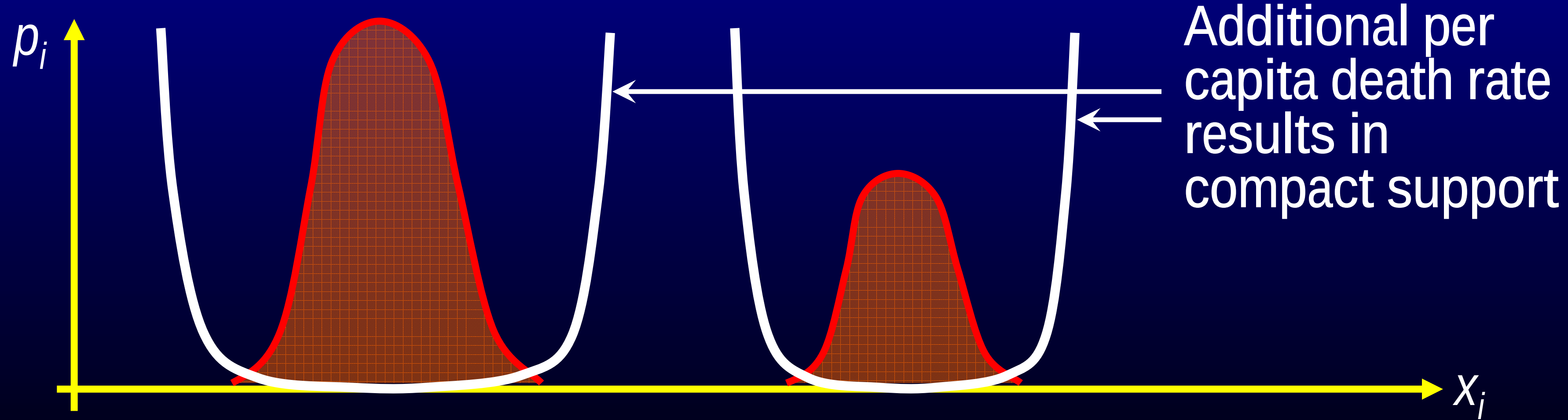
Polymorphic and Deterministic

Dieckmann (unpublished)

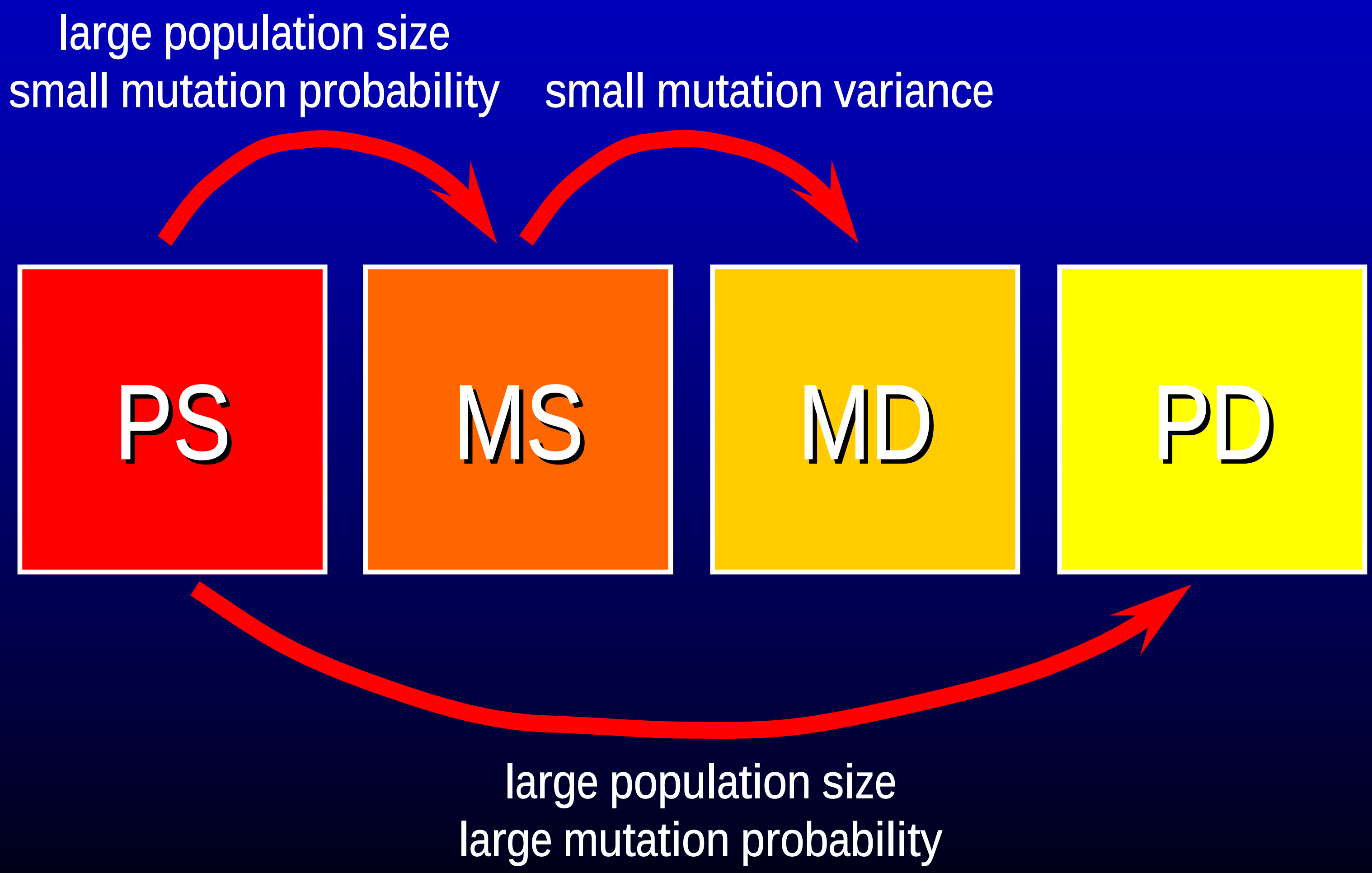
- Kimura limit

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

- Finite-size correction



Summary of Derivations



Overview Part B

1. Evolutionary Invasion Analysis
2. Example: Resource Competition
3. Evolutionary Bifurcations

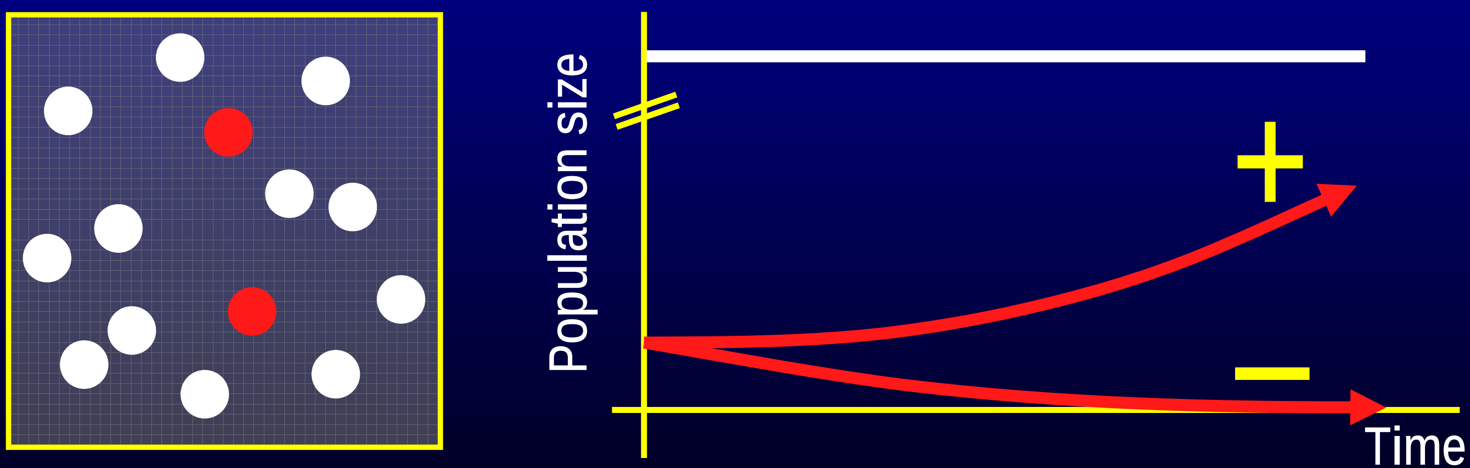
3 Evolutionary Invasion Analysis

Invasion Fitness

Metz et al. (1992)

- Definition

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



Invasion Fitness

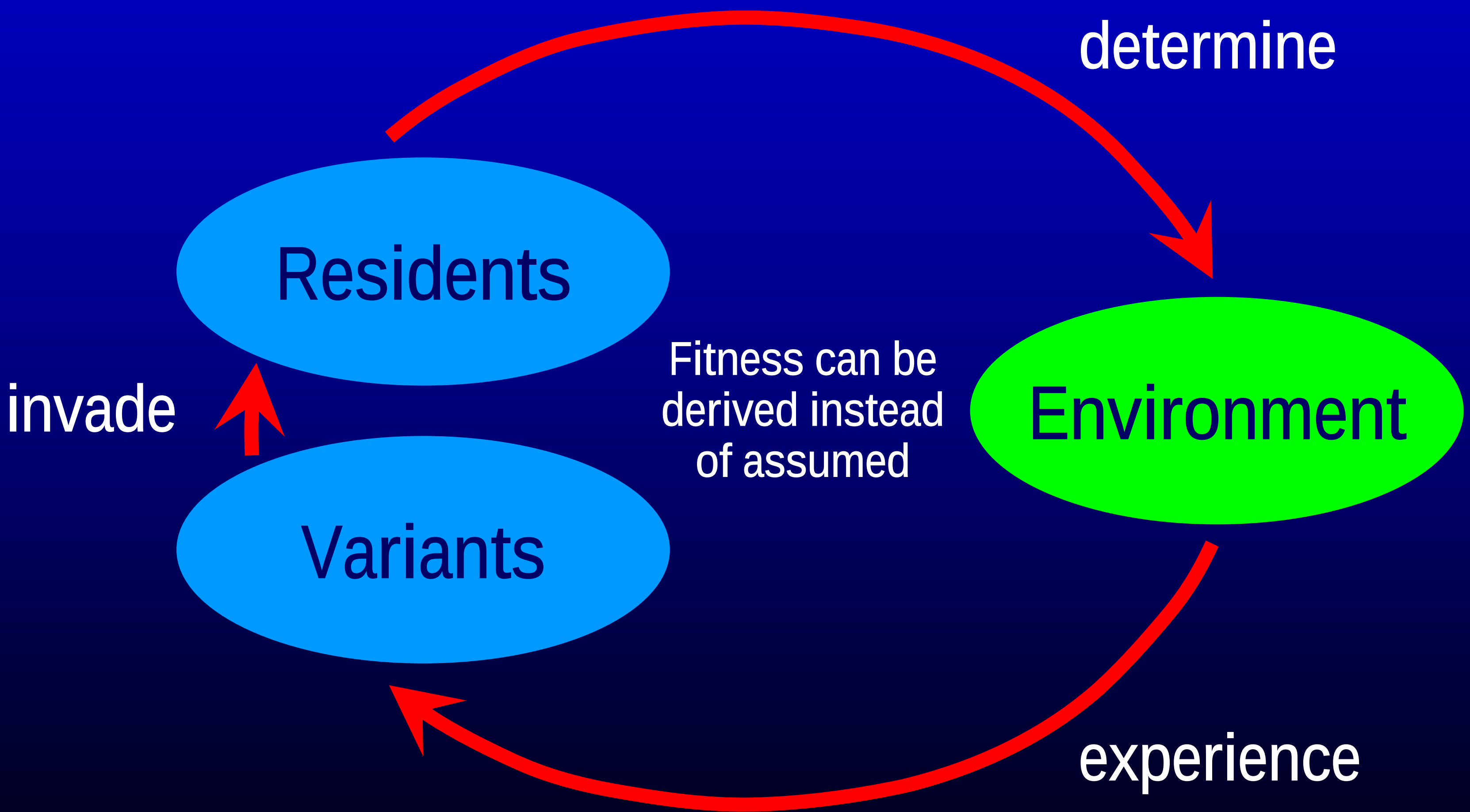
- Fitness is a function of two variables:

$$f(x'; x)$$

x': Mutant trait

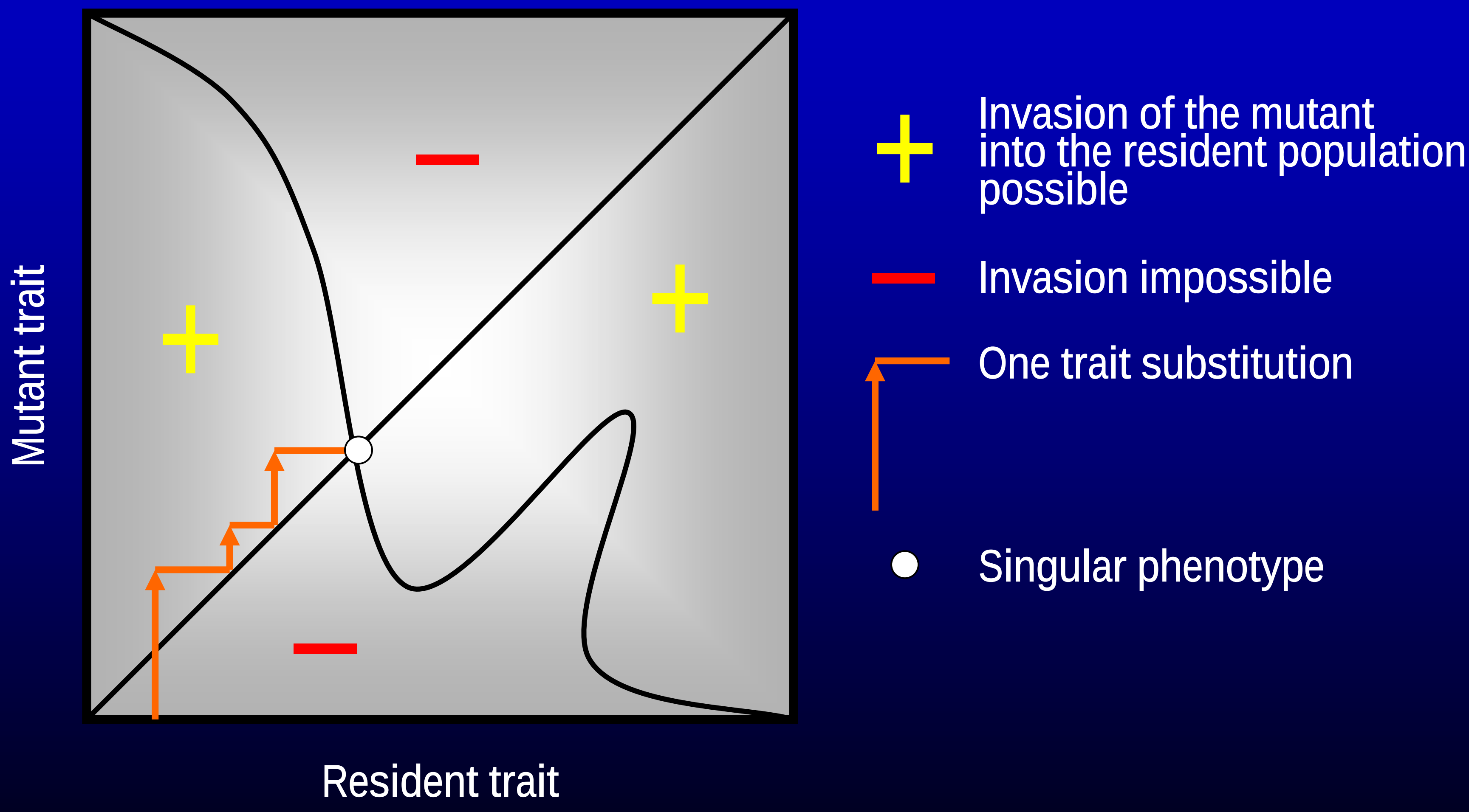
x: Resident trait: determines environment

Eco-Evolutionary Feedback



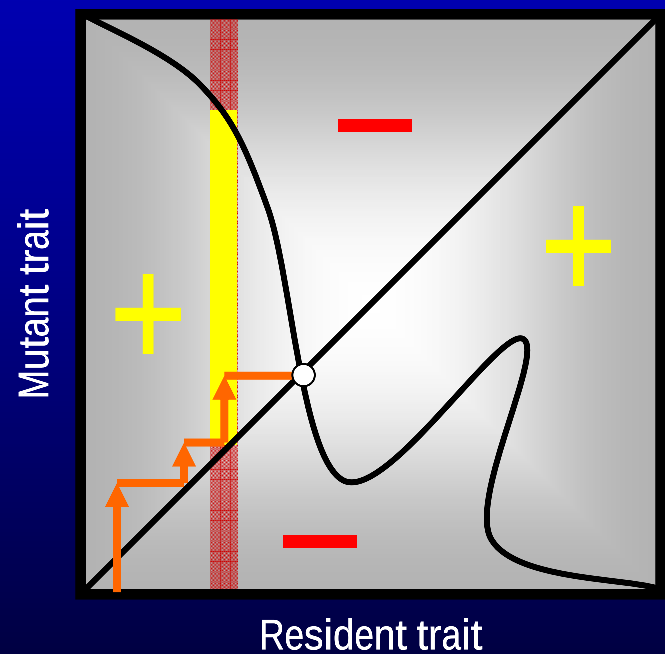
Geritz et al. (1997)

Pairwise Invasibility Plots (PIPs)



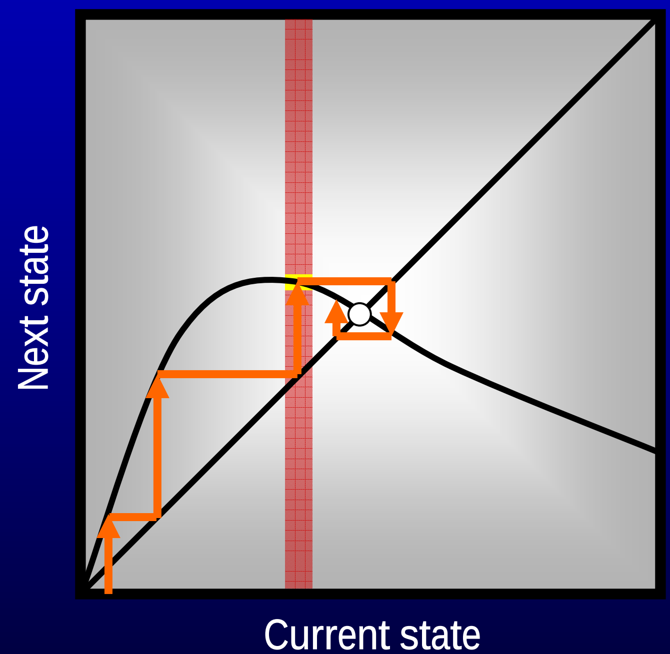
Reading PIPs: Comparison with Recursions

- Trait substitutions



Size of vertical steps stochastic

- Recursion relations

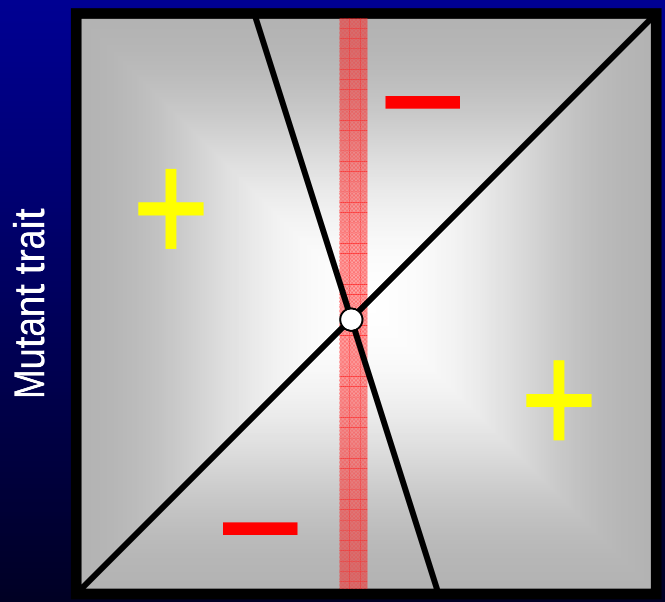


Size of vertical steps deterministic

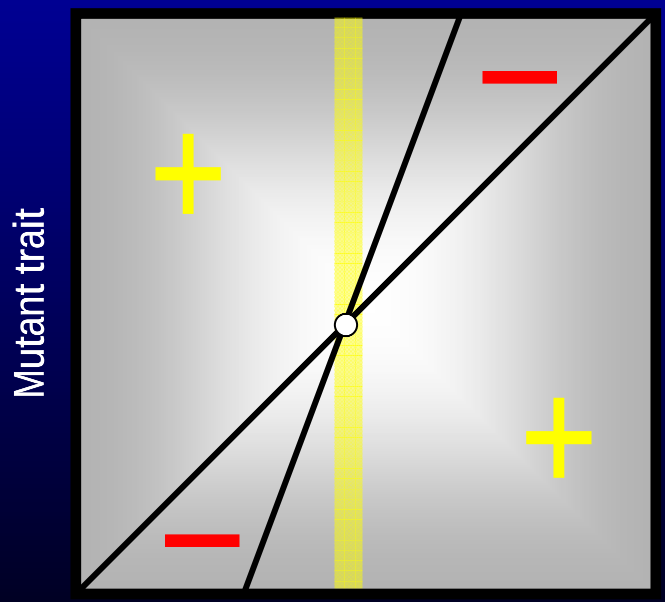
Reading PIPs: Evolutionary Stability

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

Yes:



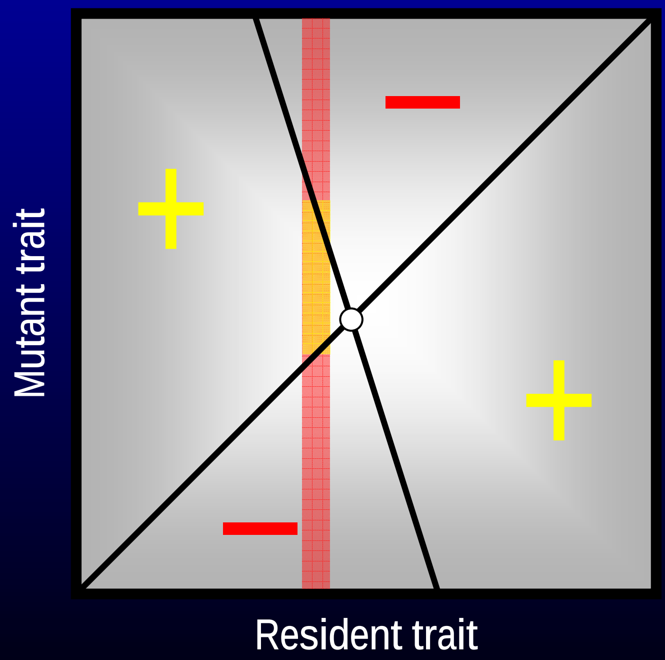
No:



Reading PIPs: Convergence Stability

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

Yes:



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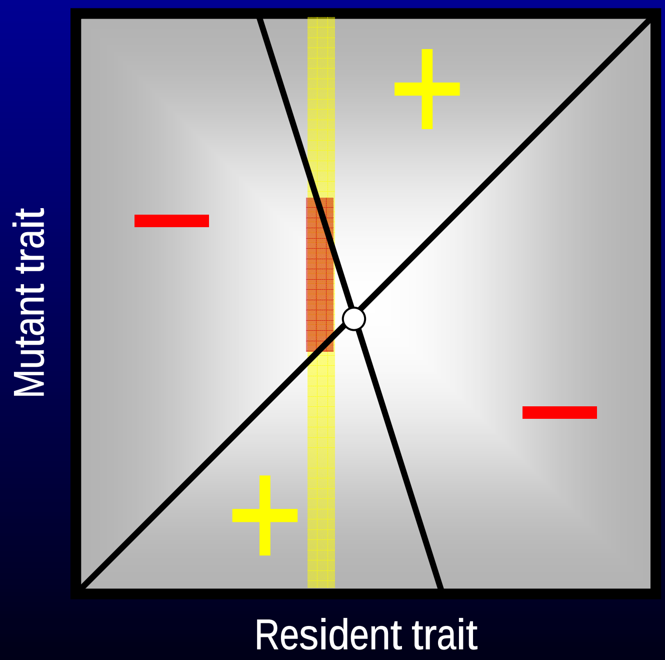
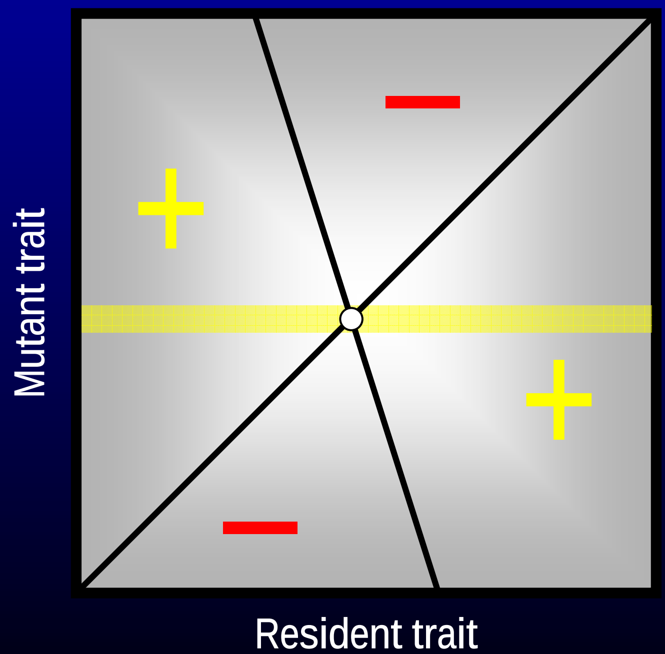


Reading PIPs: Invasion Potential

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

Yes:



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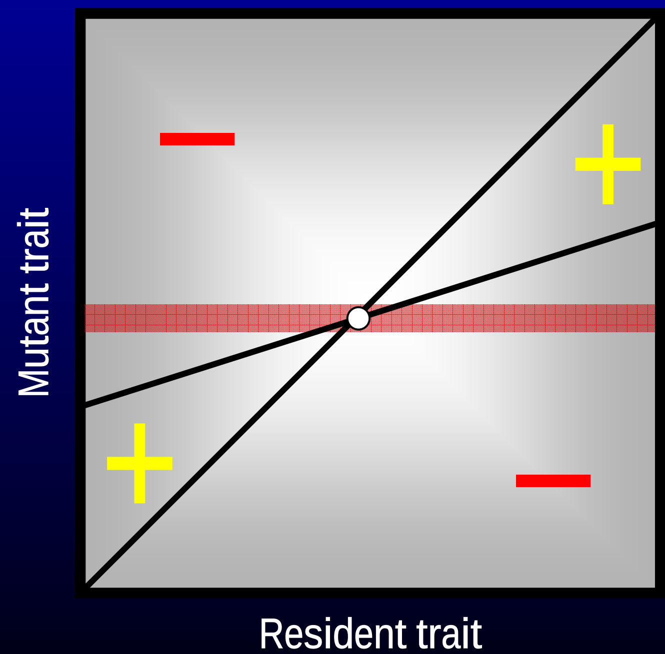
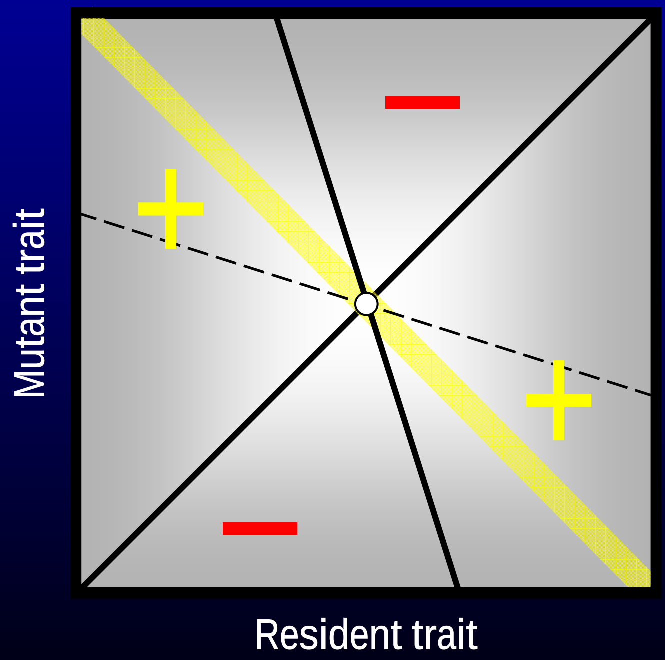


Reading PIPs: Mutual Invasibility

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

Yes:



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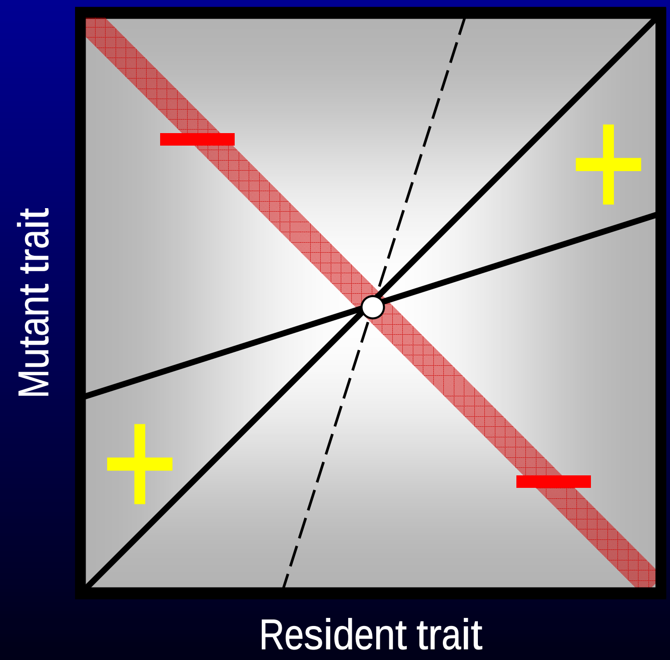
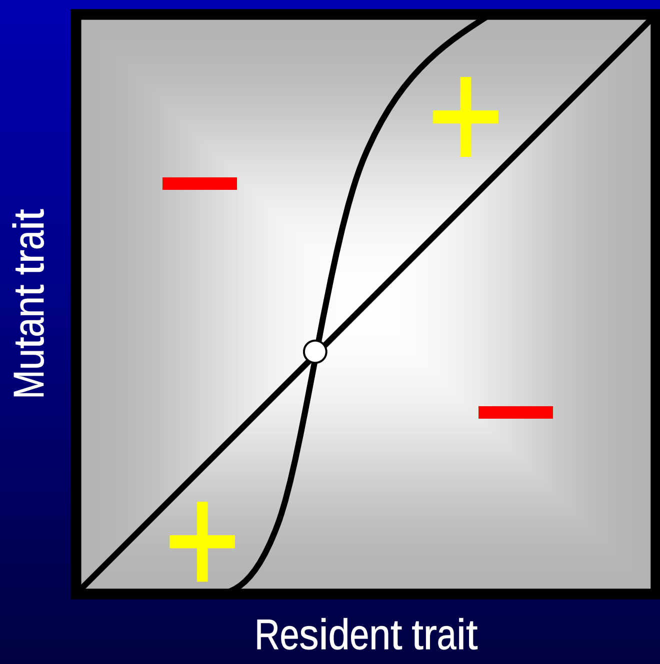


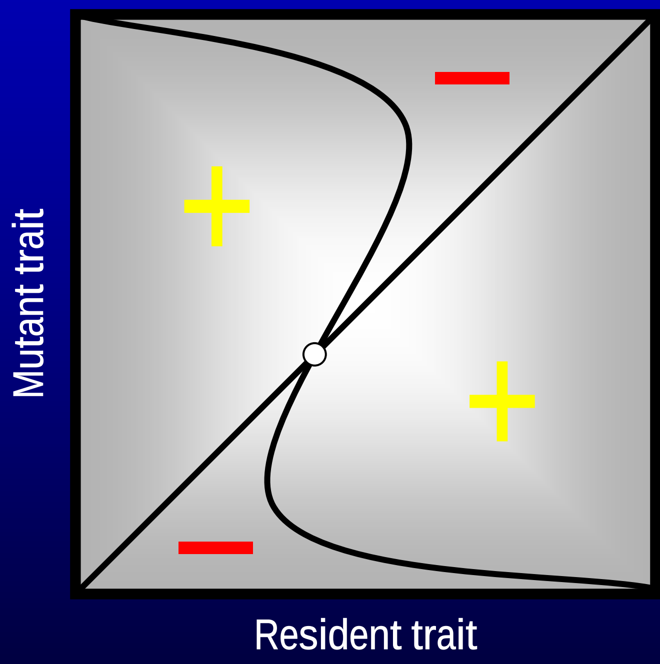
Two Especially Interesting Types of PIP

- Garden of Eden



Evolutionarily stable,
but not convergence stable

- Branching Point

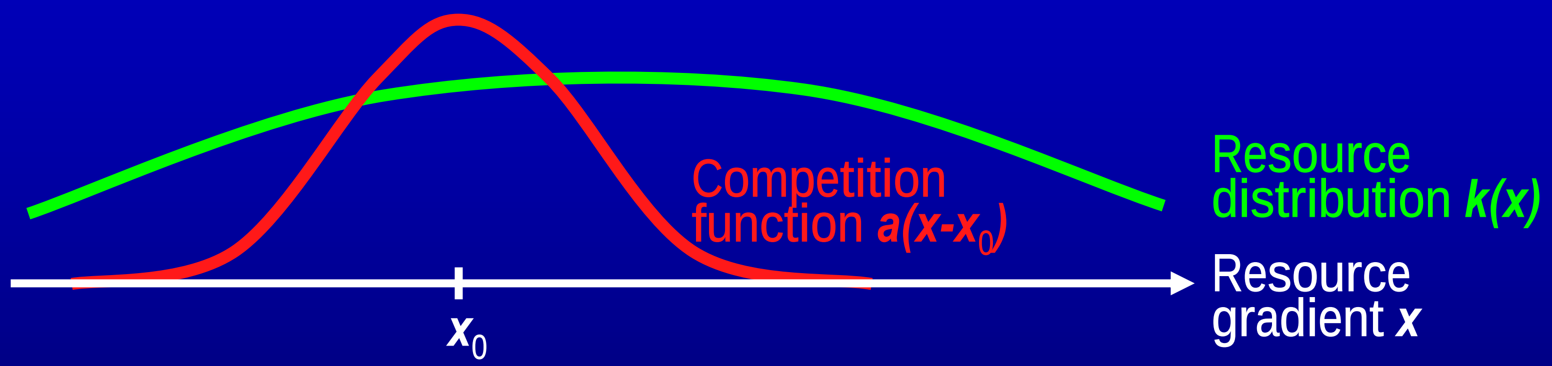


Convergence stable,
but not evolutionarily stable

4 Example: Resource Competition

Roughgarden (1976)

Example: Resource Competition



Dynamics of population sizes n_i of strategy x_i

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

Analysis of Example

- Invasion Fitness

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

1. $$n' \to 0$$

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

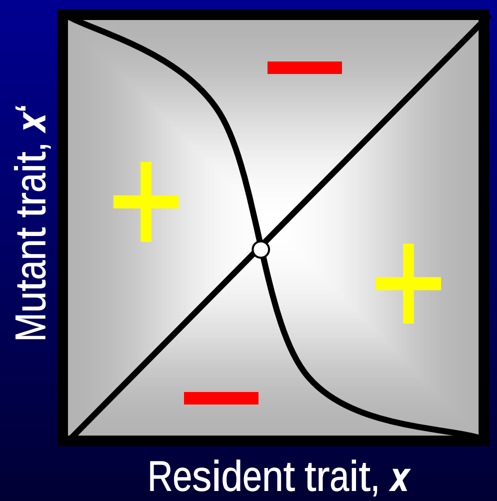
$$f(x', x) = r\left[1 - a(x' - x)\frac{k(x)}{k(x')}\right]$$

Analysis of Example

- Pairwise Invasibility Plots

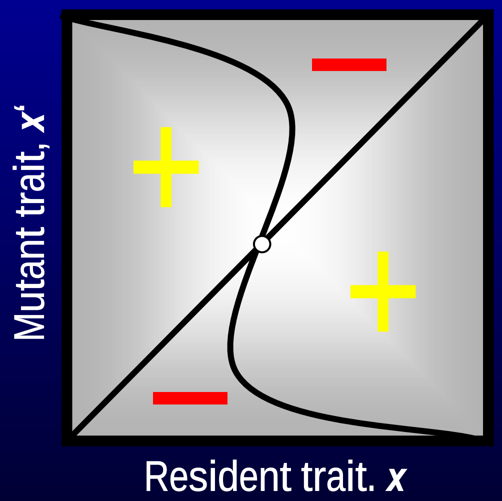
With $k = k_0\, N(0,\sigma_k)$ and $a = N(0,\sigma_a)$ we obtain

for $\sigma_a > \sigma_k$



Evolutionary Stability

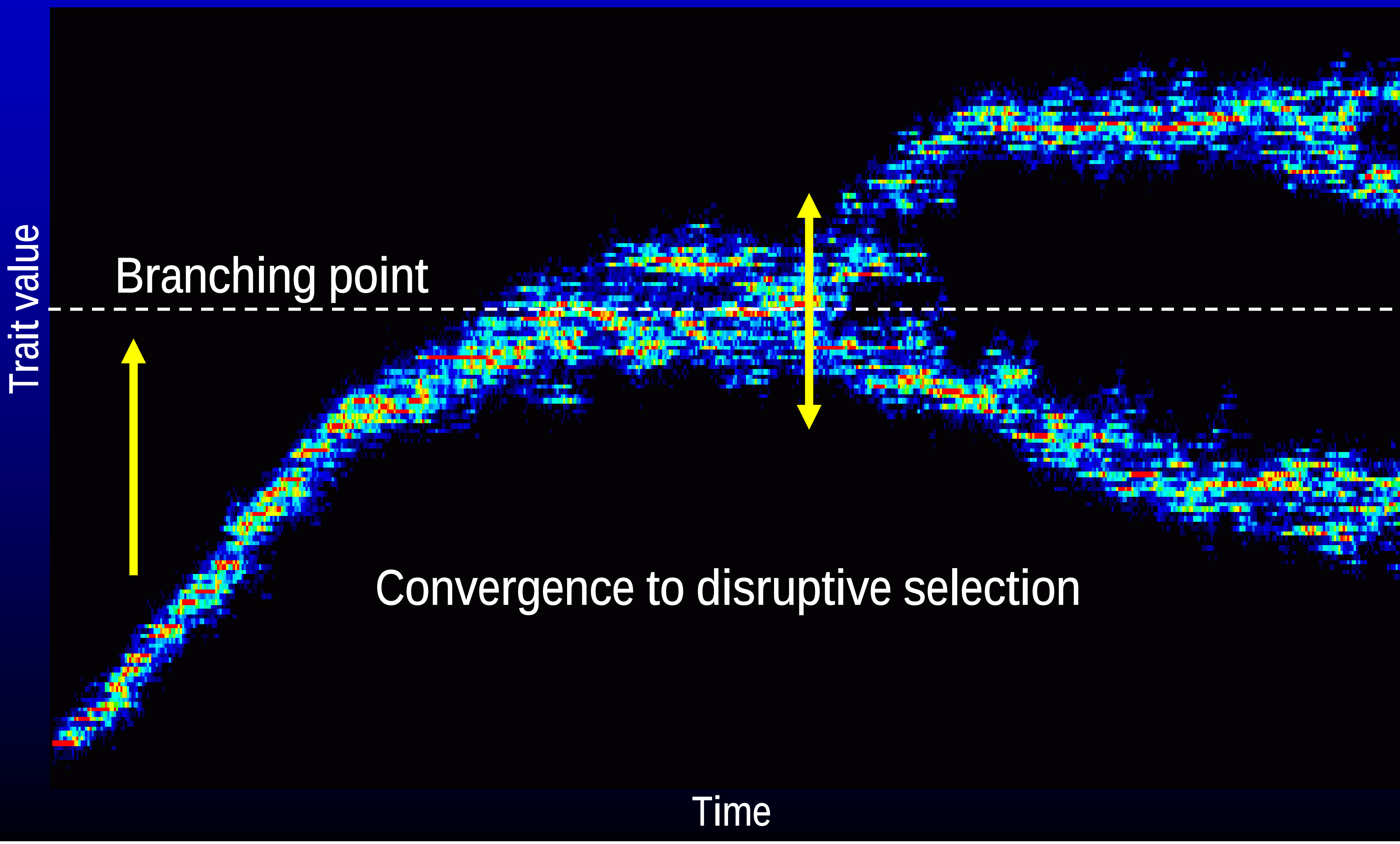
for $\sigma_a < \sigma_k$



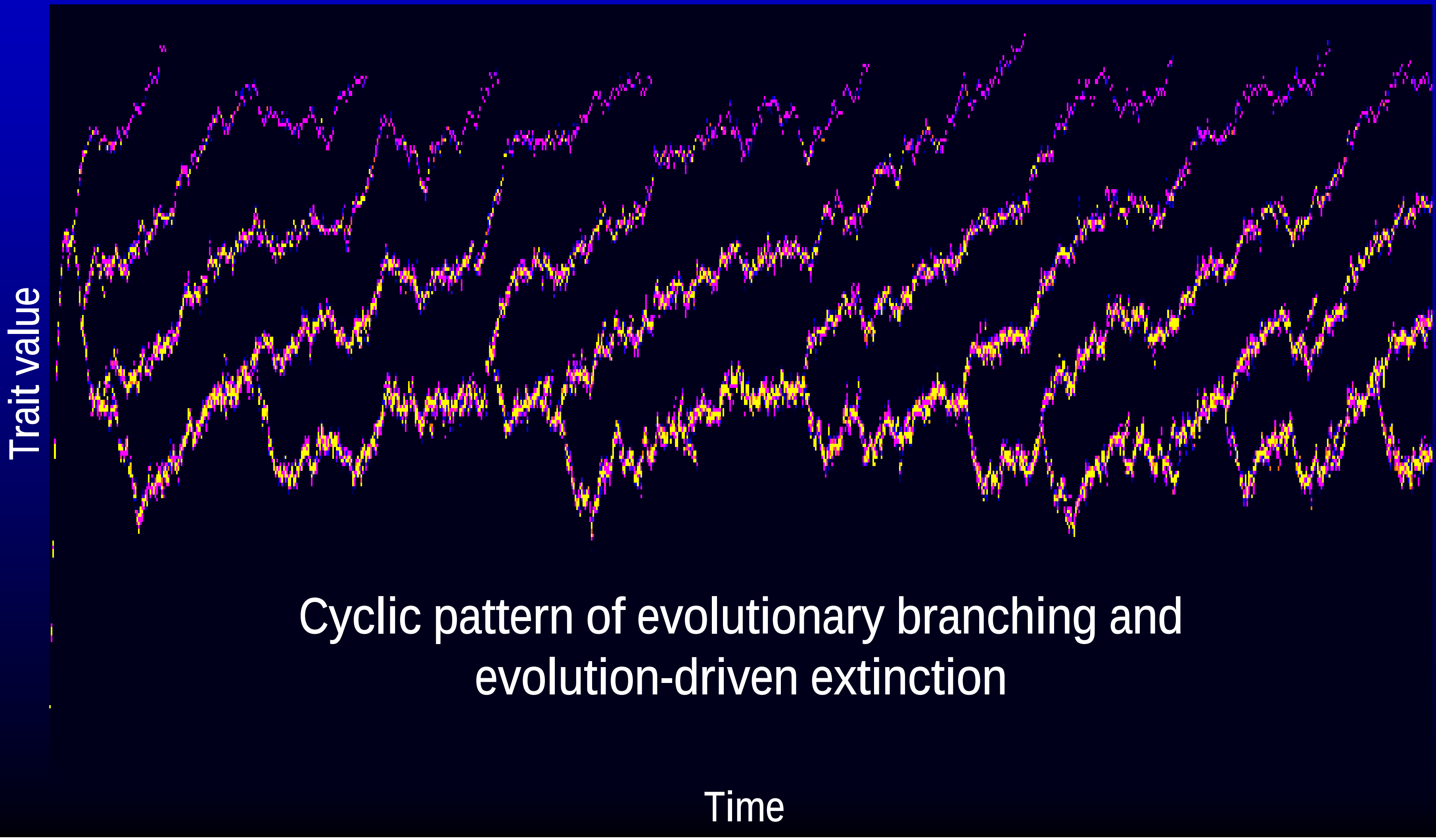
Evolutionary Branching

Evolutionary Branching

Metz et al. (1992)



Asymmetric Competition: Taxon Cycles



5 Evolutionary Bifurcation Analysis

Analytic Conditions

for One-dimensional Traits

Geritz et al. (1997)

- Evolutionary stability

$$\frac{\partial^2}{\partial x'^2} f(x', x)\Big|_{x'=x=x^*} < 0$$

Important if not monomorphic

- Convergence stability

$$\left(\frac{\partial^2}{\partial x'^2} - \frac{\partial^2}{\partial x^2}\right) f(x', x)\Big|_{x'=x=x^*} < 0$$

Central to monomorphic analysis

- Invasion potential

$$\frac{\partial^2}{\partial x^2} f(x', x)\Big|_{x'=x=x^*} > 0$$

Not important for small mutations

- Mutual invasibility

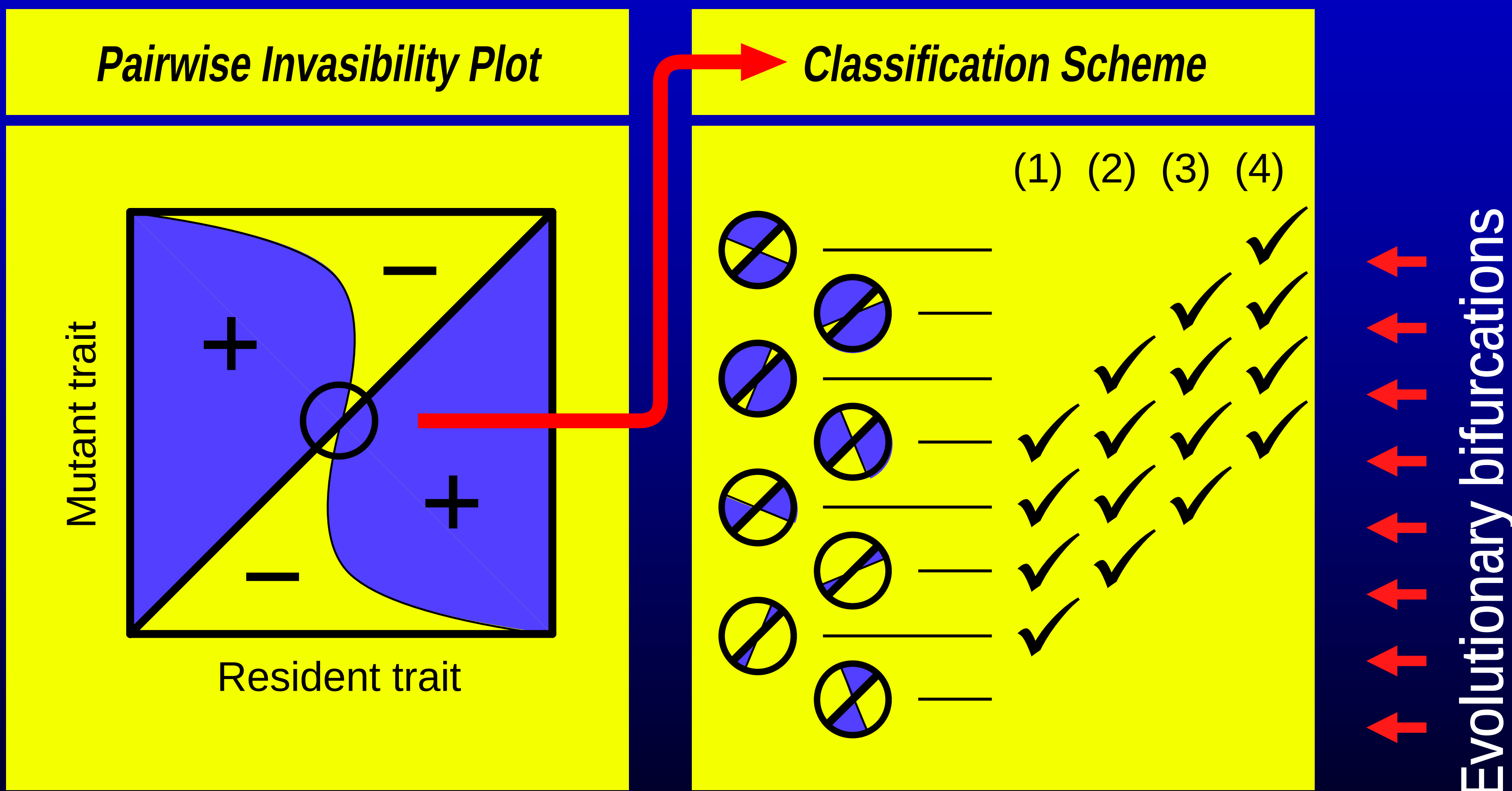
$$\left(\frac{\partial^2}{\partial x'^2} + \frac{\partial^2}{\partial x^2}\right) f(x', x)\Big|_{x'=x=x^*} > 0$$

Important if not monomorphic

Eightfold Classification

of One-dimensional Evolutionary Singularities

Geritz et al. (1997)



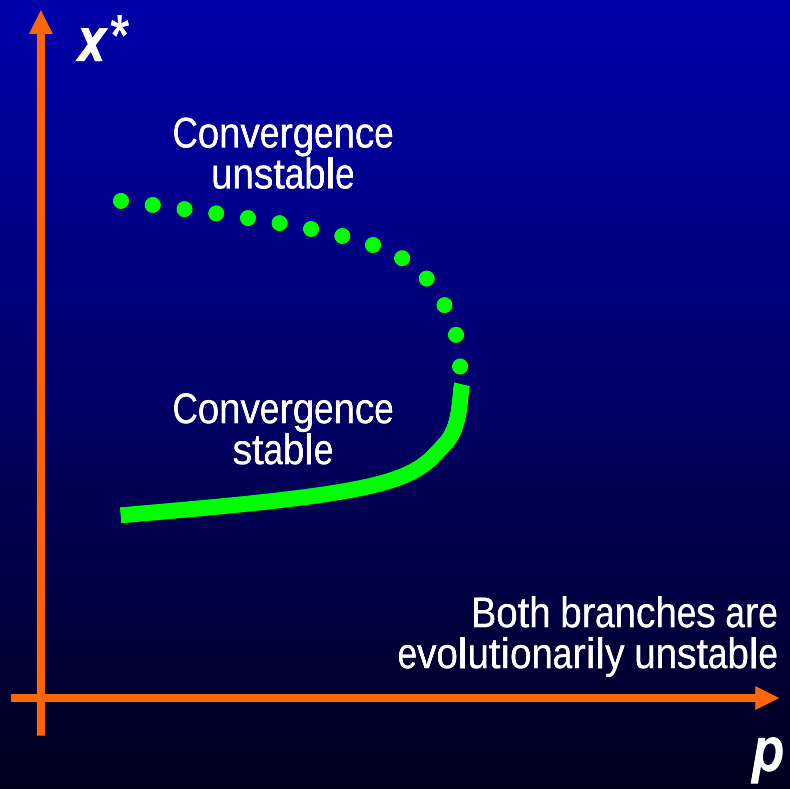
(1) Evolutionary instability, (2) Convergence stability, (3) Invasion potential, (4) Mutual invasibility.

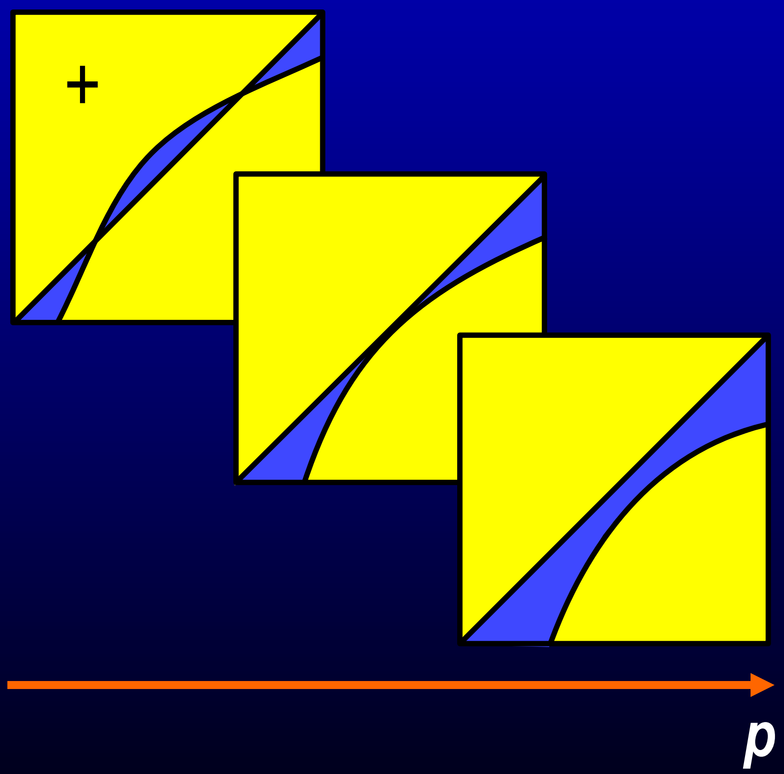
Evolutionary Bifurcations

of One-dimensional Adaptive Dynamics

Metz & Geritz (unpublished)

- Example 1: Evolutionary saddle-node bifurcation

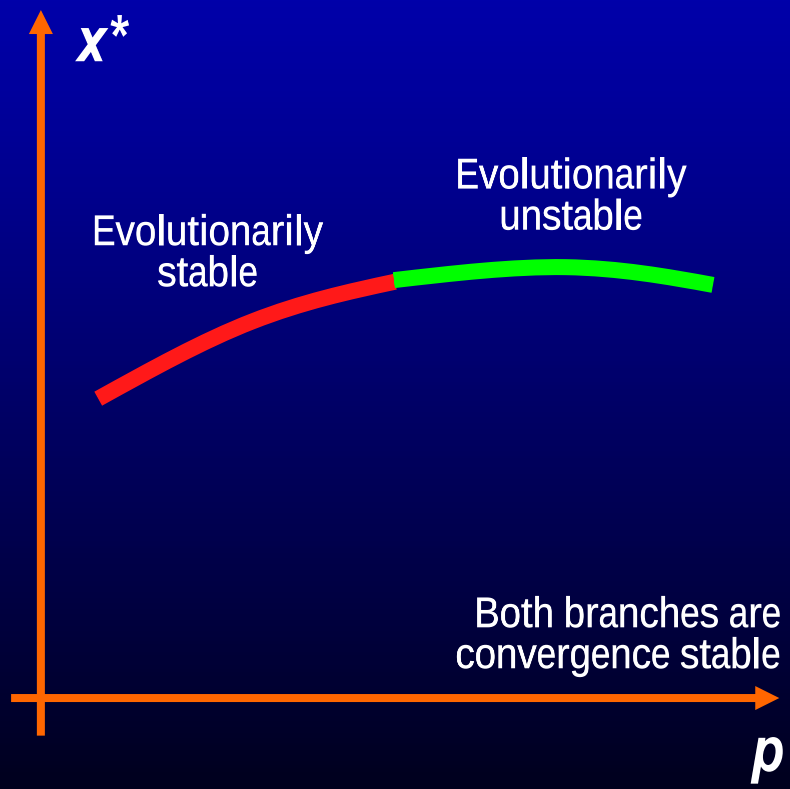


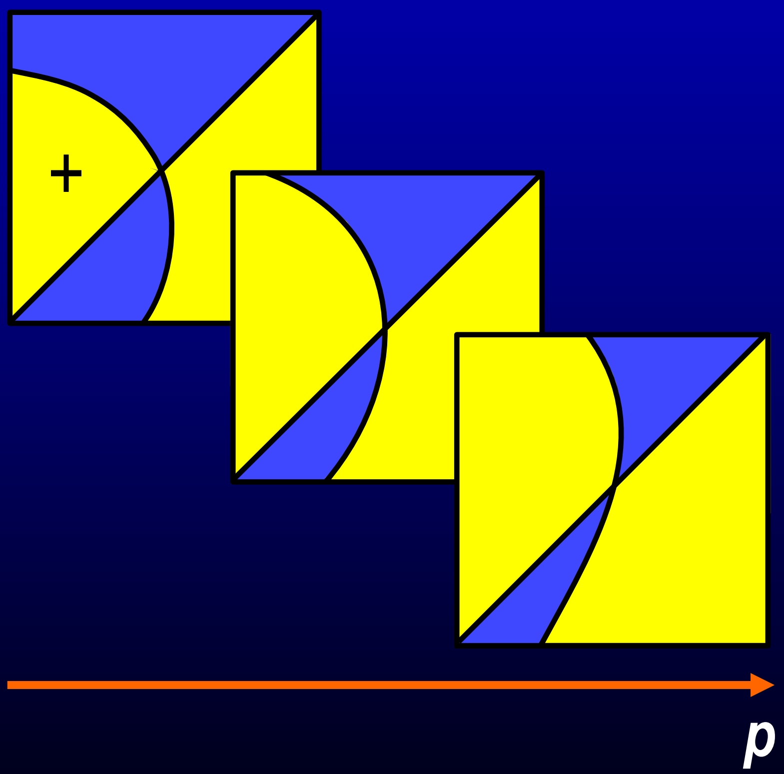


Evolutionary Bifurcations

of One-dimensional Adaptive Dynamics Metz & Geritz (unpublished)

- Example 2: Gain/loss of evolutionary stability





Evolutionary Bifurcations

of Higher-dimensional Adaptive Dynamics

- In one dimension, convergence stability and evolutionary instability imply mutual invasibility, and this constraint extends to higher dimensions as well.
- However, multi-dimensional convergence cannot be described based on one-dimensional convergence stability. Instead, multi-dimensional convergence stability has to be evaluated through the asymptotic stability of fixed points of the canonical equation. Mutational variances and covariances then start to matter.
- Multi-dimensional convergence can now occur together with evolutionary instability and an absence of mutual invasibility. Also the divergence directions allowed by evolutionary instability and mutual invasibility, respectively, have to match.
- Thus, the conditions for multi-dimensional evolutionary branching involve extra subtleties relative to the one-dimensional case.

Further Reading on Adaptive Dynamics

- Metz JAJ, Geritz SAH, Meszéna G, Jacobs FJA, van Heerwaarden JS: ***Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction.*** In: van Strien SJ, Verduyn Lunel SM (eds.) ***Stochastic and Spatial Structures of Dynamical Systems***, Proceedings of the Royal Dutch Academy of Science, North Holland, Amsterdam, pp.183-231 (1996).

- Dieckmann U, Law R: ***The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes.*** ***Journal of Mathematical Biology*** 34: 579-612 (1996).

- Geritz SAH, Metz JAJ, Kisdi É, Meszéna G: ***The Dynamics of Adaptation and Evolutionary Branching.*** ***Physical Review Letters*** 78: 2024-2027 (1997).

- Dieckmann U: ***Can Adaptive Dynamics Invade?*** ***Trends in Ecology and Evolution*** 12: 128-131 (1997).

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www.iiasa.ac.at/Research/ADN/Series.html