Adaptive Dynamics and Ecosystem Evolution

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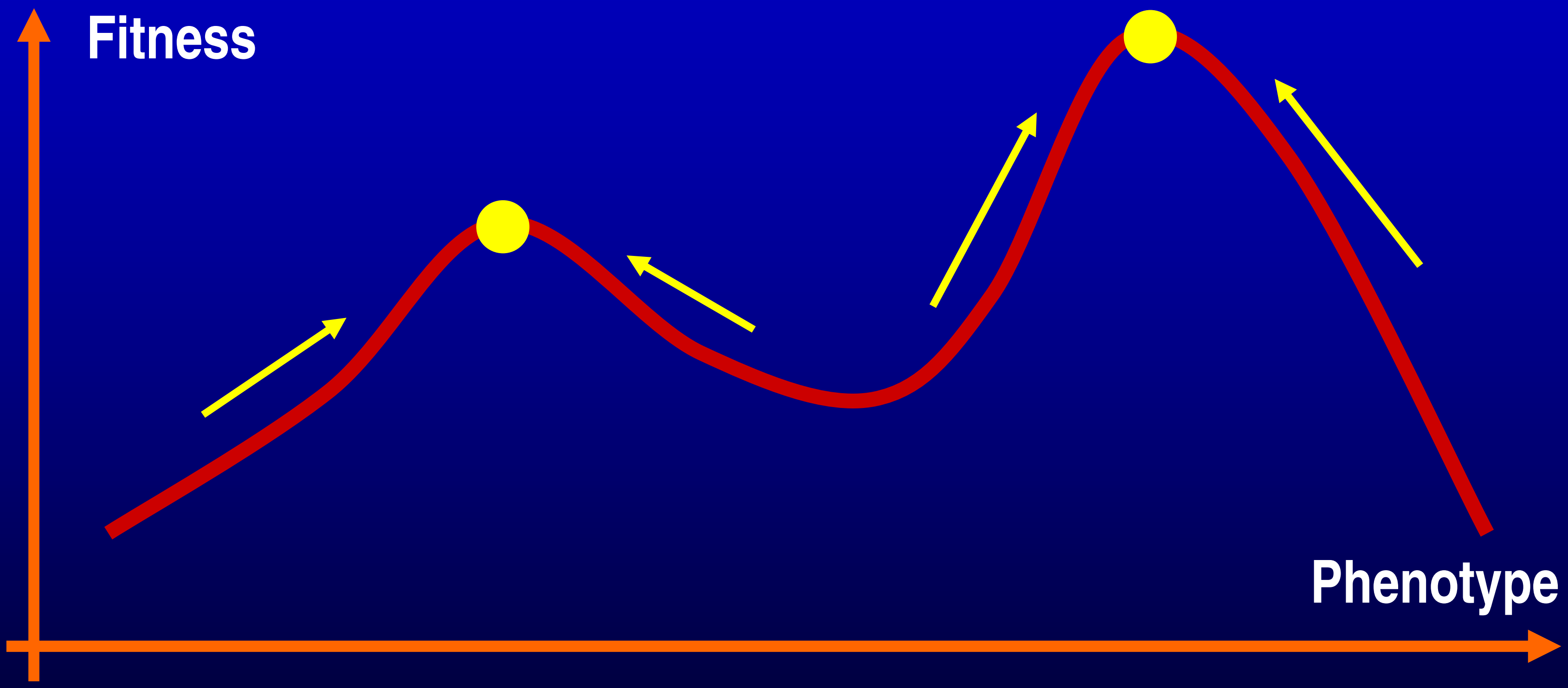
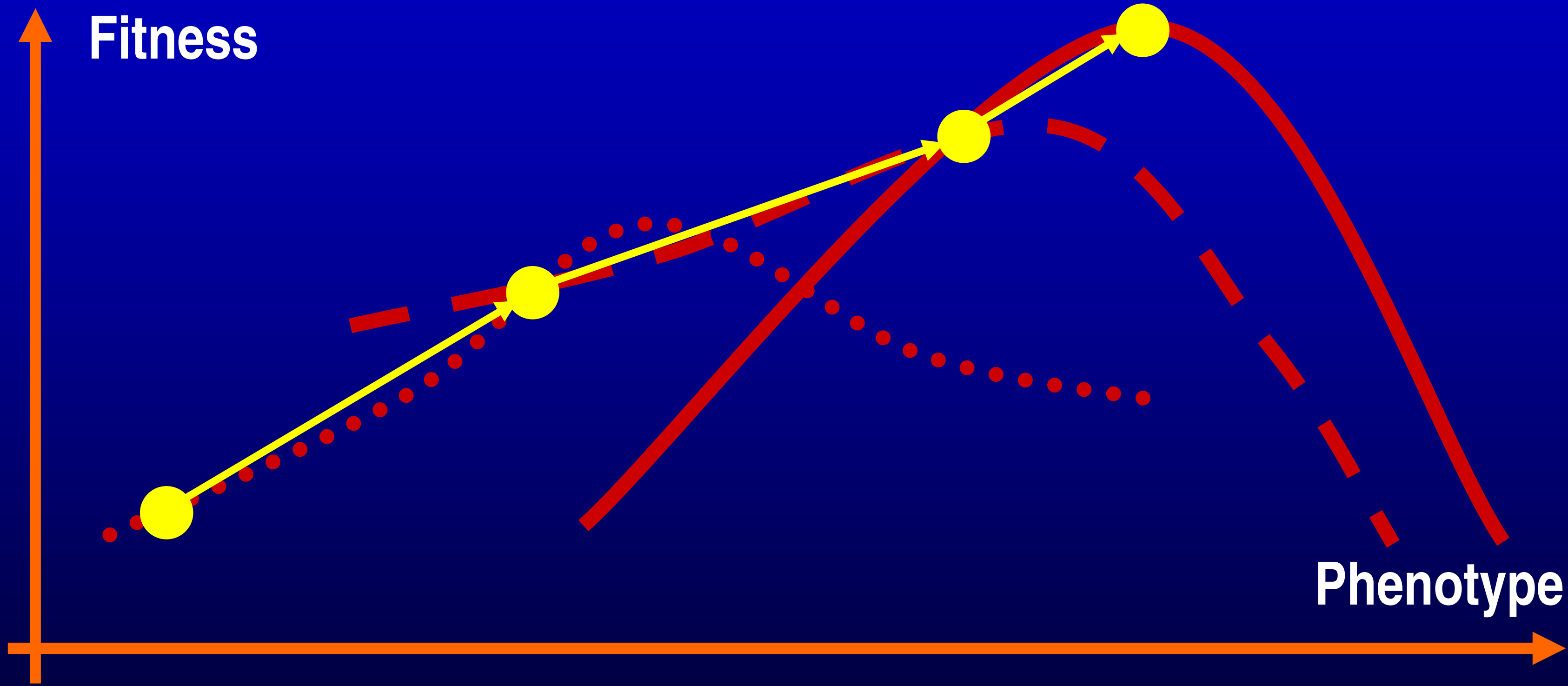
Evolutionary Optimization



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.

The Context of Evolution is Ecology

The Ecological Theater and the Evolutionary Play

G. E. Hutchinson (1967)

Limited Attention to FDS

- Sewall Wright's fitness landscapes
- Ronald Fisher's so-called fundamental theorem of natural selection (problem of 'environmental deterioration')
- Richard Levins fitness set analysis
- Life-history theory textbooks

  Roff (1992, 2002) 5 pp. out of about 500

  Stearns (1992) 2 pp. out of about 200
- Genetics textbooks

Overview

1. Adaptive Dynamics Theory
2. Evolutionary Branching
3. Evolutionary Suicide
4. Predator-Prey Coevolution
5. Mutualistic Coevolution
6. Altruism
7. Concerted Reproduction

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Adaptive Dynamics Theory

Adaptive Dynamics

Sacrificing genetic for ecological detail, adaptive dynamics theory extends evolutionary game theory:

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

Characteristic tools:

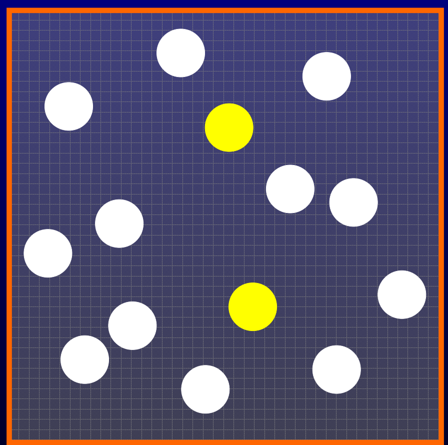
- Invasion fitness
- Pairwise invasibility plots
- Canonical equation
- Evolutionary bifurcation analysis

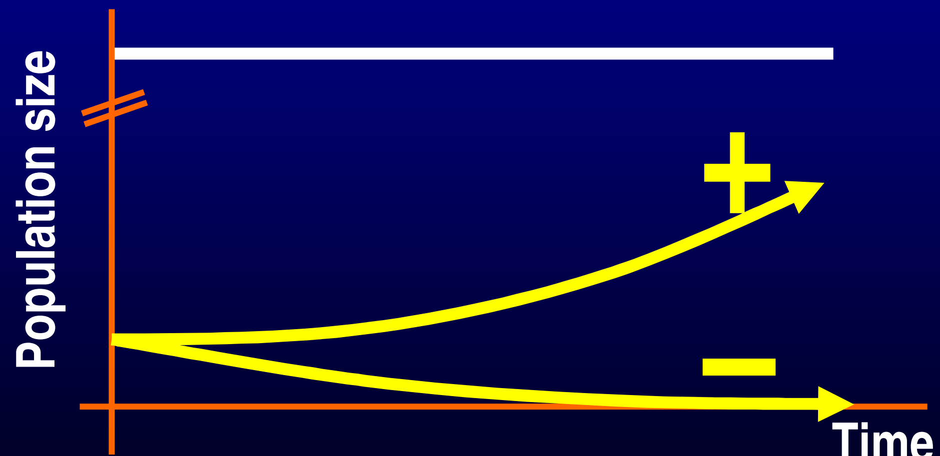
Invasion Fitness

Metz *et al.* (1992)

- **Definition**

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





Invasion Fitness

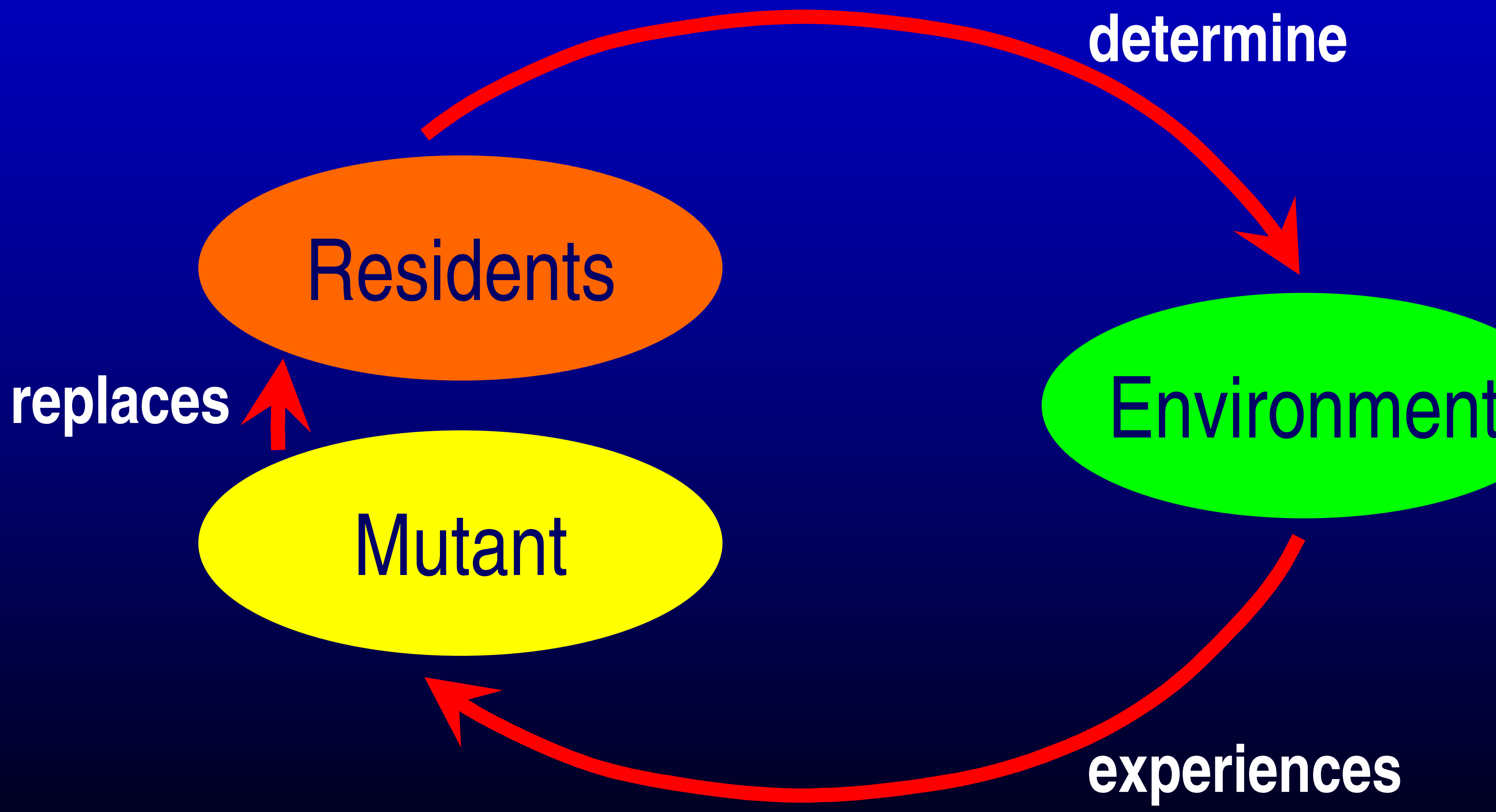
- Fitness is a function of two variables:

$$f\,(\,x\,';\,x\,)$$

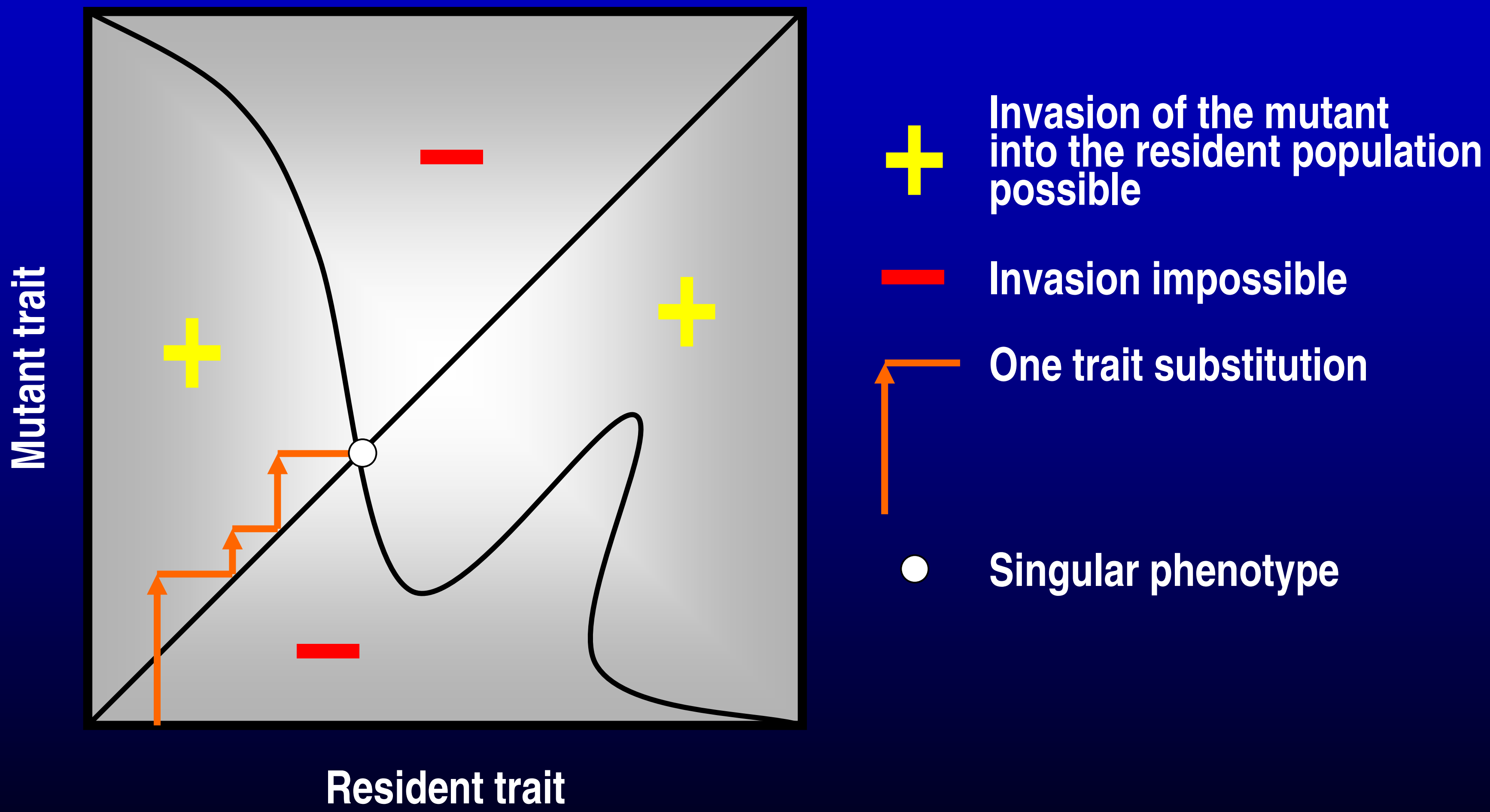
mutant trait

resident trait: determines environment

Environmental Feedback

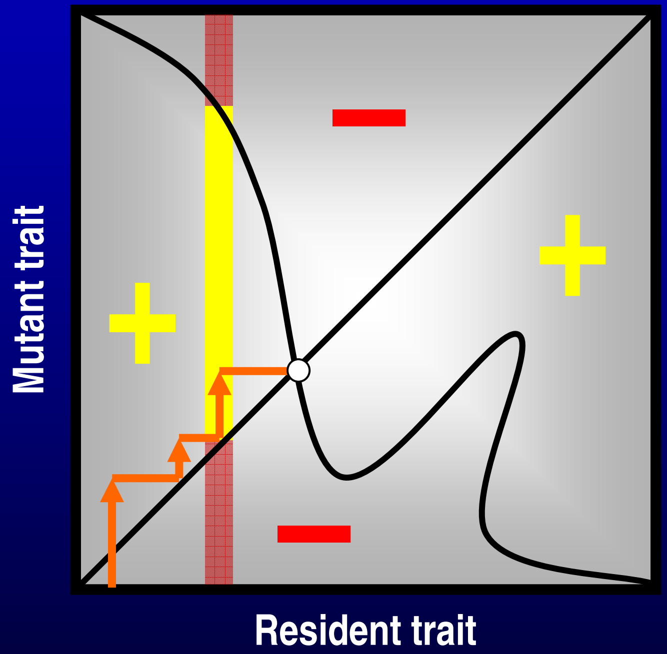


Pairwise Invasibility Plots (PIPs)



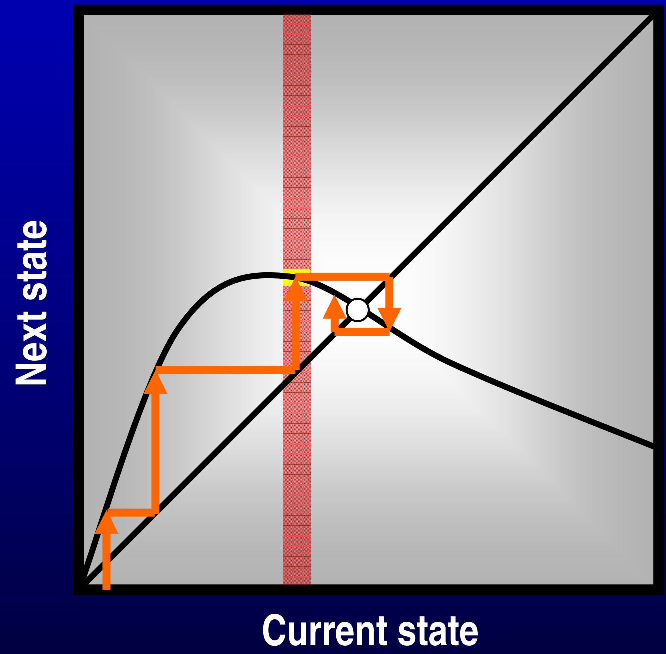
Reading PIPs: Comparison with Recursions

- **Trait substitutions**



Size of vertical steps probabilistic

- **Recursion relations**

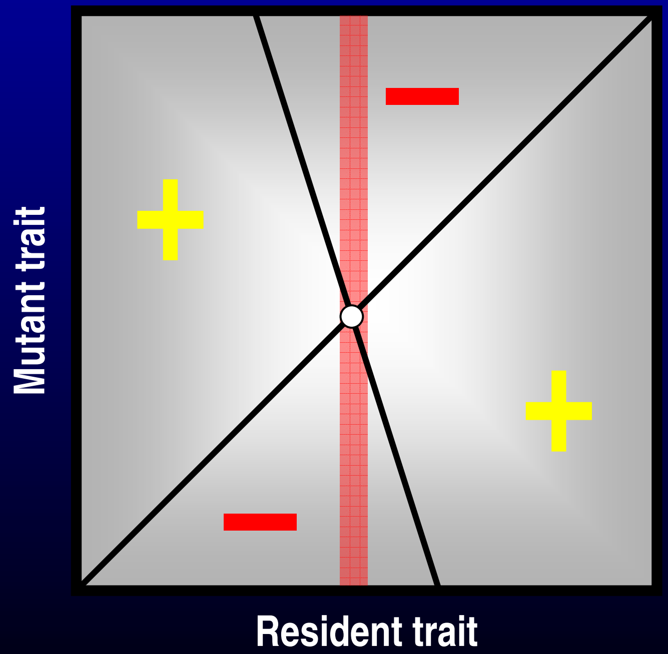


Size of vertical steps deterministic

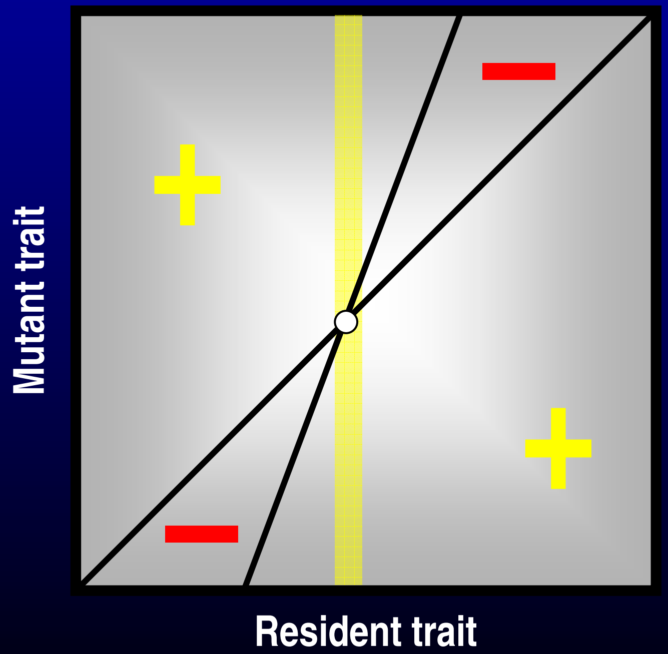
Reading PIPs: Evolutionary Stability

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

Yes:



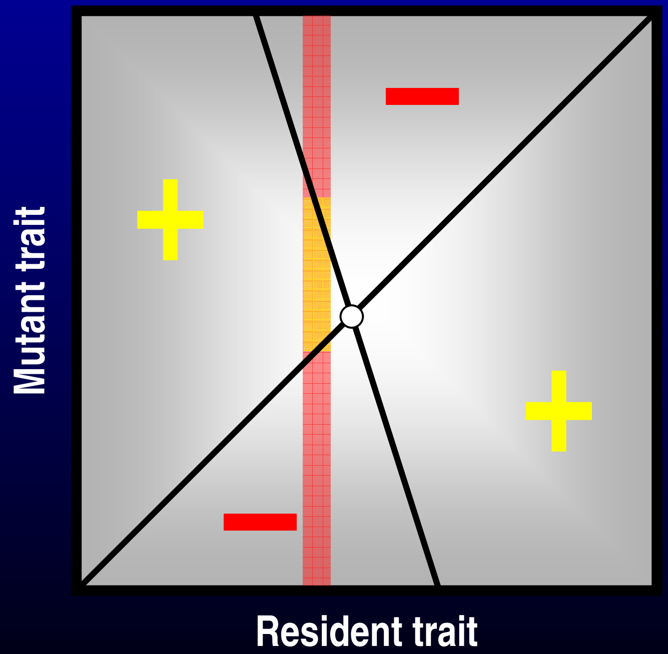
No:



Reading PIPs: Convergence Stability

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

Yes:



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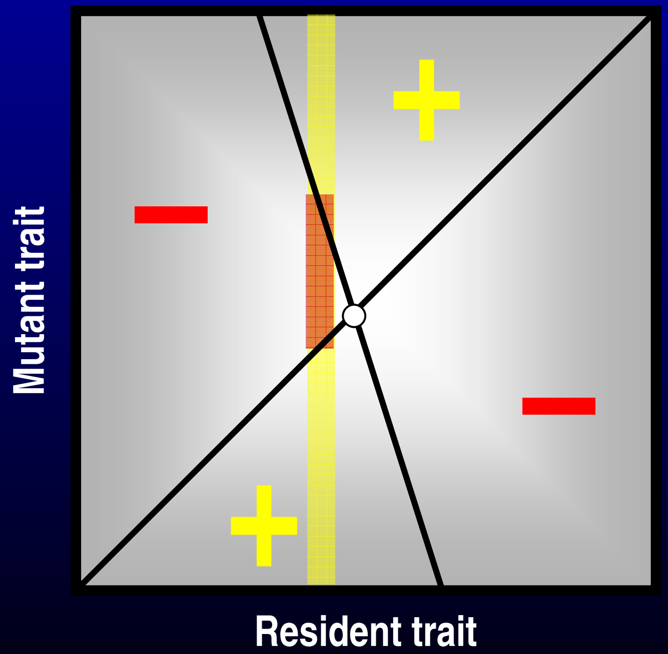
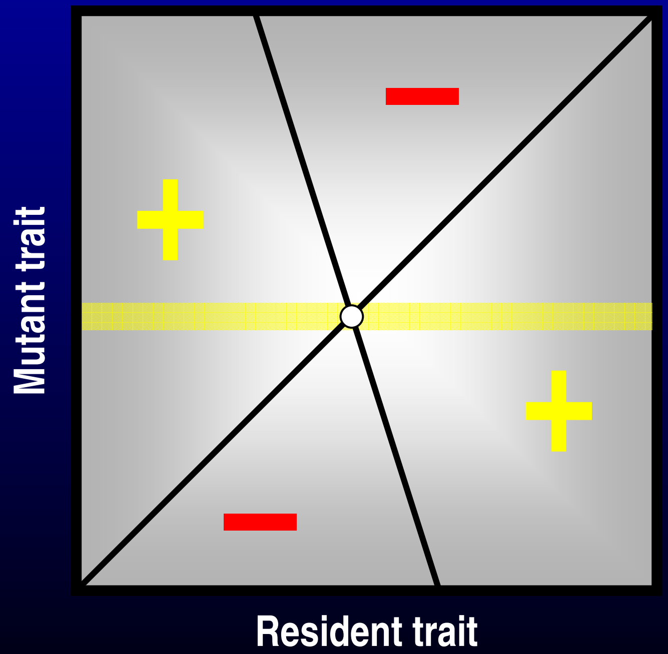


Reading PIPs: Invasion Potential

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

Yes:



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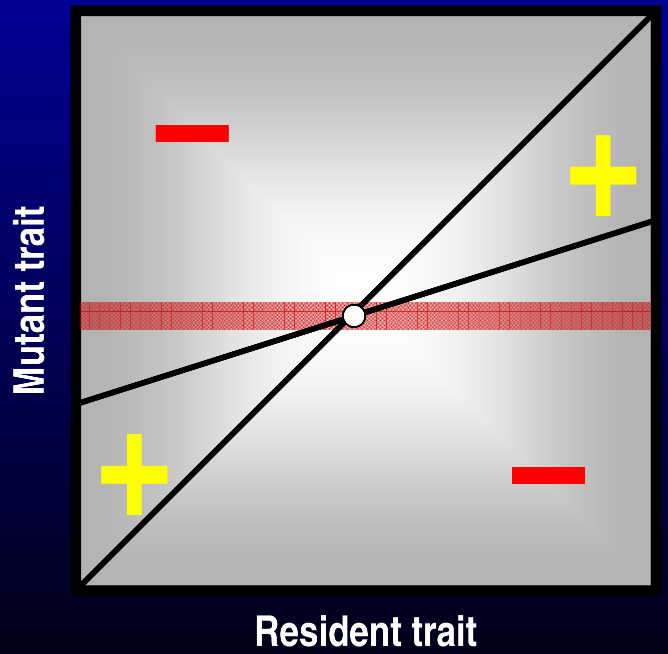
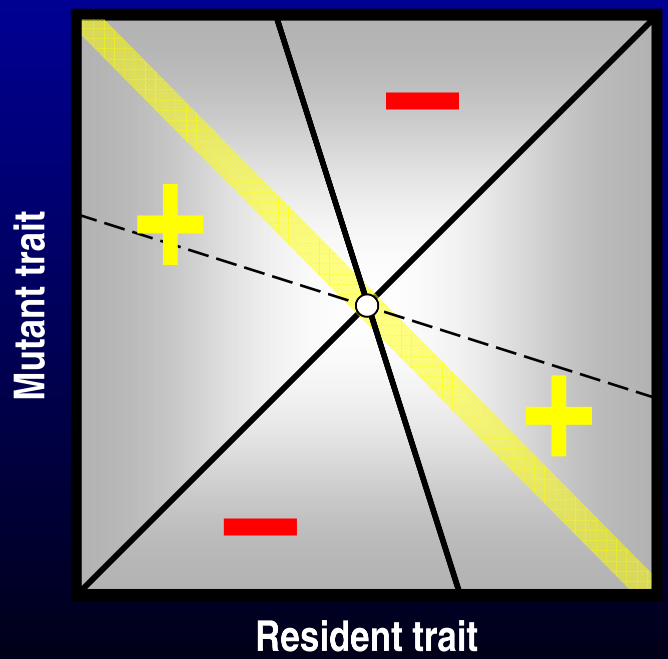


Reading PIPs: Mutual Invasibility

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

Yes:



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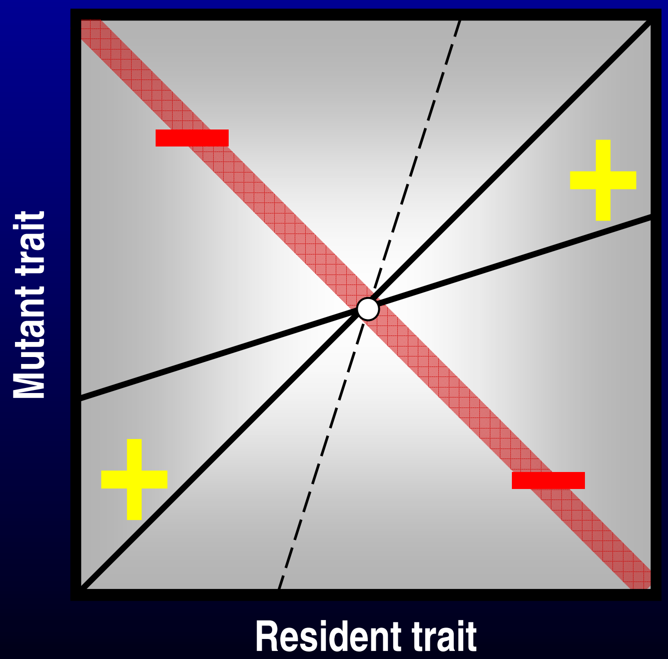
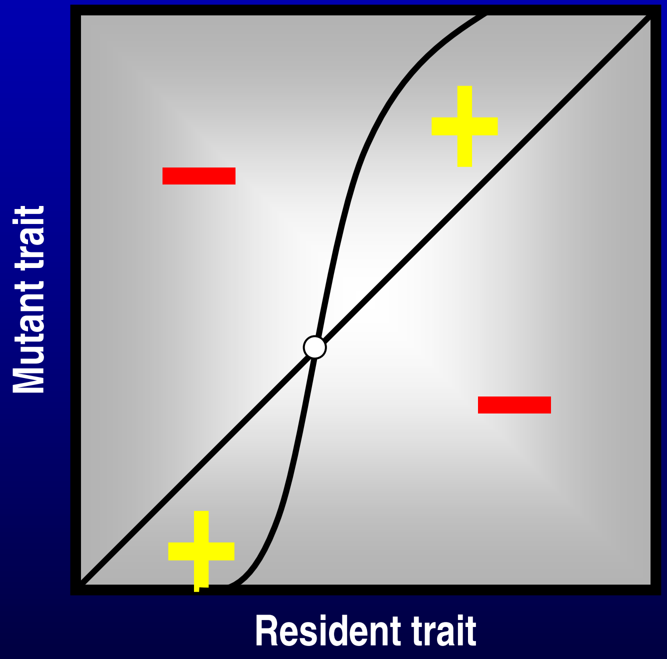


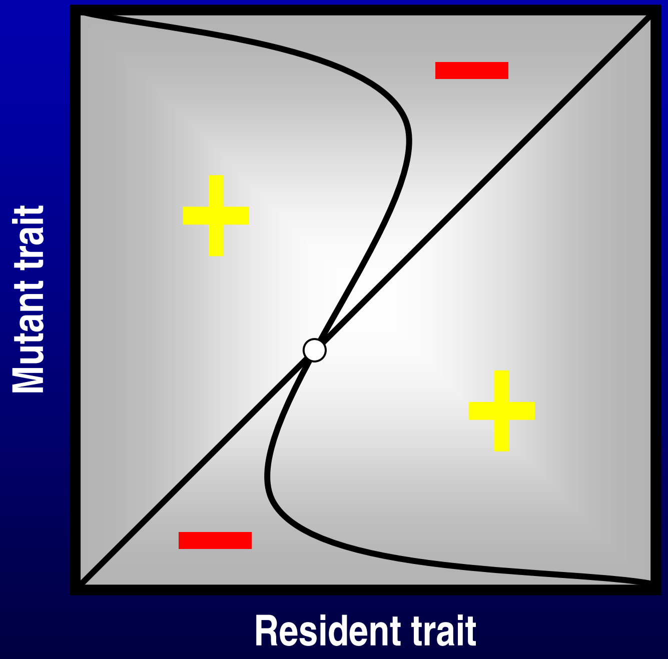
Two Especially Interesting Types of PIP

- Garden of Eden



Evolutionarily stable,
but not convergence stable

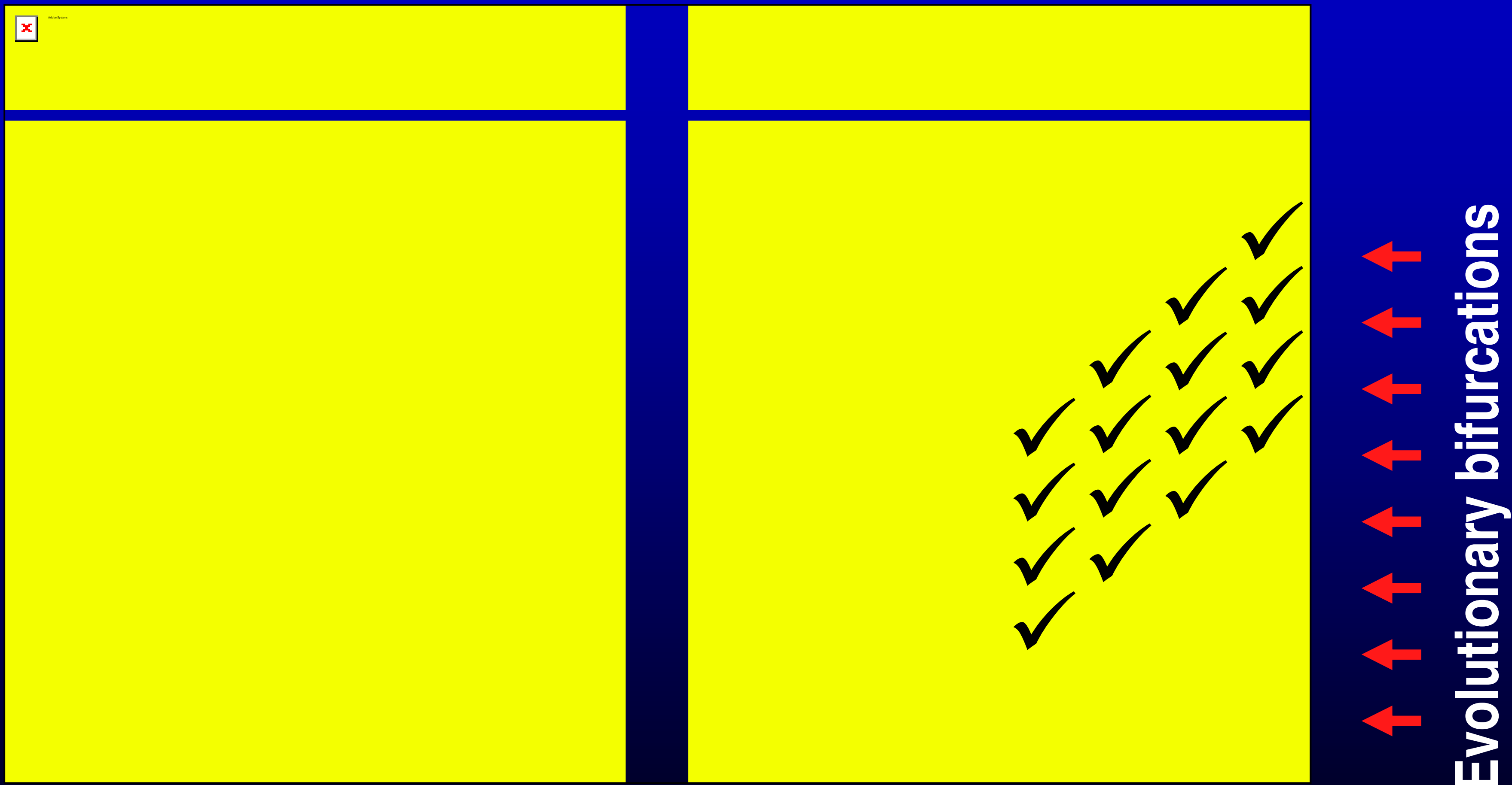
- Branching Point



Convergence stable,
but not evolutionarily stable

Eightfold Classification

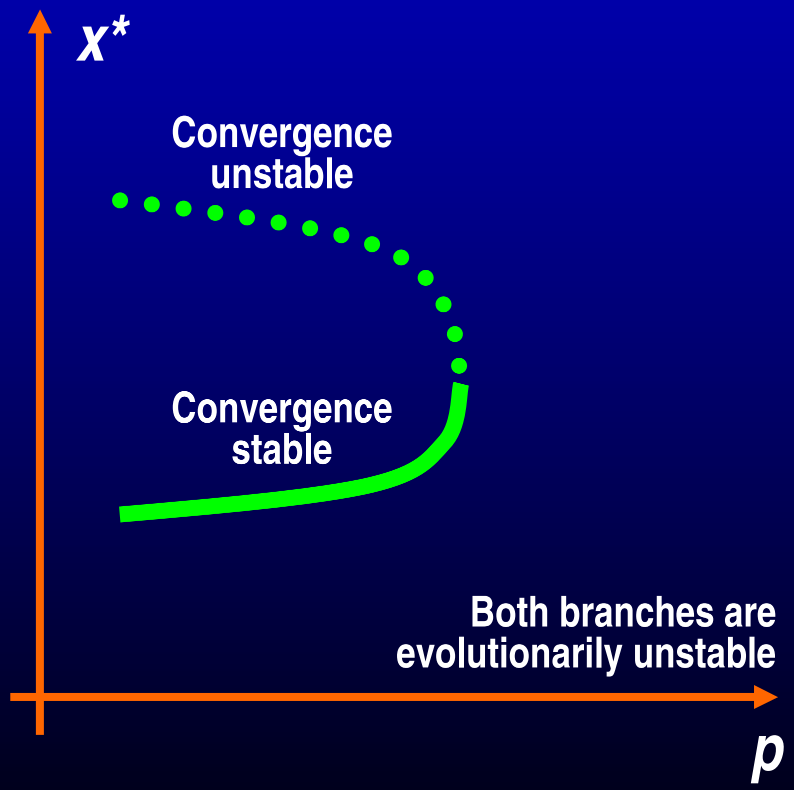
Geritz *et al.* (1997)

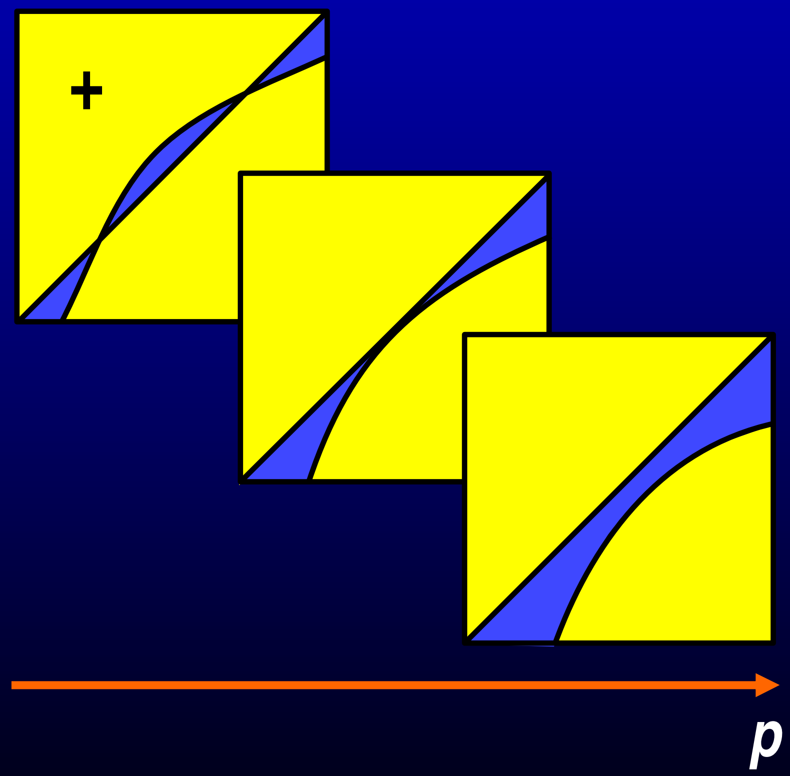


(1) Evolutionary stability, (2) Convergence stability, (3) Invasion potential, (4) Mutual invasibility.

Evolutionary Bifurcations

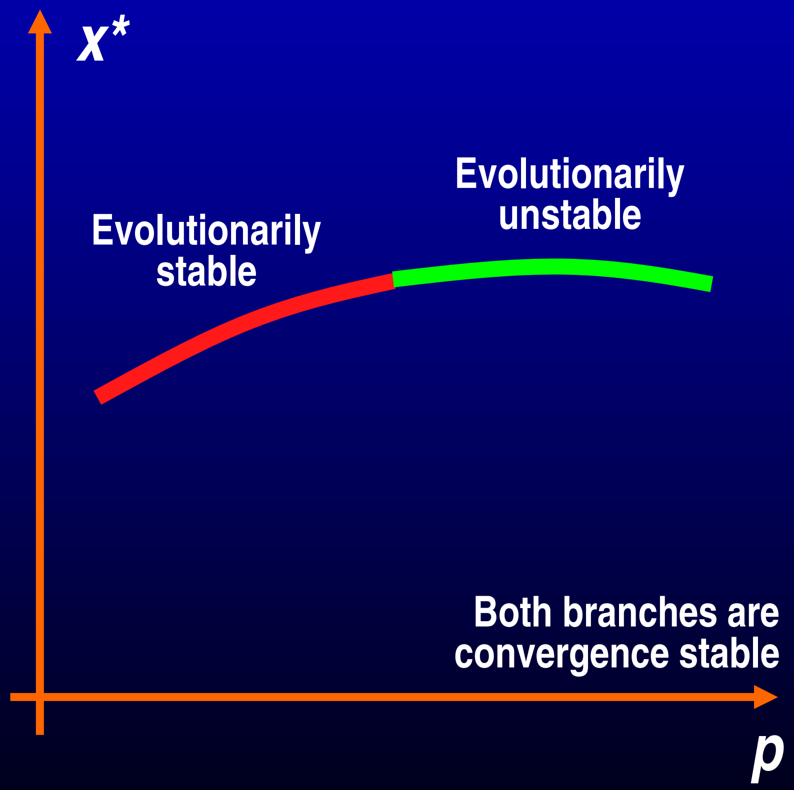
- Example 1: Evolutionary saddle-node bifurcation

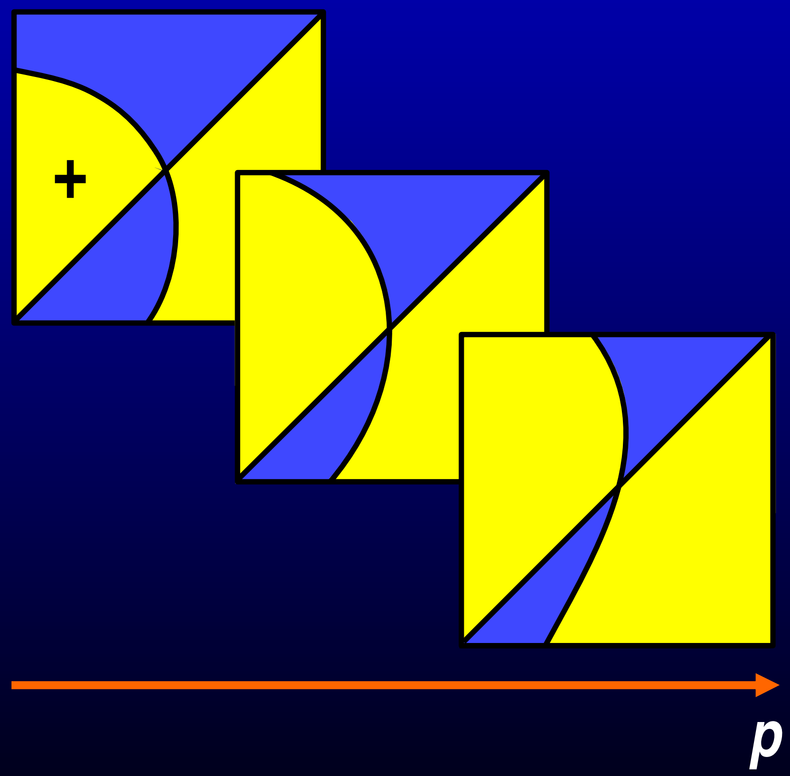




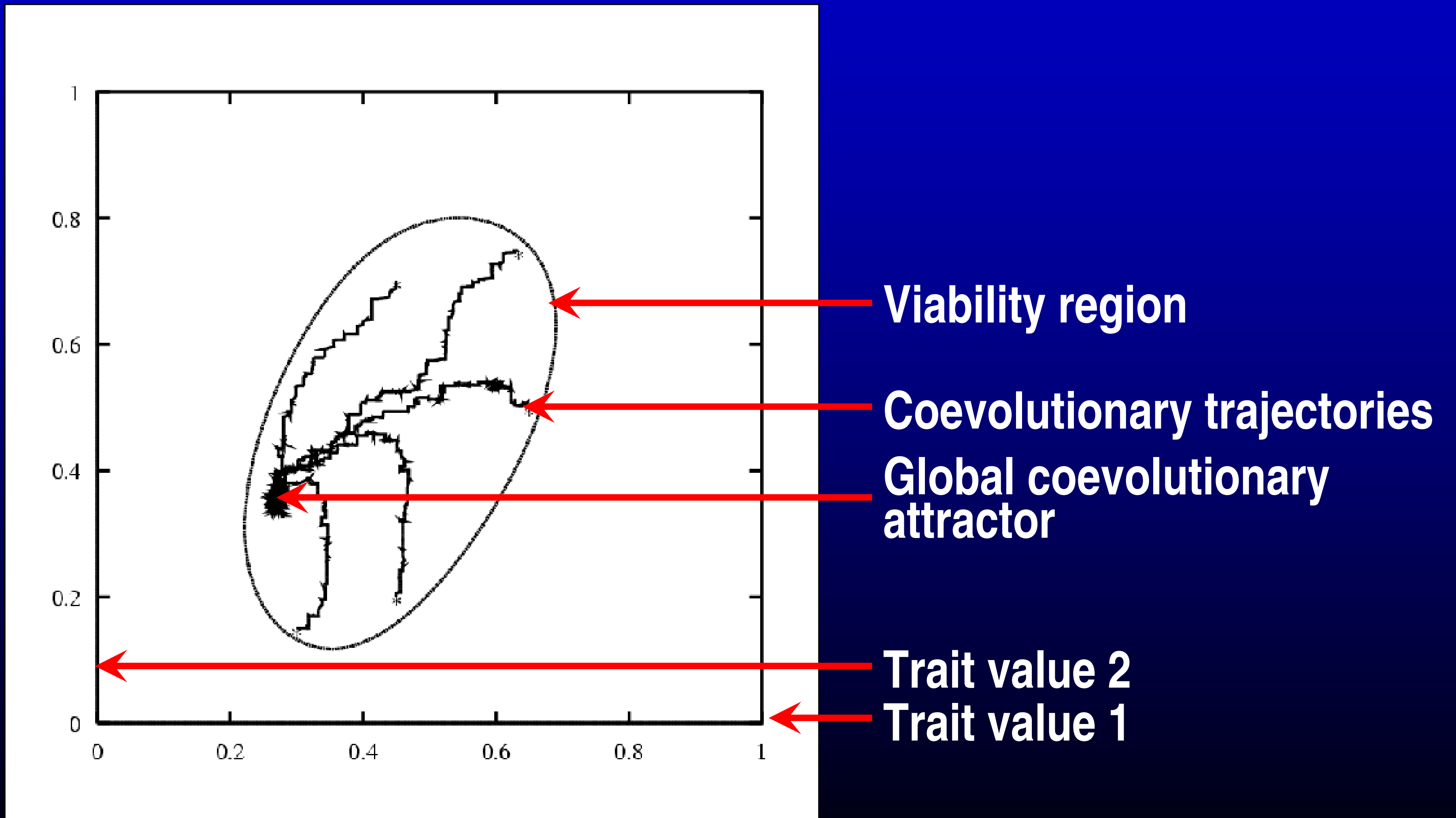
Evolutionary Bifurcations

- Example 2: Gain/loss of evolutionary stability

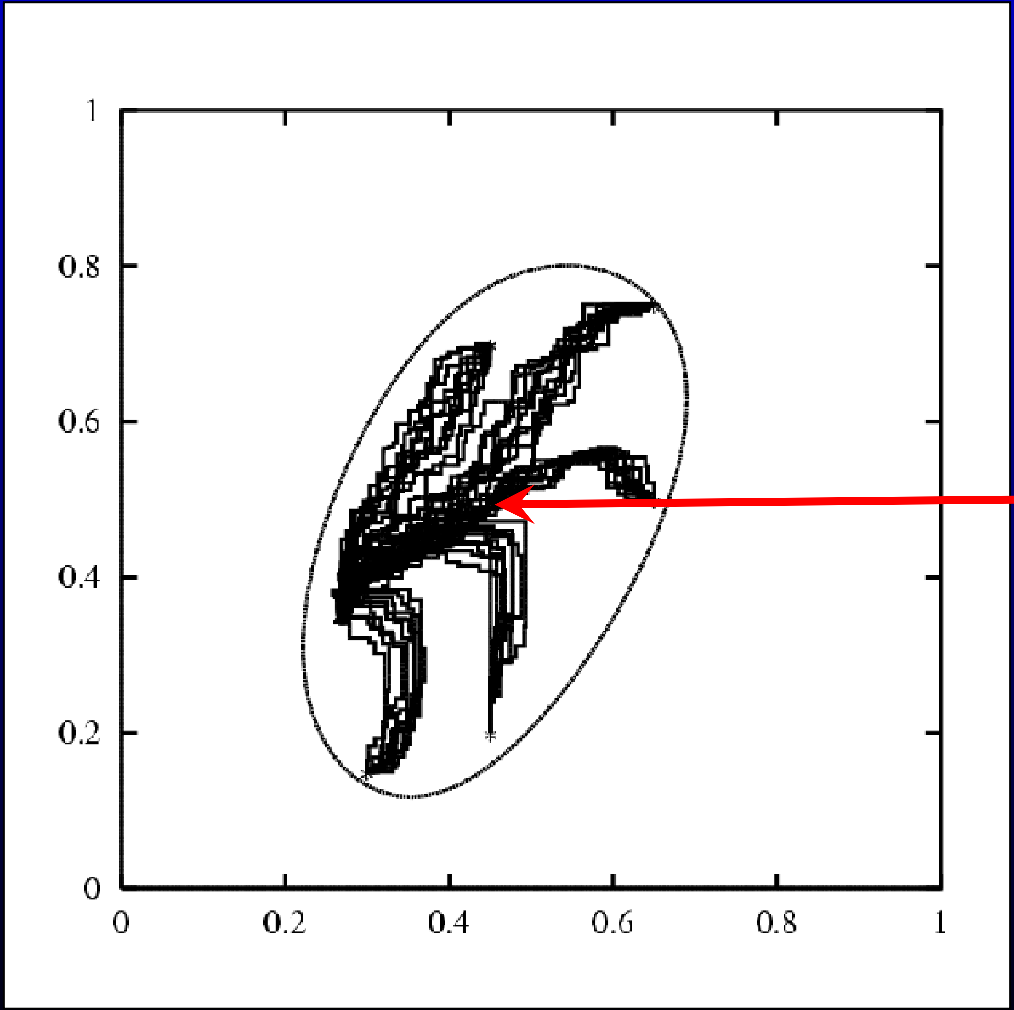




Individual-based Coevolution

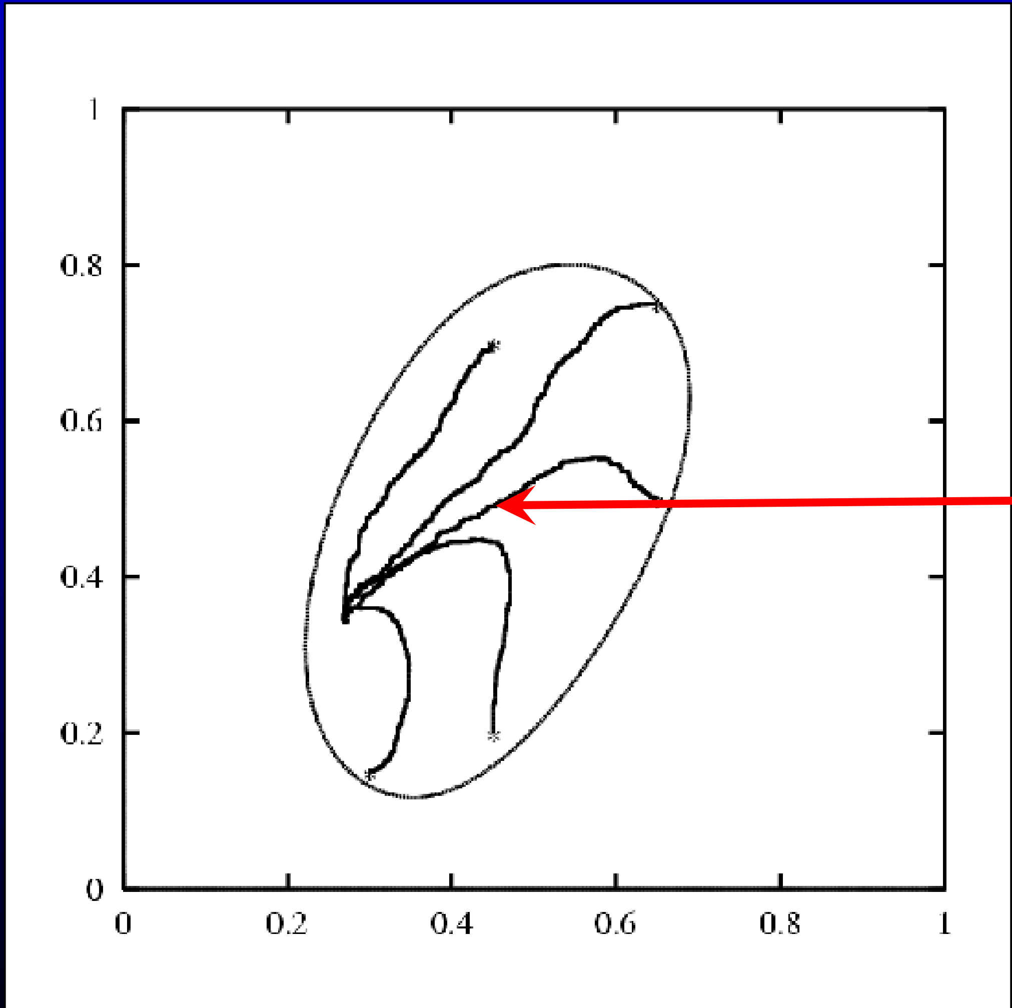


Random Walks in Trait Space



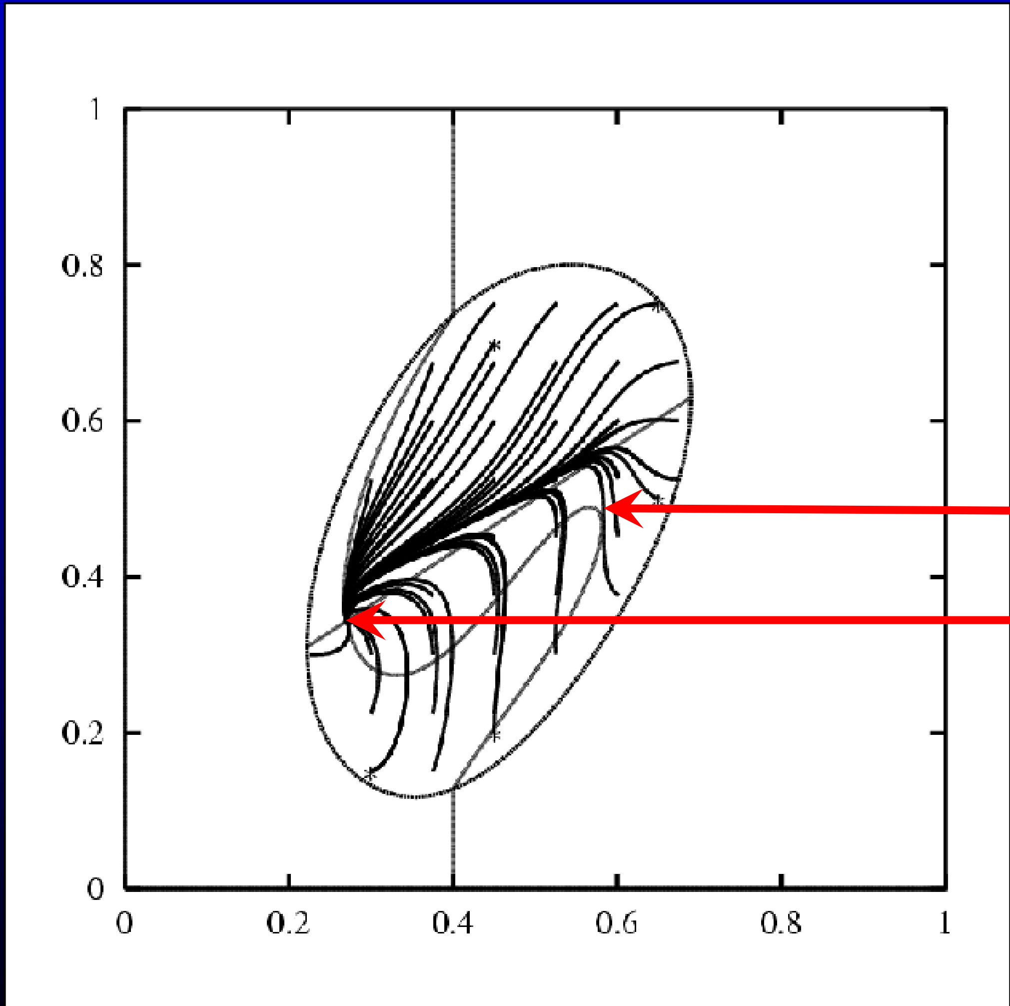
Bundles of coevolutionary trajectories

Average of Random Walks



Mean
coevolutionary trajectories

Deterministic Approximation



Coevolutionary isoclines

Global coevolutionary attractor

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

Result is formally similar to Lande's (1979) approximation based on quantitative genetics.

Dieckmann & Law, J Math Biol, 1996

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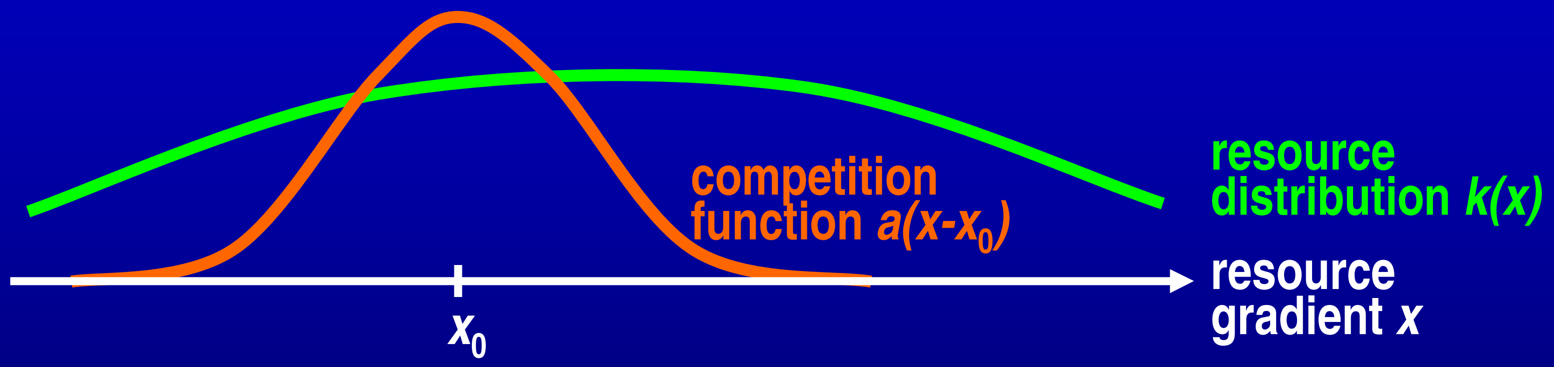
Evolutionary Branching

Resource Competition



Dynamics of population sizes n_i of strategy x_i

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

Step 1: Invasion Fitness

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

1. $n' \rightarrow 0$

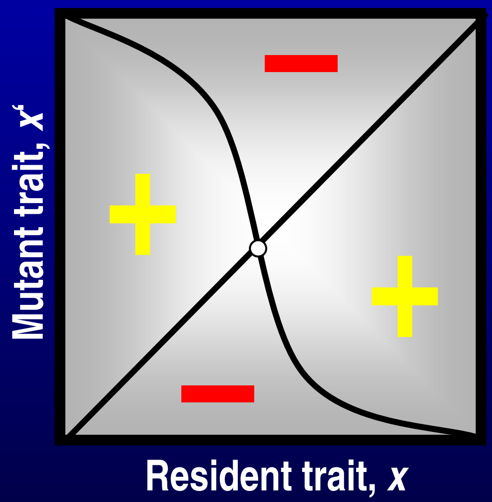
2. $n \rightarrow n_{\text{eq}} = k(x)$

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

Step 2: Pairwise Invasibility Plots

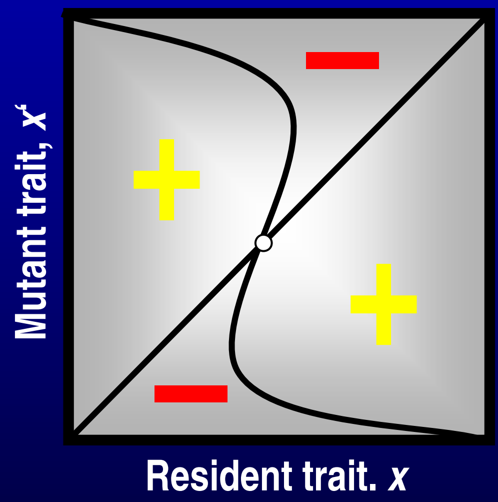
With $k = k_0\, N(0,\sigma_k)$ and $a = N(0,\sigma_a)$ we obtain:

for $\sigma_a > \sigma_k$



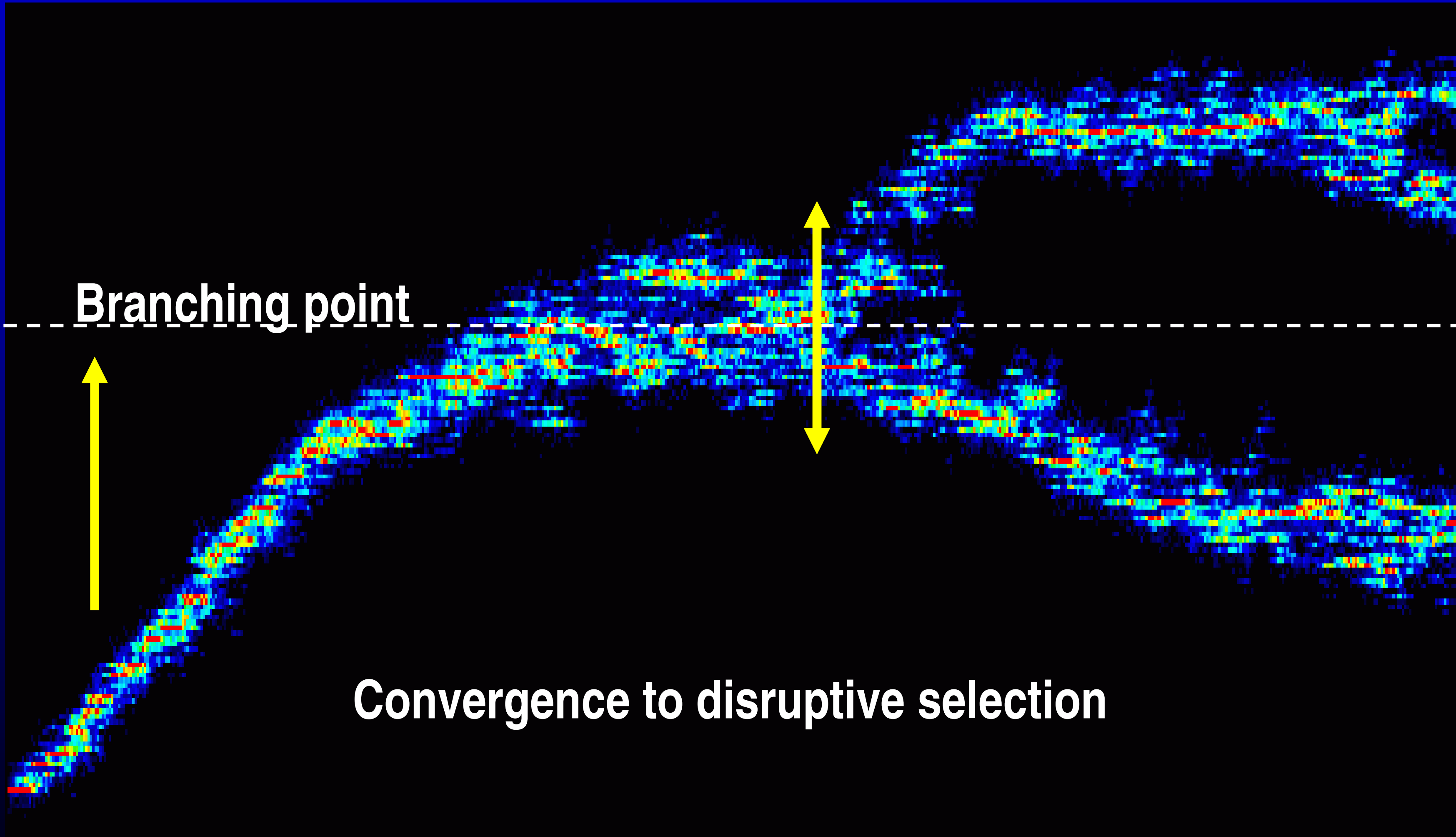
Evolutionary Stability

for $\sigma_a < \sigma_k$

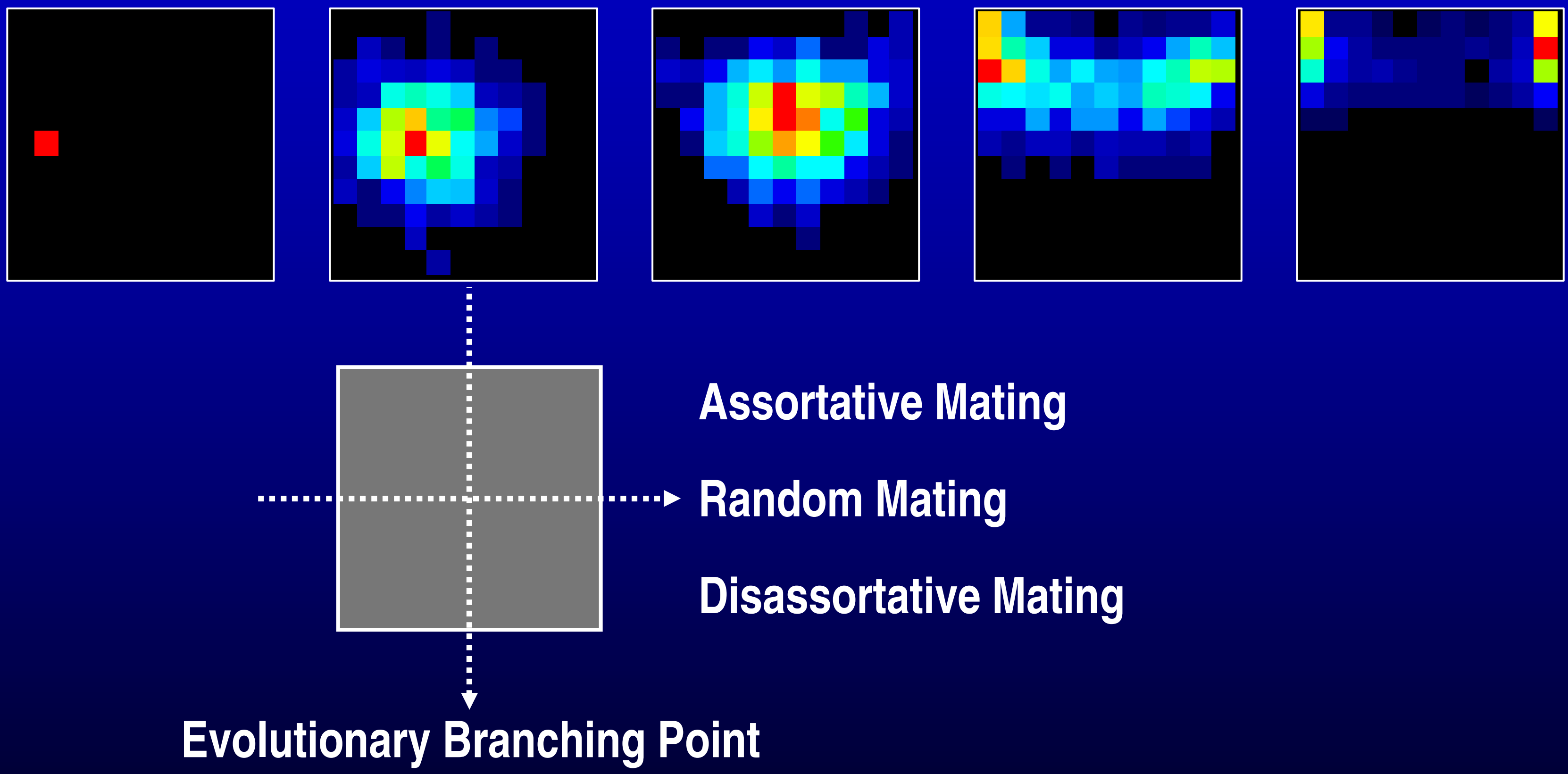


Evolutionary Branching

Evolutionary Branching

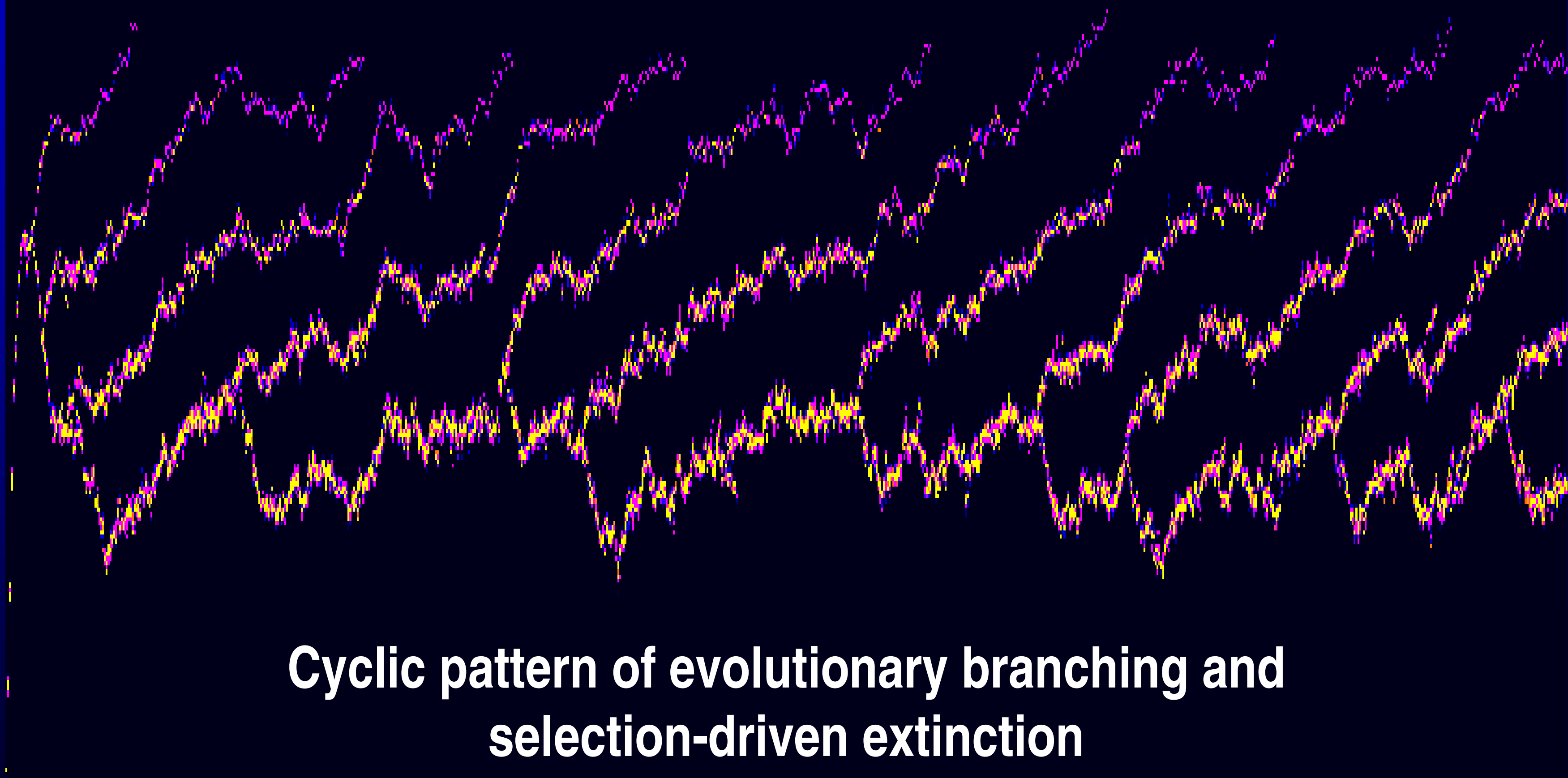


Sexual Evolutionary Branching



Dieckmann & Doebeli, Nature, 1999 (marker character)
Doebeli & Dieckmann, American Naturalist, 2000 (interspecific interactions)

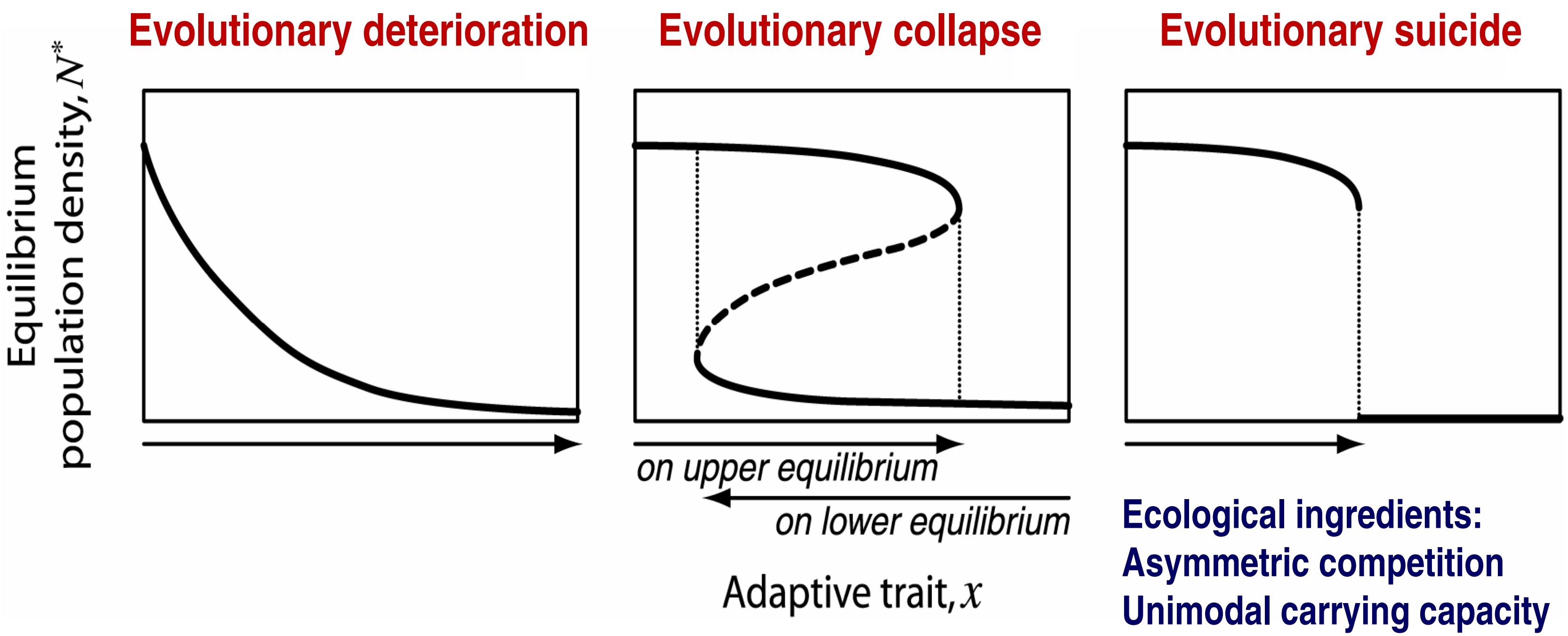
Asymmetric Competition: Taxon Cycles



Cyclic pattern of evolutionary branching and selection-driven extinction

3 Evolutionary Suicide

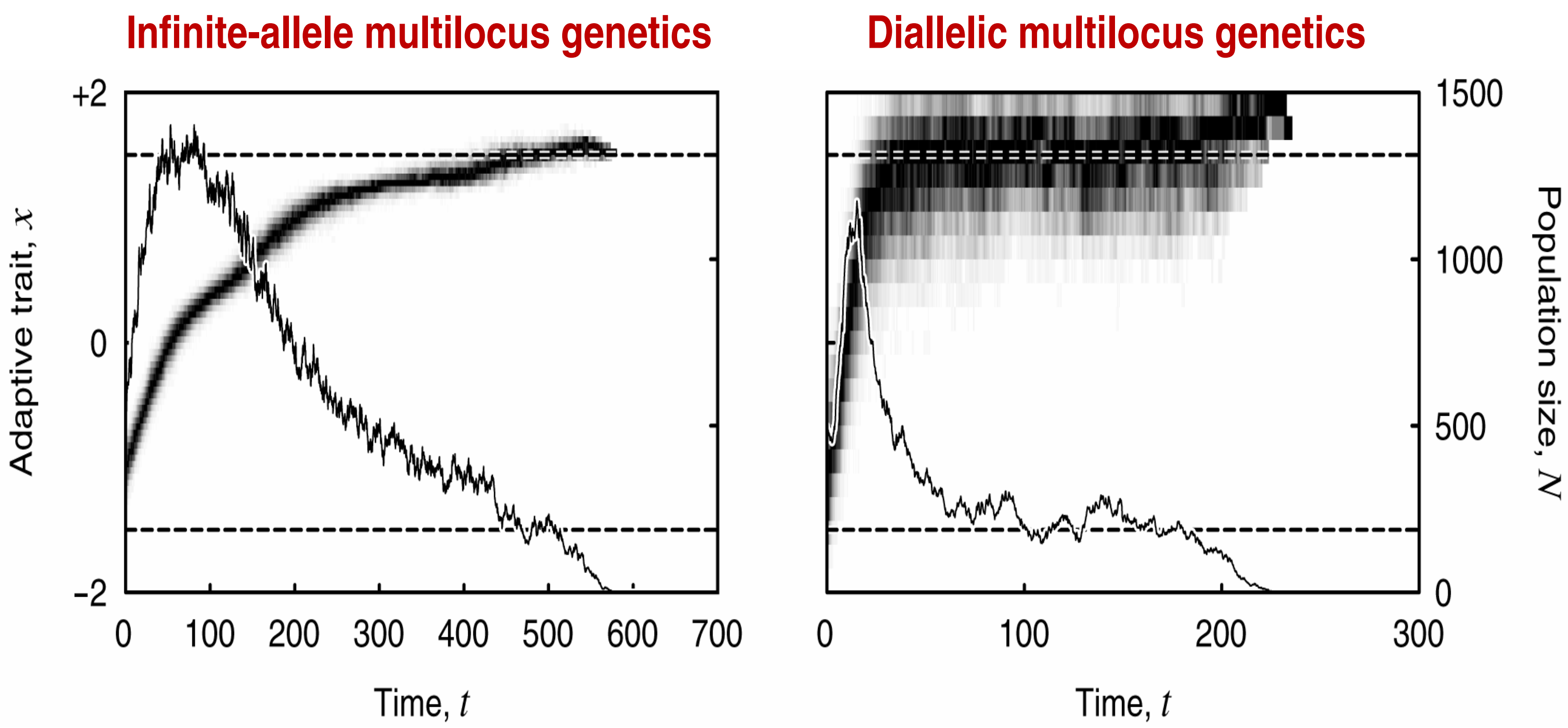
Selection-driven Loss of Viability



Ecological ingredients:
Asymmetric competition
Unimodal carrying capacity
Allee effect

Dieckmann & Ferriere, chapter in *Evolutionary Conservation Biology*, 2003 (in press)

Sexual Evolutionary Suicide

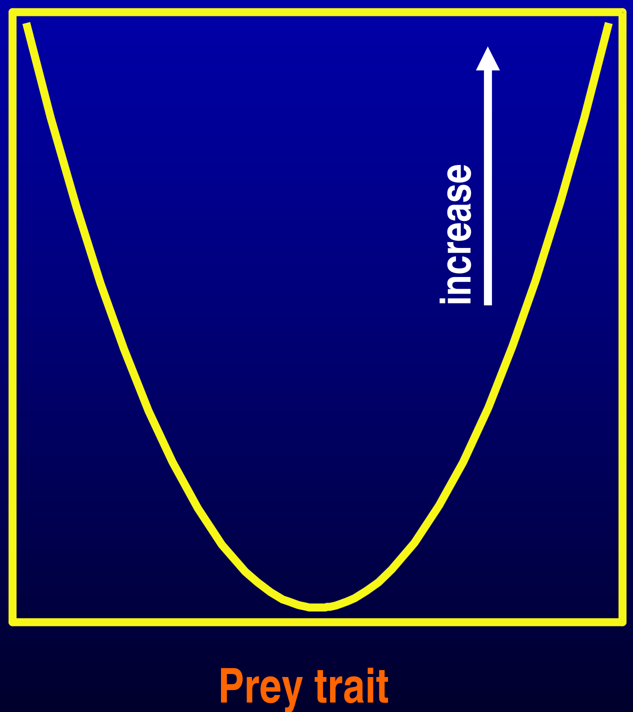


Dieckmann & Ferriere, chapter in *Evolutionary Conservation Biology*, 2003 (in press)

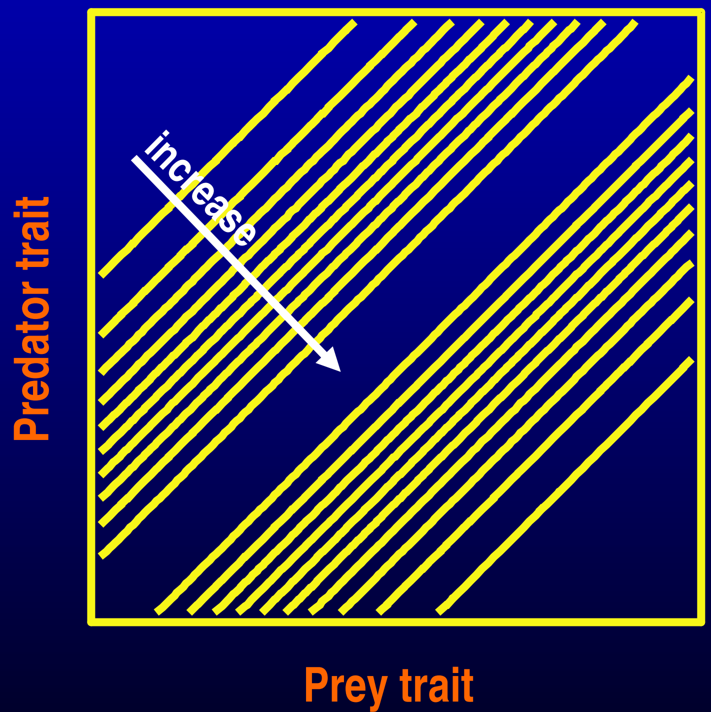
4 Predator-Prey Coevolution

Coevolving Traits

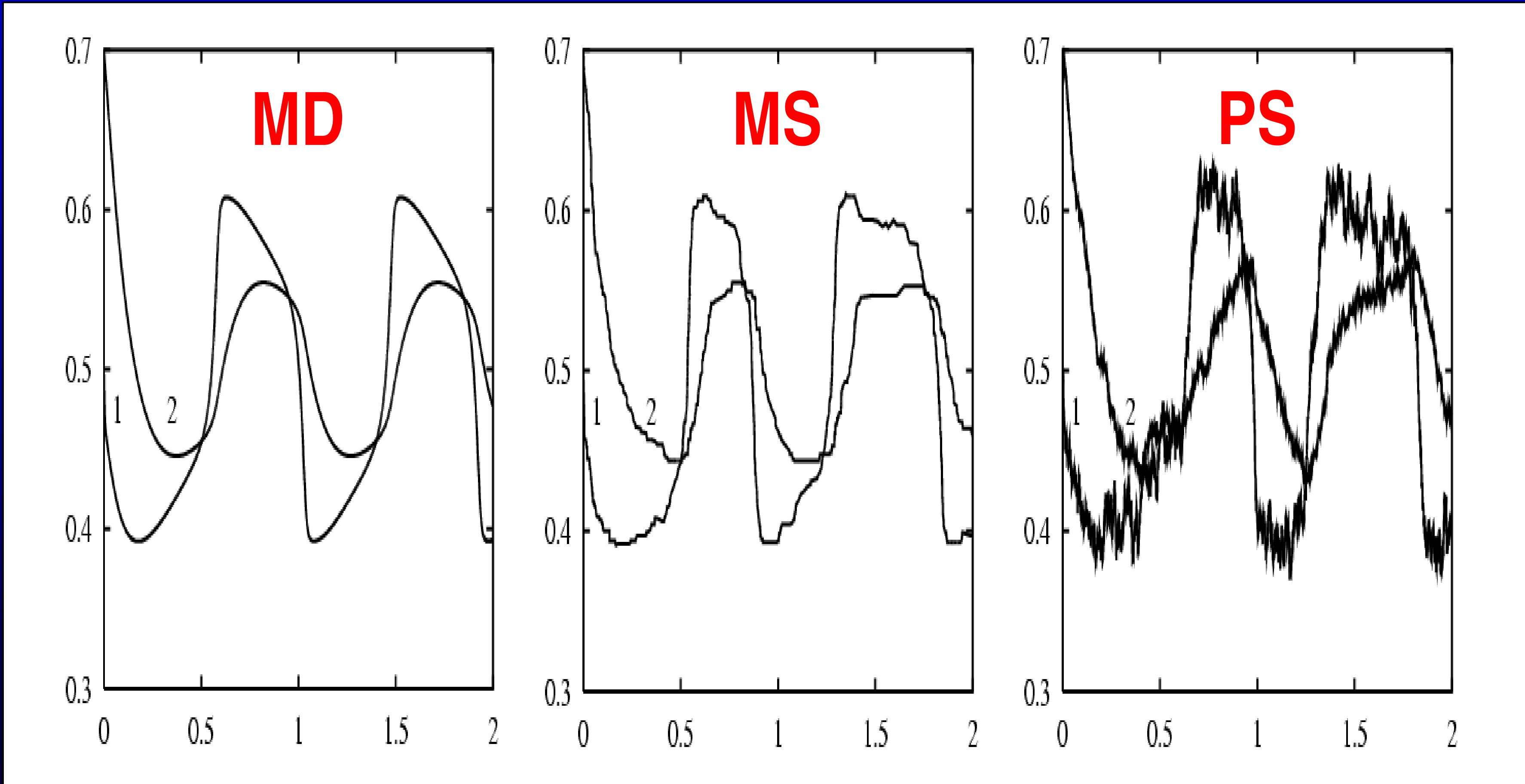
- Natural prey mortality



- Predator-induced prey mortality

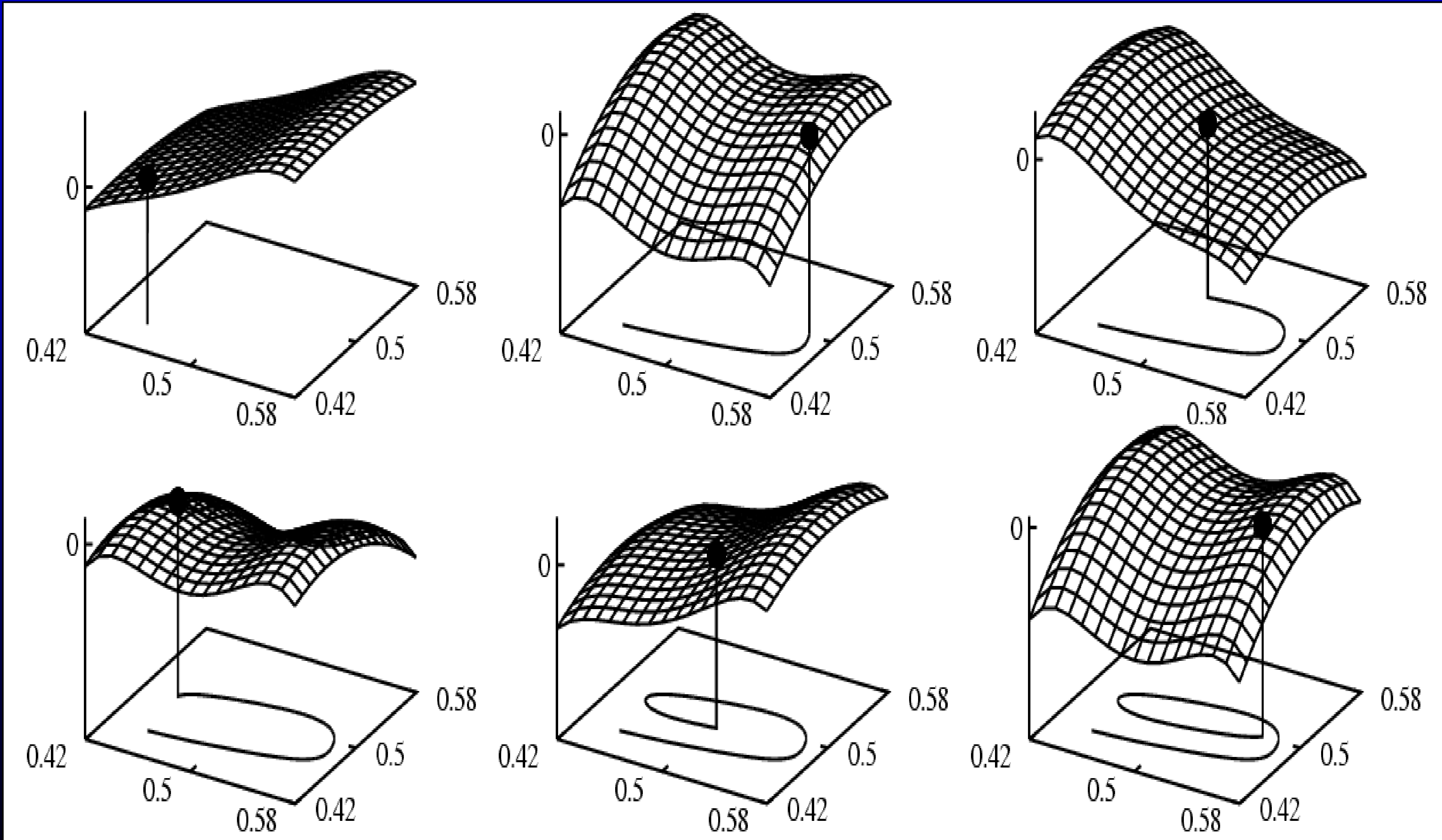


Evolutionary Cycling

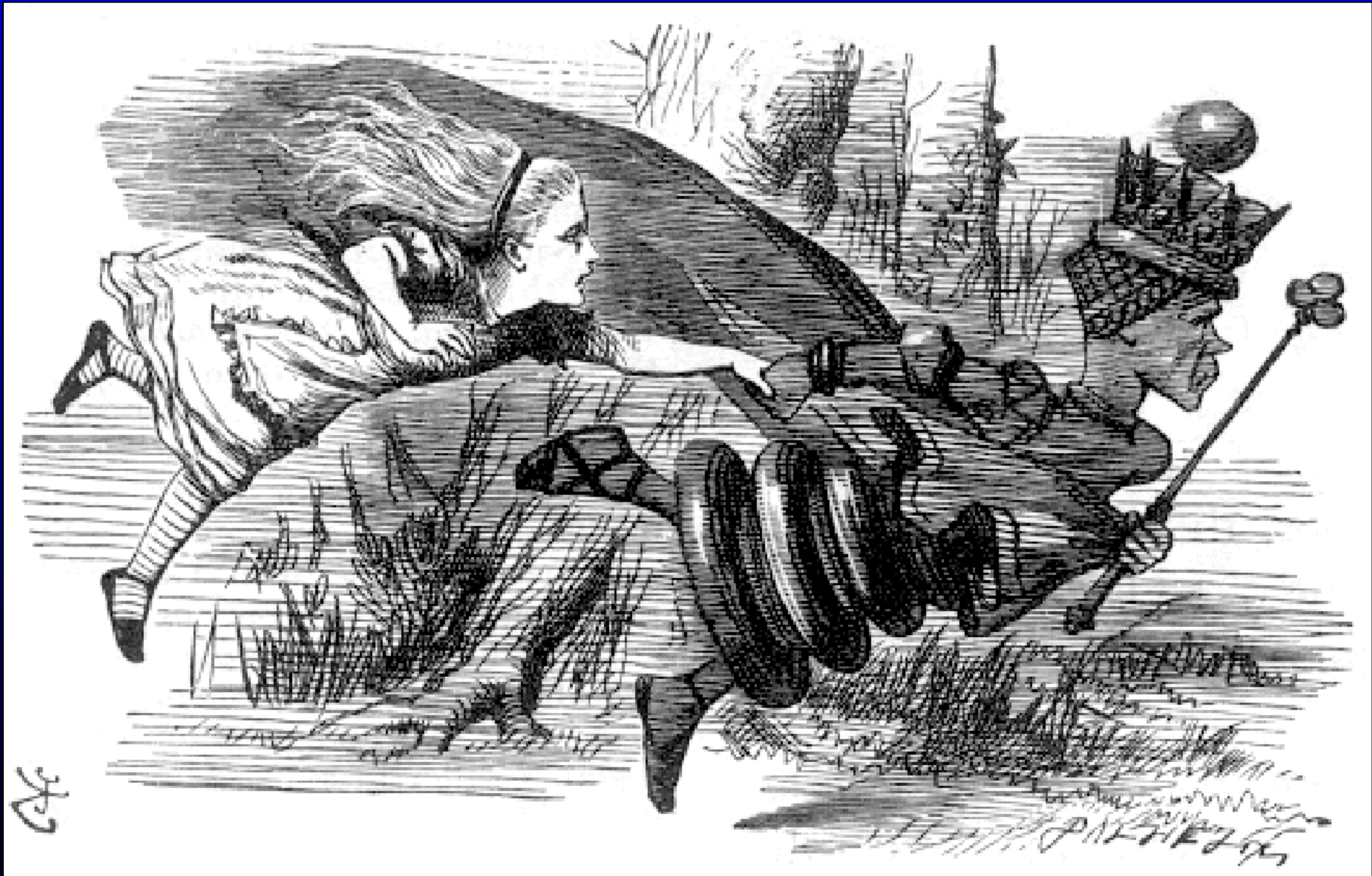


Dieckmann, Marrow & Law, Proc R Soc B, 1995

Variable Adaptive Landscapes



Red Queen Dynamics



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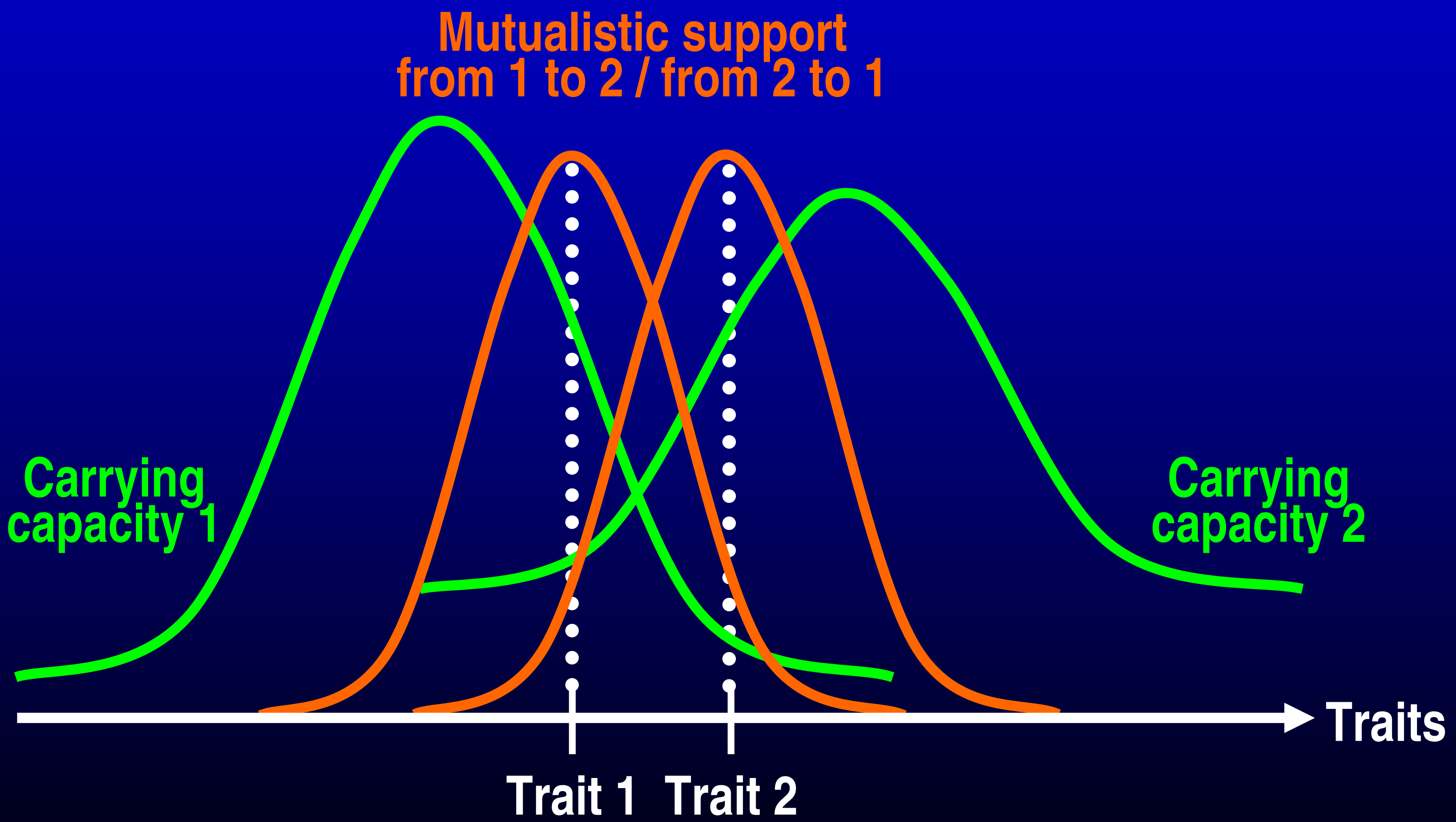
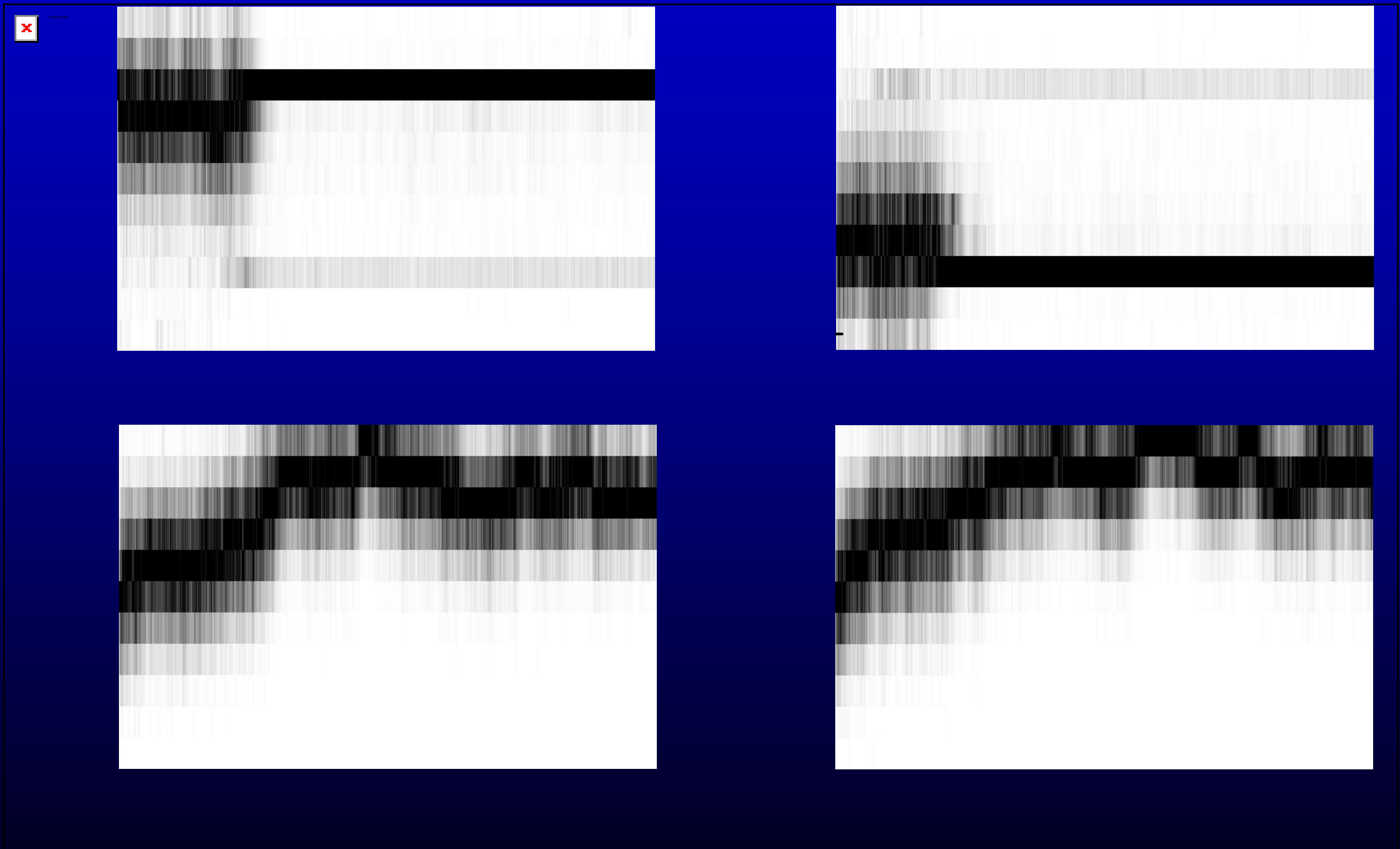
Mutualistic Coevolution

Coevolving Traits



Coevolutionary Branching



Doebeli & Dieckmann, American Naturalist, 2000

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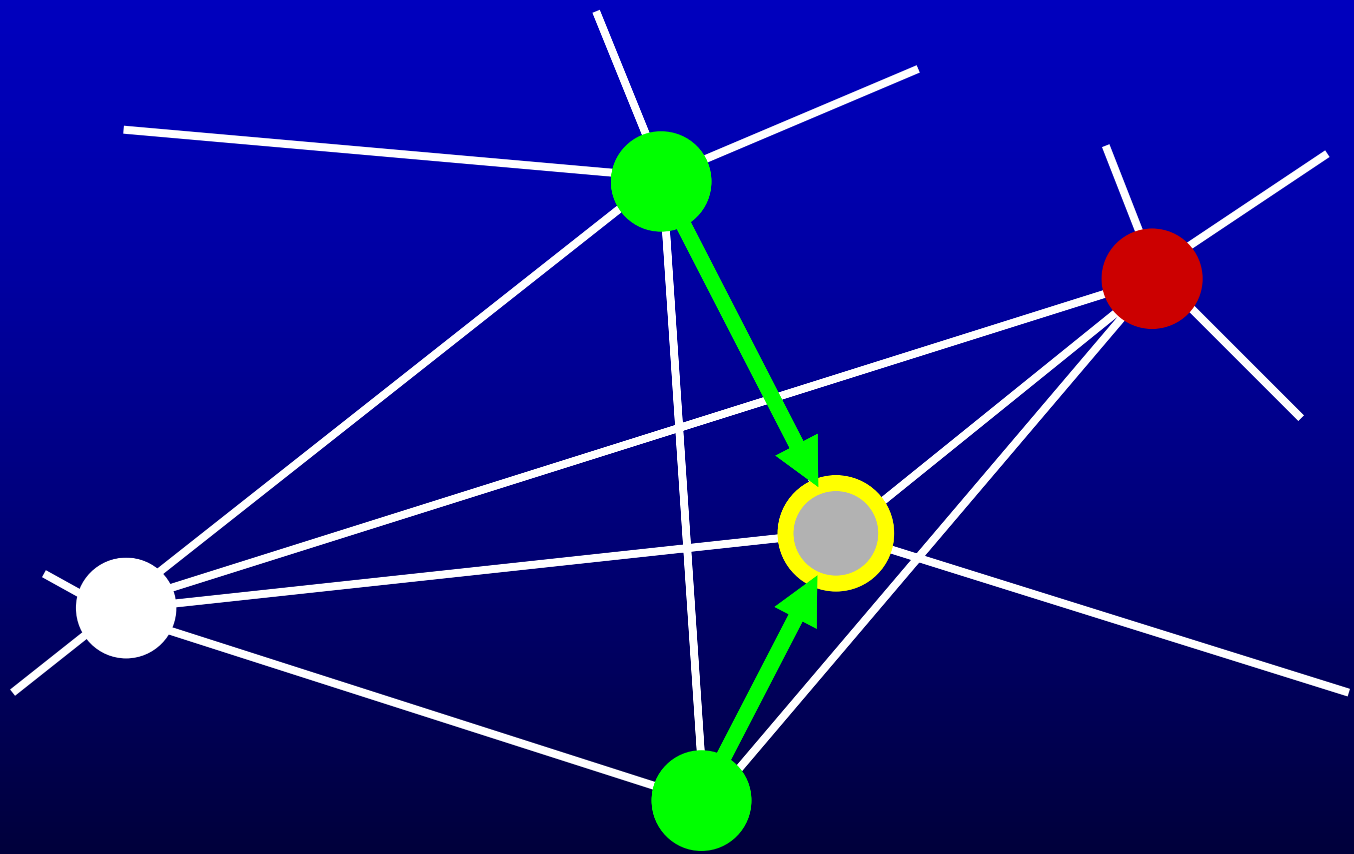
Altruism

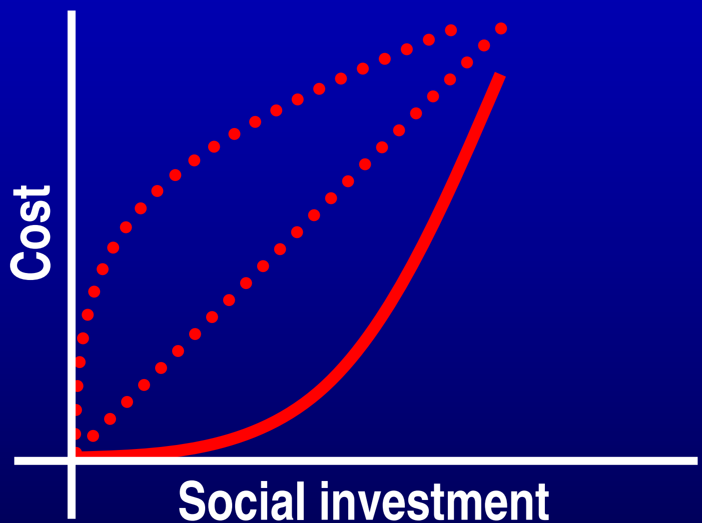
Evolution on Random Contact Networks



Individuals possess two adaptive traits, determining, respectively, their degree of sociality and mobility.

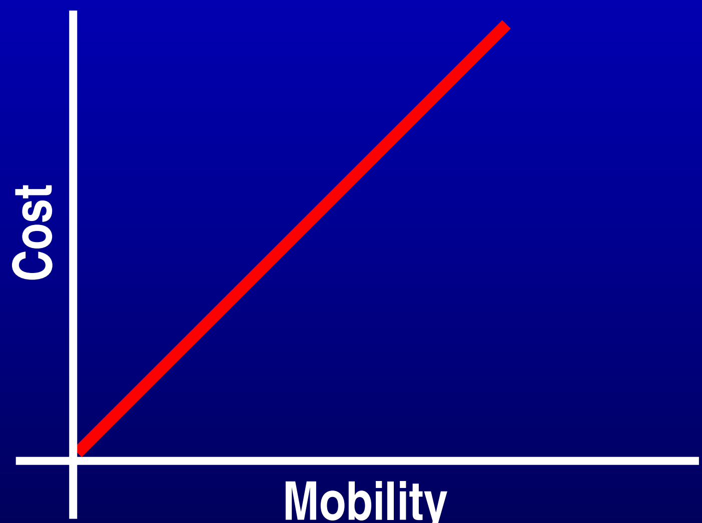
Joint Evolution of Sociality and Mobility

- **Sociality**



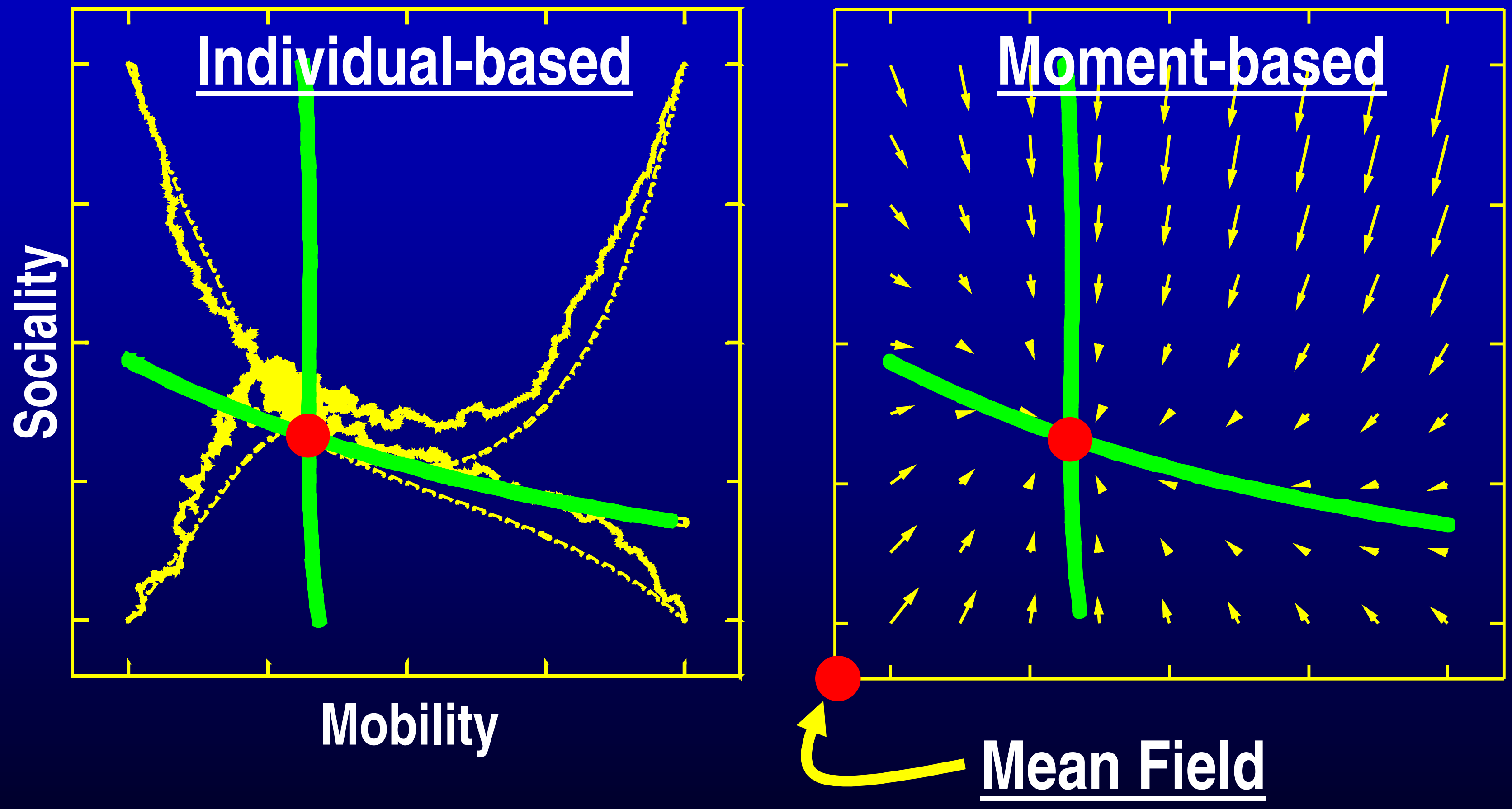
Social investment benefits the fecundity of receiving neighbors, but comes at an accelerating cost to the donor.

- **Mobility**



Also higher mobility comes at a linearly increasing cost.

Evolutionary Outcome



Le Galliard, Ferriere & Dieckmann, Evolution, 2003 (2nd ms in preparation)

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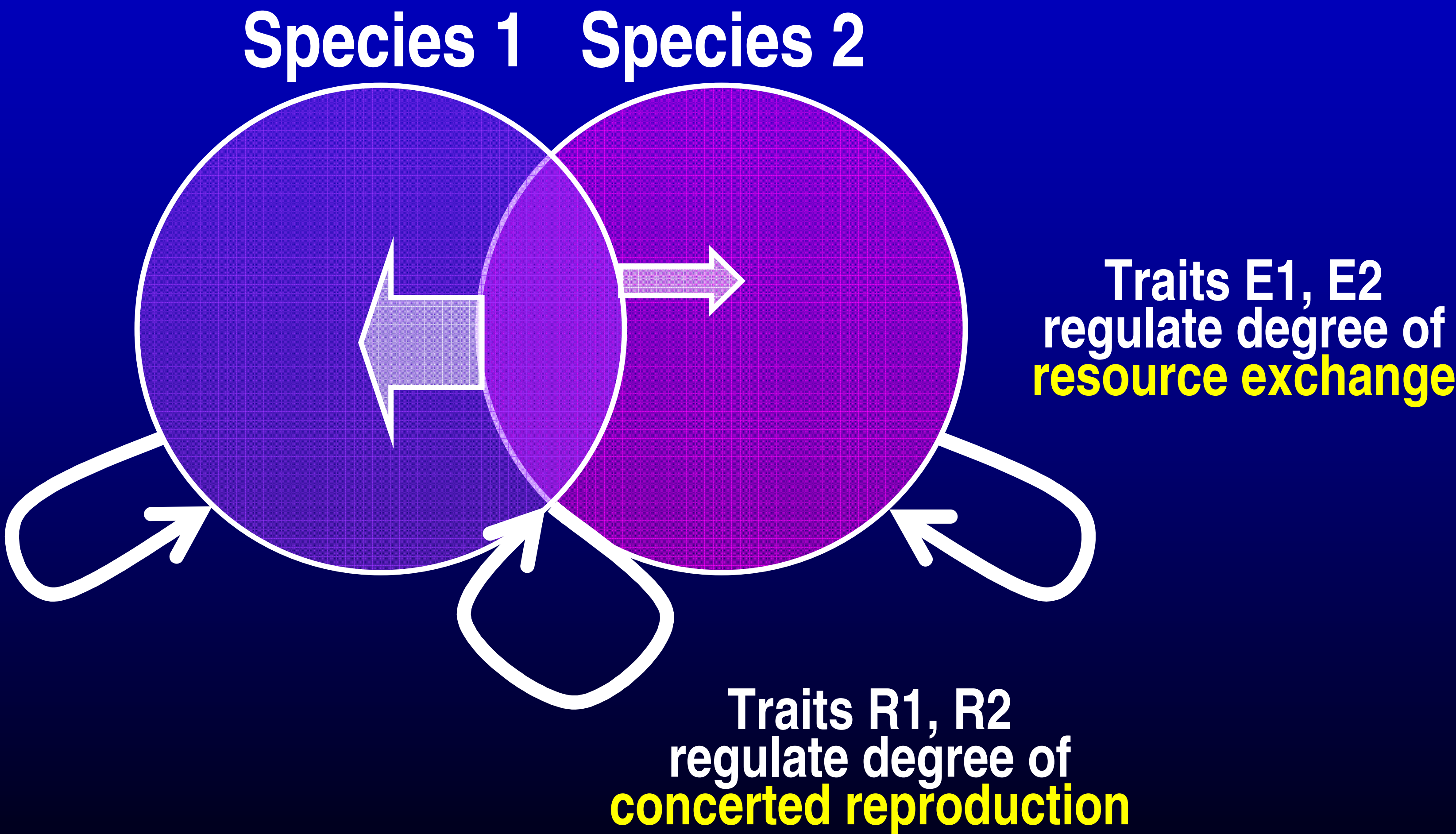
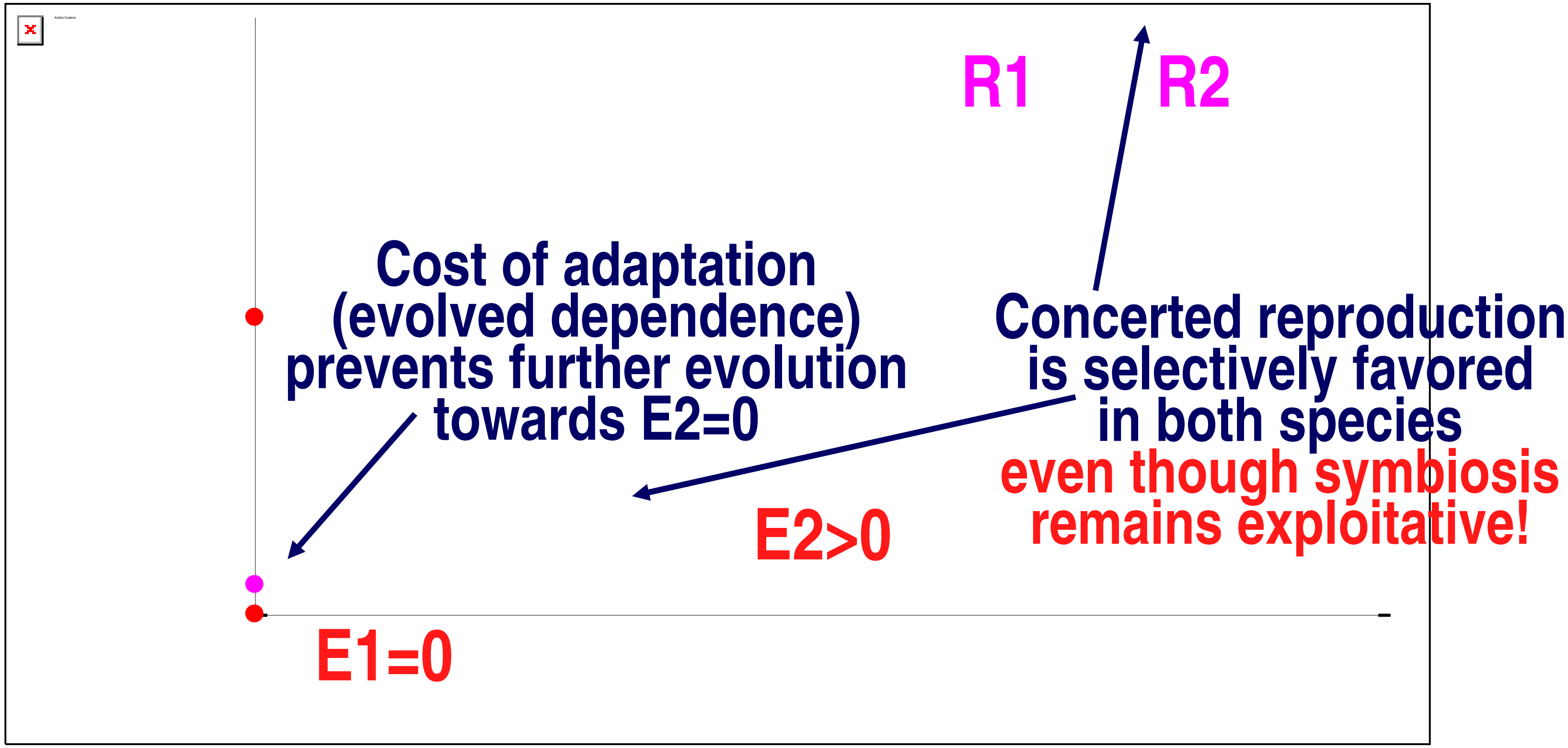
Concerted Reproduction

Coevolving Traits in a Symbiotic Unit



Coevolution of Concerted Reproduction



Law & Dieckmann, Proc R Soc B, 1997

Summary

	Only evolution	Also coevolution
Only individual-level selection	Evolutionary branching Evolutionary suicide	Predator-prey Mutualism
Also higher-level selection	Altruism	Concerted reproduction

- Frequency-dependent selection is crucial for understanding ecosystem evolution.
- Adaptive dynamics theory is set up to account for it, closely linking adaptive dynamics and population dynamics.
- Within the same framework, coevolution and higher-level selection are readily captured.

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.
  IIASA Working Paper WP-95-099.
  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.
  IIASA Working Paper WP-96-001.
  Journal of Mathematical Biology 34, 579-612 (1996).

- Geritz SAH, Metz JAJ, Kisdi É, Meszéna G:
  The Dynamics of Adaptation and Evolutionary Branching.
  IIASA Working Paper WP-96-077.
  Physical Review Letters 78, 2024-2027 (1997).

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  Can Adaptive Dynamics Invade?
  IIASA Working Paper WP-96-152.
  Trends in Ecology and Evolution 12, 128-131 (1997).

Available online at

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