Evolutionary Dimensions of Ecosystem Ecology

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Ecology and Evolution Are Intimately Linked

The Ecological Theater and the Evolutionary Play

G. E. Hutchinson (1967)

Two Common Misperceptions about Evolution

- **Evolution is always slow**

  On the contrary, rapid contemporary evolution is widespread, in particular in response to anthropogenic environmental change.

- **Evolution is always optimizing**

  On the contrary, frequency-dependent selection is ubiquitous, implying that population-level features will rarely get optimized by evolution.

The Need for and Potential of Evolutionary Considerations in Ecosystem Ecology

- **Understanding ecosystem constraints**

  With evolution being the architect of ecosystems, many ecosystem features require evolutionary explanations.

  Example: Evolutionary community assembly.

- **Predicting ecosystem responses**

  Whenever rapid evolution cannot be ruled out, understanding past and future ecosystem responses to anthropogenic change and managerial interventions requires evolutionary considerations.

Overview

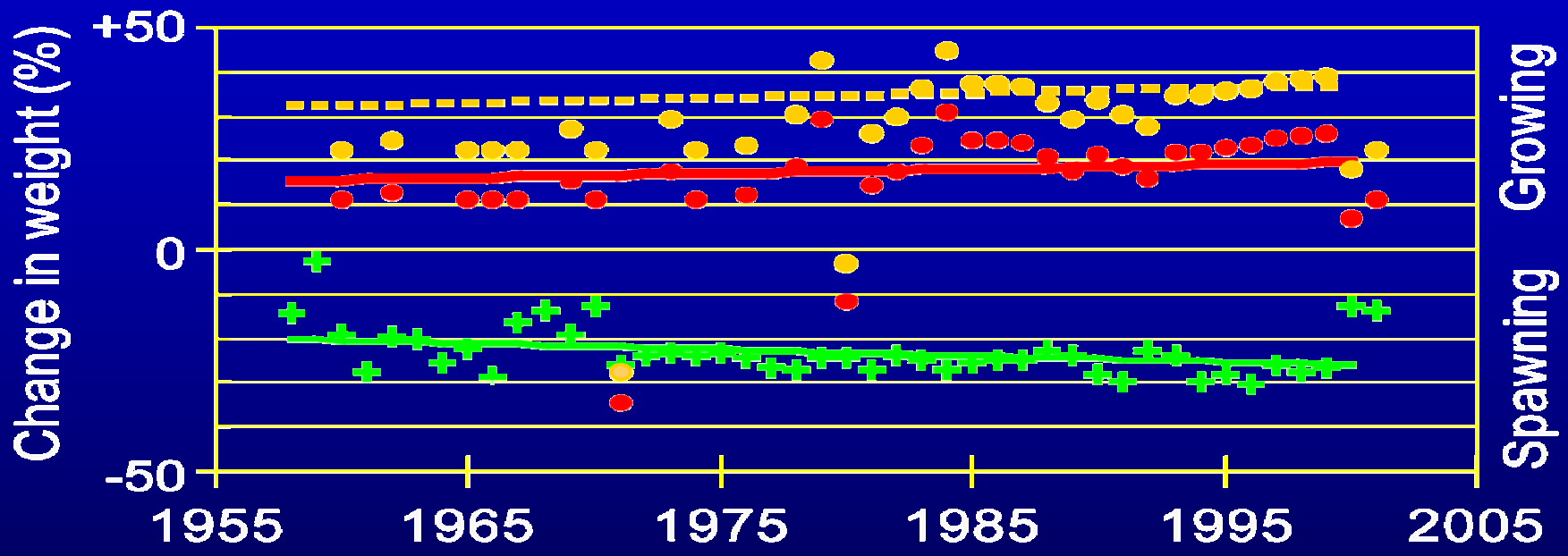
1. Rapid Evolution
2. Frequency-dependent Selection
3. Adaptive Speciation
4. Evolutionary Suicide
5. Coevolution
6. Evolutionary Timescales

1 Rapid Evolution

The Overlooked Evolutionary Dimension of Modern Fisheries

- Modern fishing results in such substantial changes of mortality patterns that evolutionary responses of stocks are inevitable.
- Such changes are not as slow as is widely believed: Significant evolution can occur within 10 or 20 years.
- Evolutionary changes are not necessarily beneficial, neither to the stock nor to the exploiting agents.
- Once evolutionary changes have occurred, they may be very difficult to reverse.
- Fishing does not only change the numbers, but also the traits of exploited fish.

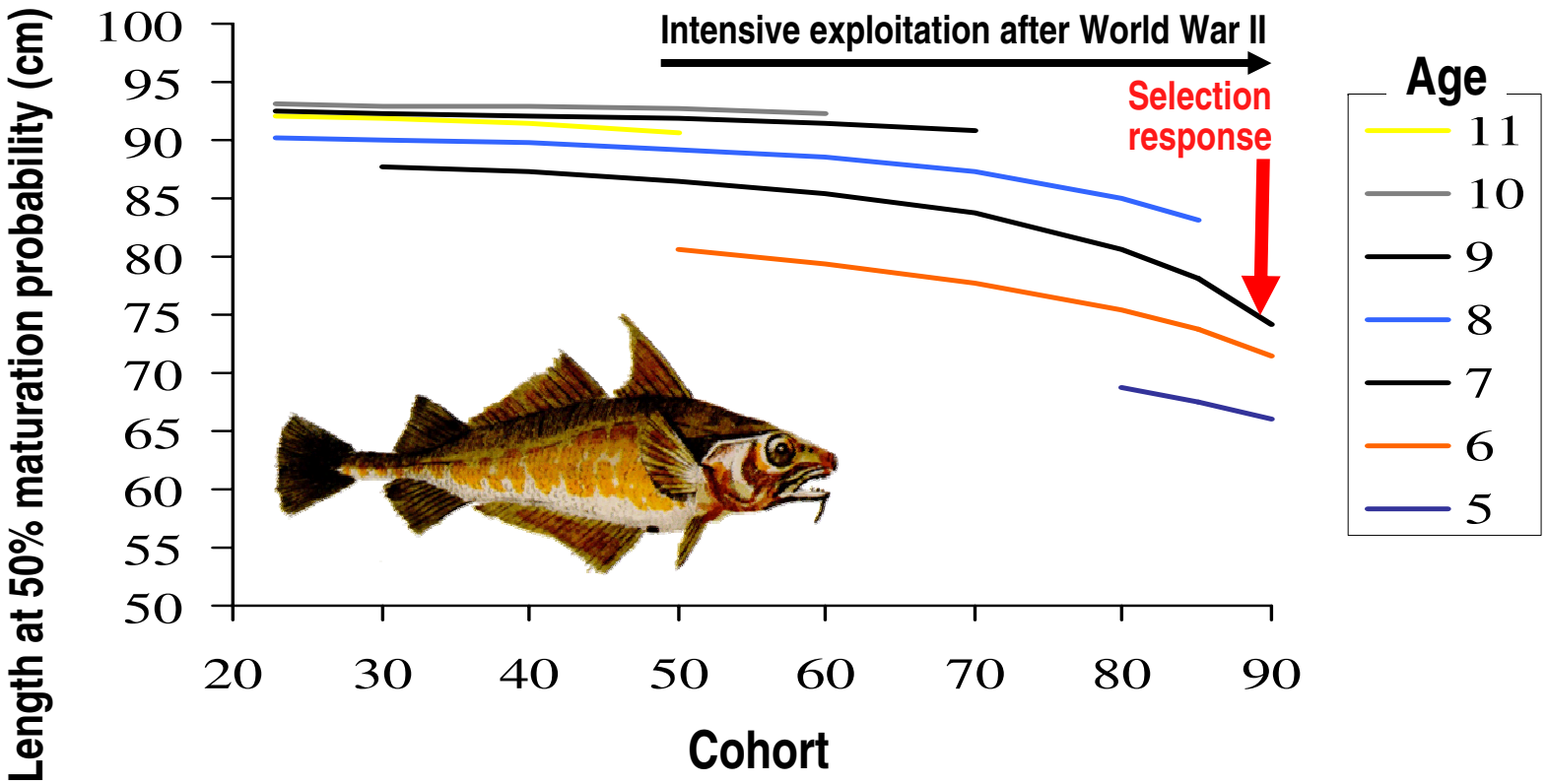
North Sea Plaice



- Loss spawning season
- Gain growing season (30 cm)
- Gain growing season (50 cm)

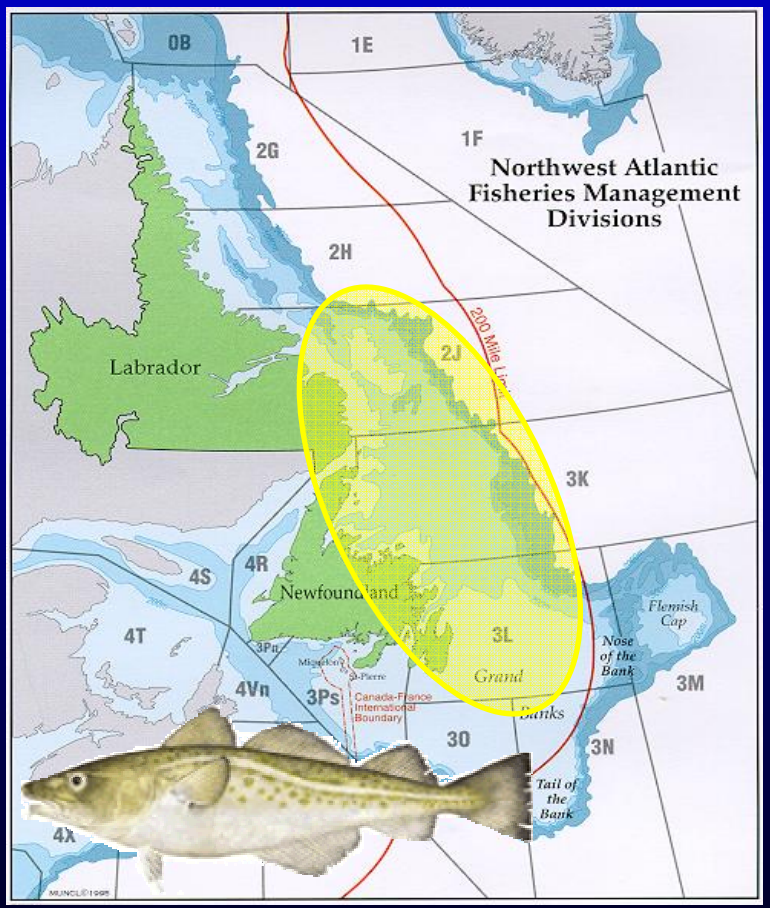
Grift, Rijnsdorp, Barot, Heino & Dieckmann. *Marine Ecology Progress Series* (2003)

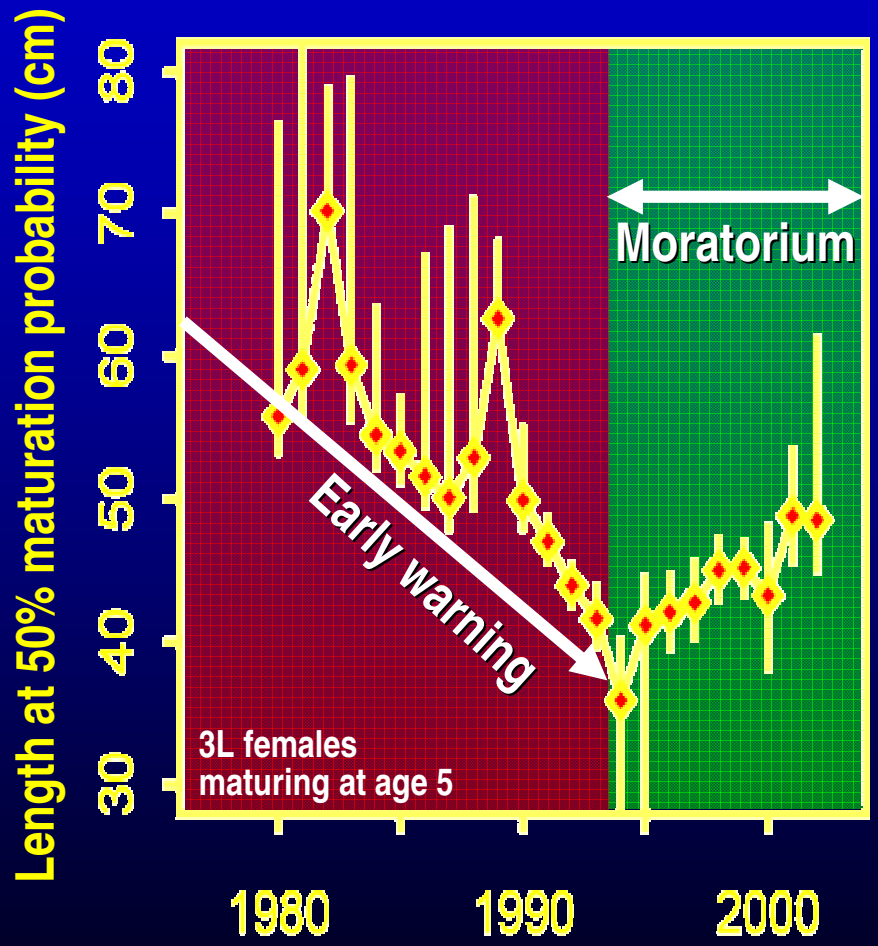
Northeast Arctic Cod



Godø, Yaragina, Heino & Dieckmann. In: *Fisheries-induced Adaptive Change*, CUP (in press)

Northern Cod





Olsen, Heino, Lilly, Morgan, Brattey, Ernande & Dieckmann. *Nature* (2004)

Which Traits Are at Risk?

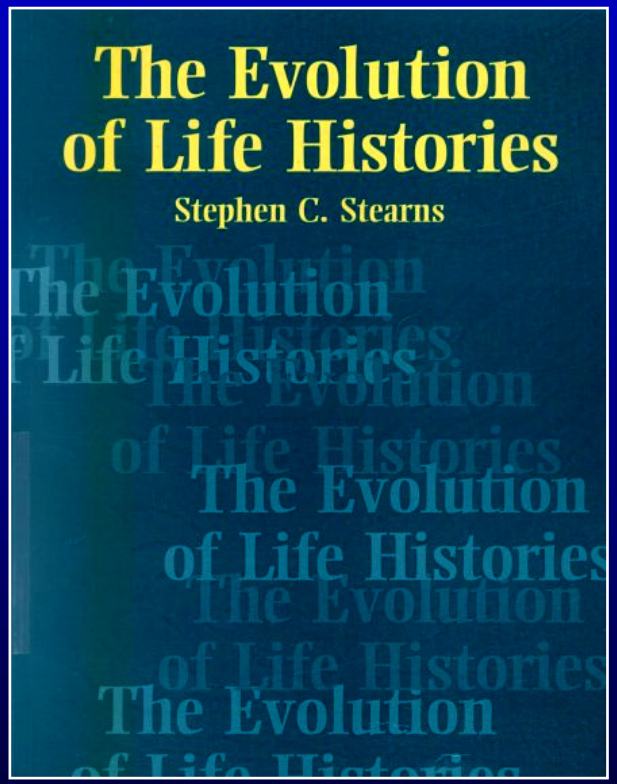
- **Age and size at maturation:**
  Reproducing late may not be a viable option.
- **Reproductive effort:**
  Saving for future reproduction may become futile.
- **Growth rate:**
  Staying below mesh size pays.
- **Behavior:**
  Reducing exposure to fishing is selected.

2 Frequency-dependent Selection

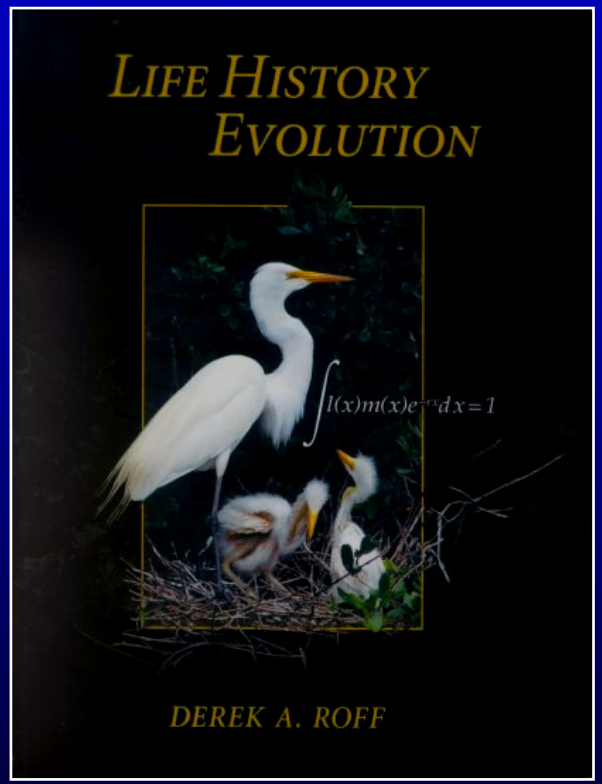
Frequency-dependent Selection

- Coping with frequency-dependent selection arguably is the biggest challenge for modern life-history 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



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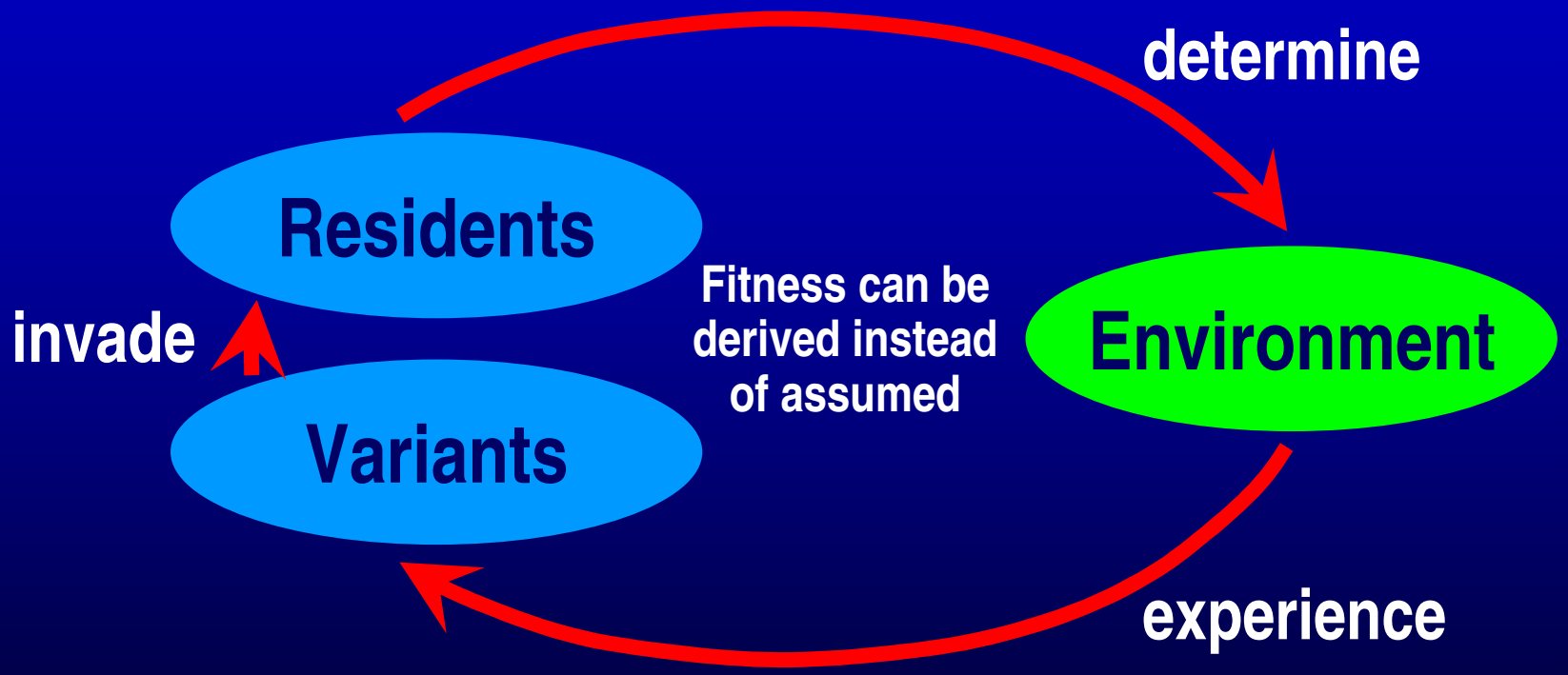
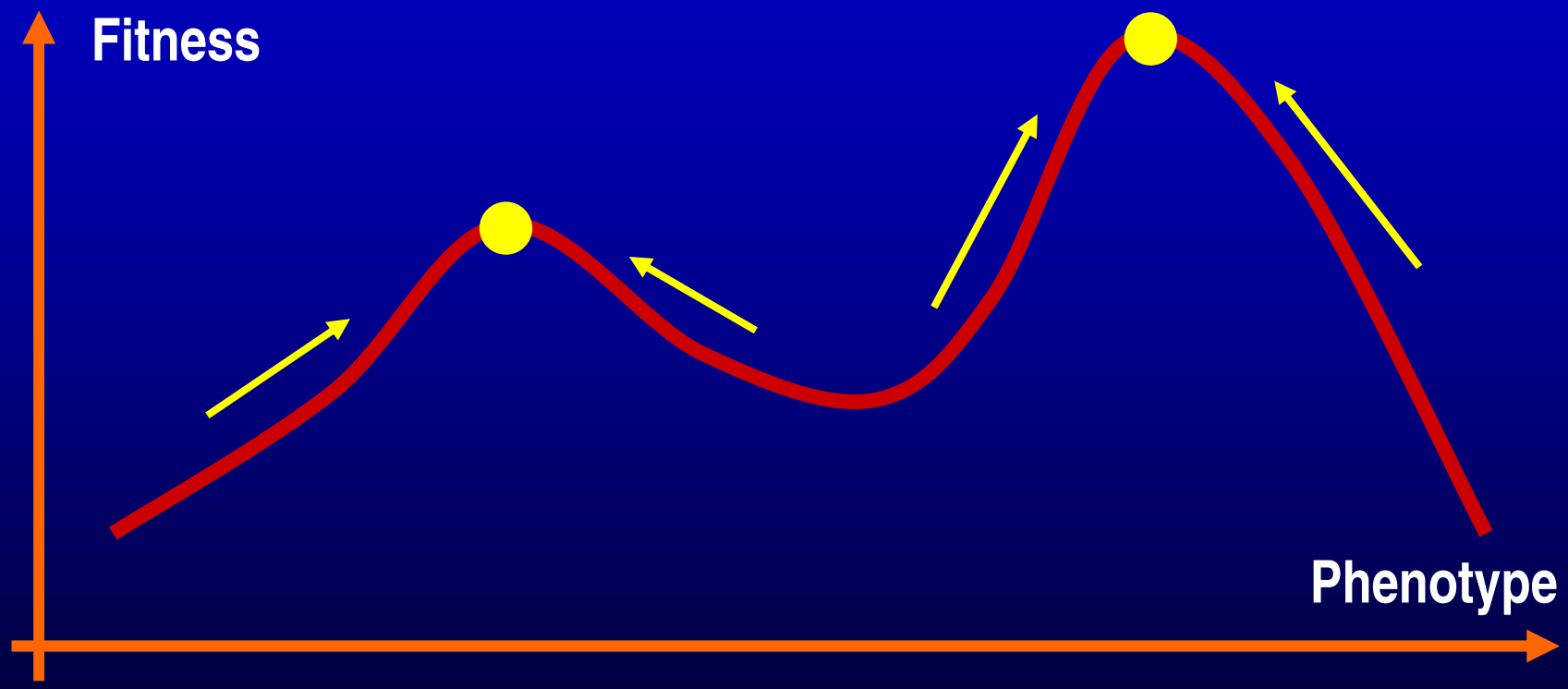
Eco-Evolutionary Feedback



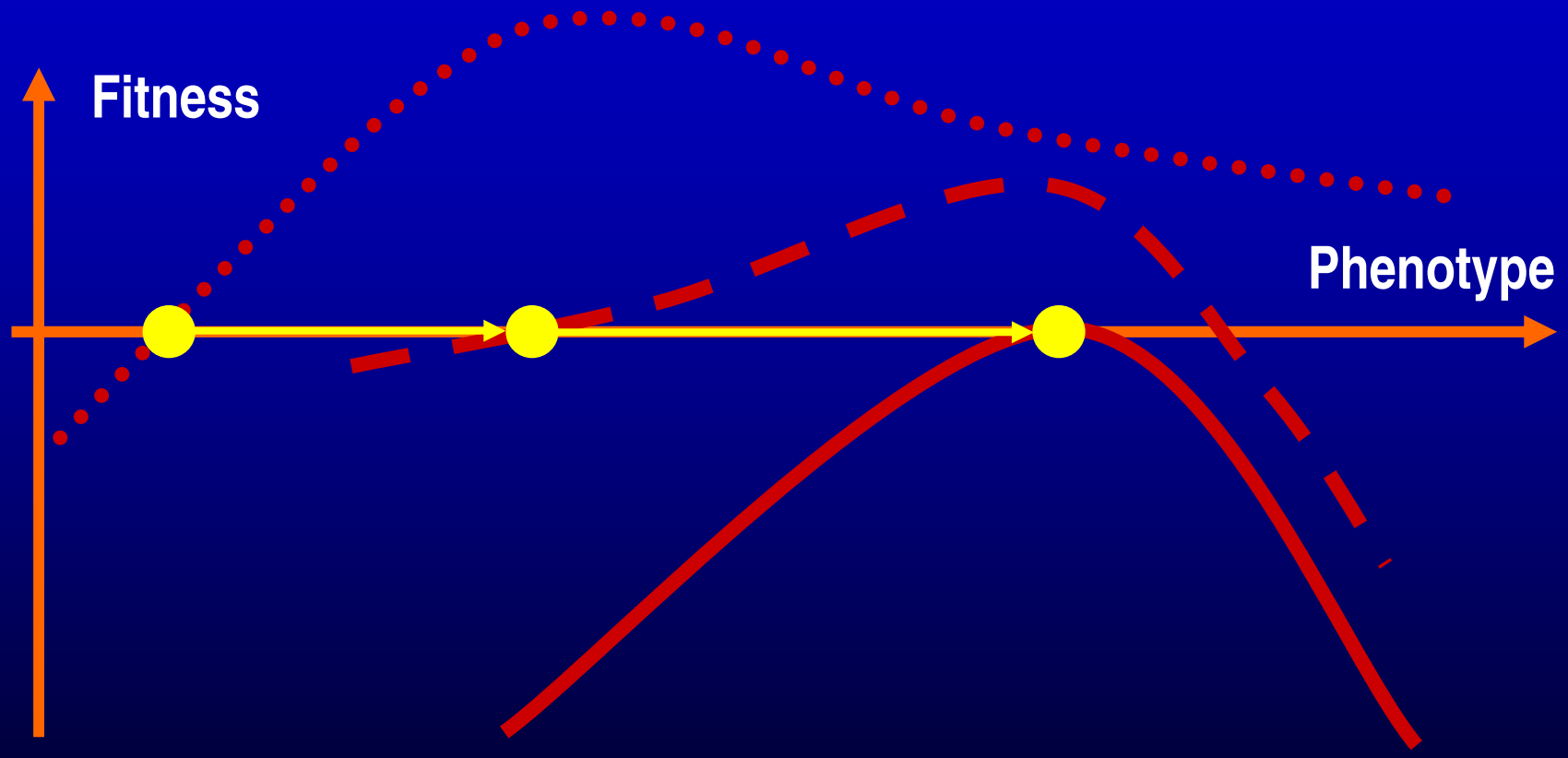
If residents are monomorphic or oligomorphic, adaptive dynamics theory offers useful tools; if they are continuously polymorphic, quantitative genetics theory is appropriate.

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.

Invasion Fitness

- Invasion fitness is a function of two variables

$$f(x', x)$$

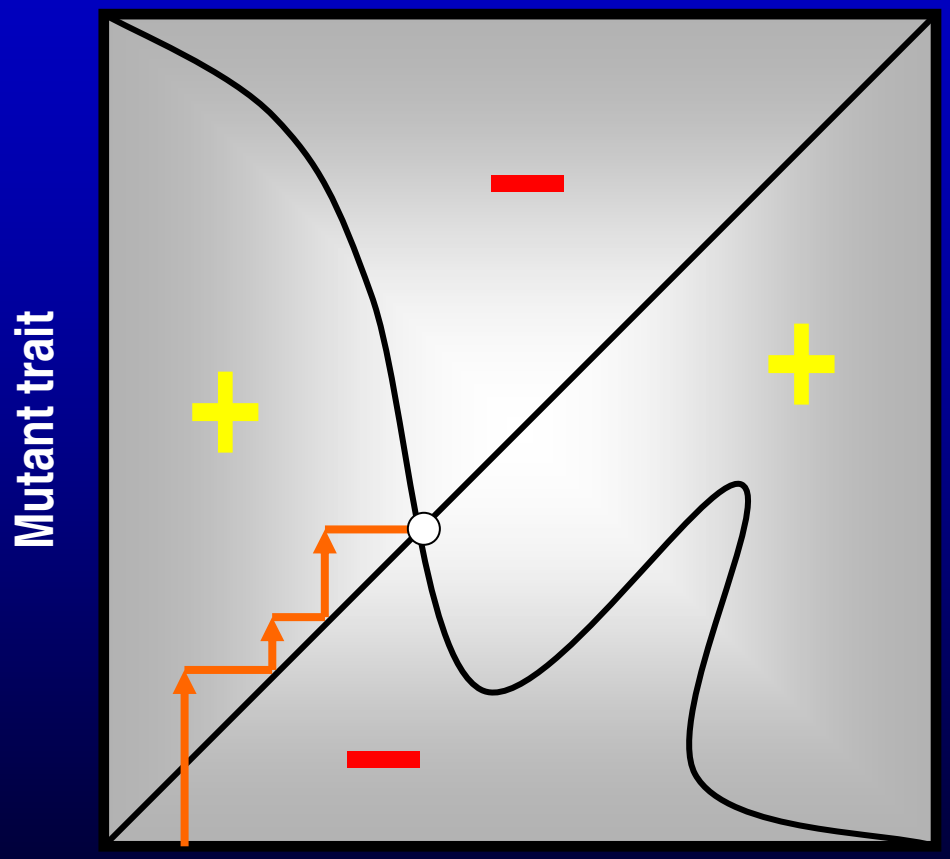
Growth rate of *x'* in *x*-environment: if positive, *x'* can invade into *x*, otherwise not

Variant trait

Resident trait: determines environment

Metz, Nisbet & Geritz. *Trends in Ecology and Evolution* (1992)

Pairwise Invasibility Plots (PIPs)



+ Invasion of the variant into the resident population possible

− Invasion impossible

One trait substitution

Singular phenotype

Matsuda (1985) / van Tienderen & de Jong (1986) / Geritz et al. (1997)

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

Direct coupling of ecology and evolution

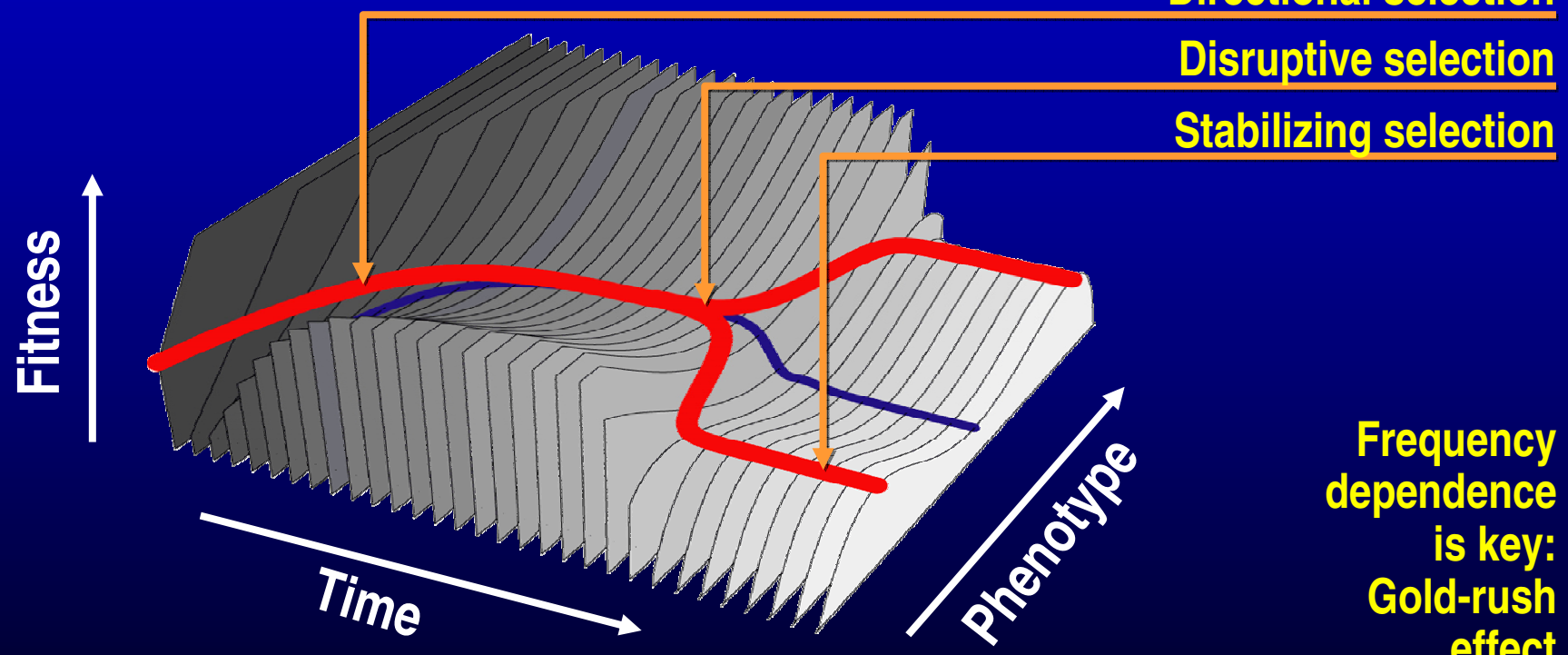
A similar result is available in quantitative genetics (Lande 1979)

Dieckmann & Law. *Journal of Mathematical Biology* (1996)

3 Adaptive Speciation

Adaptive Speciation

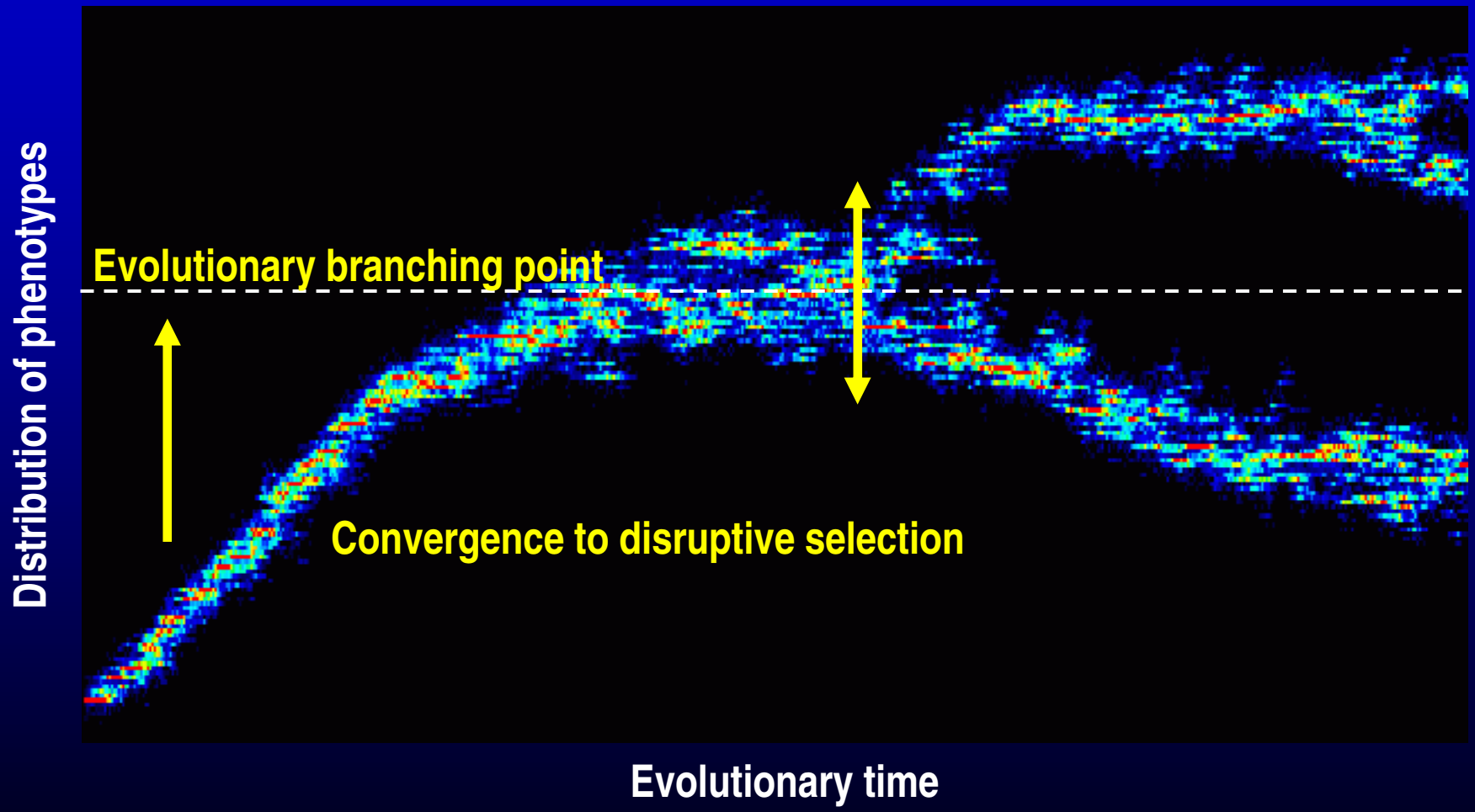
- Convergence to fitness minima



Frequency dependence is key: Gold-rush effect

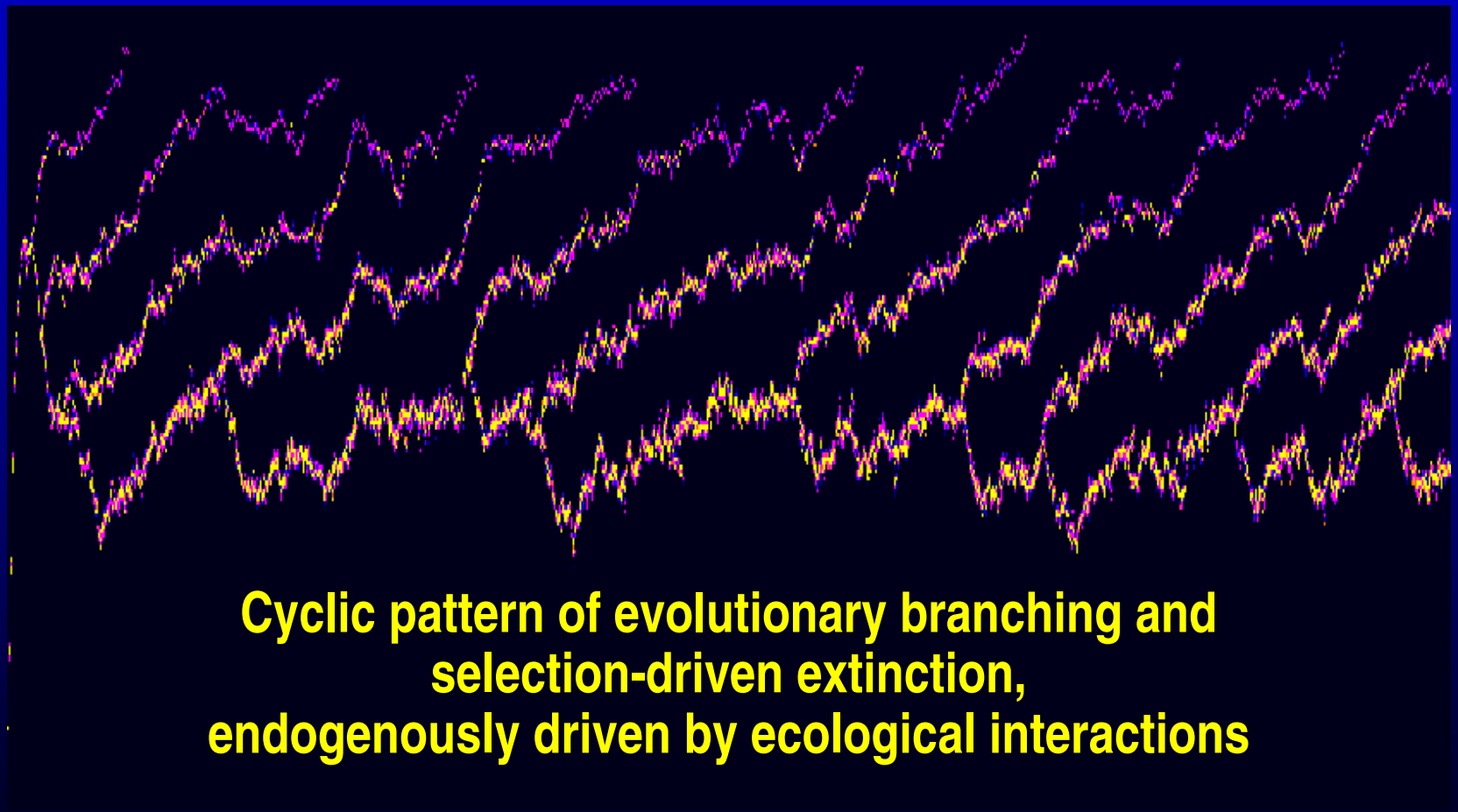
Dieckmann, Metz, Doebeli & Tautz. In: *Adaptive Speciation*, CUP (2004)

Evolutionary Branching



Metz, Nisbet & Geritz. *Trends in Ecology and Evolution* (1992)

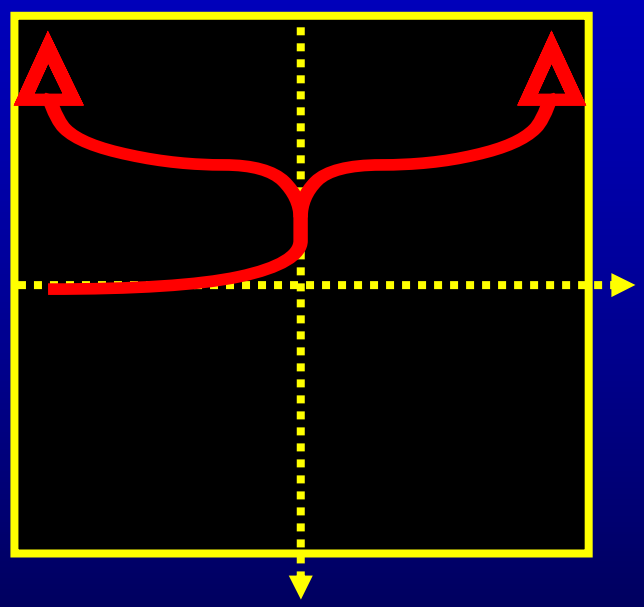
Biodiversity Formation



Distribution of phenotypes

Evolutionary time

Sexual Adaptive Speciation

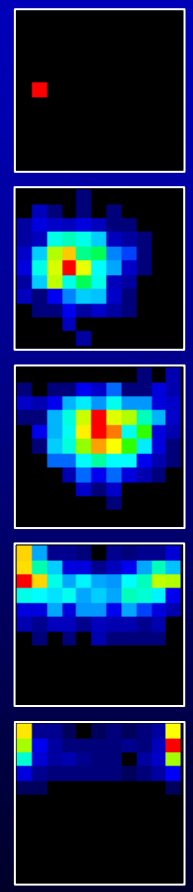


Assortative mating

Random mating

Disassortative mating

Fitness minimum



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

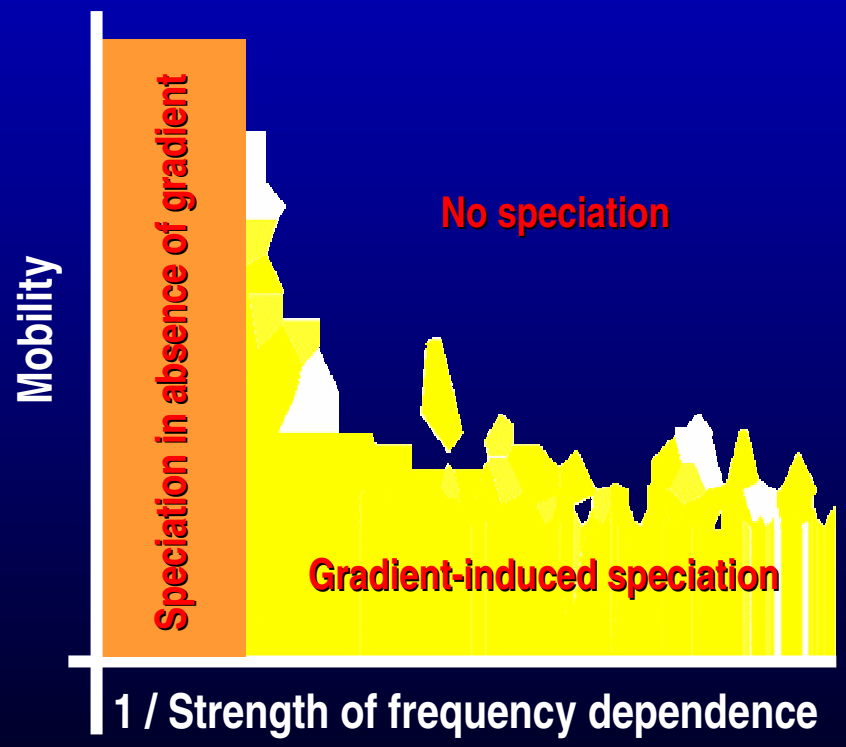
Dieckmann & Doebeli. *Nature* (1999)

Characteristics of Adaptive Speciation

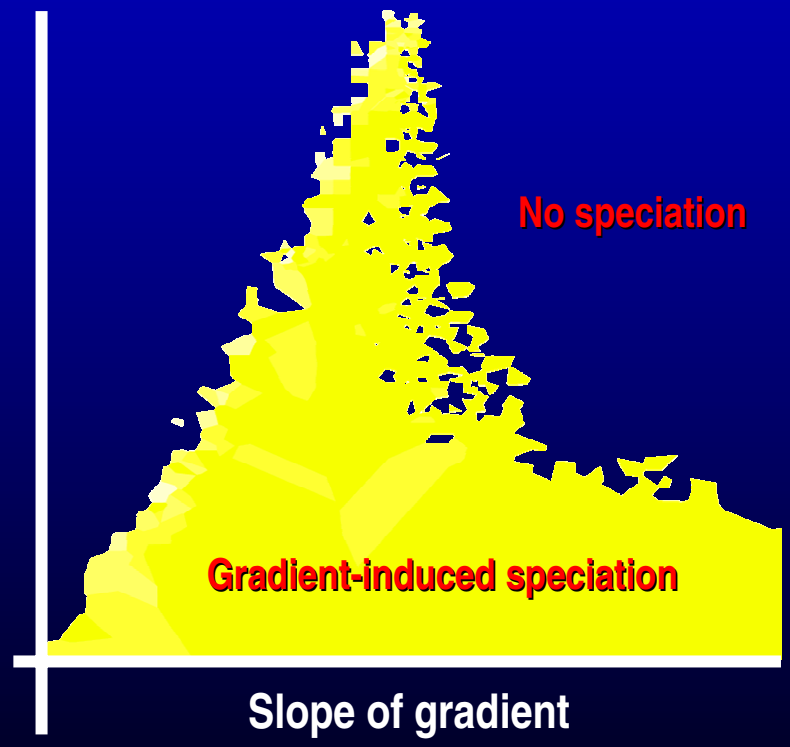
- In adaptive speciation, the speciation process itself is adaptive, enabling a population to resolve a challenge posed by the eco-evolutionary feedback.
- Adaptive speciation is driven by biological interactions, and thus does not require invoking incidental external factors for splitting a population's 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.

Spatial Adaptive Speciation

- Spatial gradients facilitate adaptive speciation



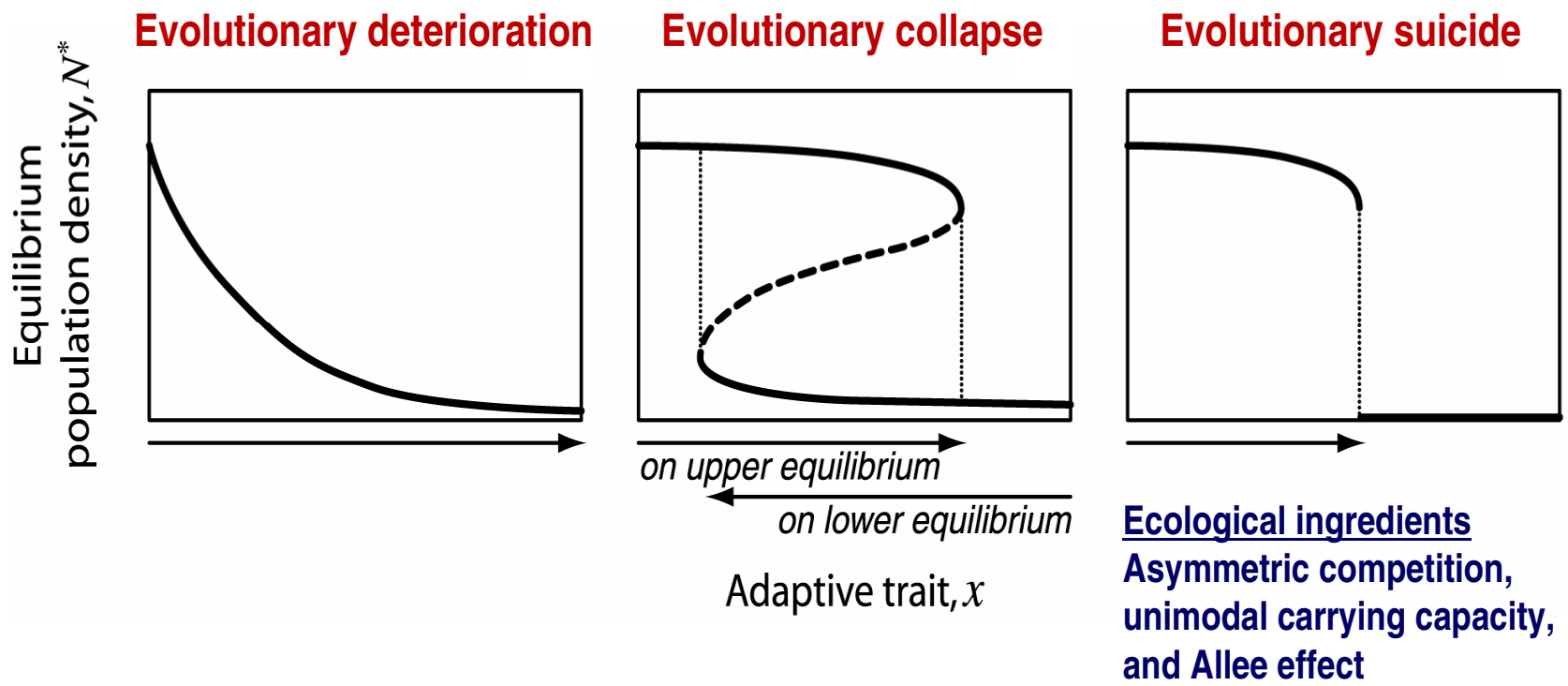
- Gradients of intermediate slope are most speciation-prone



Doebeli & Dieckmann. *Nature* (2003)

4 Evolutionary Suicide

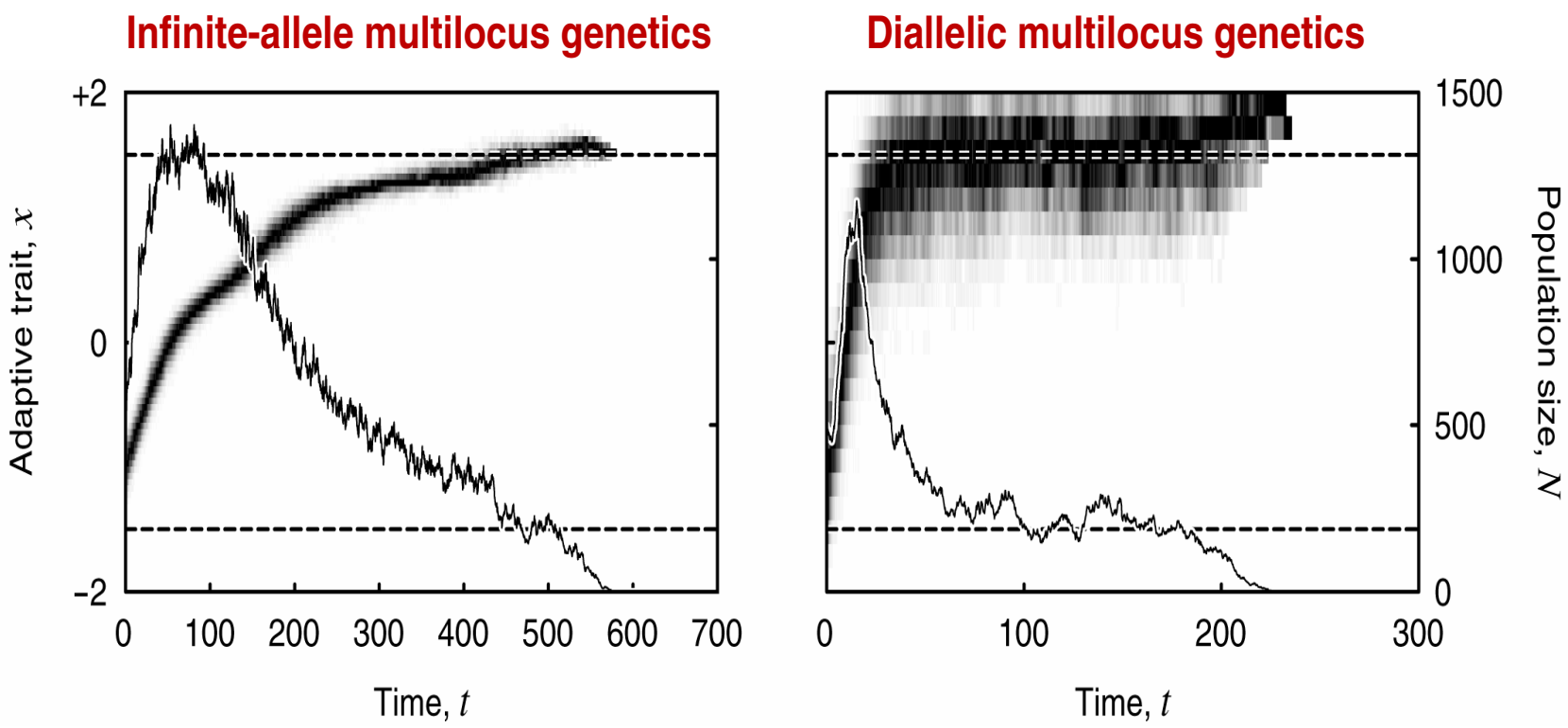
Selection-driven Extinctions



Ecological ingredients
Asymmetric competition, unimodal carrying capacity, and Allee effect

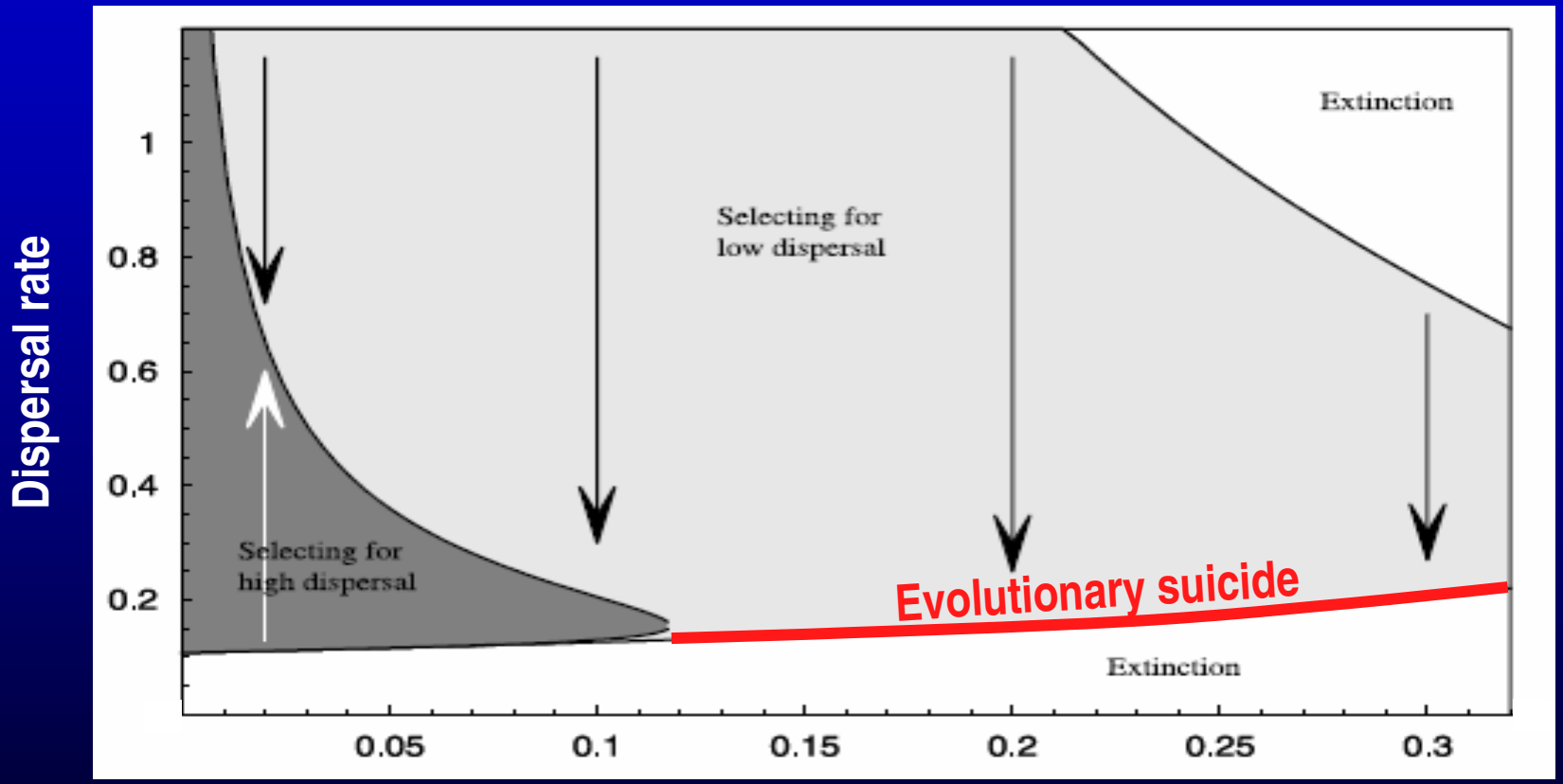
Dieckmann & Ferriere. In: *Evolutionary Conservation Biology*, CUP (2004)

Sexual Evolutionary Suicide



Dieckmann & Ferriere. In: *Evolutionary Conservation Biology*, CUP (2004)

Evolutionary Suicide through Dispersal Evolution

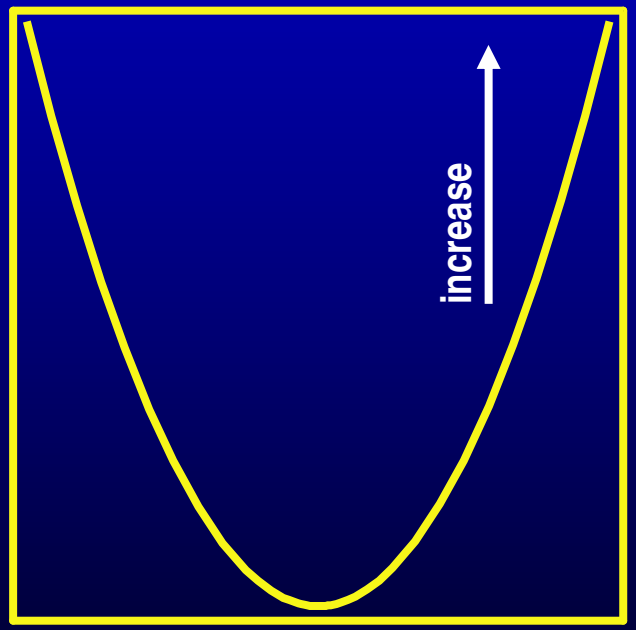


Gyllenberg, Parvinen & Dieckmann. *Journal of Mathematical Biology* (2002)

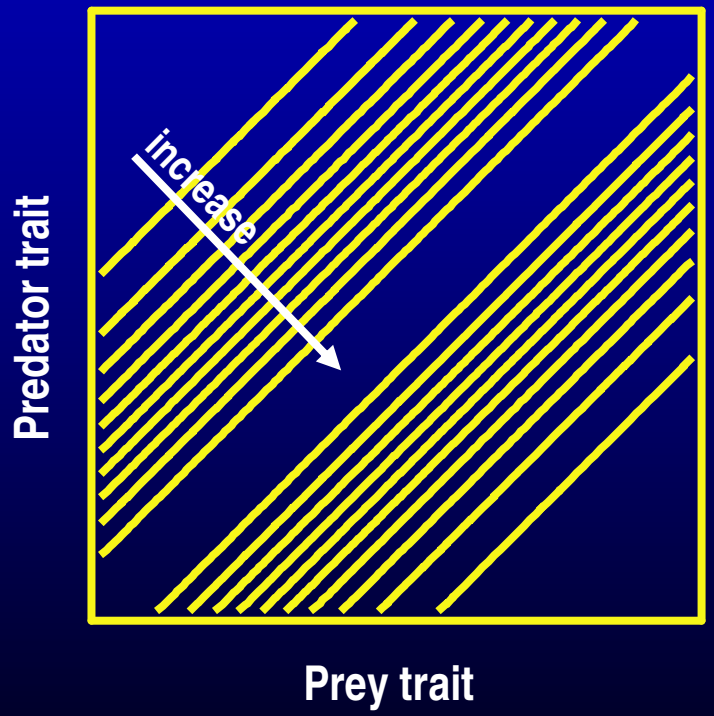
5 Coevolution

Predator-Prey Coevolution: Traits

- Natural prey mortality

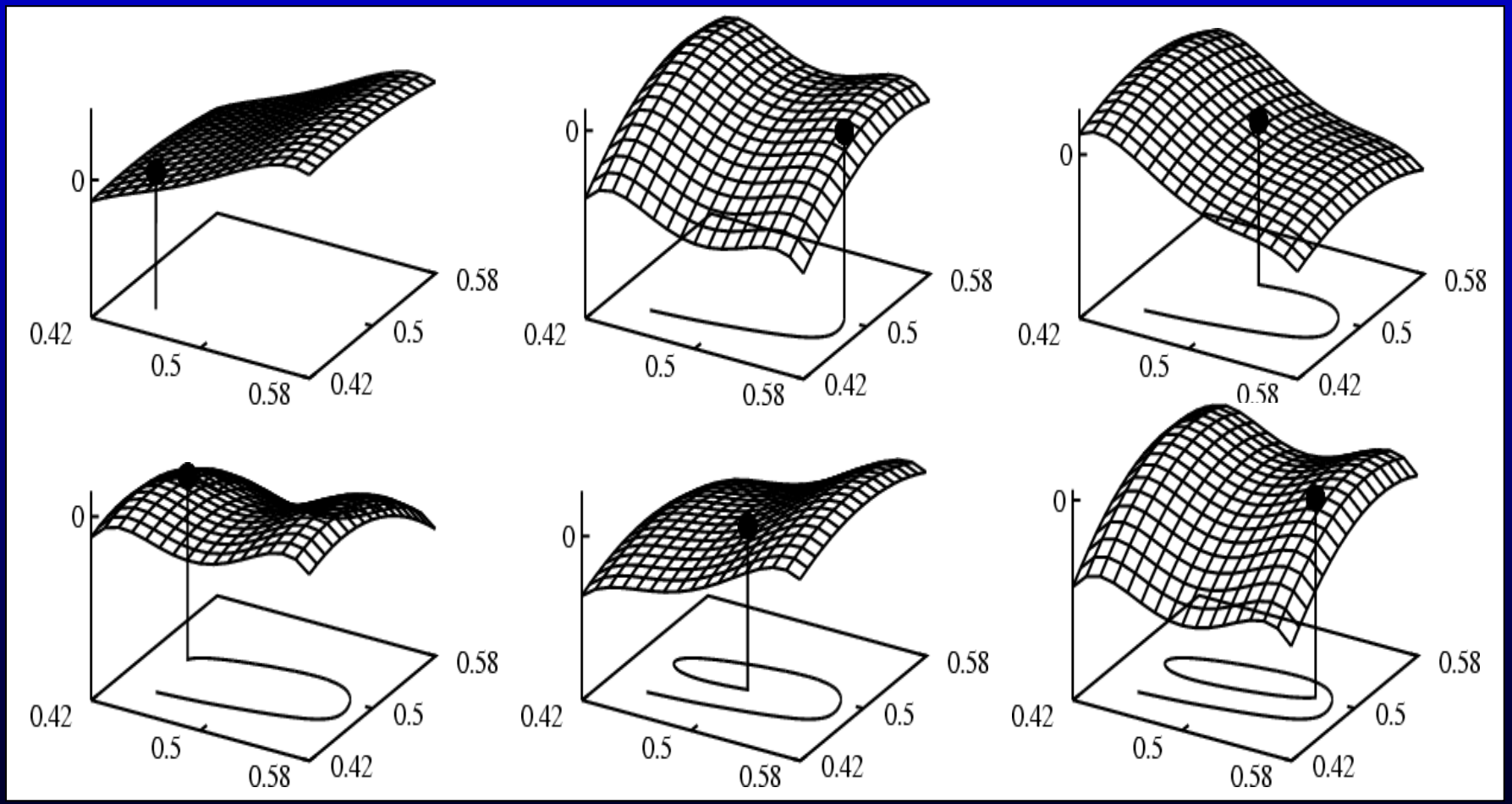


- Predator-induced prey mortality



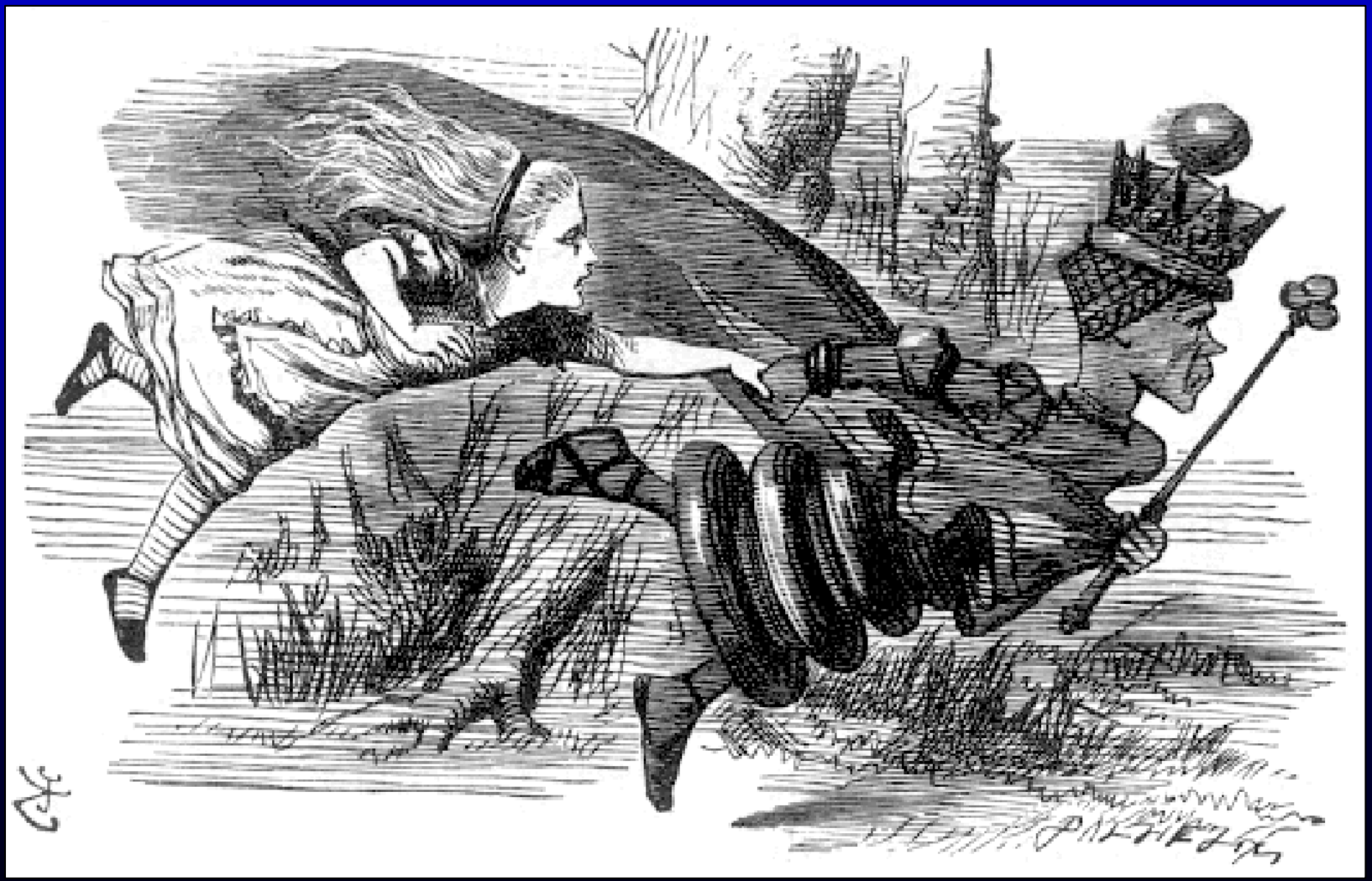
Dieckmann, Marrow & Law. *Journal of Theoretical Biology* (1995)

Predator-Prey Coevolution: Dynamics

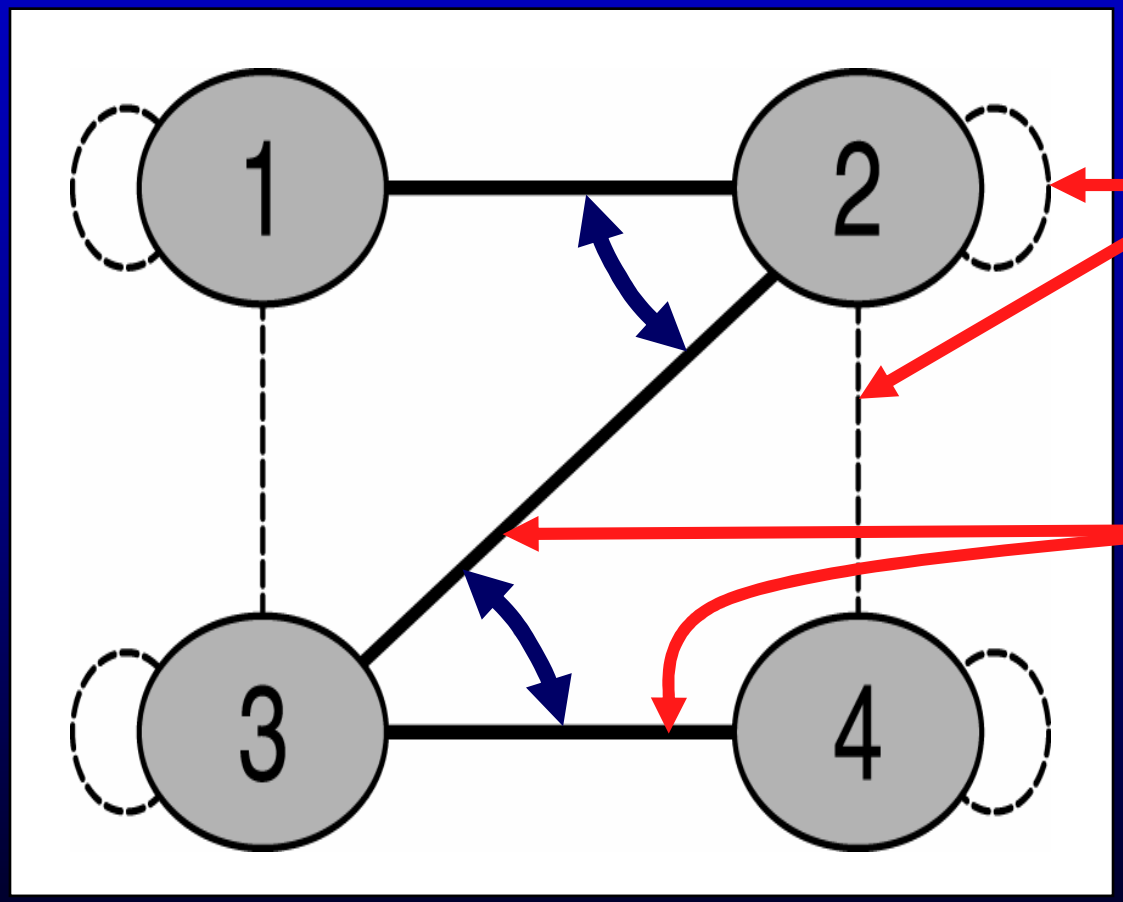


Dieckmann, Marrow & Law. *Journal of Theoretical Biology* (1995)

Red Queen Dynamics



Mutualistic Coevolution: Traits

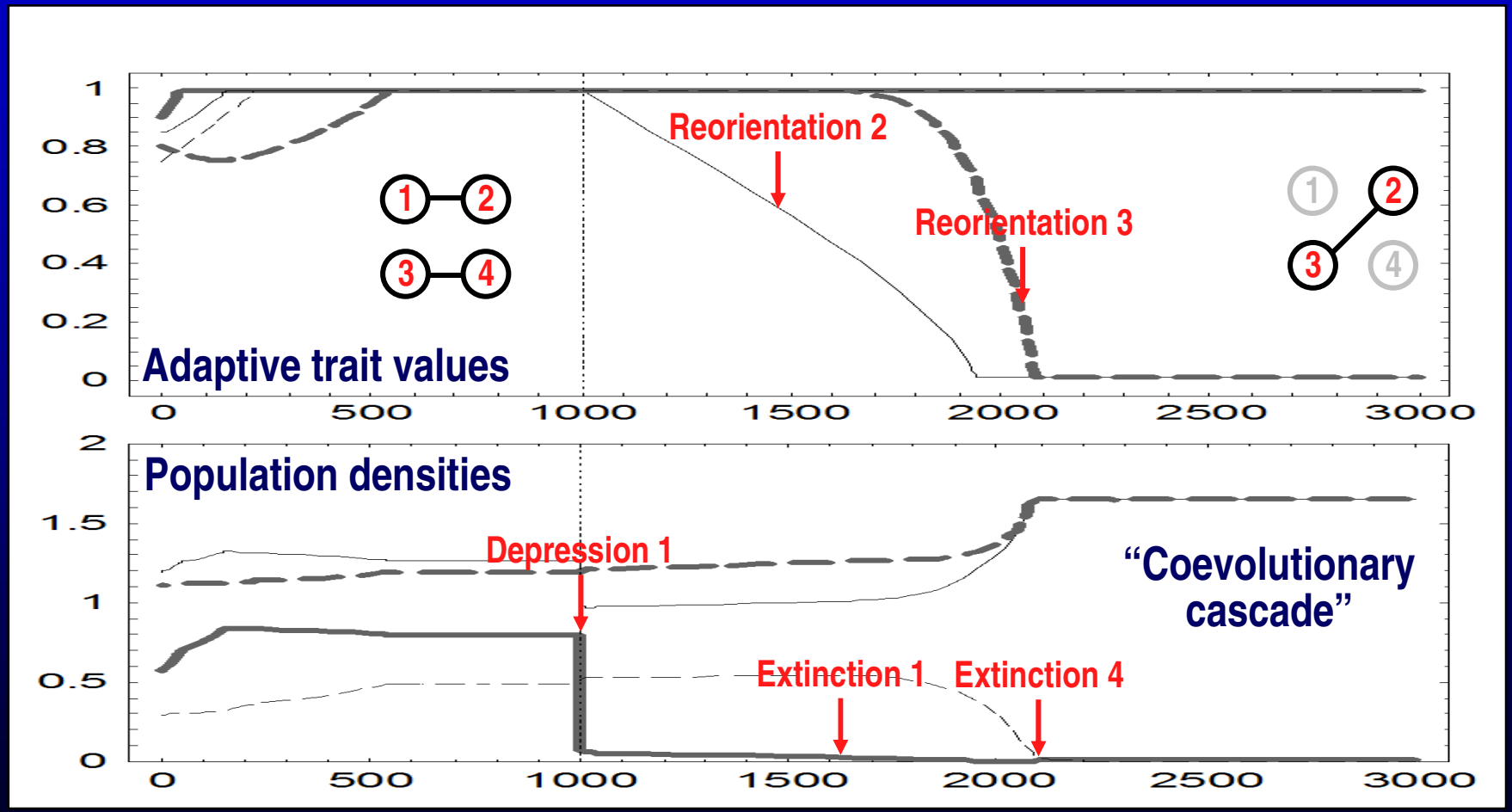


Competitive interactions

Adapting mutualistic interactions

Bronstein, Dieckmann & Ferriere. In: *Evolutionary Conservation Biology*, CUP (2004)

Mutualistic Coevolution: Dynamics

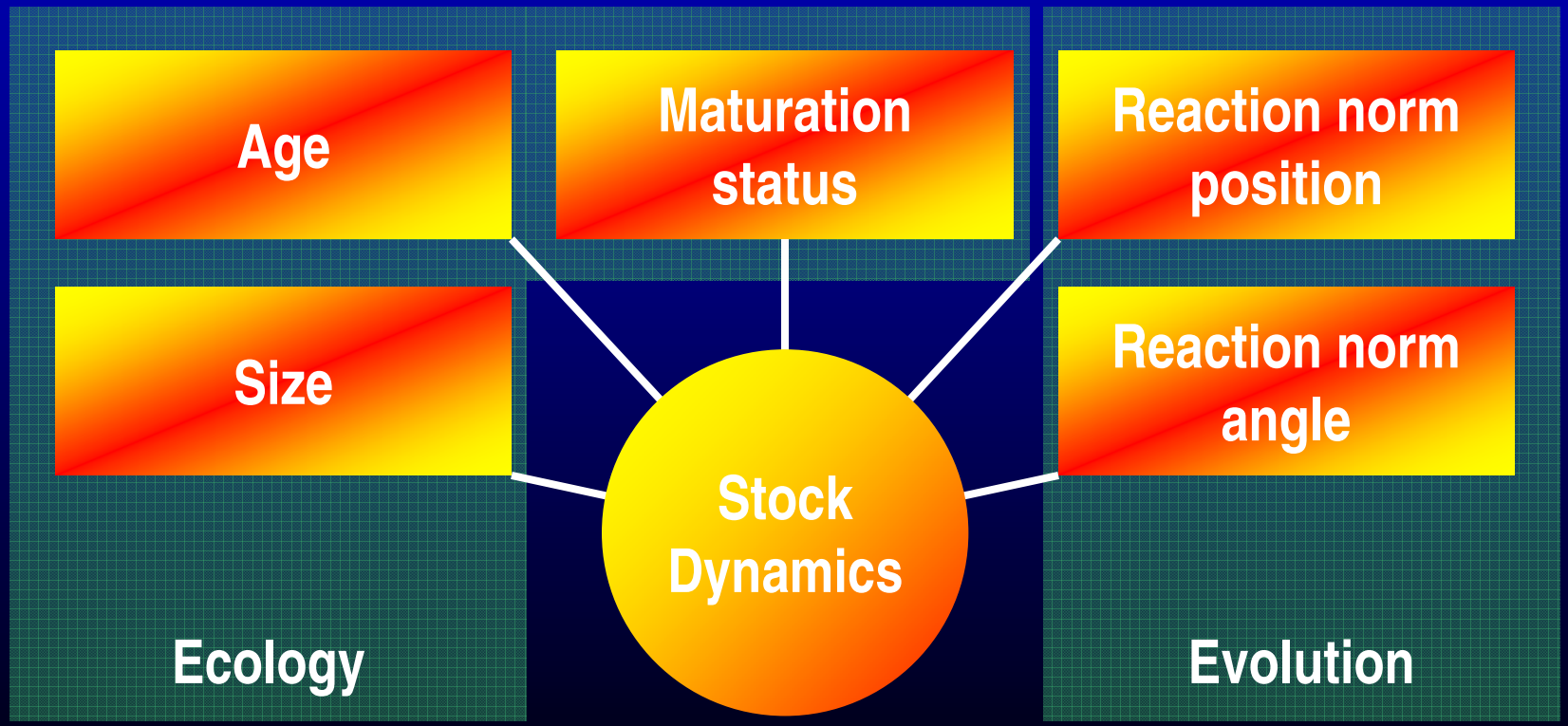


Bronstein, Dieckmann & Ferriere. In: *Evolutionary Conservation Biology*, CUP (2004)

6 Evolutionary Timescales

Eco-Genetic Models

- Frequencies of individuals are tracked through time in dependence on five characteristics:



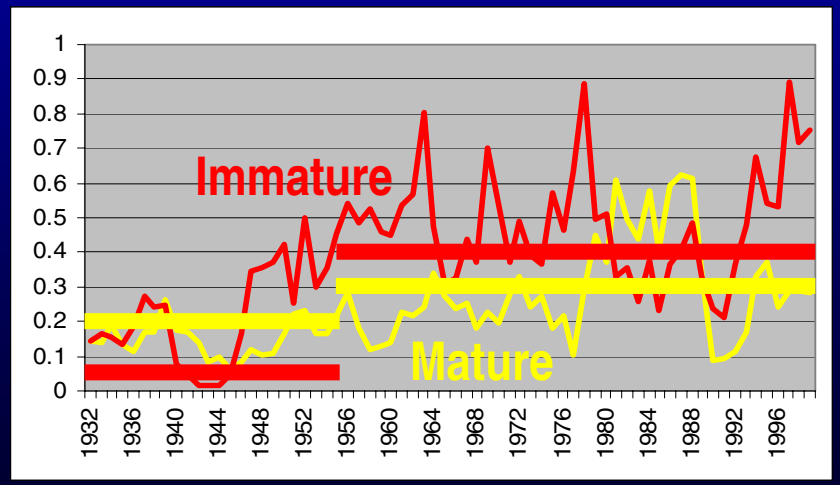
Modeling Northeast Arctic Cod

Demography

- Linear growth before maturation
- Growth increments negatively correlated with stock biomass
- Growth increments of mature individuals depend on size and gonadosomatic index
- Natural mortality of 0.2
- Density-dependent newborn mortality
- Density-dependent cannibalism on age classes 1 and 2
- Linear maturation reaction norm of constant width
- Fecundity allometrically depends on size

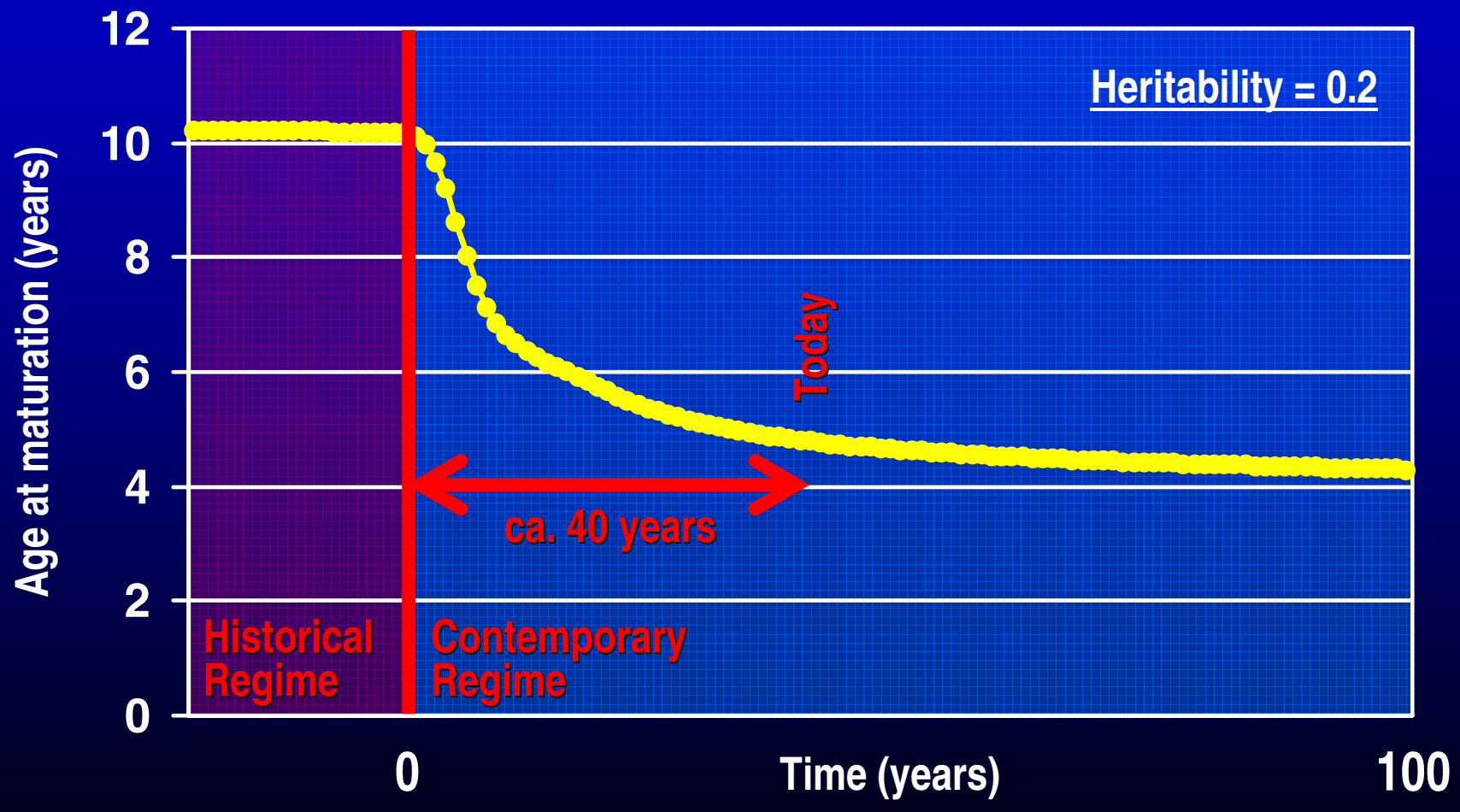
Fishing Mortality

- Historical regime:
  $F_{immature} = 0.05$ and $F_{mature} = 0.2$
- Contemporary regime:
  $F_{immature} = 0.4$ and $F_{mature} = 0.3$

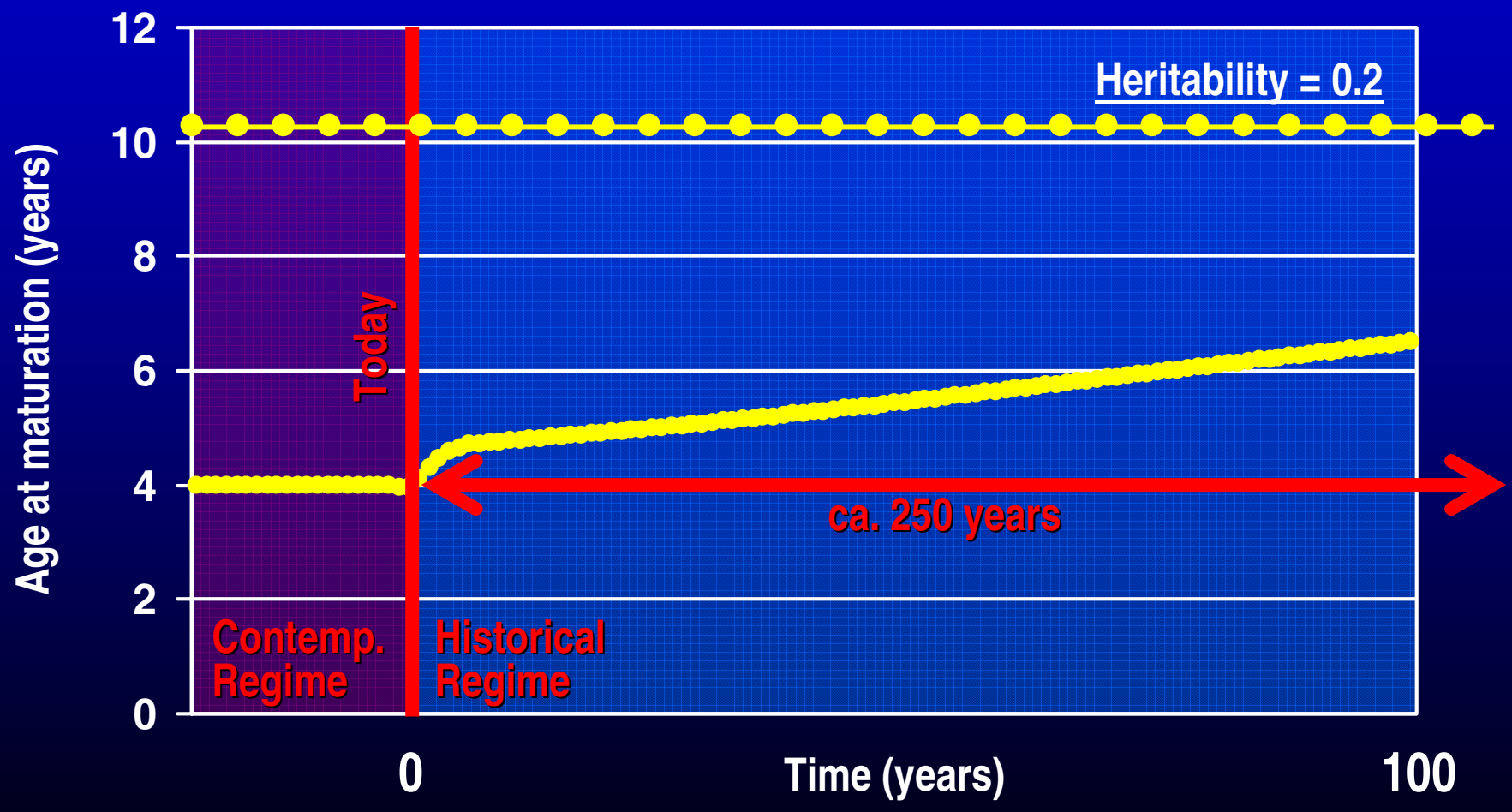


- Estimated size selectivity of fishing gear taken into account

Evolutionary Transient



Reverse Evolutionary Transient



General Conclusions

- Frequency-dependent selection is crucial for understanding ecosystem evolution. Adaptive dynamics theory is geared to account for it, by closely linking evolutionary dynamics and population dynamics.
- Key determinants of biodiversity – including selection responses to environmental change, adaptive speciation, evolutionary suicide, and coevolutionary dynamics – can thus be analyzed.
- Future directions: Ecologically reasonable models of food web evolution are just now emerging (see also WS 5).