Overview

Eco-Evolutionary Dynamics

Modelling Frameworks

Biodiversity Dynamics

Mathematical Connections

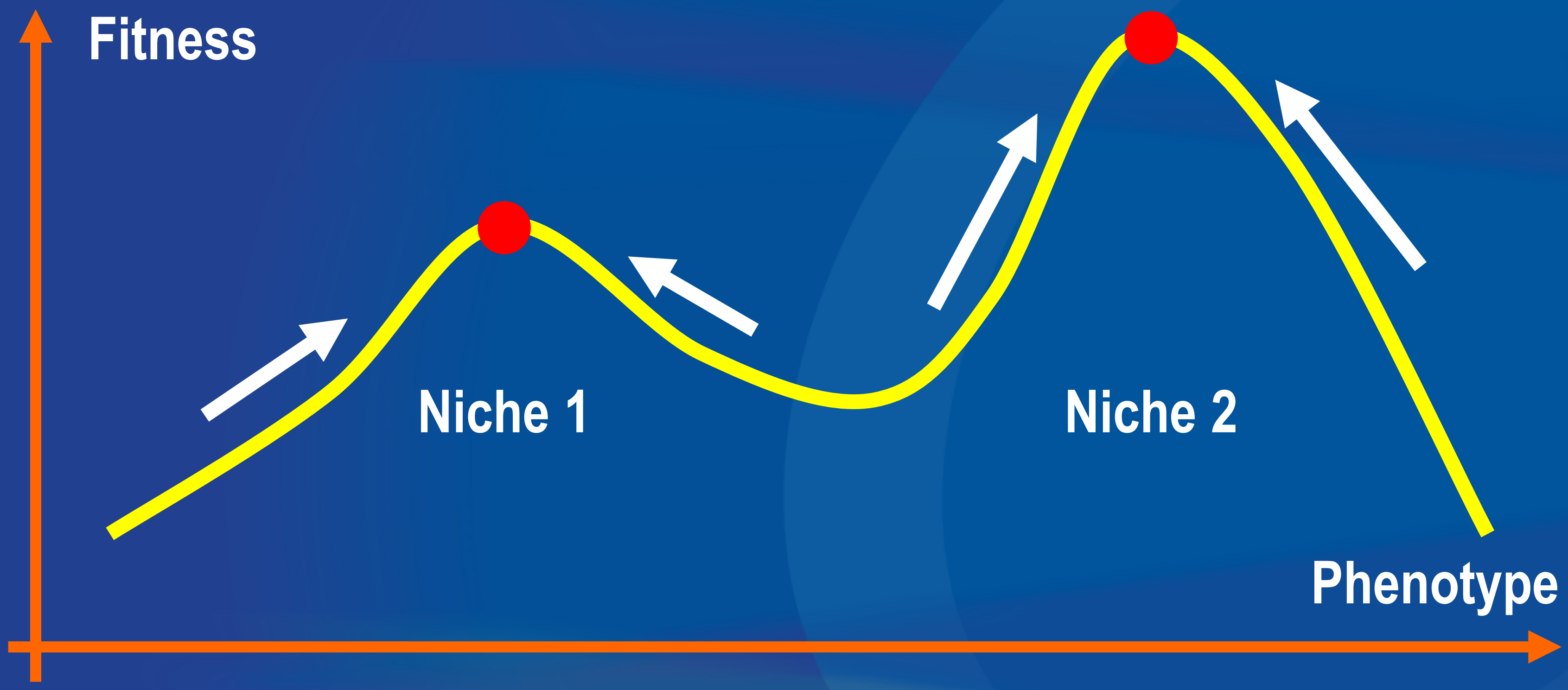
Adaptive Speciation

Niche Theory

2 Modelling Frameworks

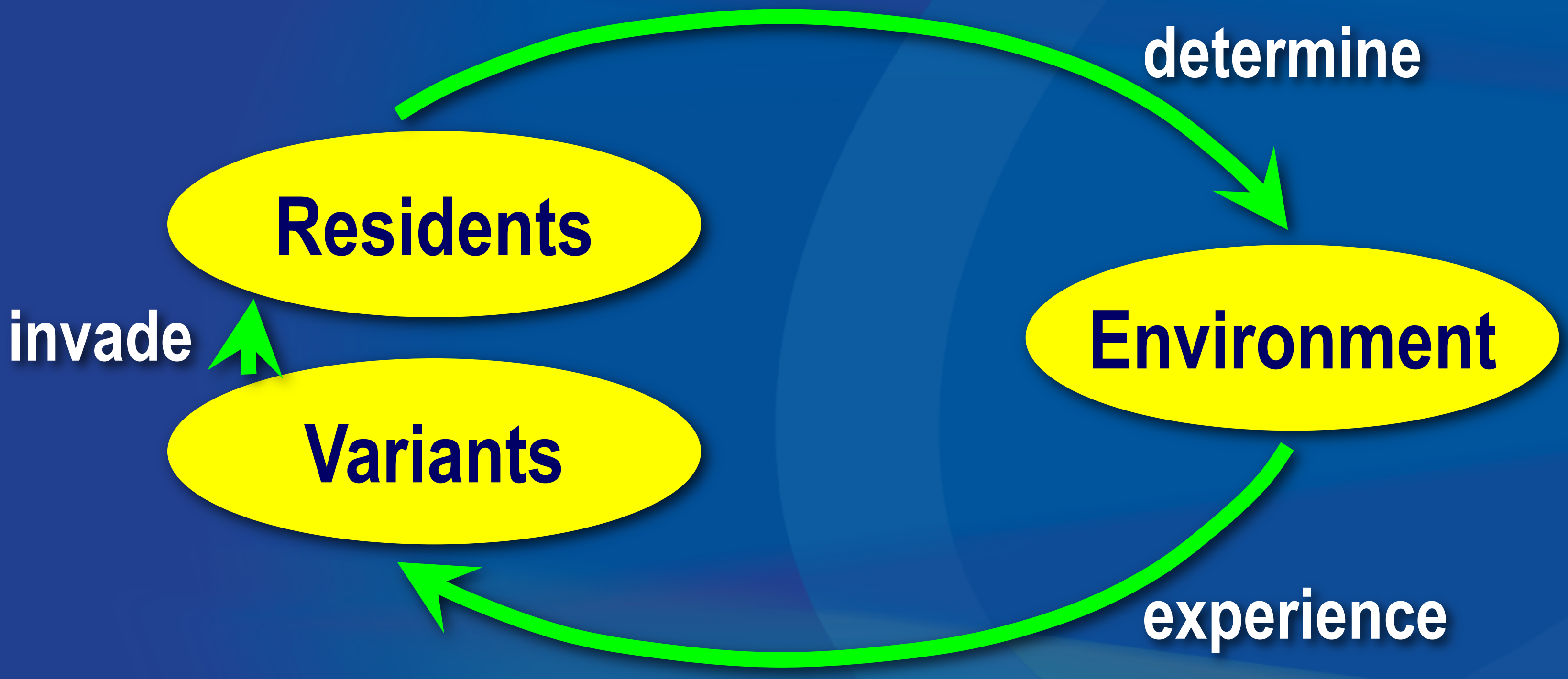
2a Eco-evolutionary feedback

Traditional View of Evolution

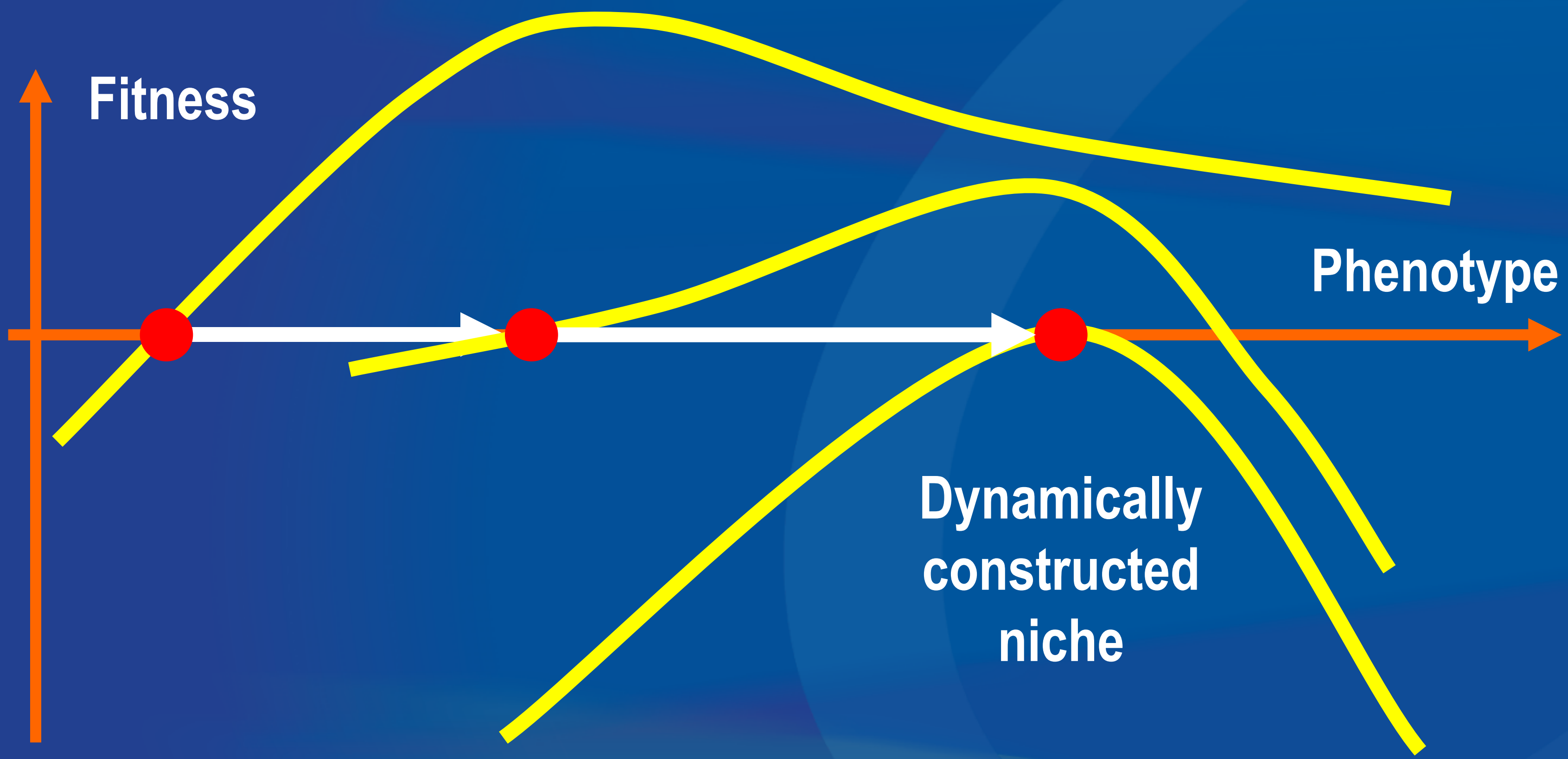


Envisaging evolution as a hill-climbing process on a static fitness landscape is attractively simple, but essentially wrong, especially in community ecology

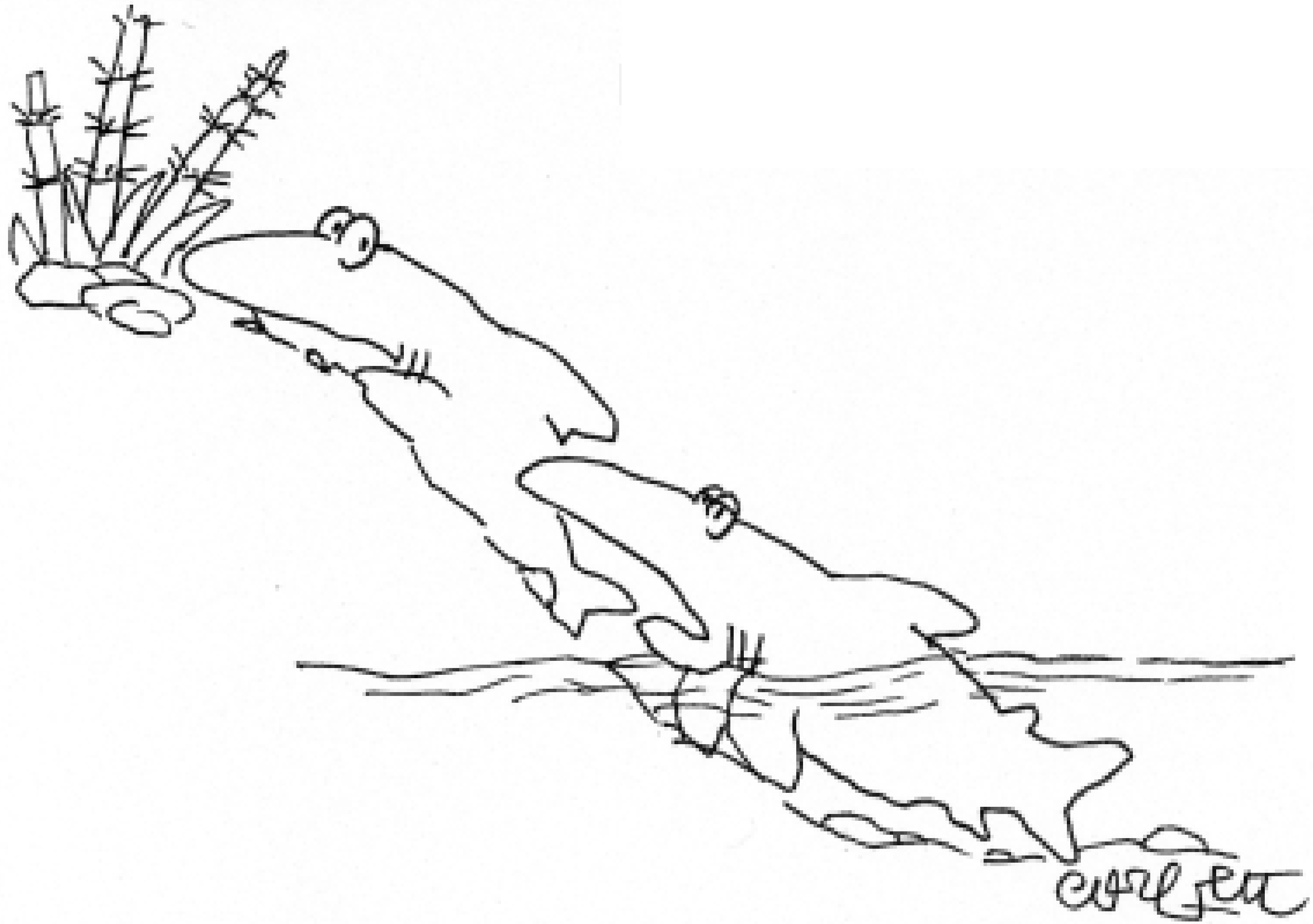
Eco-Evolutionary Feedback



Modern View of Evolution



Generically, fitness landscapes change in dependence on a community's current composition



"WRITE, IF YOU ESTABLISH A NICHE."

Niche Construction

- Through niche construction, an organism alters its environment, creating a feedback with natural selection
- Niche construction is especially evident when environmental alterations persist for generations, leading to ecological inheritance

Frequency-dependent Selection

- **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

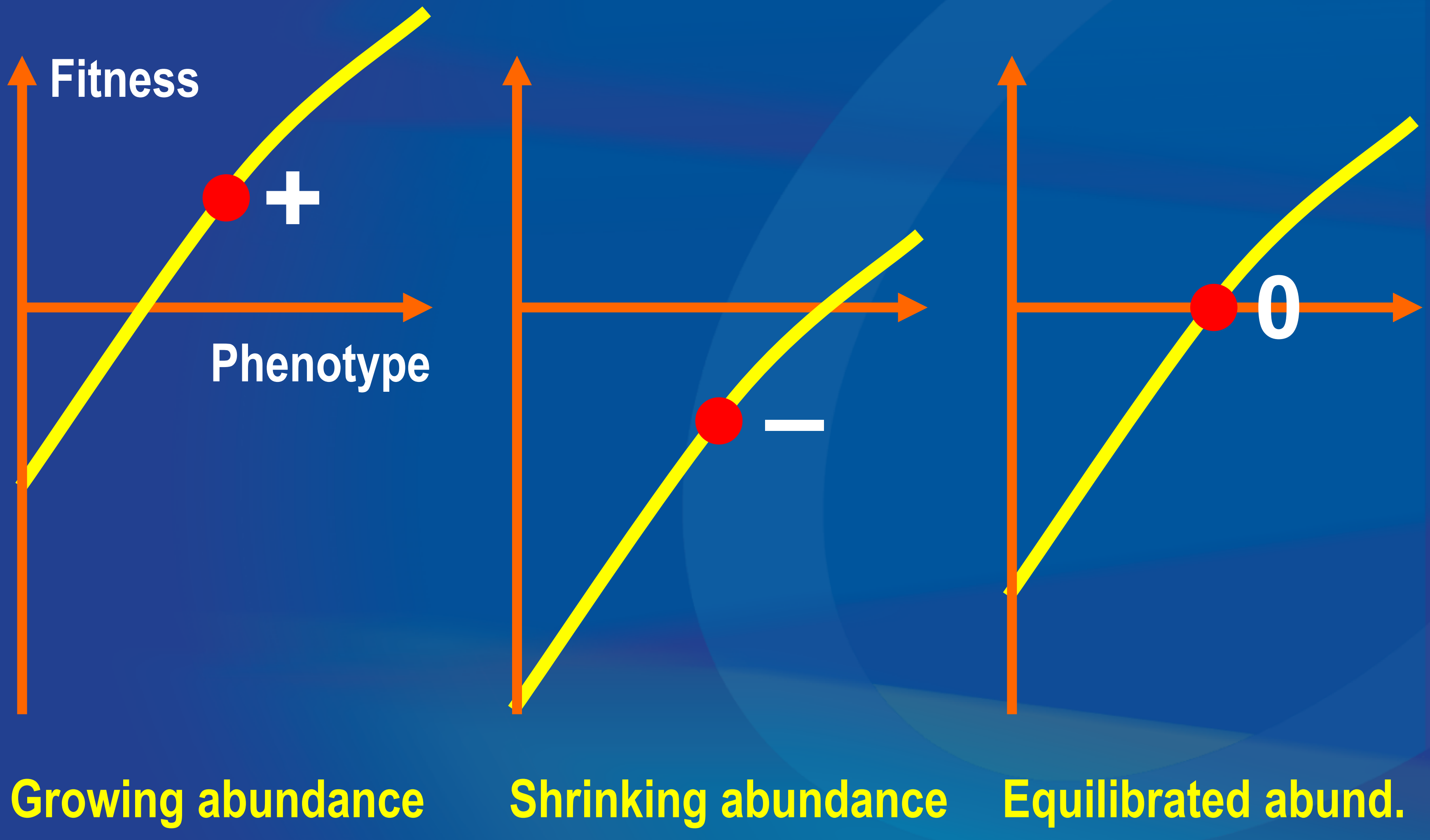
- Frequency dependence arises whenever selection pressures in a population vary with its phenotypic composition
- Virtually any ecologically serious consideration of life-history evolution implies frequency-dependent selection
- Only carefully crafted (or ecologically unrealistic) models circumvent this complication

Origin of Frequency-dependent Selection

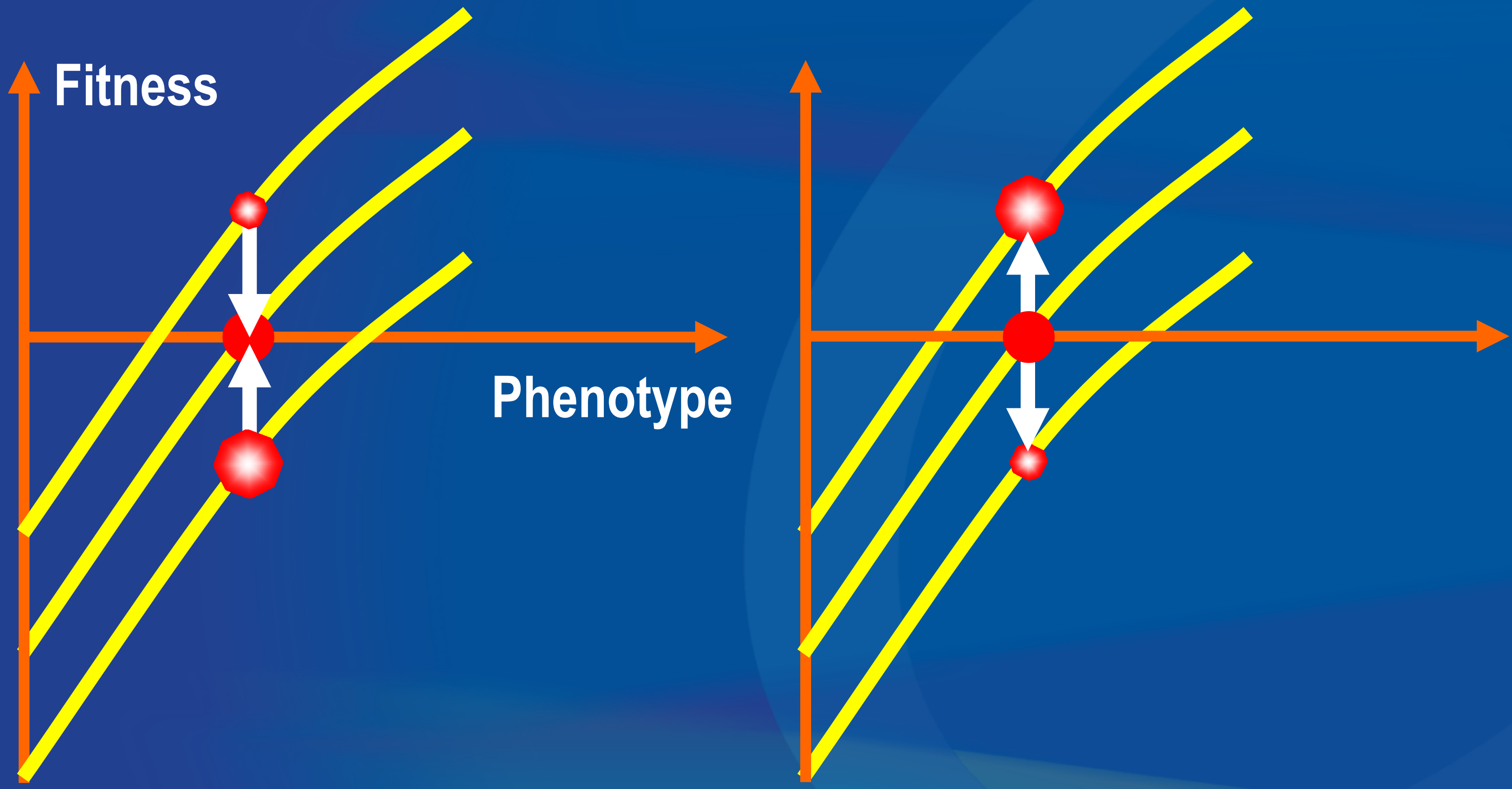
When
trait dependence
and
density regulation
overlap along a life cycle, eco-evolutionary feedback and frequency-dependent selection typically ensue

2b Dynamic fitness landscapes

Ecological Equilibration



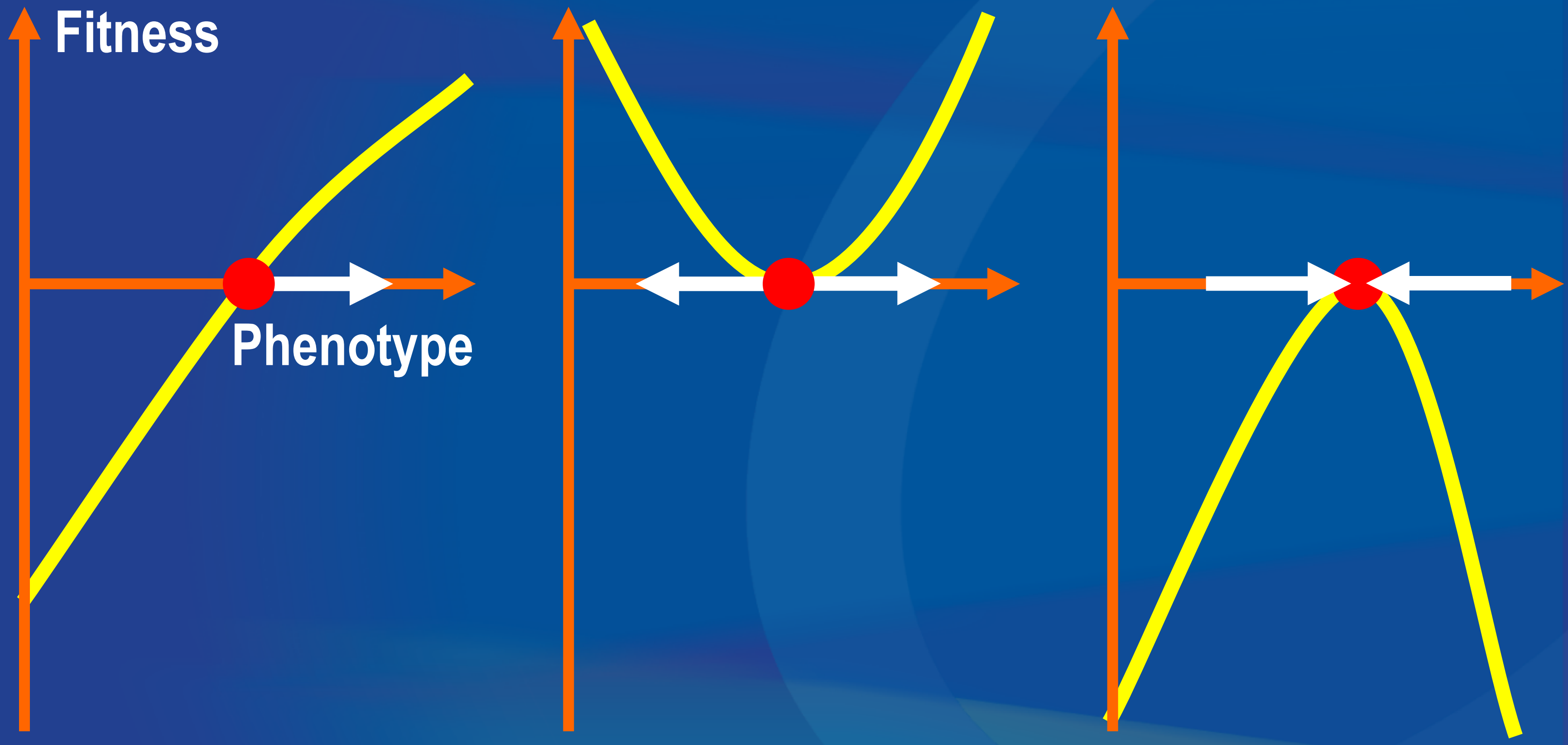
Ecological Stability



Ecologically stable

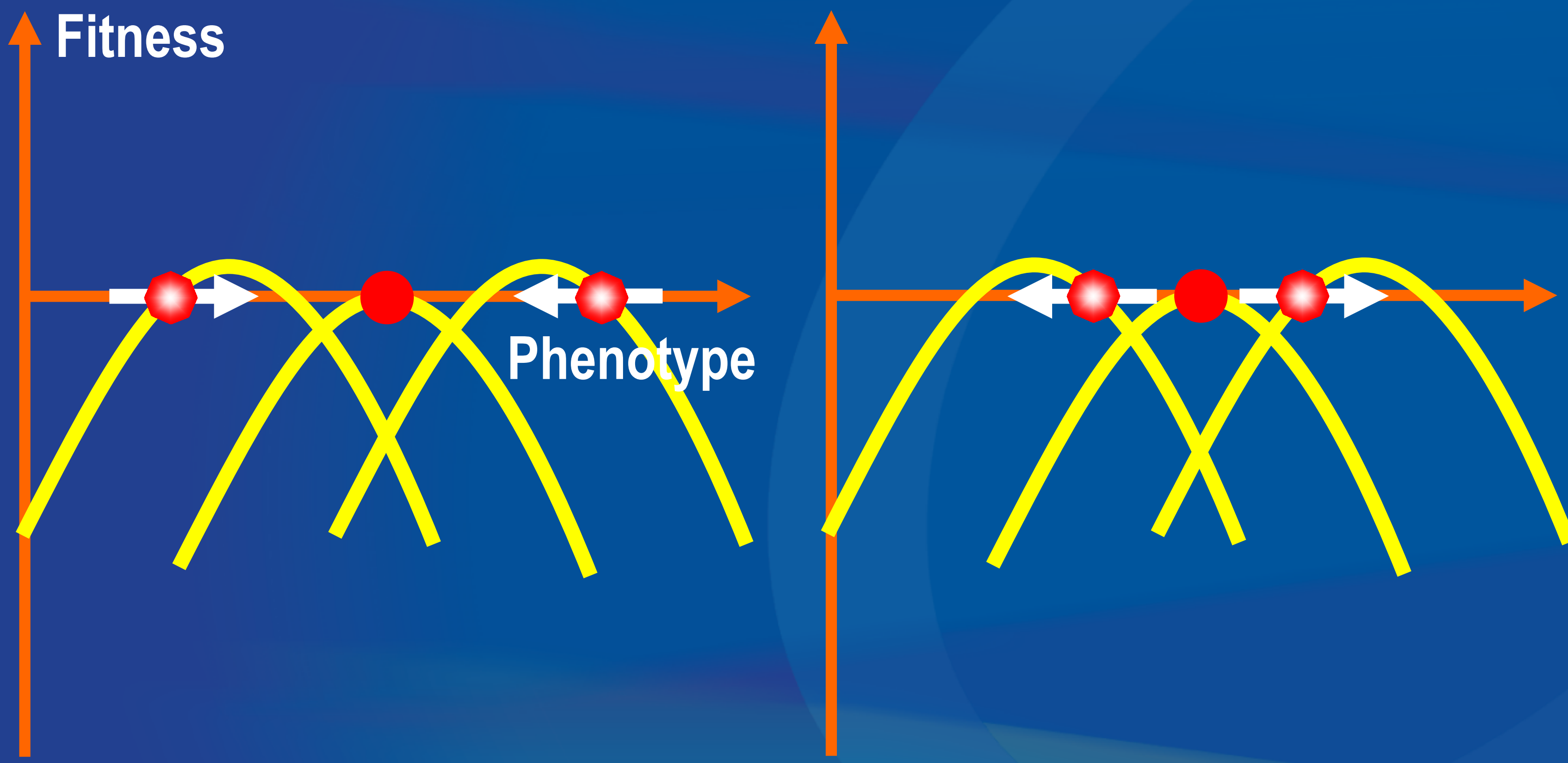
Ecologically unstable

Evolutionary Equilibration



Directional selection | Disruptive selection | Stabilizing selection

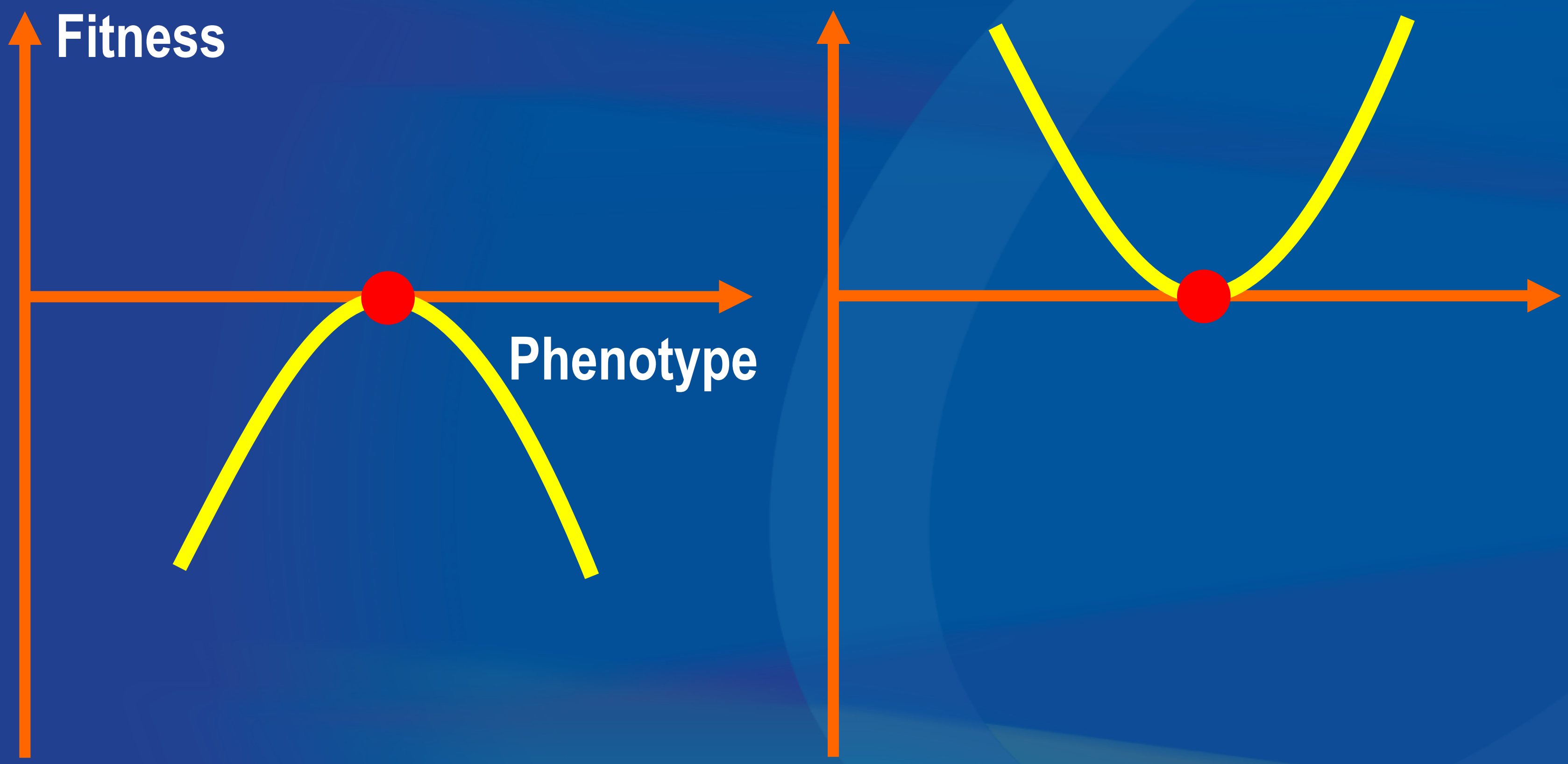
Convergence Stability



Convergence stable

Convergence unstable

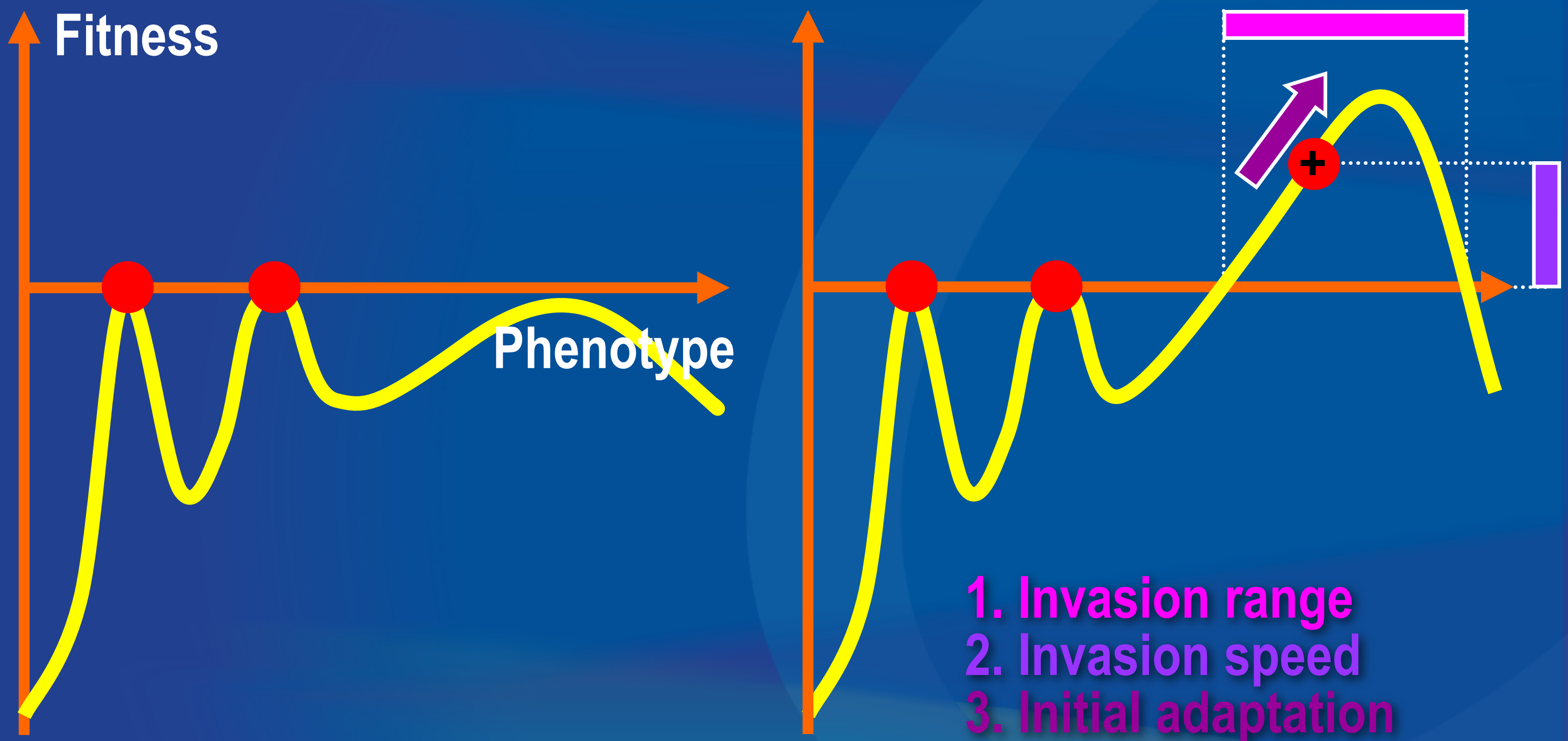
Evolutionary Stability



Evolutionarily stable

Evolutionarily unstable

Community Closure

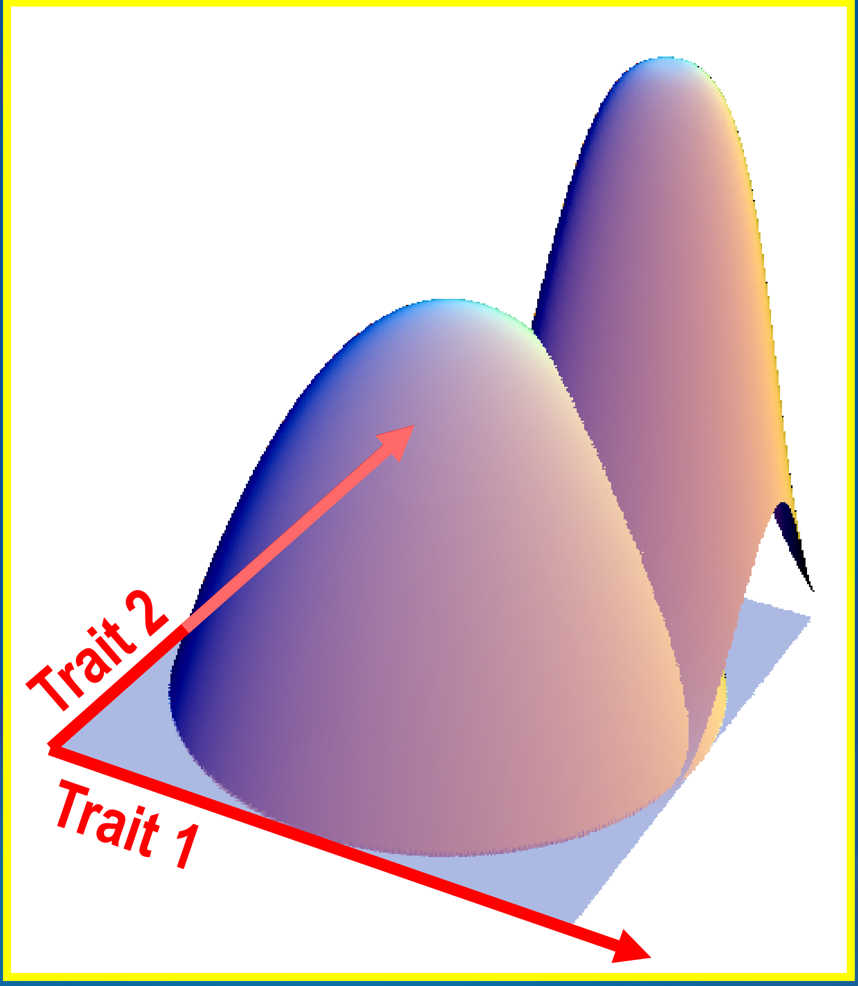


Closed to invasion

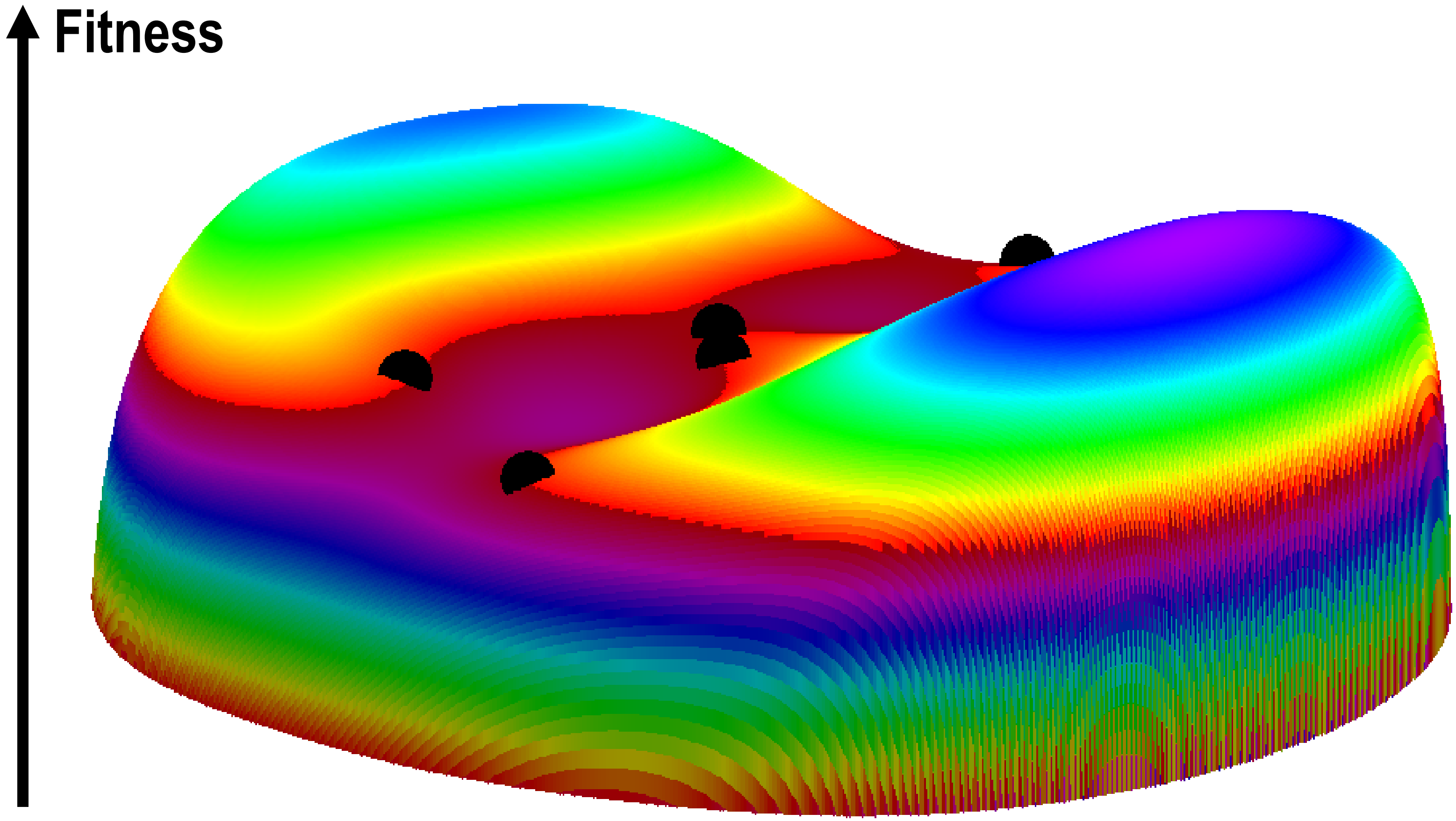
Open to invasion

Illustration of Niche Evolution

- Two functional traits
- Unimodal carrying capacity
- Strength of competition attenuates with trait difference

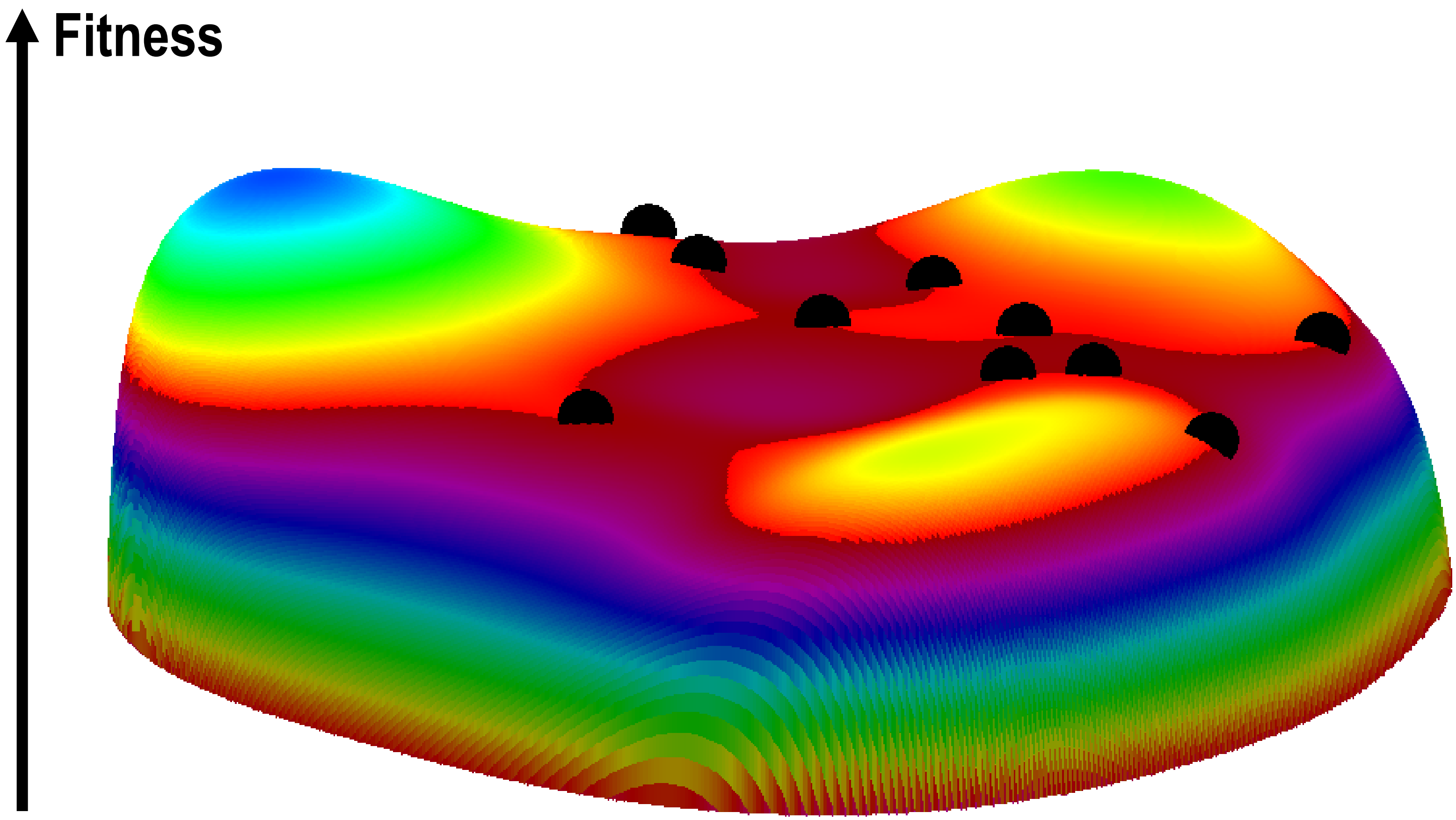


Low Initial Biodiversity



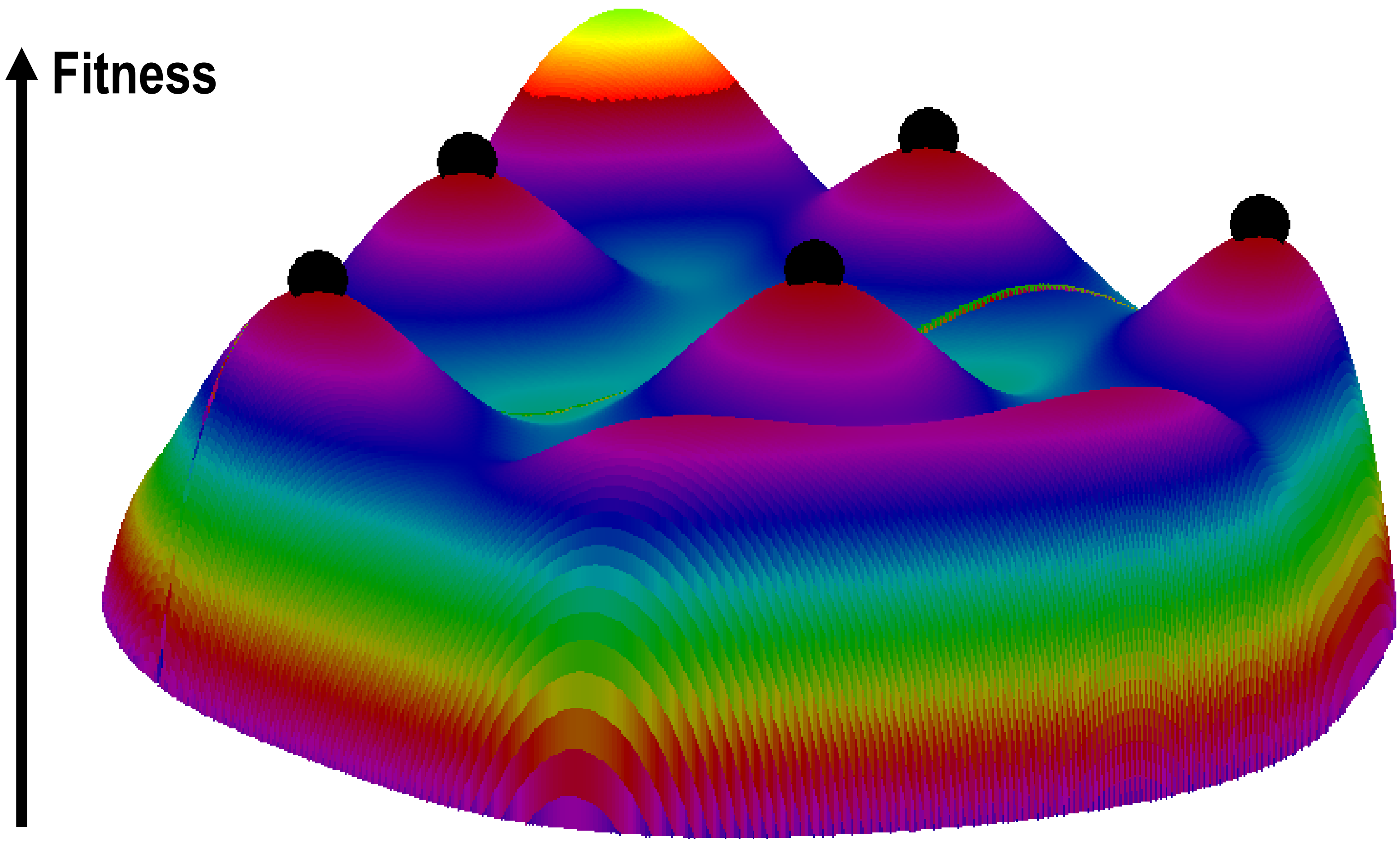
Bright colors: positive fitness; dark colors: negative fitness

Higher Initial Biodiversity



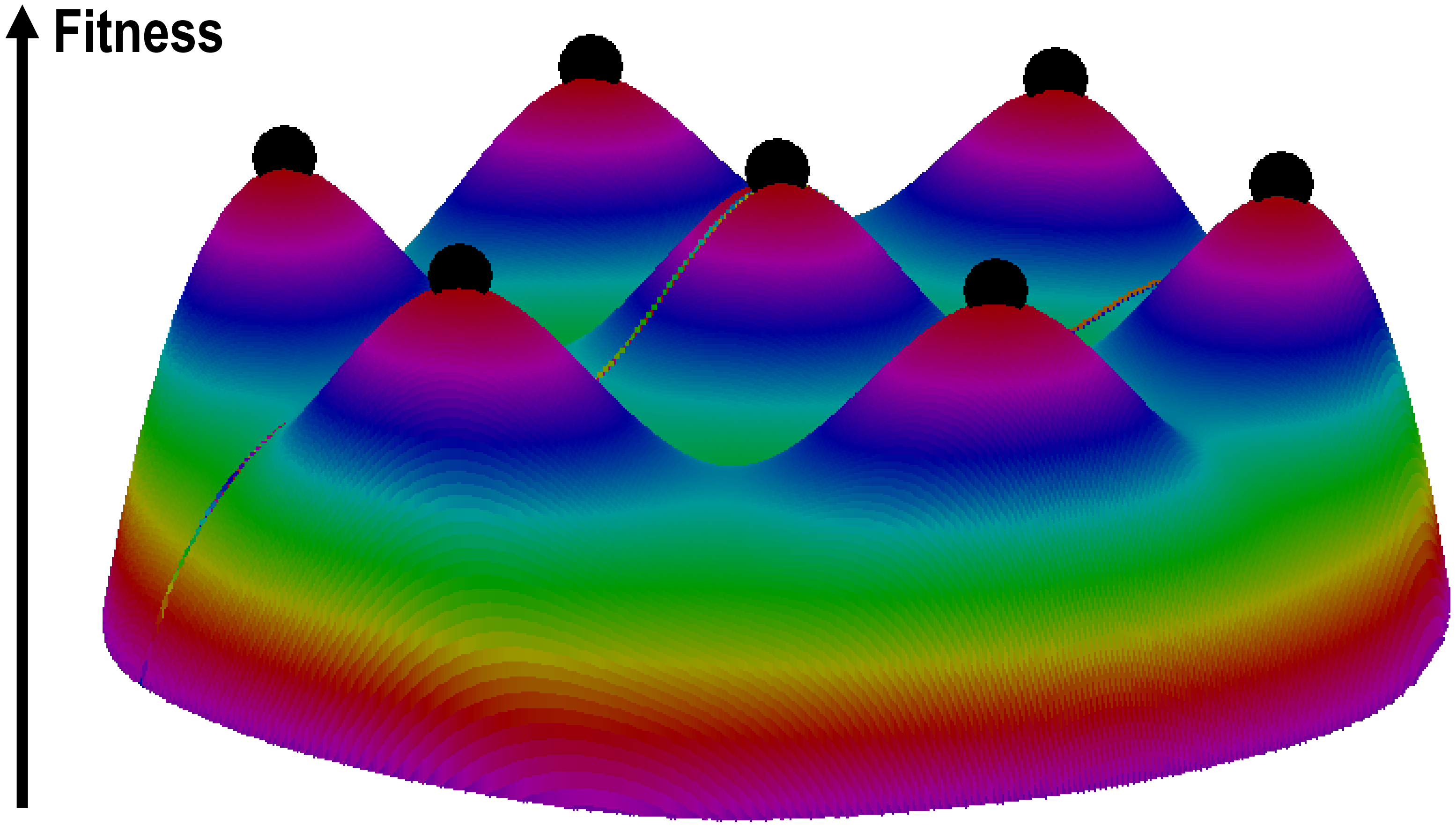
Bright colors: positive fitness; dark colors: negative fitness

With Gradual Evolution



Bright colors: positive fitness; dark colors: negative fitness

With Speciation



Bright colors: positive fitness; dark colors: negative fitness

Summary

- Dynamic fitness landscapes permit assessing
  (1) ecological equilibration, ecological stability,
  (2) evolutionary equilibration, evolutionary stability, convergence stability, and
  (3) community closure
- In the absence of community closure, such fitness landscapes reveal open niches, the speed or likelihood of their being invaded, and the initial direction of invader adaptation

2c Evolutionary games

Strategies and Payoffs

- Evolutionary games are often based on **discrete strategies** and on **pairwise interactions**
- Pairwise interactions result in **payoffs** that depend on the strategies chosen by the interacting players
- The payoff values are compiled in a **payoff matrix** and define the evolutionary game:

If I play…	… and my opponent plays… A	B
	… I receive this payoff:	
A	W_{AA}	W_{AB}
B	W_{BA}	W_{BB}

Example: Hawk-Dove Game

- A hawk (H) strategist fights for a resource
- A dove (D) strategist yields to a hawk and shares with a dove, both without fighting
- Getting the resource confers a benefit *b* and losing fights implies a cost *c*

If I play…	… and my opponent plays… H	D
	… I receive this payoff:	
H	$b/2 - c/2$	b
D	0	$b/2$

Average Payoffs

- **Assumptions:** Populations are large, and individuals encounter each other at random
- If strategies A and B have abundances n_A and n_B, their average payoffs are then given by $W_{AA}\, n_A + W_{AB}\, n_B$ and $W_{BA}\, n_A + W_{BB}\, n_B$, respectively
- Using the matrix W and the vector $n = (n_A\,, n_B)$, we see that these expressions are simply the entries of Wn:

$$Wn = \begin{pmatrix} W_{AA} & W_{AB} \\ W_{BA} & W_{BB} \end{pmatrix} \begin{pmatrix} n_A \\ n_B \end{pmatrix} = \begin{pmatrix} W_{AA} n_A + W_{AB} n_B \\ W_{BA} n_A + W_{BB} n_B \end{pmatrix}$$

Replicator Dynamics

- **Assumption:** The abundances n_i of strategies i = A, B, … increase according to their average payoffs:

$$\frac{d}{dt} n_i = (Wn)_i$$

- Their relative frequencies p_i then follow the **replicator equation:**

$$\frac{d}{dt} p_i = (Wp)_i - \underbrace{p \cdot Wp}_{\text{Average payoff in entire population}}$$

Outcomes of Hawk-Dove Game 1/2

The evolutionary equilibrium in this game is attained after the frequency of H, $p_H = 1 - p_D$, has changed so that the payoffs for H and D have become equal:

$$
\begin{aligned}
p_{\mathrm{H}}(\tfrac{1}{2}b - \tfrac{1}{2}c) + (1 - p_{\mathrm{H}})b &= p_{\mathrm{H}}0 + (1 - p_{\mathrm{H}})\tfrac{1}{2}b \\
p_{\mathrm{H}}(\tfrac{1}{2}b - \tfrac{1}{2}c - b + \tfrac{1}{2}b) &= -b + \tfrac{1}{2}b \\
-\tfrac{1}{2}cp_{\mathrm{H}} &= -\tfrac{1}{2}b \\
p_{\mathrm{H}} &= b / c
\end{aligned}
$$

Outcomes of Hawk-Dove Game 2/2

- If the cost is **larger** than the benefit, $c > b$:

A **mixed** strategy results

- If the cost is **smaller** than the benefit, $c < b$:

A **pure** strategy results

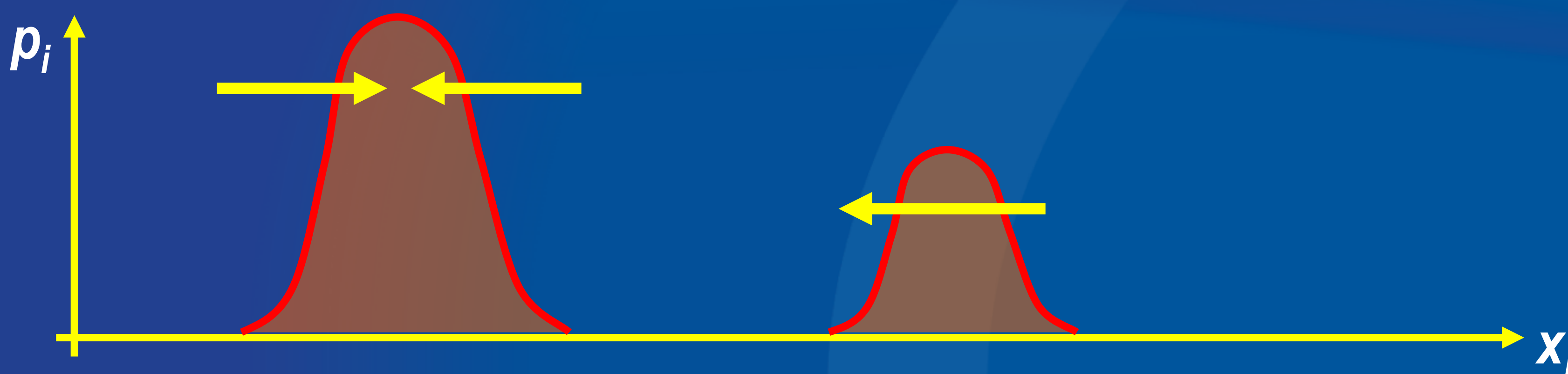
Limitations of Replicator Dynamics

- Owing to the focus on frequencies, the replicator equation cannot capture density-dependent selection
- Nonlinear payoff functions naturally arise in applications, but cannot be captured by matrix games
- Continuous strategies are often needed for comparisons with data
- Since the replicator equation cannot include innovative mutations, it describes short-term, rather than long-term, evolution

2d Quantitative genetics

Dynamics of Trait Distributions

- Models of quantitative genetics describe evolution in polymorphic populations:



- Examples are reaction-diffusion dynamics:

$$\frac{d}{dt}p_i(x_i) = \underbrace{f_i(x_i,p)\,p_i(x_i)}_{\text{Reaction dynamics}} + \underbrace{\frac{1}{2}\mu_i(x_i)\sigma_i^2(x_i) * \frac{\partial^2}{\partial x_i^2} b_i(x_i,p)\,p_i(x_i)}_{\text{Diffusion dynamics}}$$

Problem: Moment Hierarchy

- 0th moments: Population densities

$$\frac{d}{dt} n_i = \ldots n \ldots x \ldots \sigma^2 \ldots$$

- 1st moments: Mean traits

$$\frac{d}{dt} x_i = \ldots n \ldots x \ldots \sigma^2 \ldots$$

- 2nd moments: Trait variances and covariances

$$\frac{d}{dt} \sigma_i^2 = \ldots n \ldots x \ldots \sigma^2 \ldots$$ skewness

Lande's Equation

- **Assumptions:** Populations are large, and total population densities, variances, and covariances are all fixed
- Then, the rates of change in mean trait values are given by

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

rate of mean trait in species *i*

local selection gradient

fitness

current population variance-covariance