Adaptive Speciation: Linking Pattern and Process

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Speciation Modes: Pattern & Process

Pattern ↓ / Process →	Non-adaptive speciation	Adaptive speciation
Allopatric speciation	Geographic isolation, Isolation by distance, Peripheral isolates	Consumer-mediated evolutionary branching
(Parapatric Speciation)		
Sympatric speciation	Chromosomal rearrangements	Host race formation, Evolutionary branching by natural or sexual selection

Characteristics of Adaptive Speciation

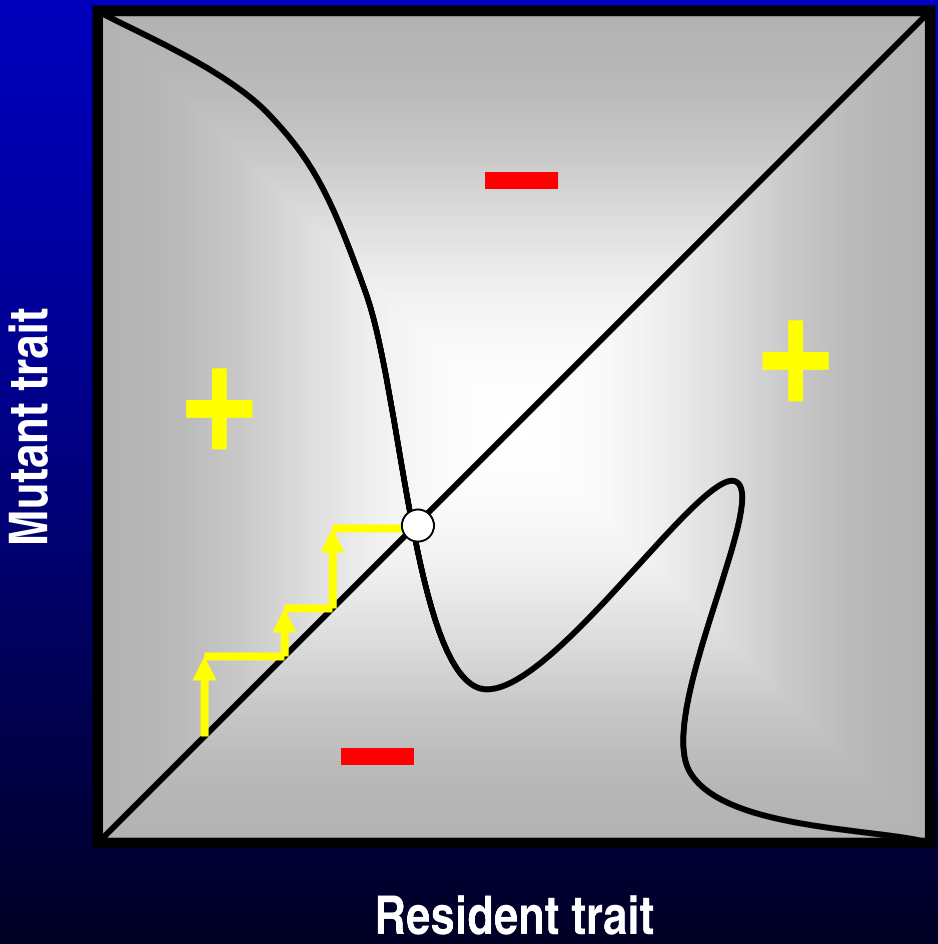
- In adaptive speciation, the speciation process itself is adaptive, enabling a population to resolve a challenge posed by the eco-evolutionary feedback.
- Adaptive speciation is driven by biological interactions, and thus does not require invoking incidental external factors for splitting a population's gene pool.
- Adaptive speciation can involve both ecological and sexual traits. The origin of variability and the stable coexistence of daughter species is automatically ensured.
- Adaptive speciation can occur in sympatry or parapatry.

Outline

1. Asexual Adaptive Speciation
2. Sexual Adaptive Speciation
3. Spatial Adaptive Speciation
4. A New Classification System

1 Asexual Adaptive Speciation

Pairwise Invasibility Plots



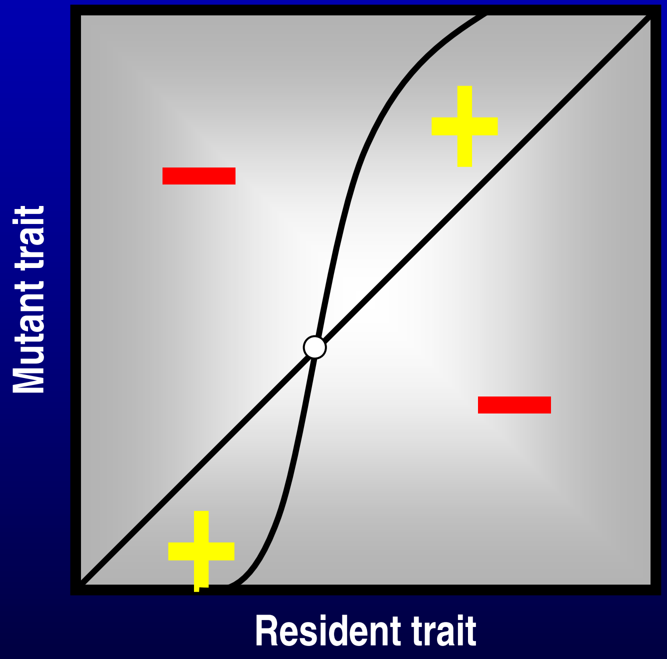
+ Invasion of the mutant into the resident population is possible

− Invasion is impossible

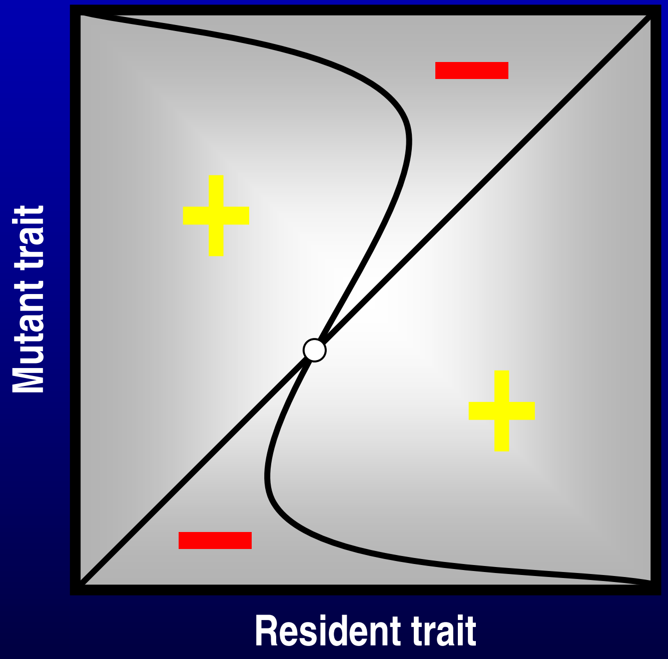
Trait substitution sequence

Examples

- Garden of Eden

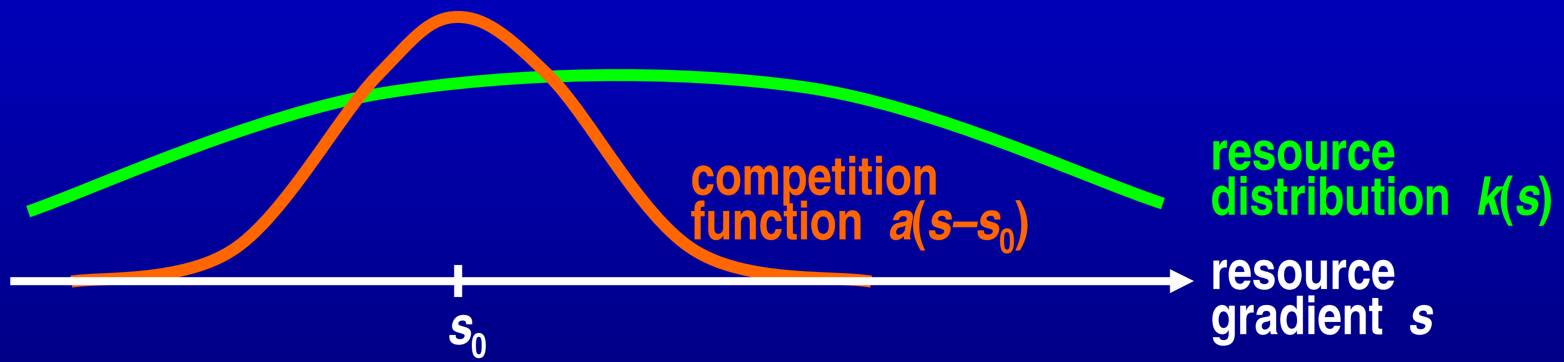


- Branching Point



Evolutionary stability and convergence stability are completely independent properties

Resource Competition



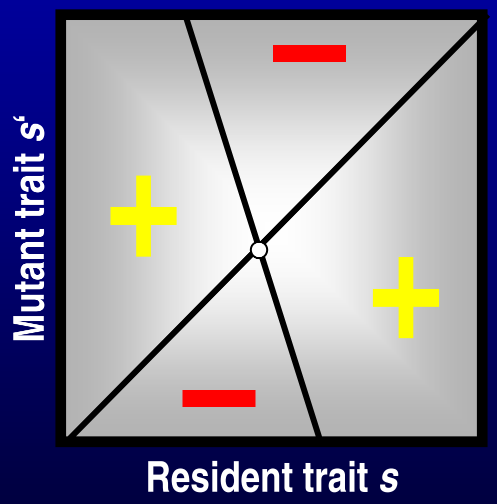
Dynamics of population sizes n_i of strategy s_i

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

Resultant Pairwise Invasibility Plots

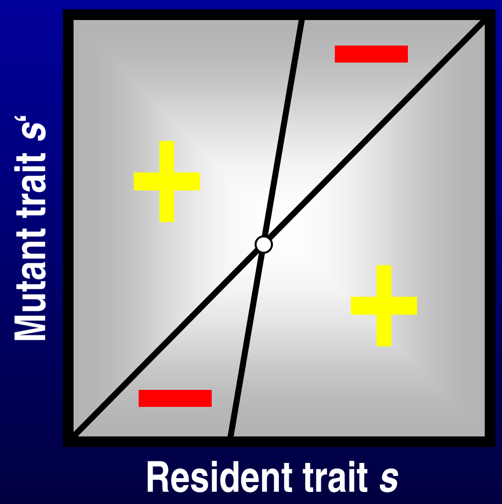
- With $k = k_0\, N(0,\sigma_k)$ and $a = N(0,\sigma_a)$ we obtain

for $\sigma_a > \sigma_k$



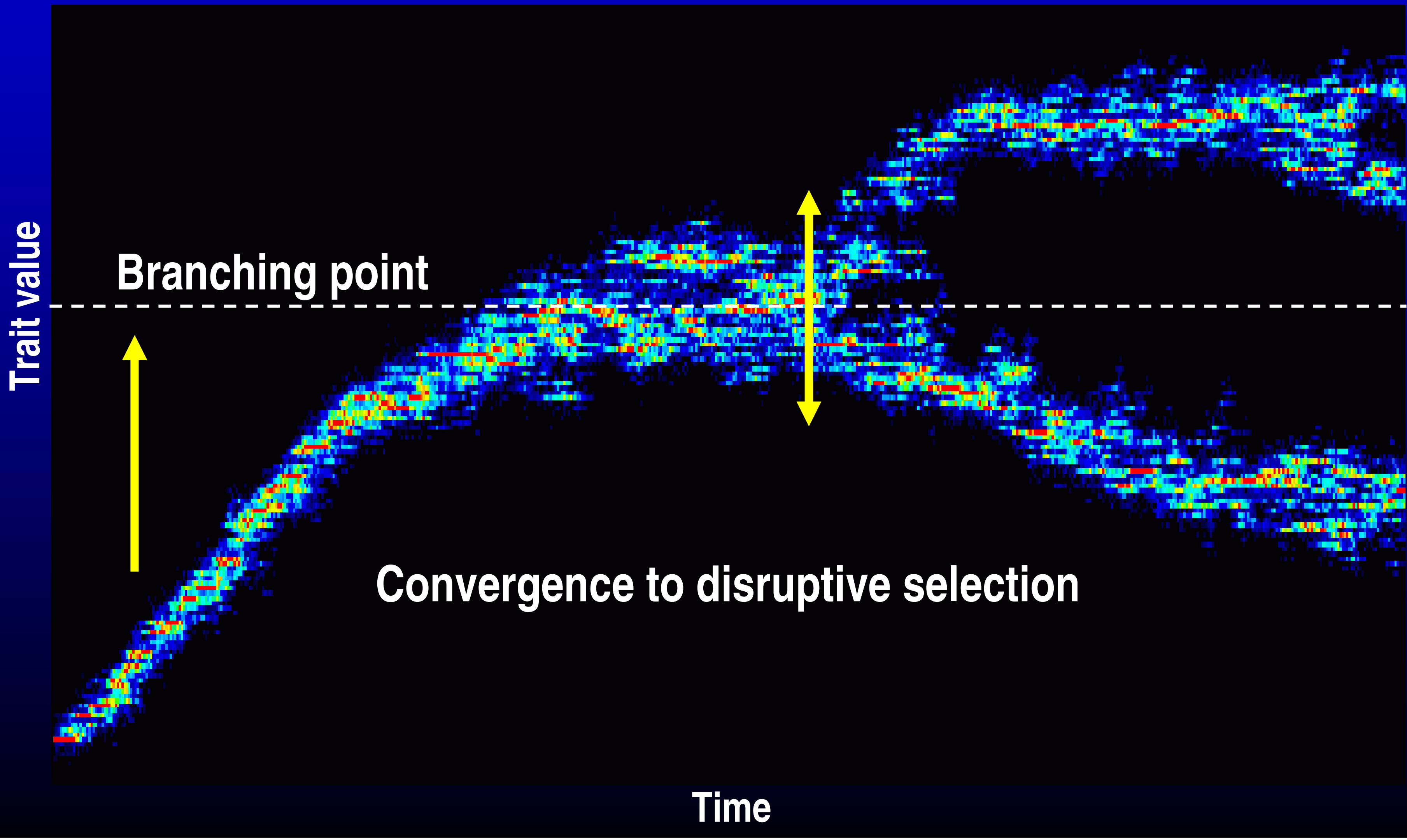
→ **Evolutionary Stability**

for $\sigma_a < \sigma_k$



→ **Evolutionary Branching**

Evolutionary Branching



2 Sexual Adaptive Speciation

Simple Multilocus Genetics

- *N* loci for each quantitative trait
- Diallelic
- Diploid
- Additive phenotypic effects
- Free recombination

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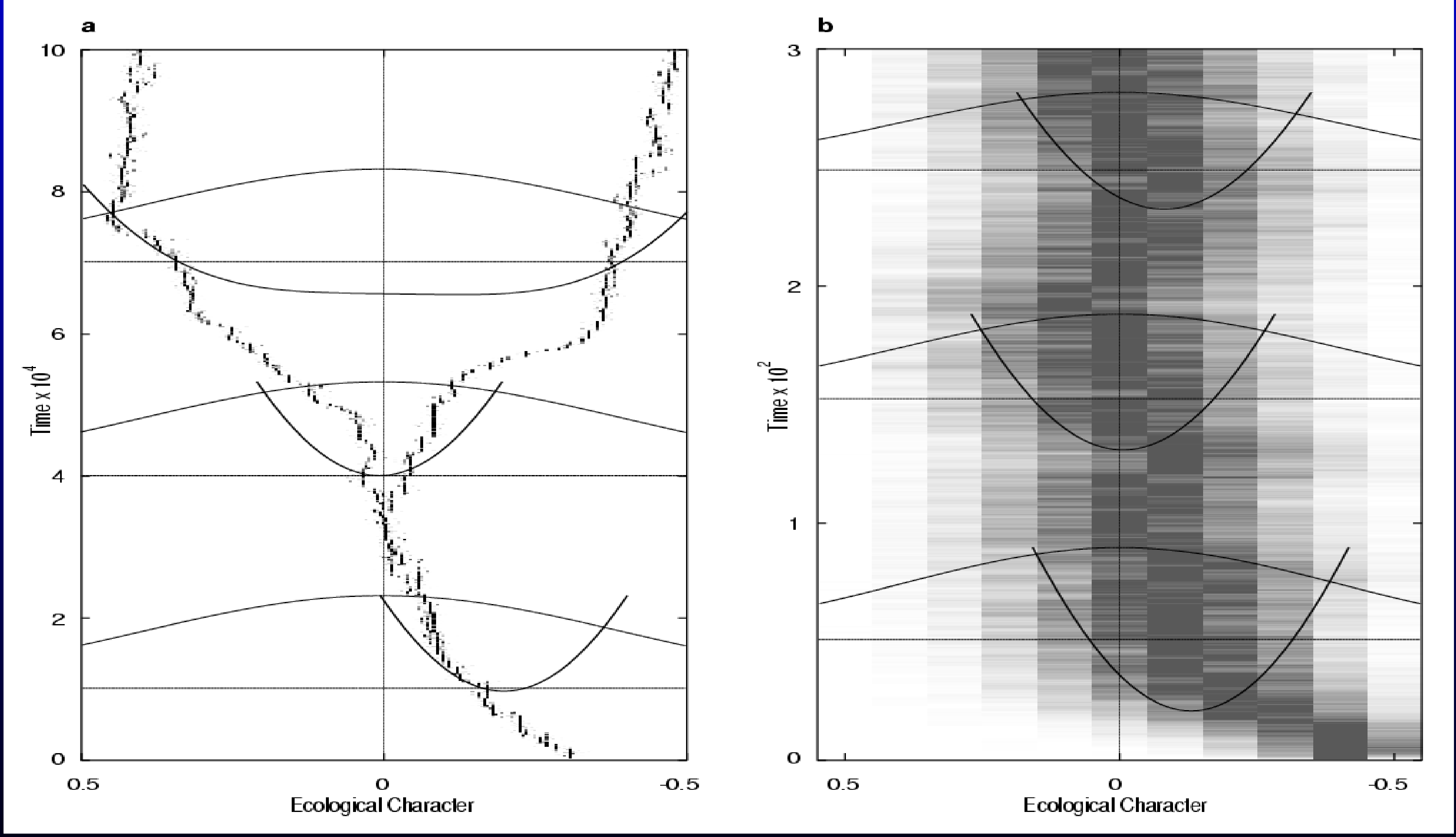
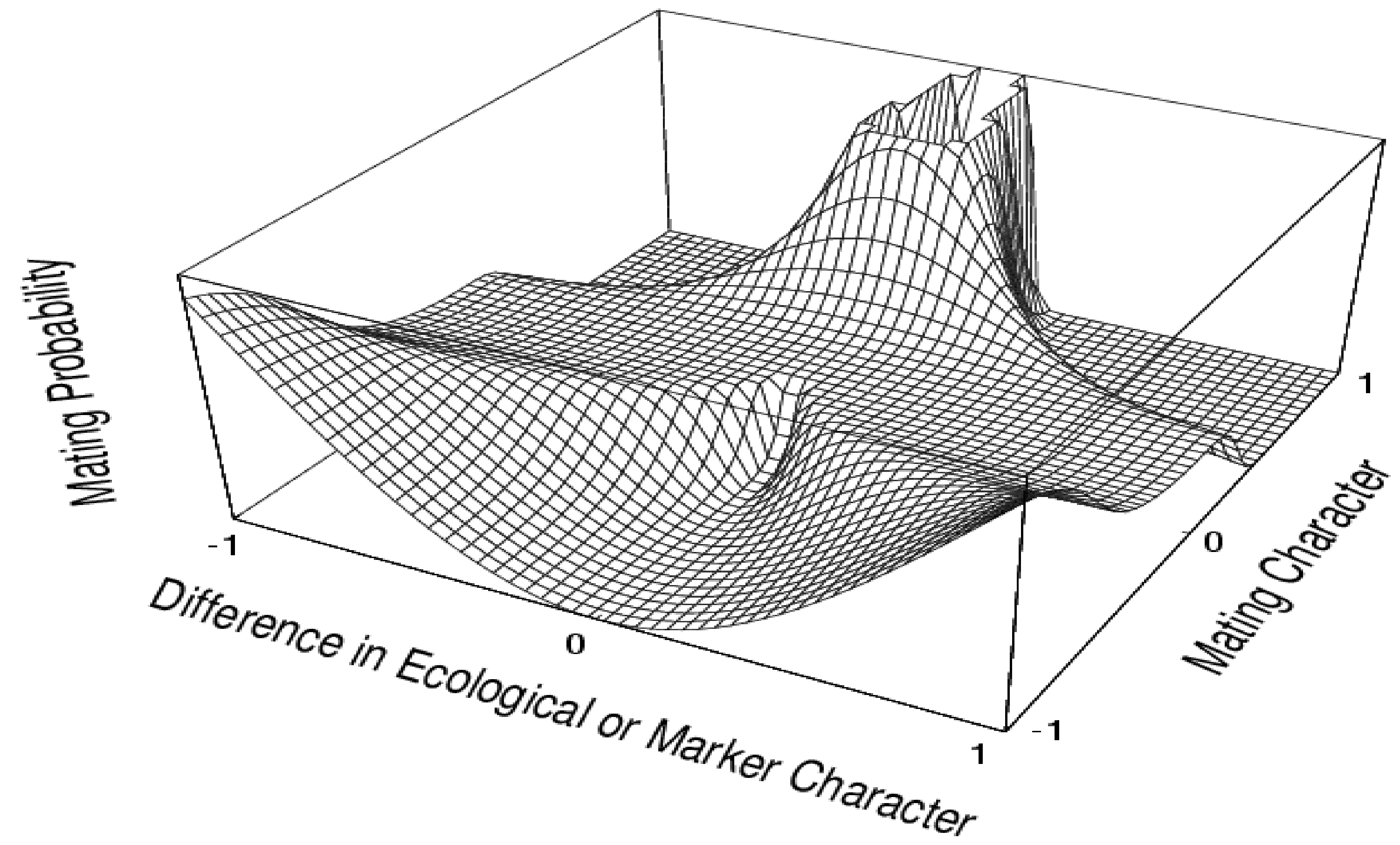
Sexual Cohesion Can Prevent Branching *Nature* (1999)

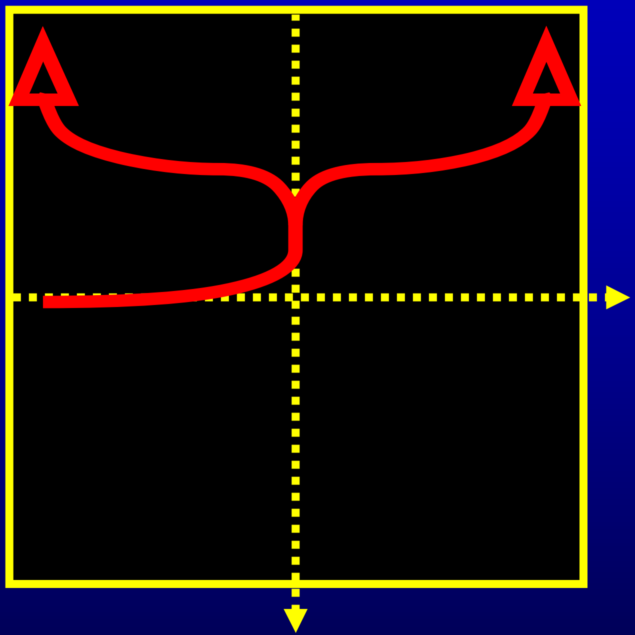


Mating Character



Sexual Adaptive Speciation

Nature (1999)

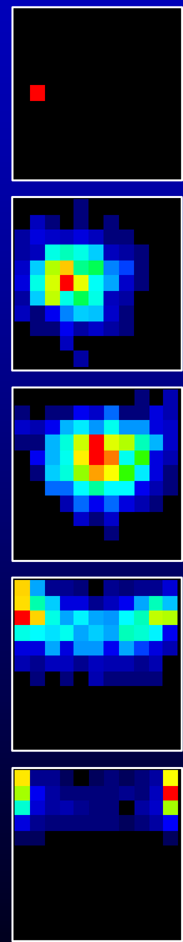


Fitness minimum

Assortative mating

Random mating

Disassortative mating

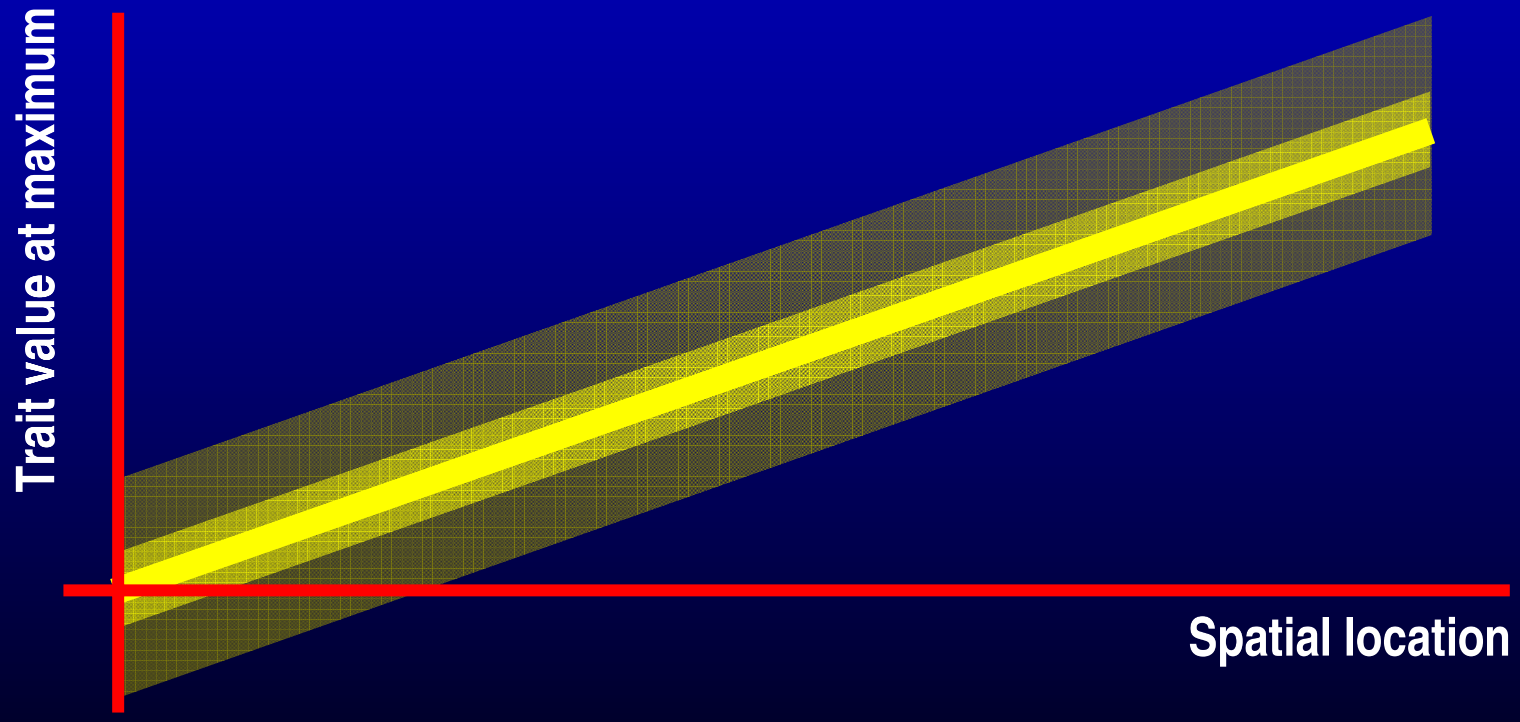


This mechanism also works when assortative mating is based on a marker character and when evolutionary branching is driven by interspecific interactions.

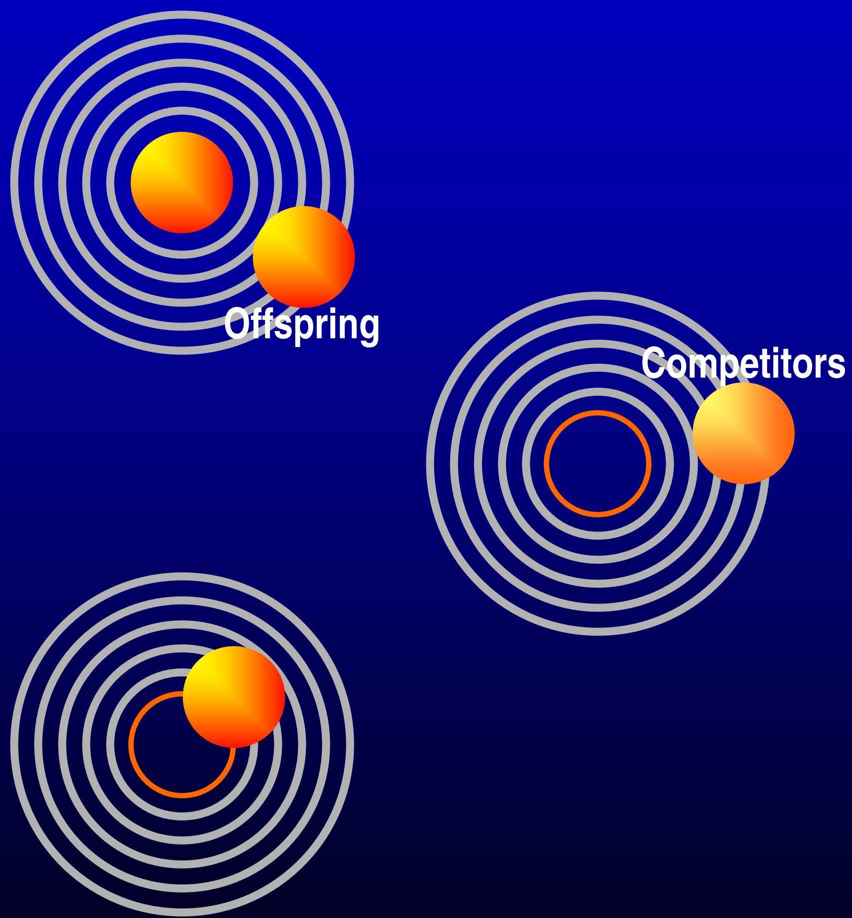
3 Spatial Adaptive Speciation

Spatial Gradient

Maximum of carrying capacity varies with location



Local Demography



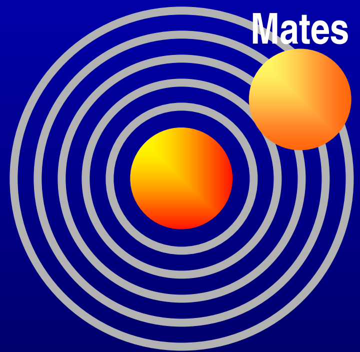
Birth

Death

Movement

Local Mating

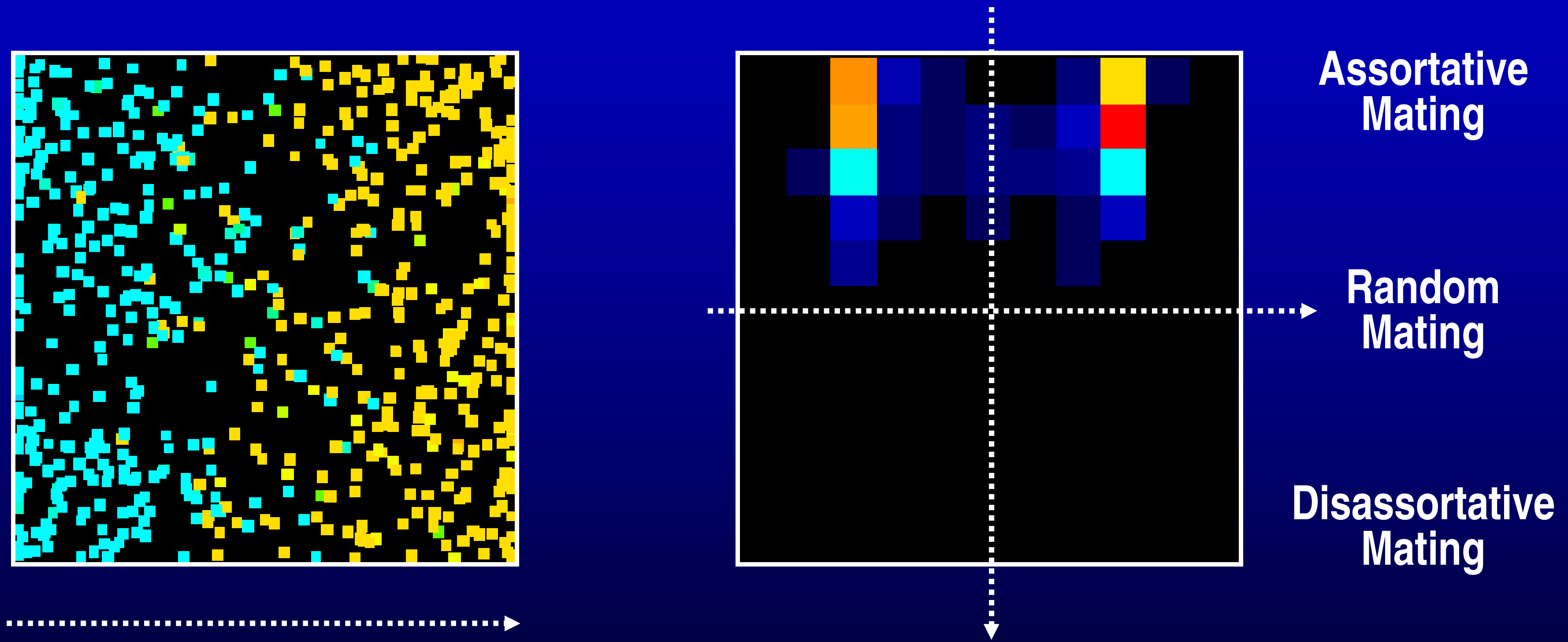
- Potential mates are discounted with spatial and (when mating is assortative) phenotypic distance



- Effective fecundity increases from zero to saturation with the number of locally available suitable mates
- This induces a cost of choosiness, in addition to the already present cost of rarity

Spatial Evolutionary Branching

Nature (2003)

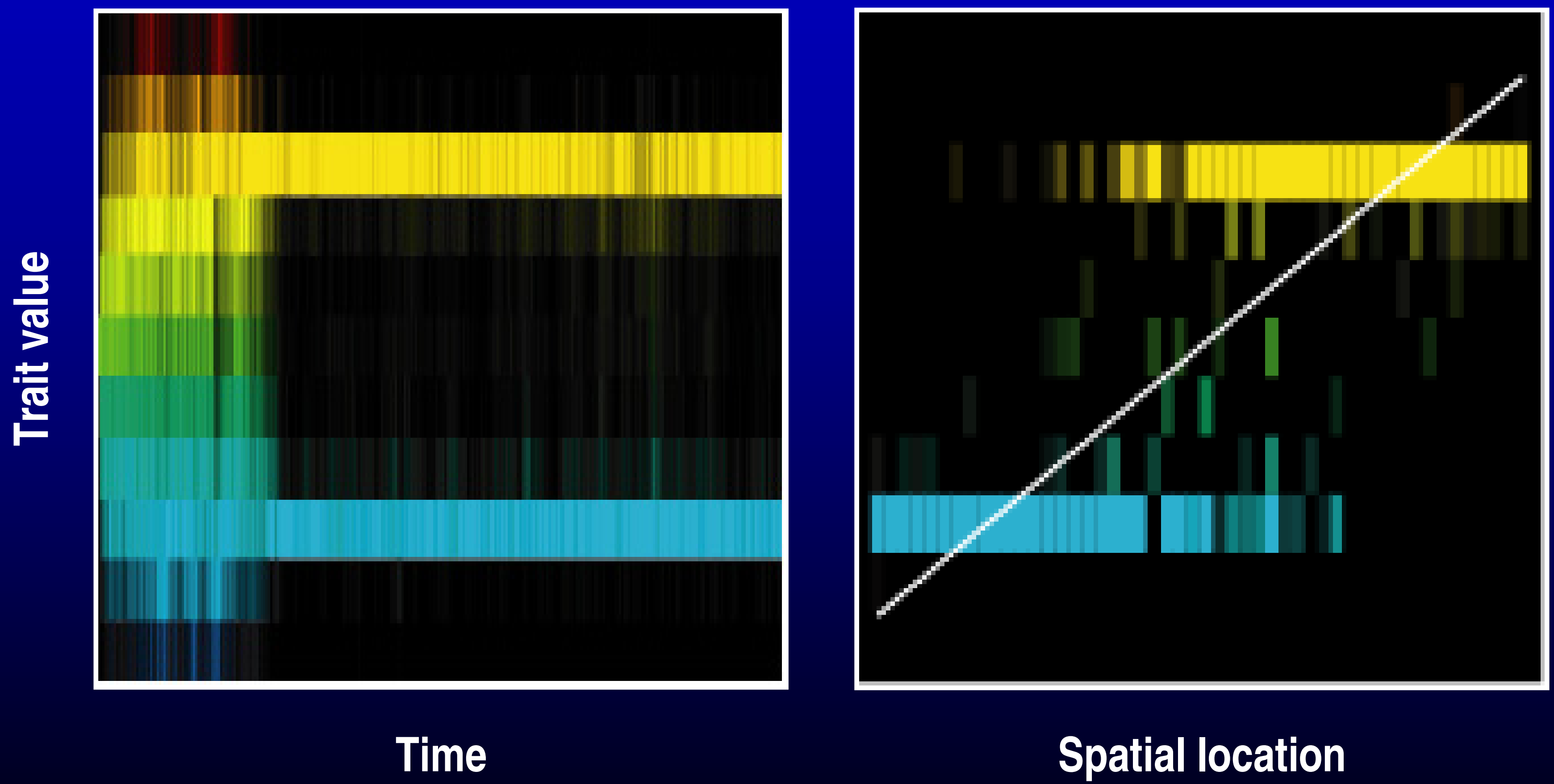


Spatial Gradient
(second direction is ecologically neutral)

Evolutionary Branching Point

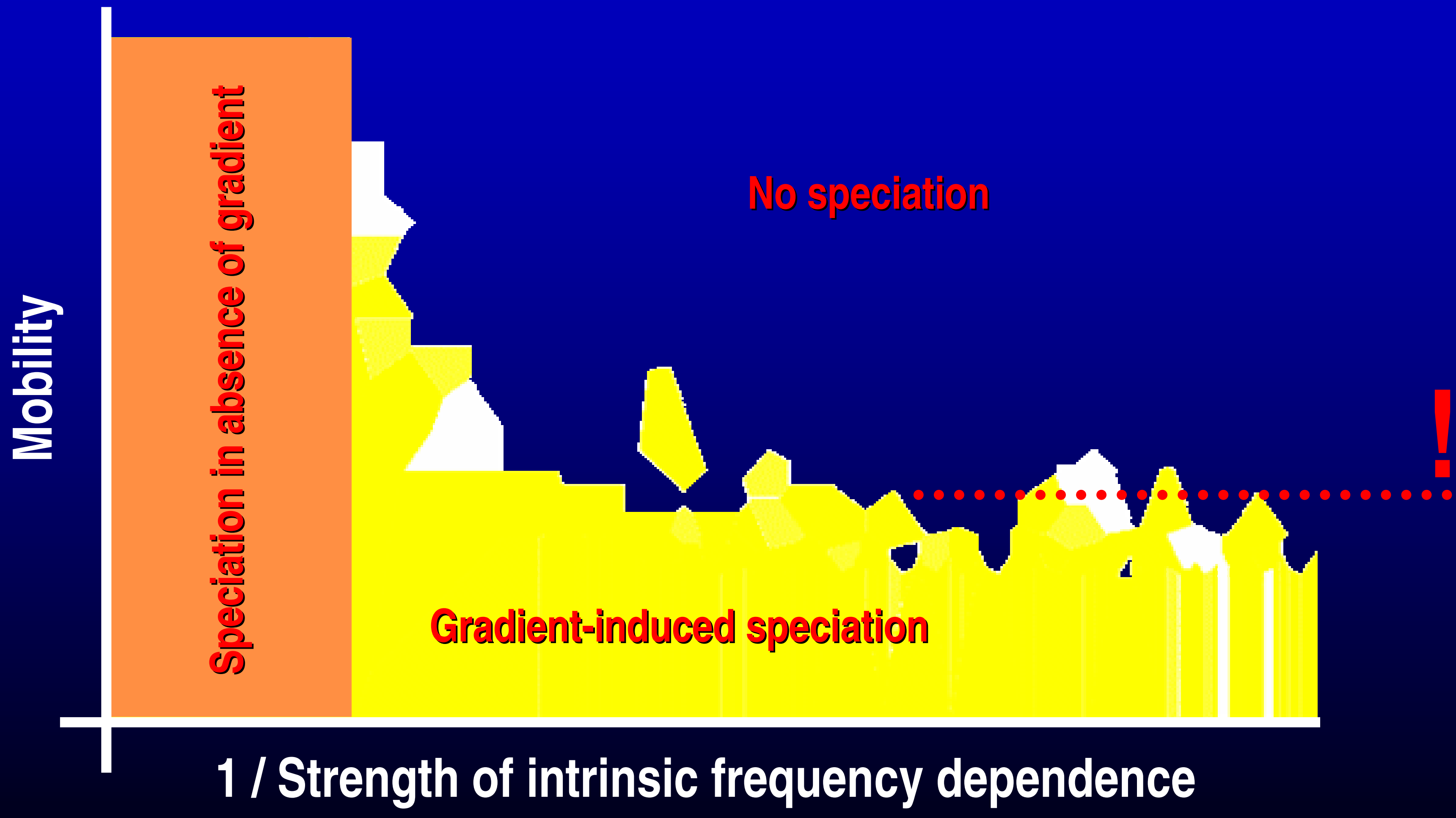
Spatial Evolutionary Branching

Nature (2003)

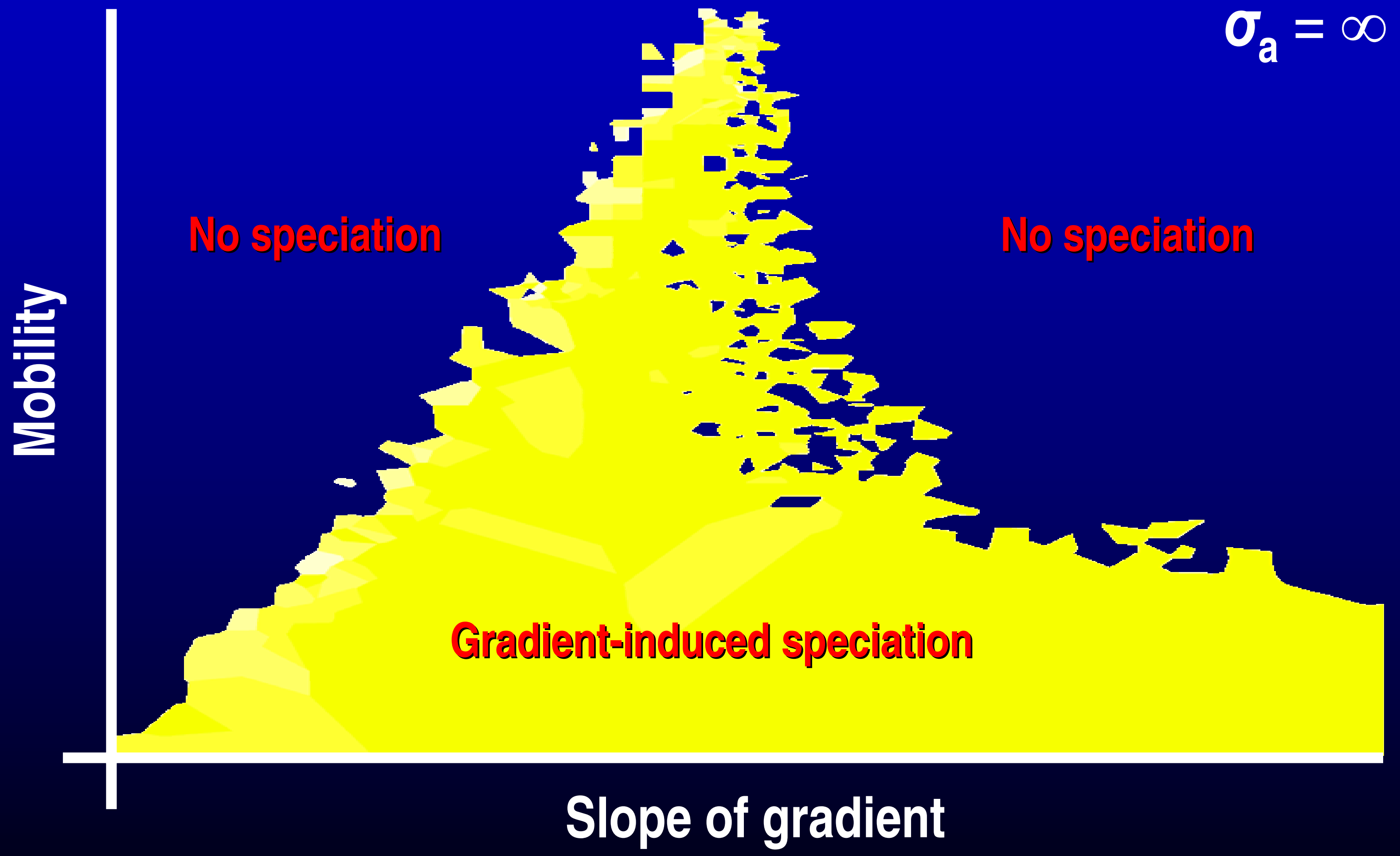


Spatial Gradient Facilitates Speciation

Nature (2003)

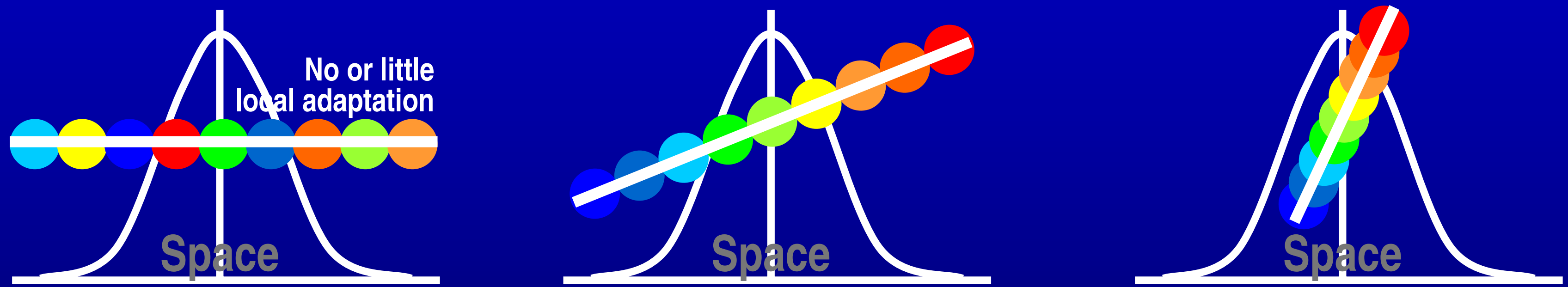


Intermediate Slopes Are Most Speciation-Prone *Nature* (2003)

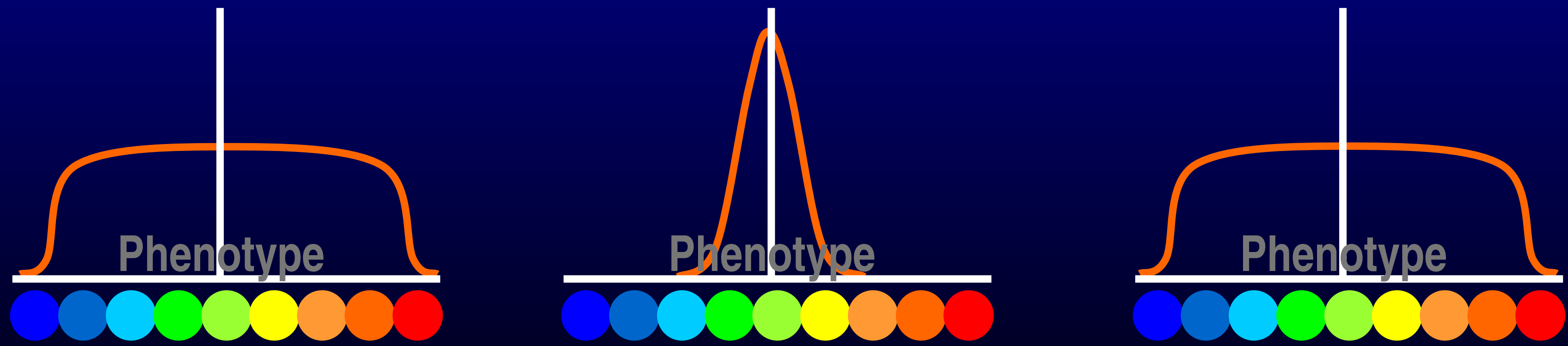


Gradient-Induced Disruptiveness

- Shallow gradient
- Intermed. gradient
- Steep gradient



Resulting effective local phenotypic competition function:



Wide | Narrow | Wide

Only 3 Dimensionless Parameters

- **Scaled width of competition function**

  focused resource utilization vs. unspecific resource utilization

- **Scaled migration distance = Mobility**

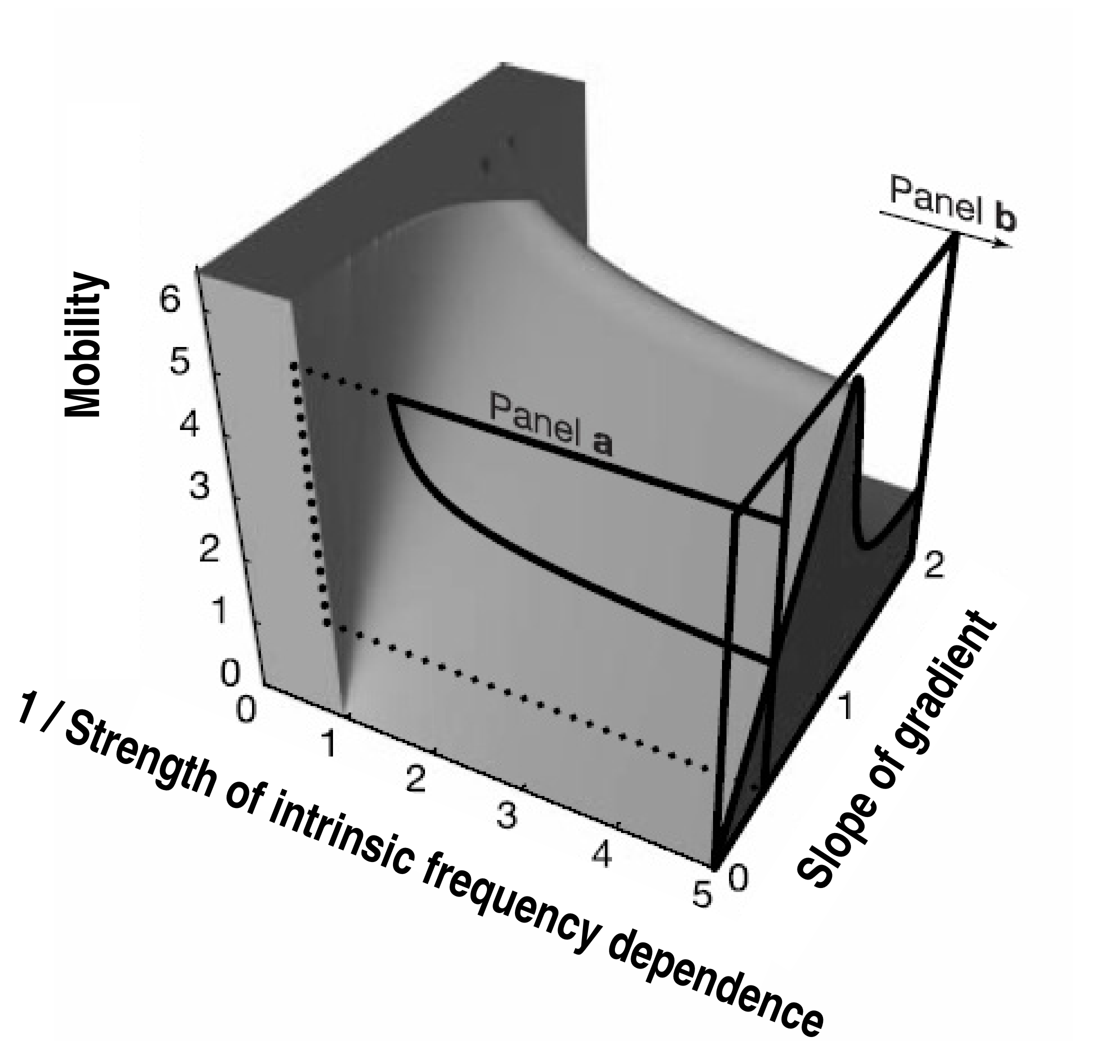
  highly viscous population vs. well-mixed population

- **Scaled slope of gradient**

  homogeneous environment vs. steep cline

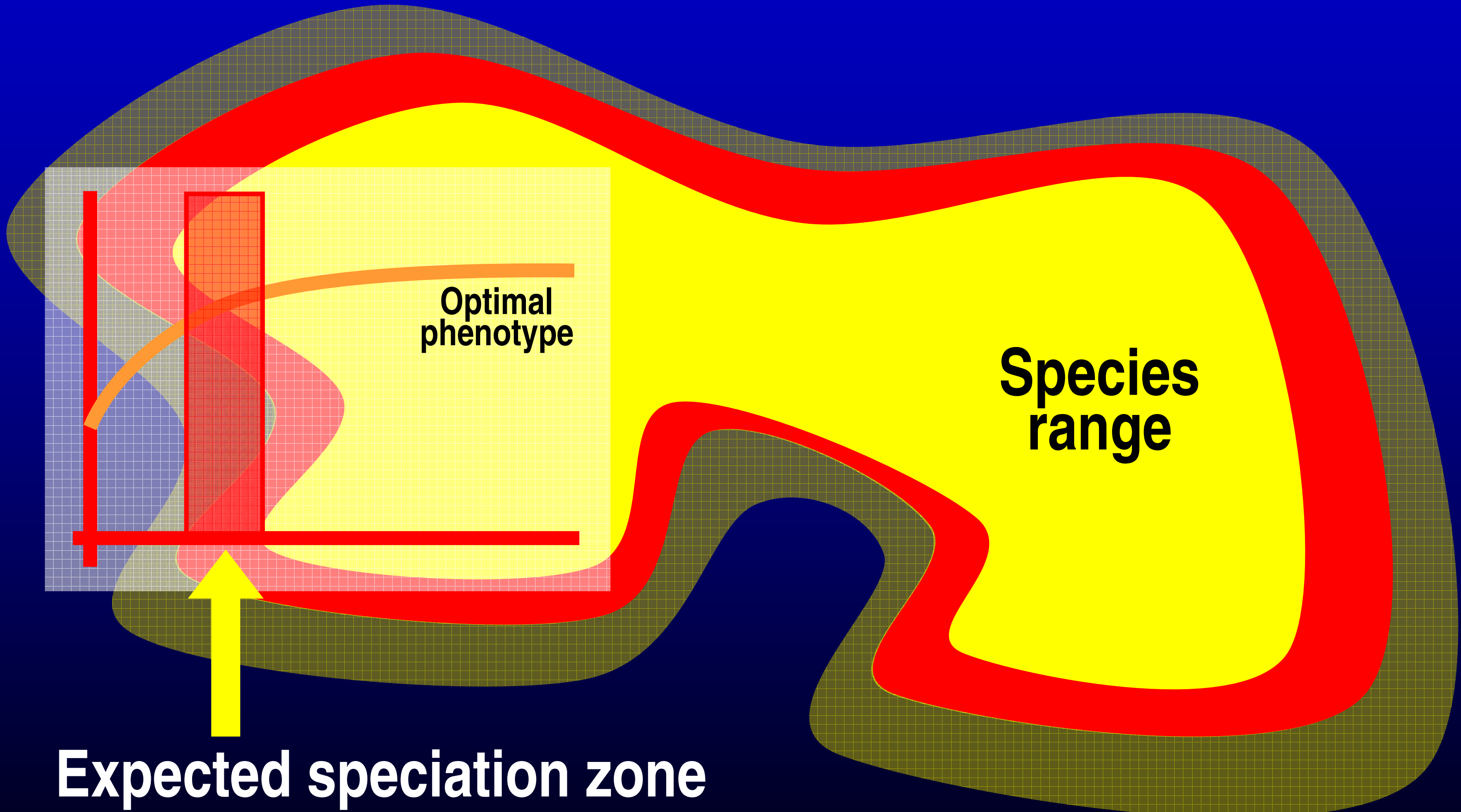
Full Characterization

Nature (2003)



Speciation
occurs for all settings
within gray block

Peripheral Speciation



4

A New Classification System

Three Key Characteristics

- **Spatial differentiation**

  Can either drive or be driven by the speciation process.

- **Ecological differentiation**

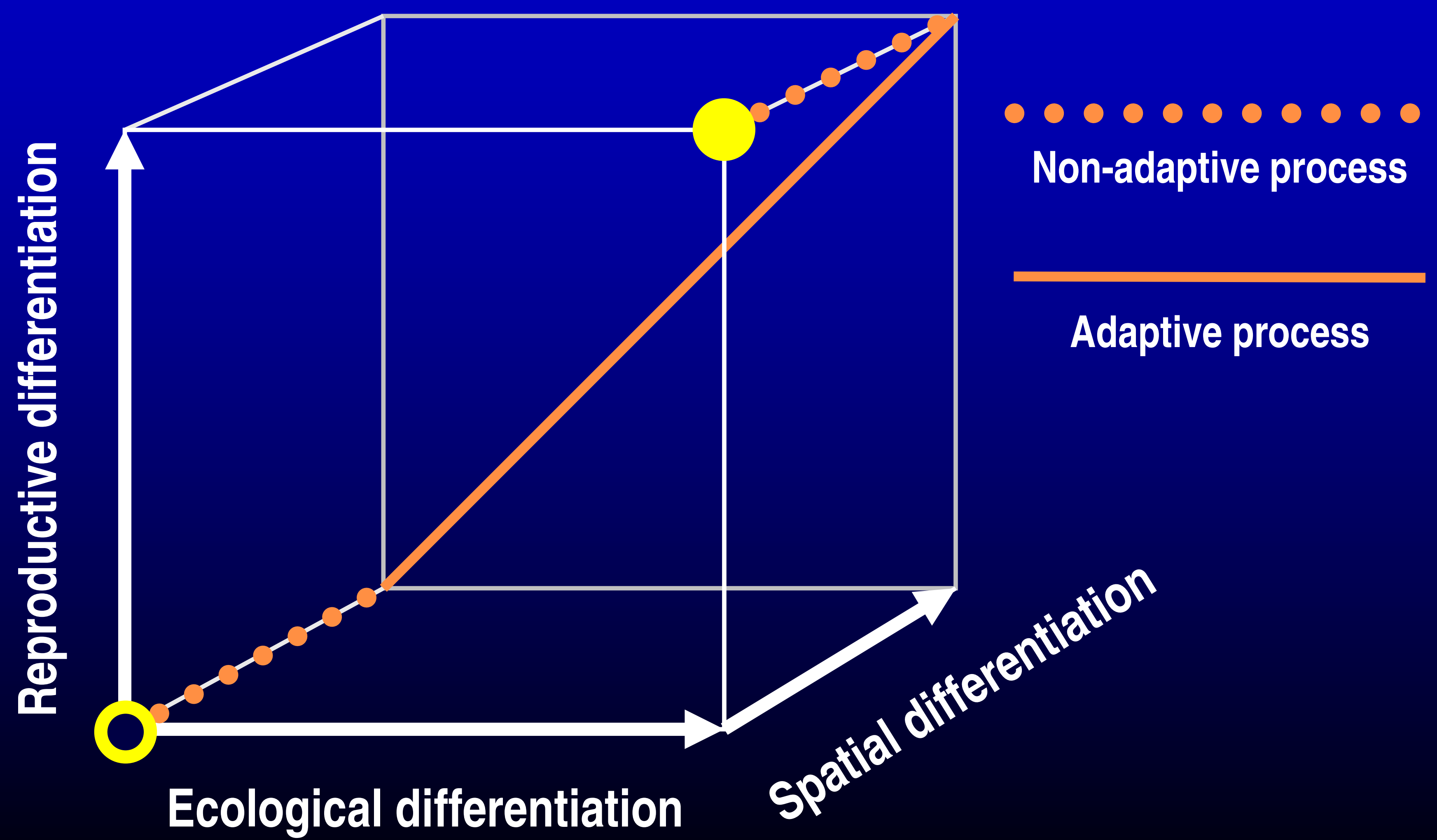
  Provides the only speciation criterion for asexuals.

- **Reproductive differentiation**

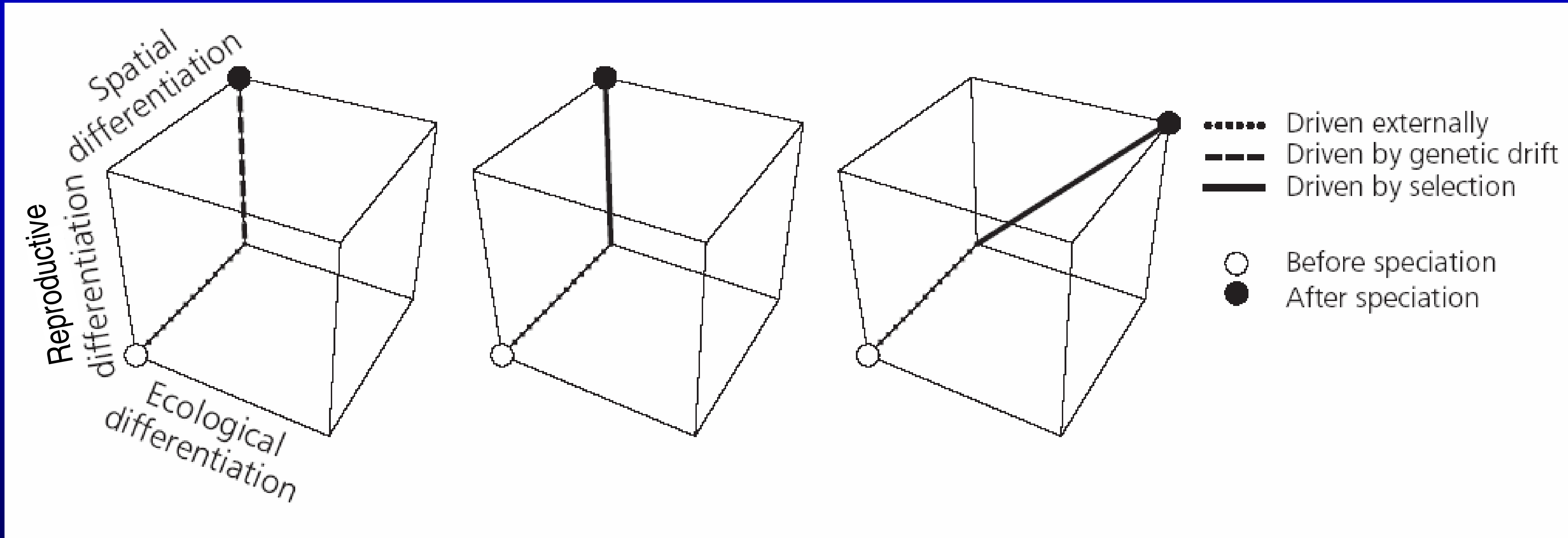
  Needs to evolve for speciation in sexuals.

- **These characteristics can arise simultaneously or sequentially, and occur gradually or in externally determined phases.**

“Speciation Cubes”

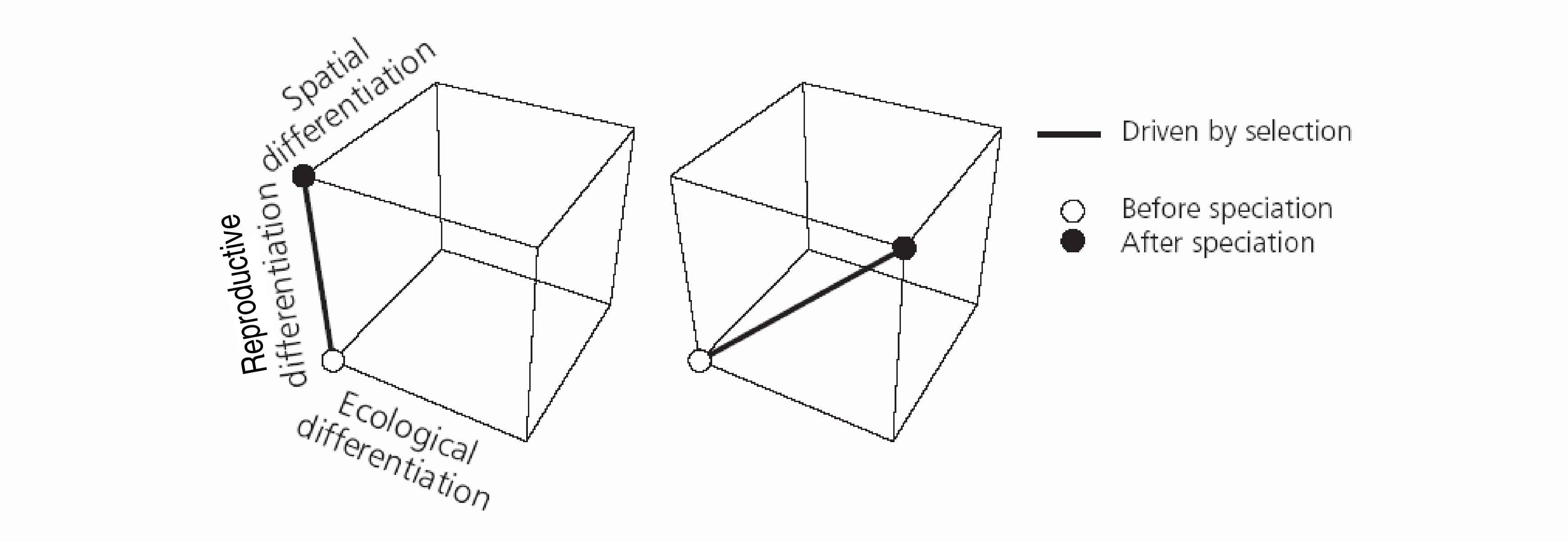


Allopatric Speciation



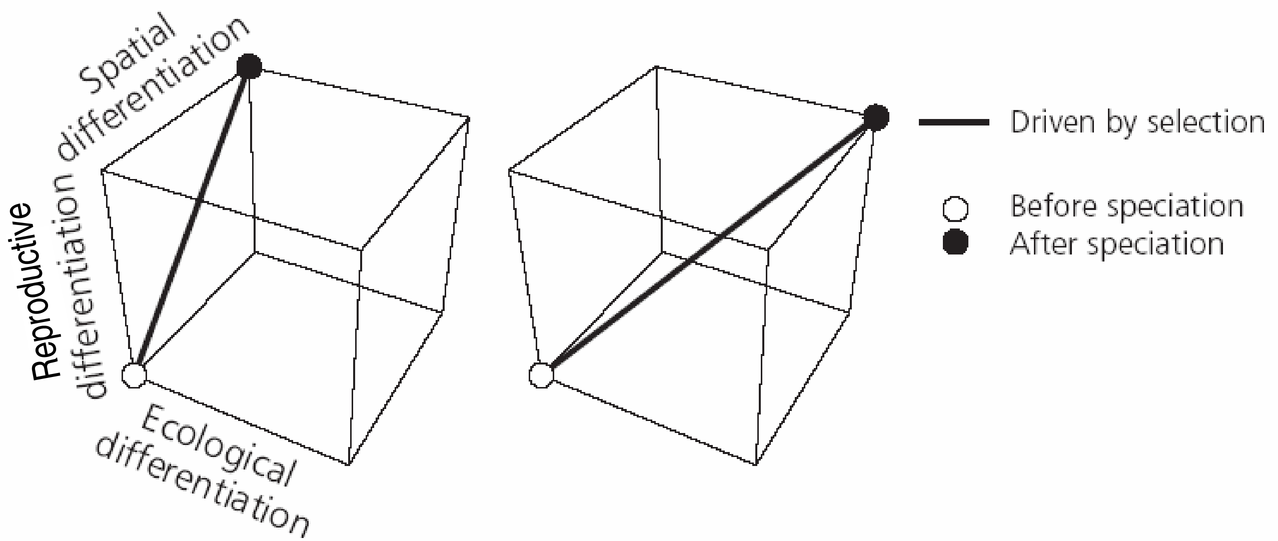
External causes first result in geographic isolation between two incipient species, and thus introduce a high degree of spatial differentiation. After that, either genetic drift (left) or sexual selection (middle) can increase reproductive differentiation. Alternatively, local adaptation with pleiotropic effects on mating (right) can increase ecological and reproductive differentiation concomitantly.

Sympatric Speciation



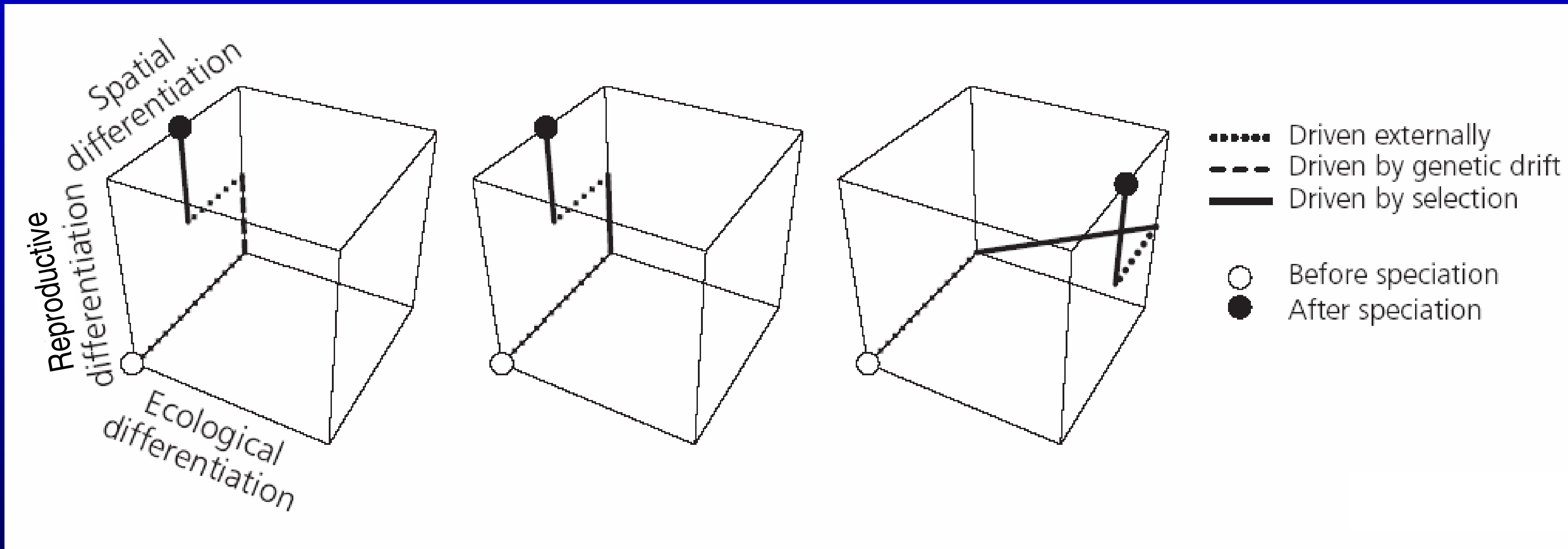
For populations that lack any spatial structure, two scenarios have been suggested: either evolution driven by sexual selection induces reproductive isolation in the absence of concomitant ecological differentiation (left; unstable), or such ecological differentiation is accompanied by the evolution of assortative mating (right).

Parapatric Speciation



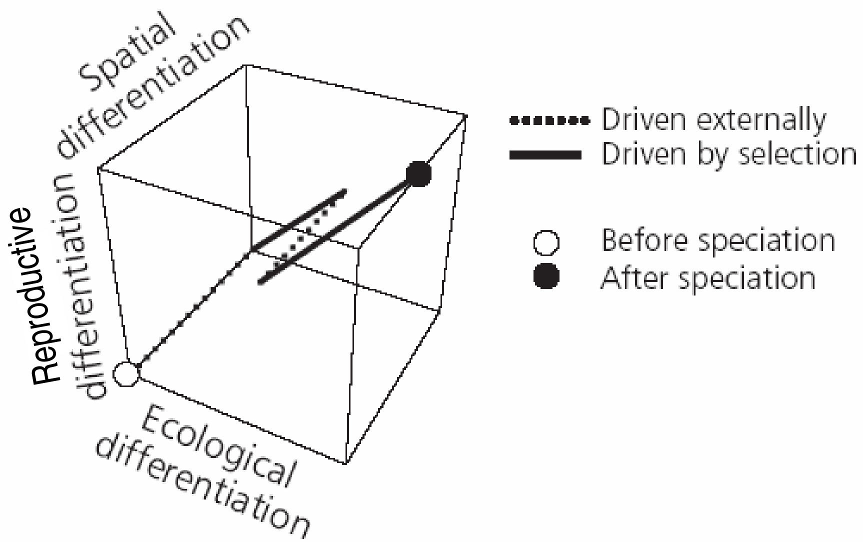
Either evolution driven by sexual selection induces reproductive isolation and spatial differentiation by giving rise to mating domains (left), or ecological differentiation is accompanied by the evolution of assortative mating and the emergence of spatial differentiation (right). The latter can occur at least in two guises: first in the course of host-race formation, and second through local adaptation and speciation along environmental gradients.

Two-Phase Speciation Processes



In the wake of geographic isolation, the incipient species develop partial reproductive isolation, through genetic drift (left), through sexual selection (middle), or through local ecological adaptation (right). This first phase is followed by the establishment of secondary contact and subsequent reinforcement.

Double Invasion



Evolution during a first phase after geographic isolation results in partial ecological differentiation and reproductive mating differentiation. In a second phase, contact between the incipient species is reestablished, and further ecological and reproductive differentiation ensues; the second phase may also involve an increase in spatial differentiation.

Summary

- Spatial gradients can greatly facilitate branching
- Intermediate slopes appear to be most speciation-prone
- The responsible mechanism is not isolation by distance but instead local adaptation leading to gradient-induced frequency-dependent disruptive selection
- Sympatric speciation processes may lead to patterns of species abutment and cause peripheral speciation
- Classification of speciation ought to be reflect the processes of spatial differentiation, ecological differentiation, and reproductive differentiation