Overview

Eco-Evolutionary Dynamics

Modelling Frameworks

Mathematical Connections

Biodiversity Dynamics

Adaptive Speciation

Niche Theory

2e Adaptive dynamics

Adaptive Dynamics Theory

The theory of adaptive dynamics extends evolutionary game theory and quantitative genetics theory in a number of respects:

- Evolving traits are continuous
- Trait dynamics are described
- Mutational covariances and constraints can be examined
- Arbitrary density and frequency dependence is allowed
- Coevolution is integrated
- Structured population dynamics are allowed
- Non-equilibrium population dynamics are allowed
- Fitness landscapes are derived

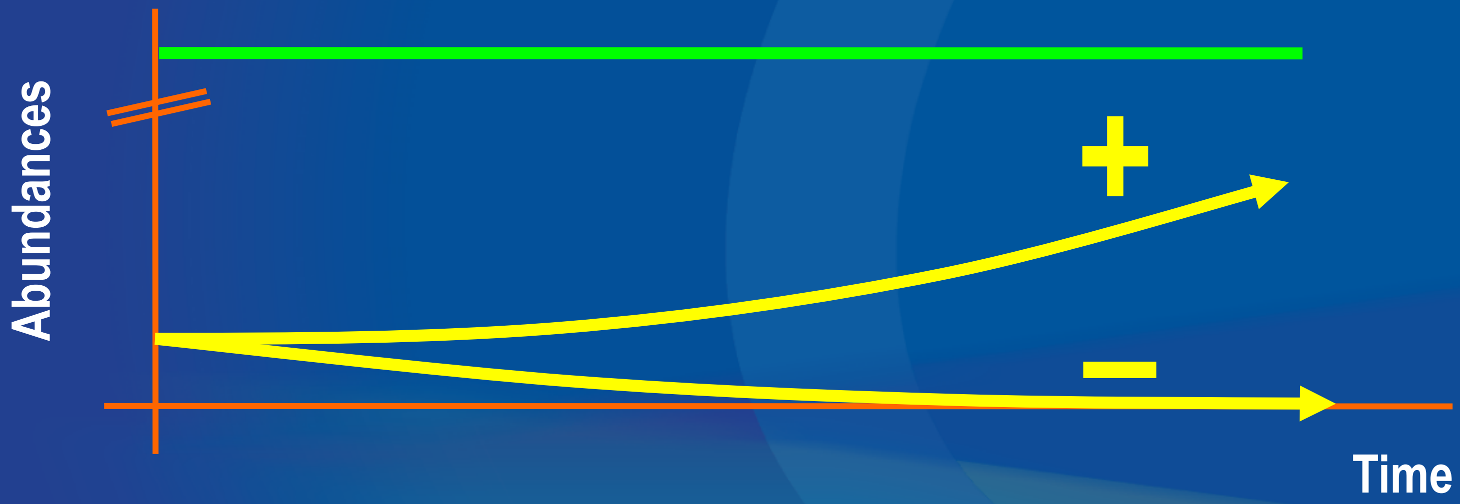
Extensions of EGT

Extensions of both EGT and QGT

Invasion Fitness

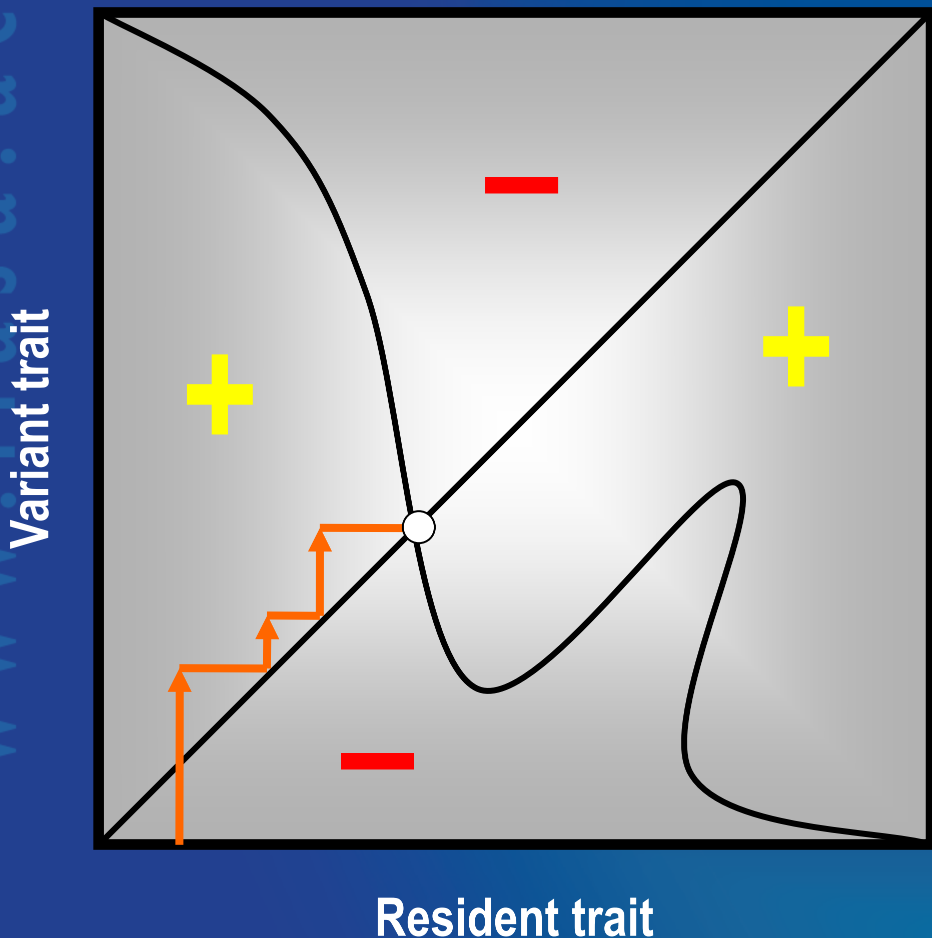
Metz et al. (1992)

- Initial per capita growth rate of a small variant population within a large resident population at ecological equilibrium:



Pairwise Invasibility Plots

Matsuda & Abrams (1985)
Metz et al. (1992)



+ Invasion of the variant into the resident population is possible

– Invasion is impossible

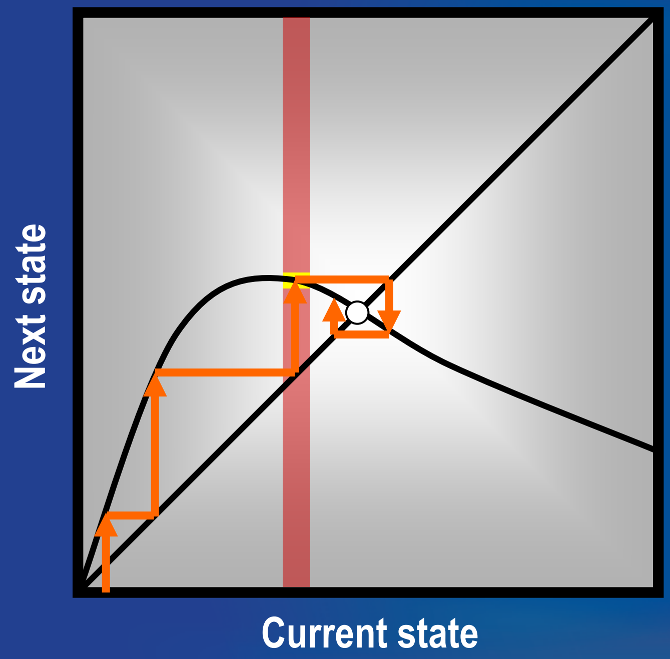
One trait substitution

Trait substitution sequence

Evolutionarily singular phenotype

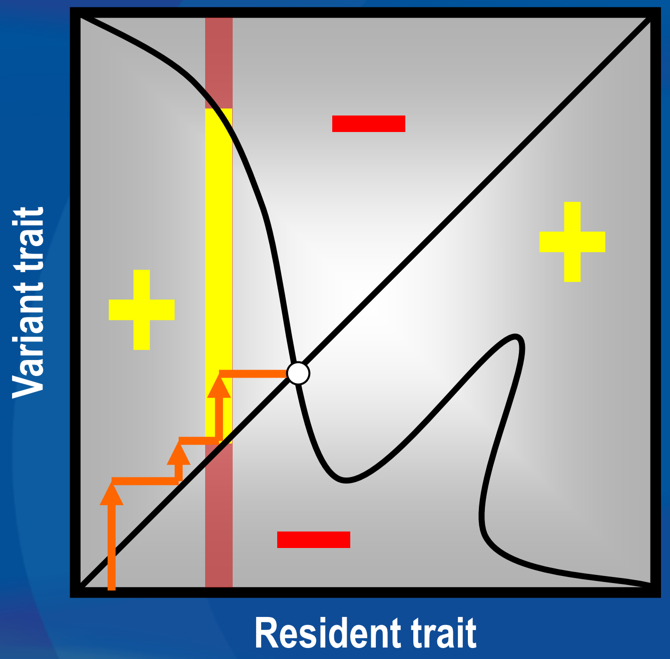
Comparison with Recursions

- Recursion relations



Size of vertical steps deterministic

- Trait substitutions

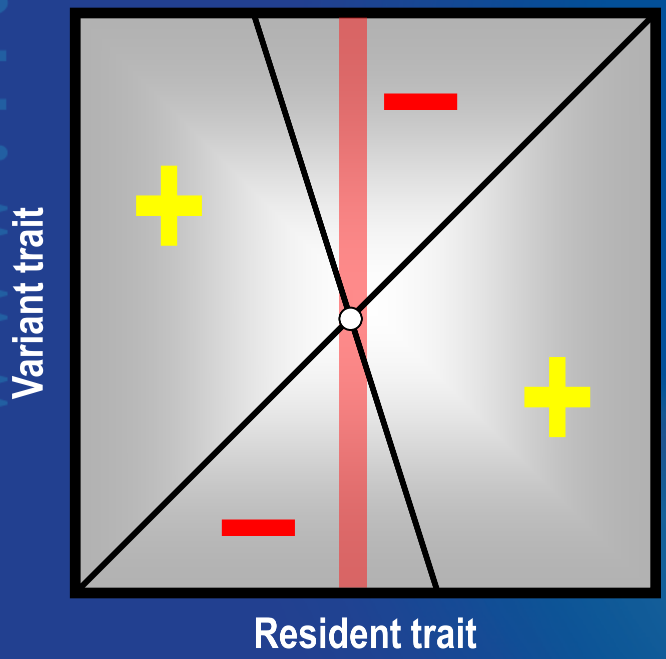


Size of vertical steps stochastic

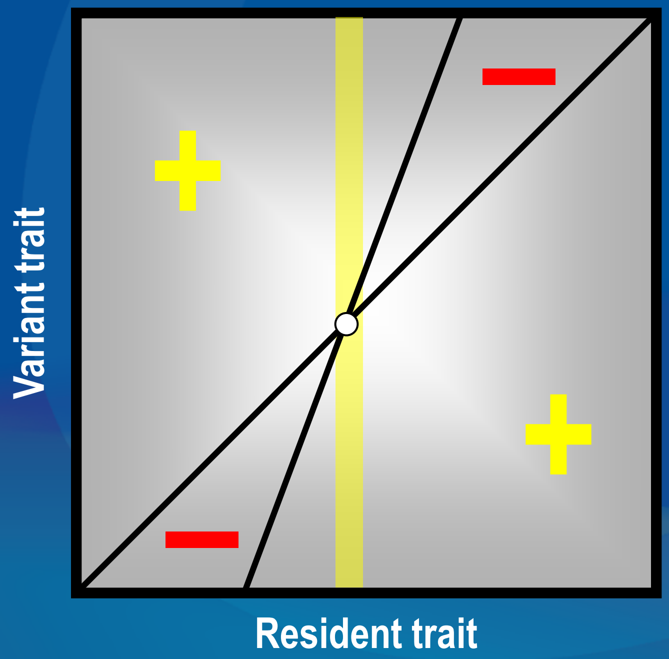
Reading PIPs: Evolutionary Stability

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

Yes:

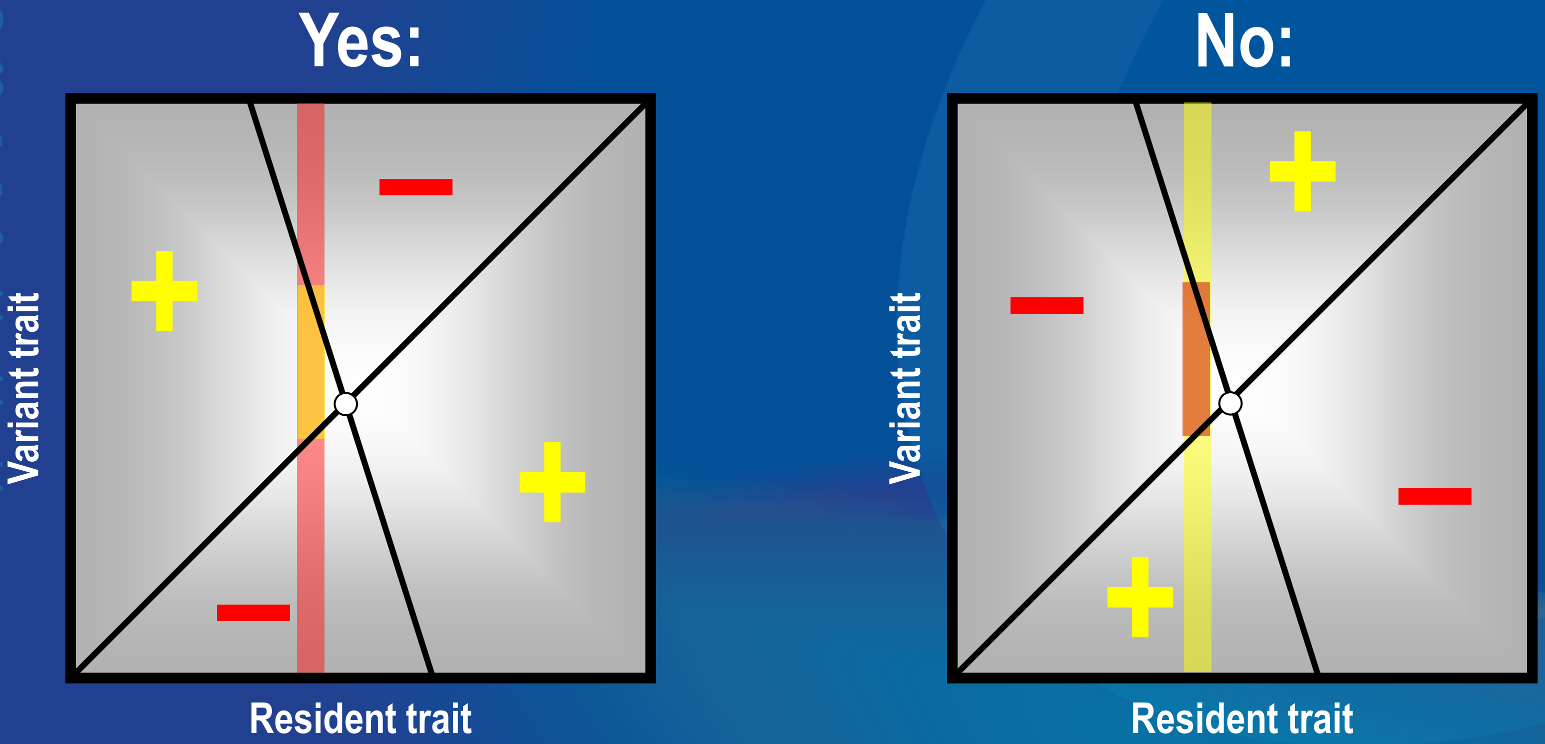


No:



Reading PIPs: Convergence Stability

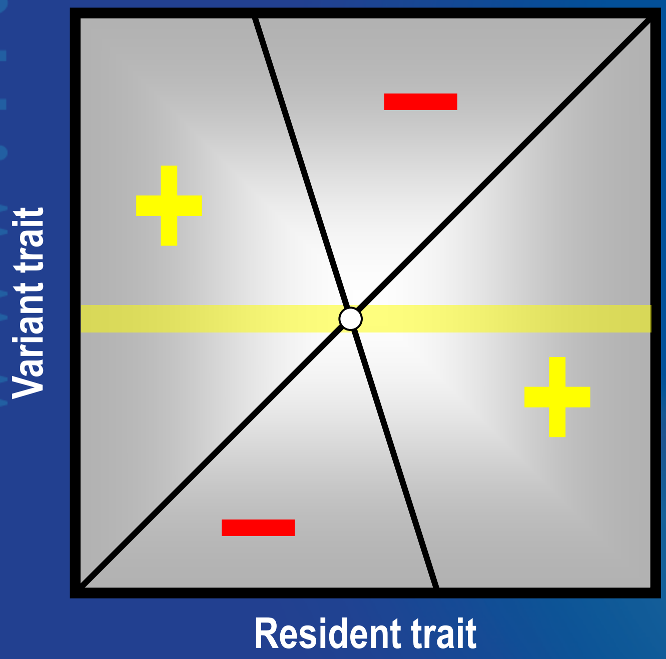
- When starting from neighboring phenotypes, do successful invaders lie closer to the singular one?



Reading PIPs: Invasion Potential

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

Yes:



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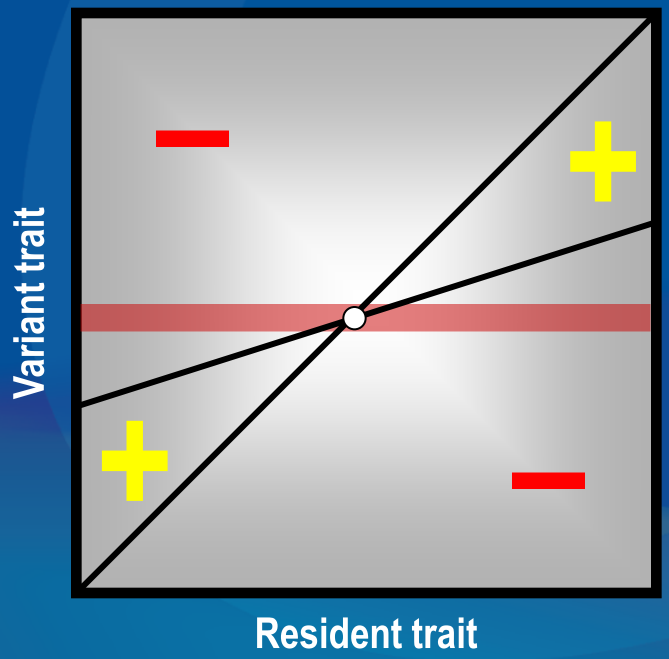
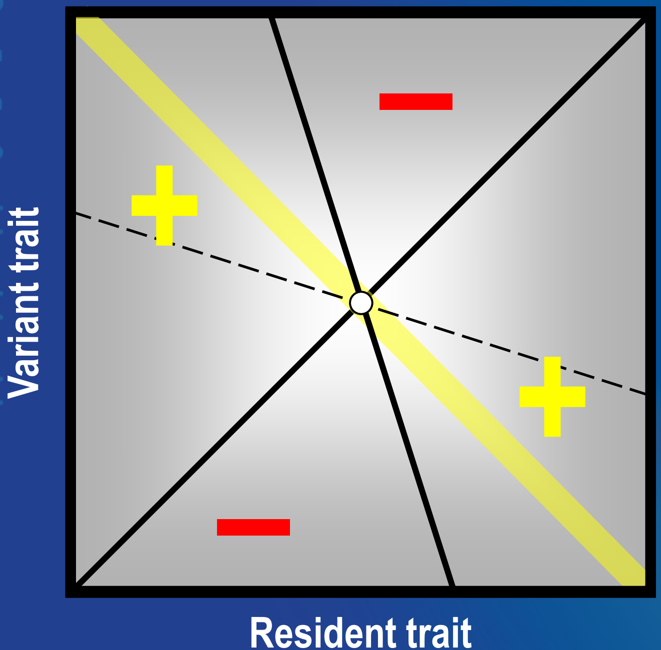


Reading PIPs: Mutual Invasibility

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

Yes:



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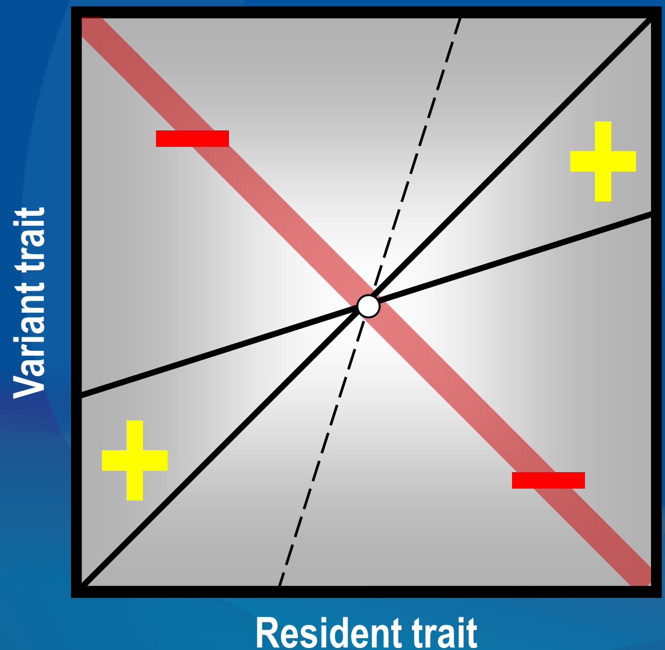
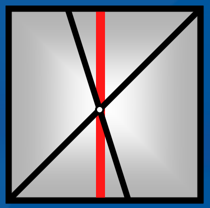


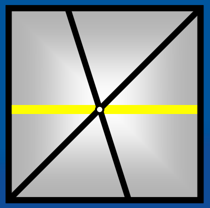
Reading PIPs: Four Independent Properties Geritz et al. (1997)

- Evolutionary stability

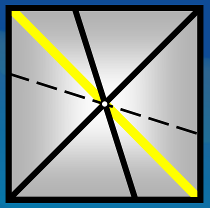


- Convergence stability

- Invasion potential

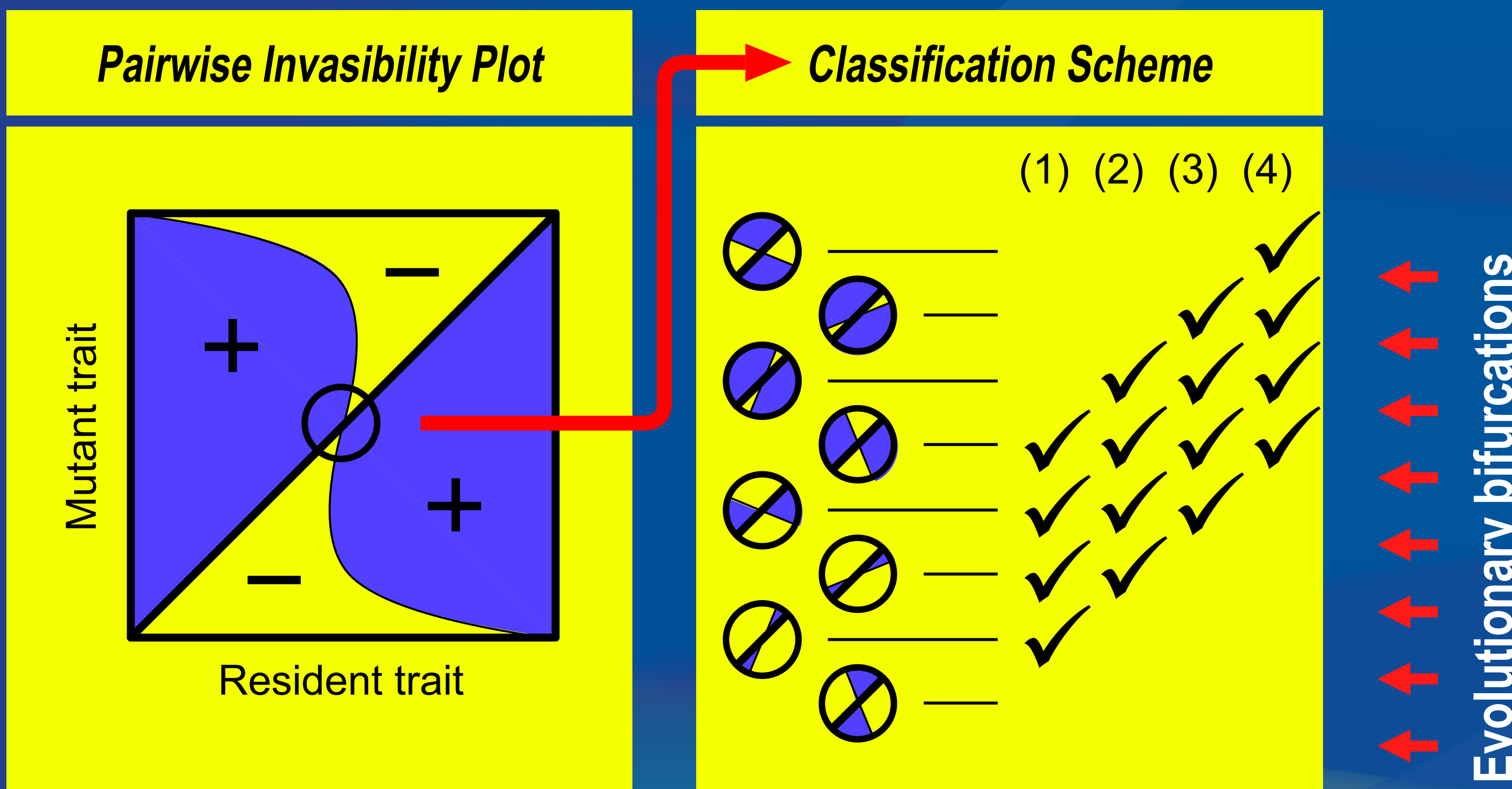


- Mutual invasibility



Reading PIPs: Eightfold Classification

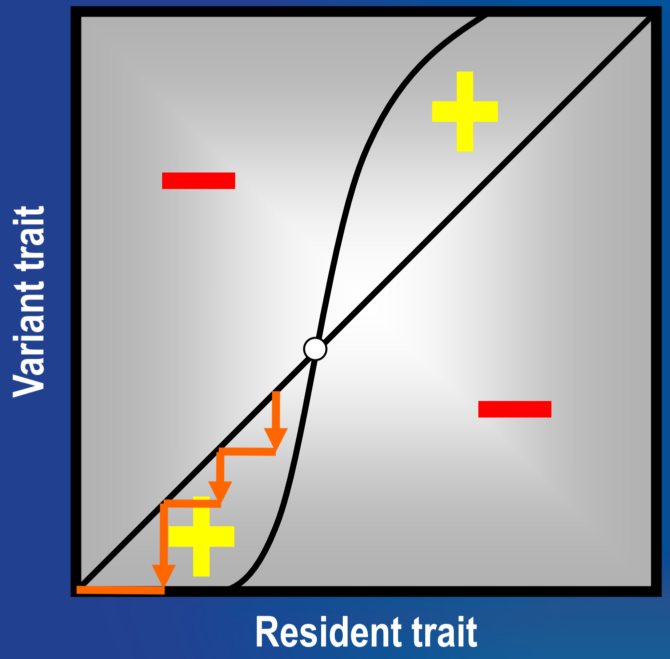
Geritz et al. (1997)
Dieckmann (1997)



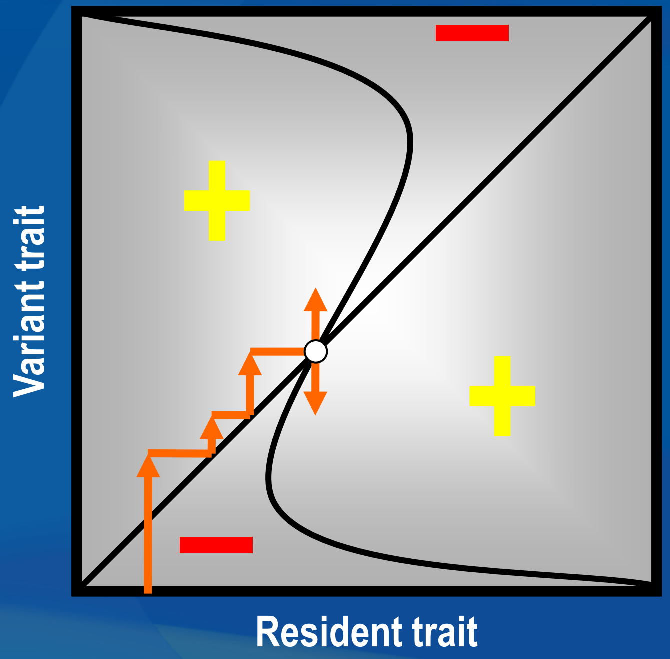
(1) Evolutionary stability, (2) Convergence stability, (3) Invasion potential, (4) Mutual invasibility

Two Interesting Types of PIPs

- Garden of Eden

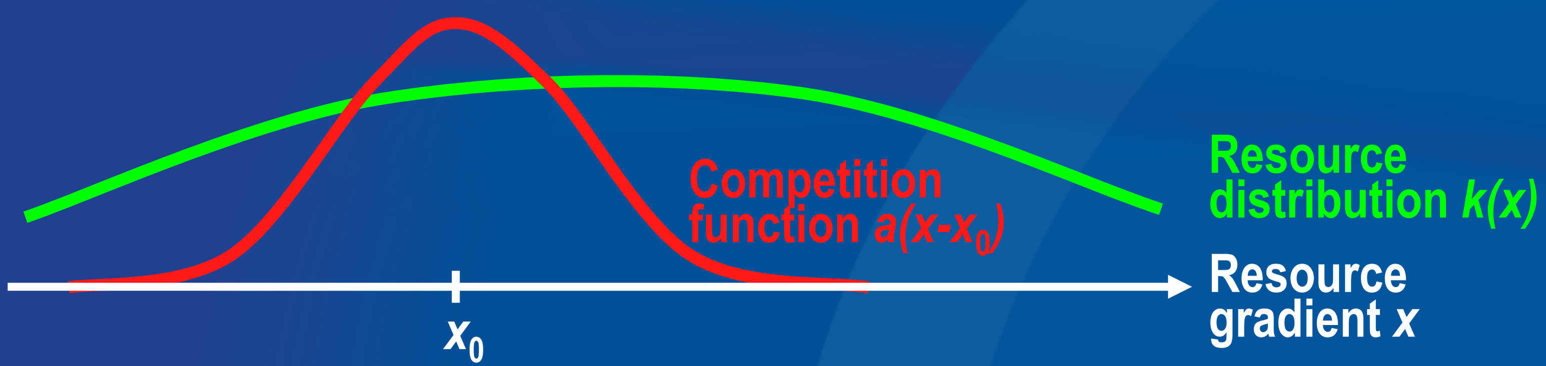


- Branching Point



Example:
Resource Competition

Roughgarden (1976)



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 1/2

- **Invasion Fitness**

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

1 $\quad n' \to 0$

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

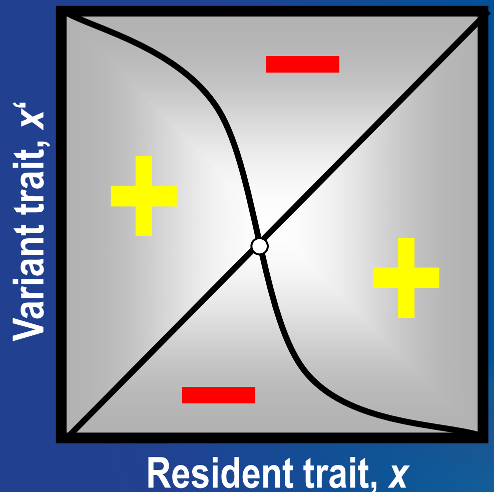
$$f(x',x) = r\left[1 - a(x'-x)\frac{k(x)}{k(x')}\right]$$

Analysis of Example 2/2

- Pairwise Invasibility Plots

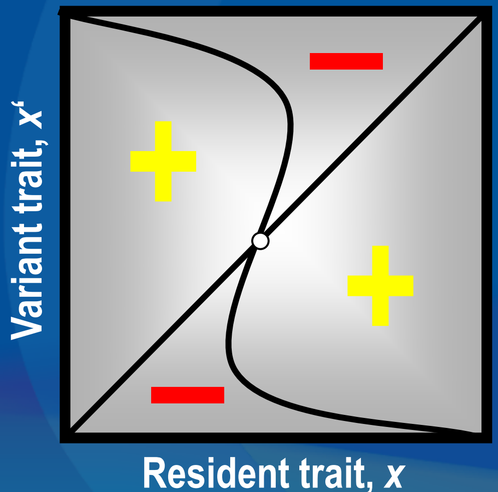
  With $k = k_0\, N(0,\sigma_k)$ and $a = N(0,\sigma_a)$ we obtain

for $\sigma_a > \sigma_k$



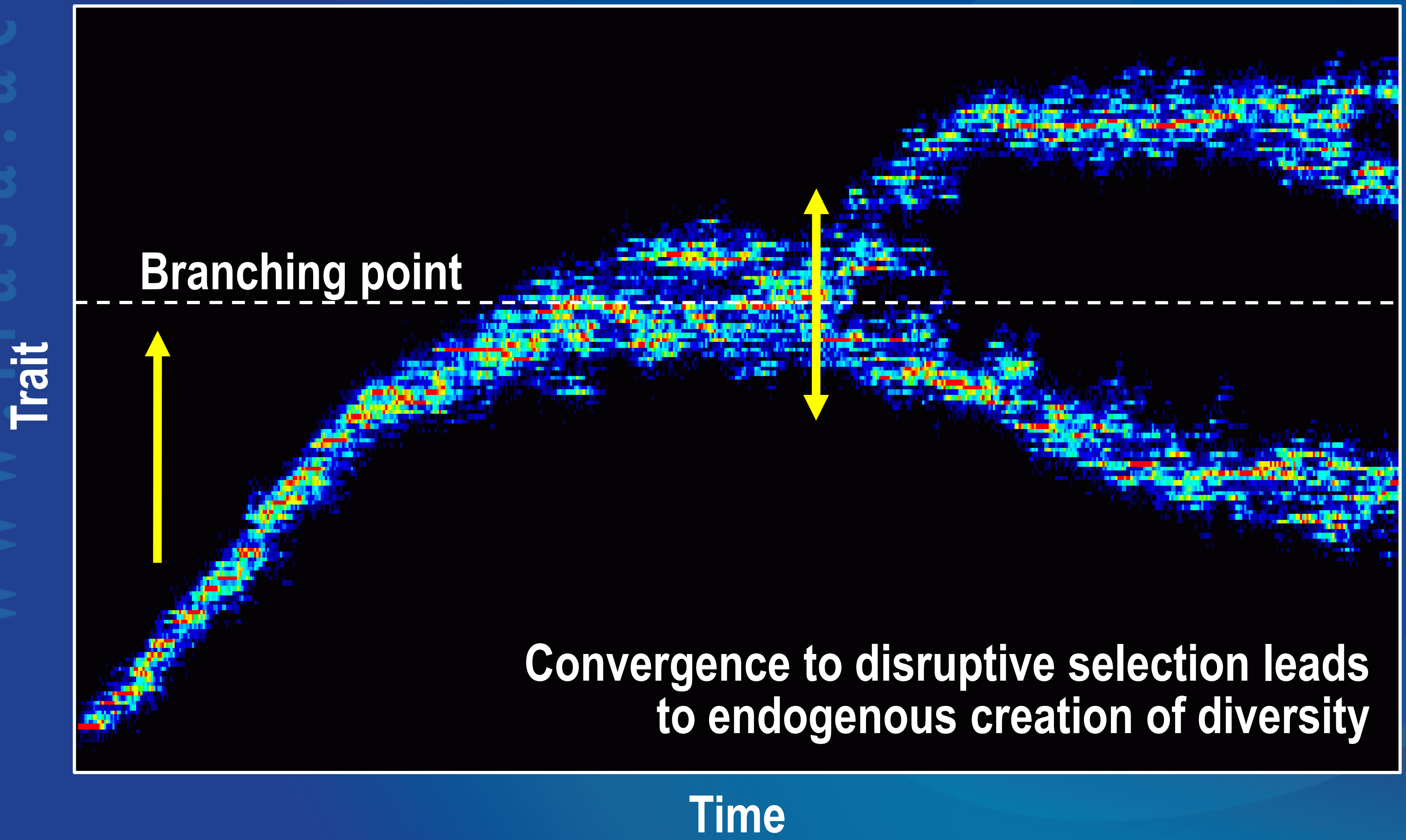
Evolutionary stability

for $\sigma_a < \sigma_k$



Evolutionary branching

Evolutionary Branching



Published Analyses 1/2

- Symmetric intraspecific competition (Doebeli 1996a, 1996b; Metz et al. 1996; Dieckmann and Doebeli 1999)
- Asymmetric intraspecific competition (Kisdi 1999; Doebeli and Dieckmann 2000; Kisdi et al. 2001)
- Interspecific competition (Law et al. 1997; Kisdi and Geritz 2001)
- Resource specialization (Meszéna et al. 1997; Geritz et al. 1998; Day 2000; Kisdi 2001; Schreiber and Tobiason 2003; Egas et al. 2004, 2005)
- Ontogenetic niche shifts (Claessen and Dieckmann 2002)
- Mixotrophy (Troost et al. 2005)
- Phenotypic plasticity (Van Dooren and Leimar 2003; Ernande and Dieckmann 2004; Leimar 2005)
- Dispersal evolution (Doebeli and Ruxton 1997; Johst et al. 1999; Parvinen 1999; Mathias et al. 2001; Parvinen and Egas 2004),
- Mutualism (Doebeli and Dieckmann 2000; Law et al. 2001; Ferdy et al. 2002; Ferriére et al. 2002; Day and Young 2004)
- Emergent cooperation (Doebeli et al. 2004)

Published Analyses 2/2

- Predator-prey interactions (Brown and Pavlovic 1992; Van der Laan and Hogeweg 1995; Doebeli and Dieckmann 2000; Bowers et al. 2003)
- Cannibalism (Dercole 2003)
- Host-parasite interactions (Boots and Haraguchi 1999; Koella and Doebeli 1999; Regoes et al. 2000; Gudelj et al. 2004)
- Sex-ratio evolution (Metz et al. 1992; Reuter et al. 2004)
- Evolution of selfing (Cheptou and Mathias 2001; De Jong and Geritz 2001)
- Evolution of mating traits (Van Doorn et al. 2001, 2004)
- Evolution of anisogamy (Maire et al. 2001)
- Seed evolution (Geritz et al. 1999; Mathias and Kisdi 2002)
- Microbial cross-feeding (Doebeli 2002)
- Prebiotic evolution (Meszéna and Szathmáry 2001)
- Community assembly (Jansen and Mulder 1999; Bonsall et al. 2004)
- Food-web formation (Loeuille and Loreau 2005; Ito et al. 2009; Brännström et al. 2010)

Canonical Equation

Dieckmann & Law (1996)

- **Assumptions:** Populations are large, and mutational steps are both rare and small
- Then, the evolutionary rates are given by

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

evolutionary rate in species *i*

mutation probability

equilibrium population size

mutation variance-covariance

local selection gradient

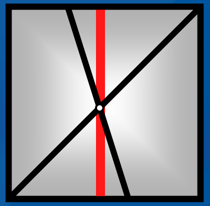
invasion fitness

Synthetic Perspective

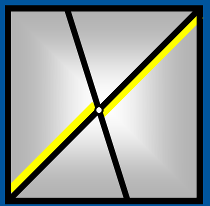
- The common form of the canonical equation of adaptive dynamics and of Lande's equation of quantitative genetics is reassuring
- In first approximation, evolutionary rates are proportional to the gradient of a frequency-dependent fitness
- Beyond this commonality, the two dynamics differ, describing different kinds of evolutionary processes

Reminder: Four Independent Properties Geritz et al. (1997)

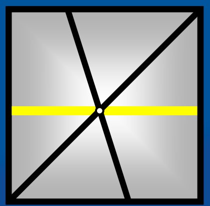
- Evolutionary stability



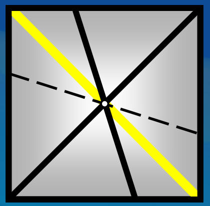
- Convergence stability



- Invasion potential



- Mutual invasibility



Fitness, Gradient, Hessians

- Invasion fitness

$$f(x', x)$$

$$f(x, x) = 0$$ at ecological equilibrium

- Selection gradient

$$g(x) = \frac{\partial}{\partial x'} f(x', x)\Big|_{x'=x}$$

$$g(x^*) = 0$$ at evolutionary equilibrium

- Hessians of invasion fitness

$$h_{mm} = \frac{\partial^2}{\partial x'^2} f(x', x)\Big|_{x'=x=x^*} \qquad h_{rm} = \frac{\partial^2}{\partial x' \partial x} f(x', x)\Big|_{x'=x=x^*}$$

$$h_{rr} = \frac{\partial^2}{\partial x^2} f(x', x)\Big|_{x'=x=x^*} \qquad h_{mr} = \frac{\partial^2}{\partial x \partial x'} f(x', x)\Big|_{x'=x=x^*}$$

Conditions for Evolutionary Branching

- Evolutionary stability: no

$$h_{mm} < 0$$

- Convergence stability: yes

$$h_{mm} - h_{rr} < 0 \quad (\text{or } h_{mm} + h_{mr} < 0)$$

- Invasion potential

$$h_{rr} > 0$$

- Mutual invasibility

$$h_{mm} + h_{rr} > 0$$

These conditions apply to one-dimensional traits.

For higher-dimensional traits, they involve matrices and are a bit more complex.

Summary:
Main Tools of Adaptive Dynamics Theory

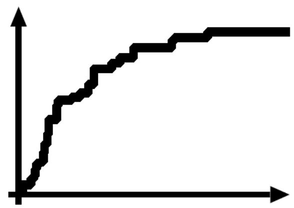
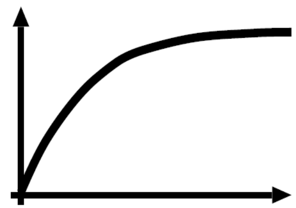
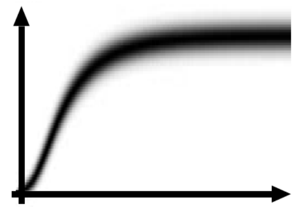
- Individual-based modelling
- Invasion fitness
- Pairwise invasibility plots
- Canonical equation
- Evolutionary branching conditions

2e

Interlude: Mathematical Connections

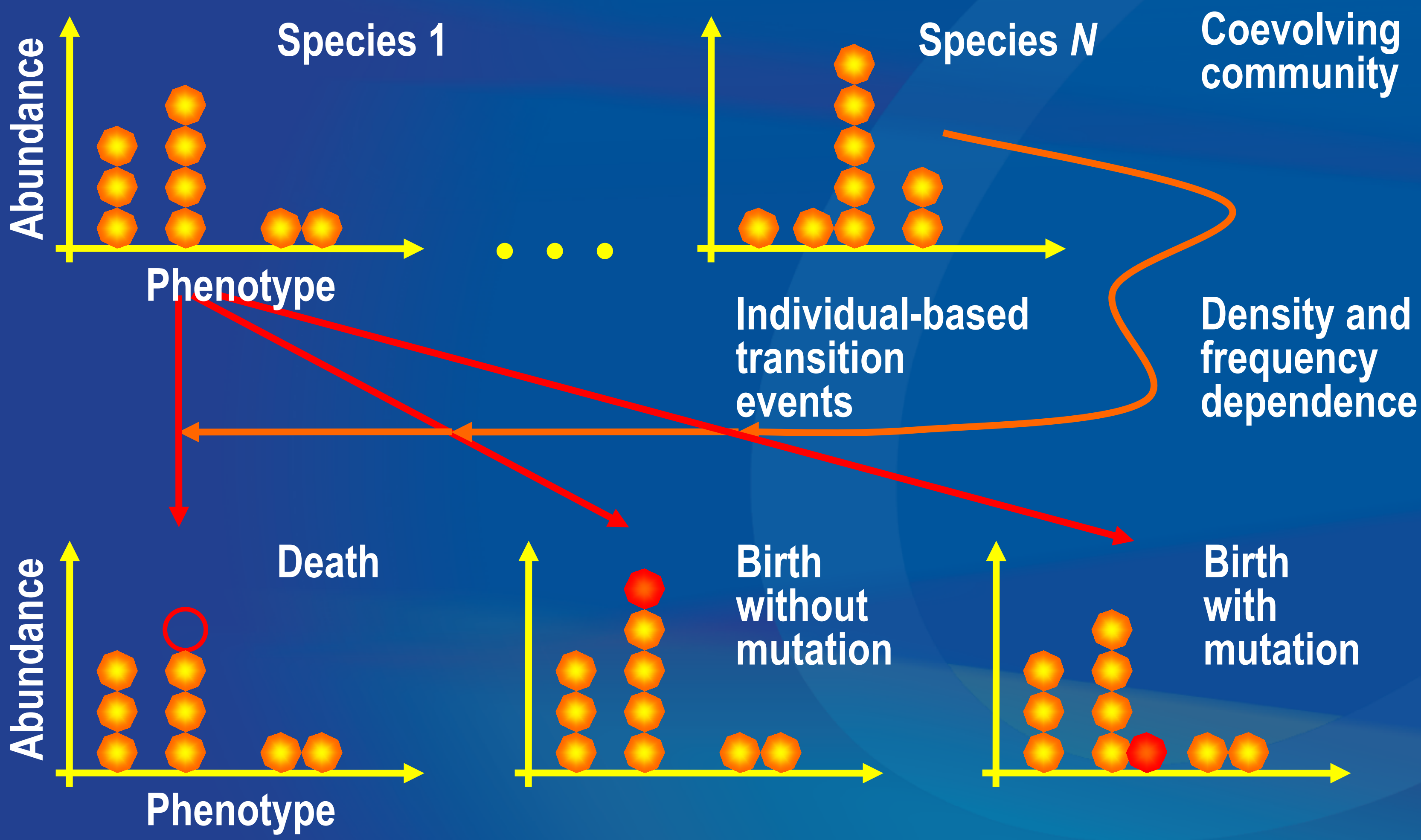
Four Types of Evolutionary Dynamics

Polymorphic stochastic	Monomorphic stochastic	Monomorphic deterministic	Polymorphic deterministic
Individual-based evolutionary dynamics	Evolutionary random walk	Gradient-ascent on adaptive landscape	Reaction-diffusion dynamics

Birth-Death-Mutation Processes

Dieckmann (1994)



Individual-based Evolutionary Dynamics

Polymorphic and Stochastic

Dieckmann (1994)

- **State variables**

$$p_i = \sum_{k=1}^{n_i} \delta_{x_{ik}}$$

Phenotypic distribution
in species *i*

$$p = (p_1, \ldots, p_N)$$

Phenotypic distribution
of entire community

- **Parameters**

$$b_i(x_i, p)$$

Per capita birth rate
in species *i*

$$d_i(x_i, p)$$

Per capita death rate
in species *i*

$$\mu_i(x_i)$$

Mutation probability
in species *i*

$$M_i(x_i', x_i)$$

Mutation distribution
in species *i*

$$f_i(x_i, p) = b_i(x_i, p) - d_i(x_i, p)$$

Fitness-generating function
in species *i*

Individual-based Evolutionary Dynamics

Polymorphic and Stochastic

Dieckmann (1994)

- **Master equation**

$$\frac{d}{dt}P(p) = \int \left[w(p \mid p')P(p') - w(p' \mid p)P(p) \right] dp'$$

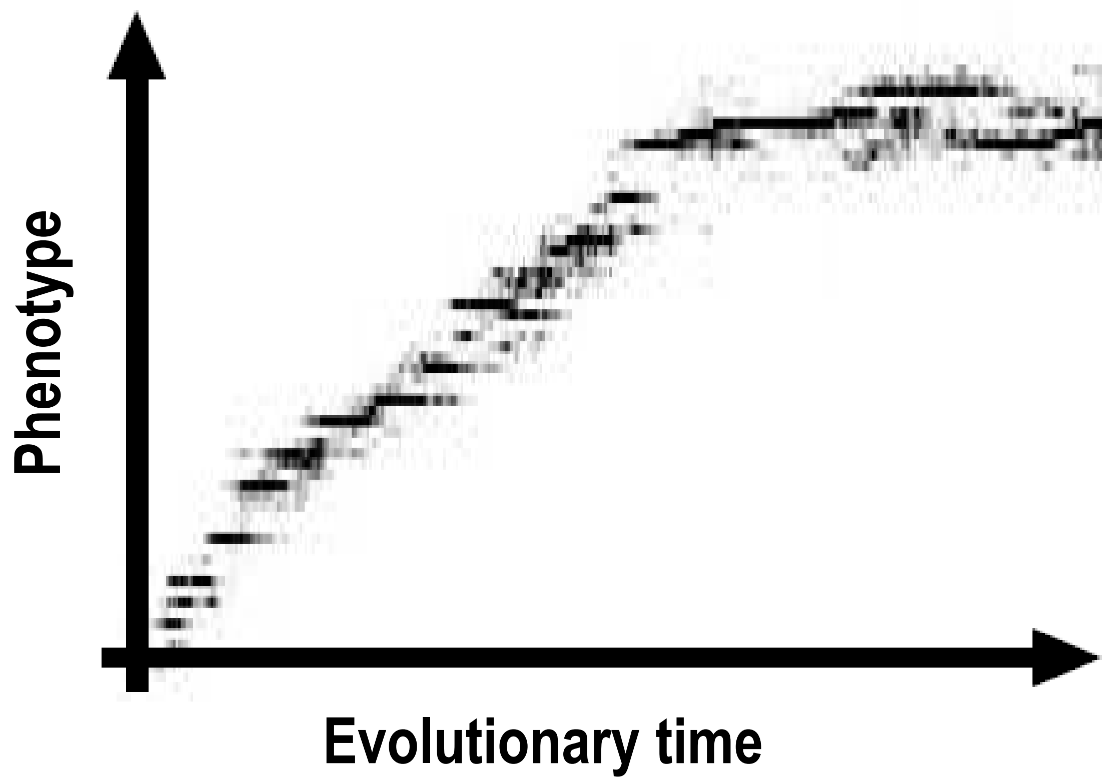
$$\begin{aligned} w(p' \mid p) &= \sum_{i=1}^{N} \int \Big[d_i(x_i', p) p_i(x_i') \, \Delta(p_i - \delta_{x_i'} - p_i') \prod_{j \neq i} \Delta(p_j' - p_j) \\ &\quad + \int b_i(x_i, p) p_i(x_i) B_i(x_i', x_i) \, dx_i \, \Delta(p_i + \delta_{x_i'} - p_i') \prod_{j \neq i} \Delta(p_j' - p_j) \Big] \, dx_i' \end{aligned}$$

Measure-valued stochastic process in the space of atomic distributions (Dirac measures)

Individual-based Evolutionary Dynamics

Polymorphic and Stochastic

Dieckmann (1994)



Effect of Mutation Probability

Large: 10%

Dynamic mutation-selection equilibrium

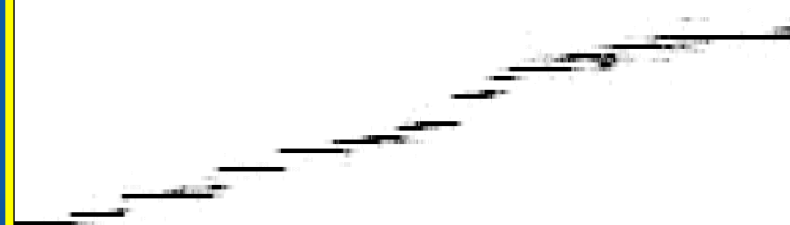
Phenotype

"Moving cloud"

Evolutionary time

Small: 0.1%

Mutation-limited evolutionary dynamics



"Staircase"

Evolutionary time

Probability for a Trait Substitution

Dieckmann & Law (1996)
Geritz et al. (2002)

Mutation

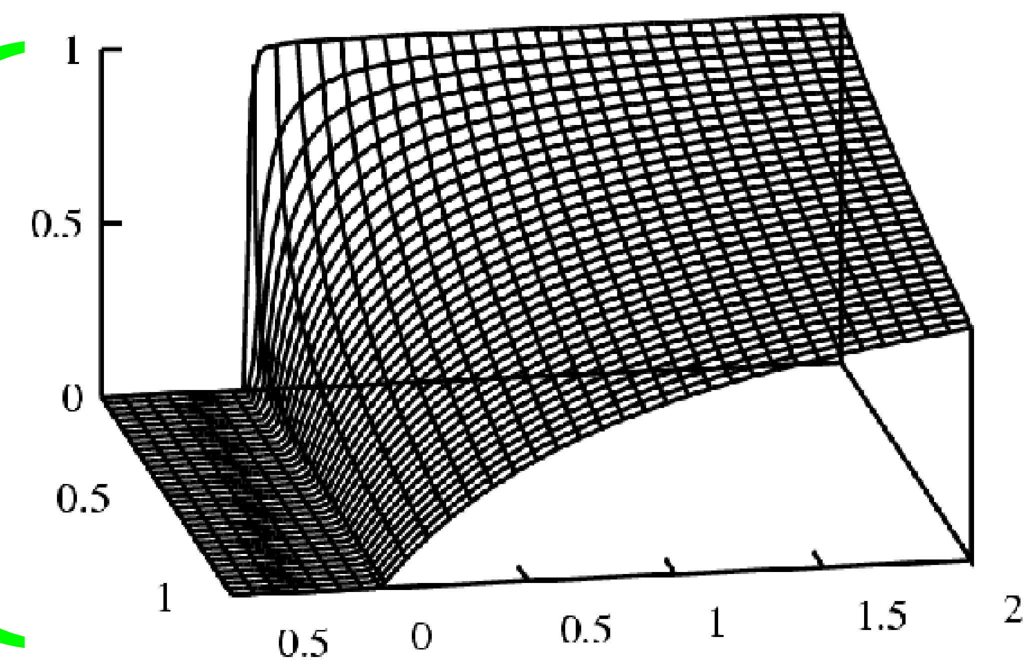
Population dynamics

Invasion

Branching process theory

Fixation

Invasion implies fixation



Invasion probabilities can alternatively be based on the Moran process, on diffusion approximations, or on graph topologies

Evolutionary Random Walk

Monomorphic and Stochastic

Dieckmann & Law (1996)

- Master equation

$$\frac{d}{dt}P(x) = \int \left[w(x \mid x')P(x') - w(x' \mid x)P(x) \right] dx'$$

$$w(x' \mid x) = \sum_{i=1}^{N} w_i(x_i', x) \prod_{j \neq i} \delta(x_j' - x_j)$$

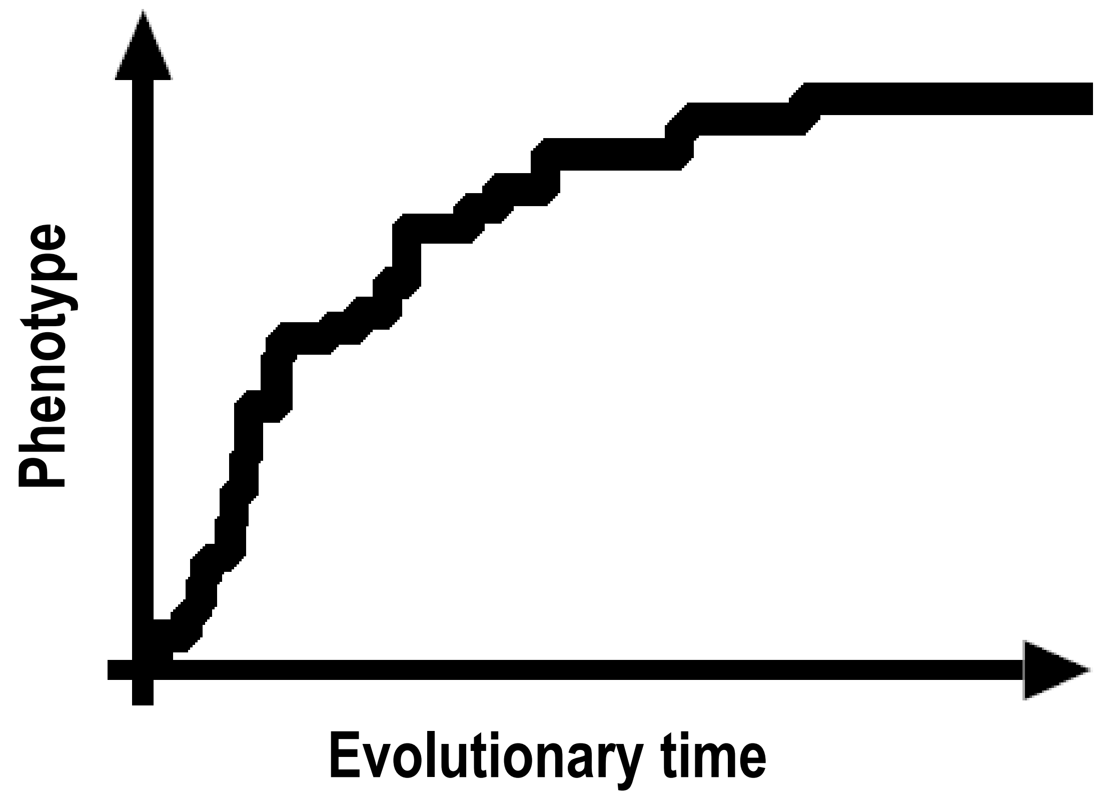
$$w_i(x_i', x) = \mu_i(x_i) b_i(x_i, x) n_i^*(x) M_i(x_i', x_i) \cdot (f_i(x_i', x))_+ / b_i(x_i', x)$$

Real-valued stochastic process in trait space

Evolutionary Random Walk

Monomorphic and Stochastic

Dieckmann & Law (1996)



Gradient-Ascent on Adaptive Landscapes

Monomorphic and Deterministic

Dieckmann & Law (1996)

- Canonical equation of adaptive dynamics

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

evolutionary rate in species *i*

mutation probability

equilibrium population size

mutation variance-covariance

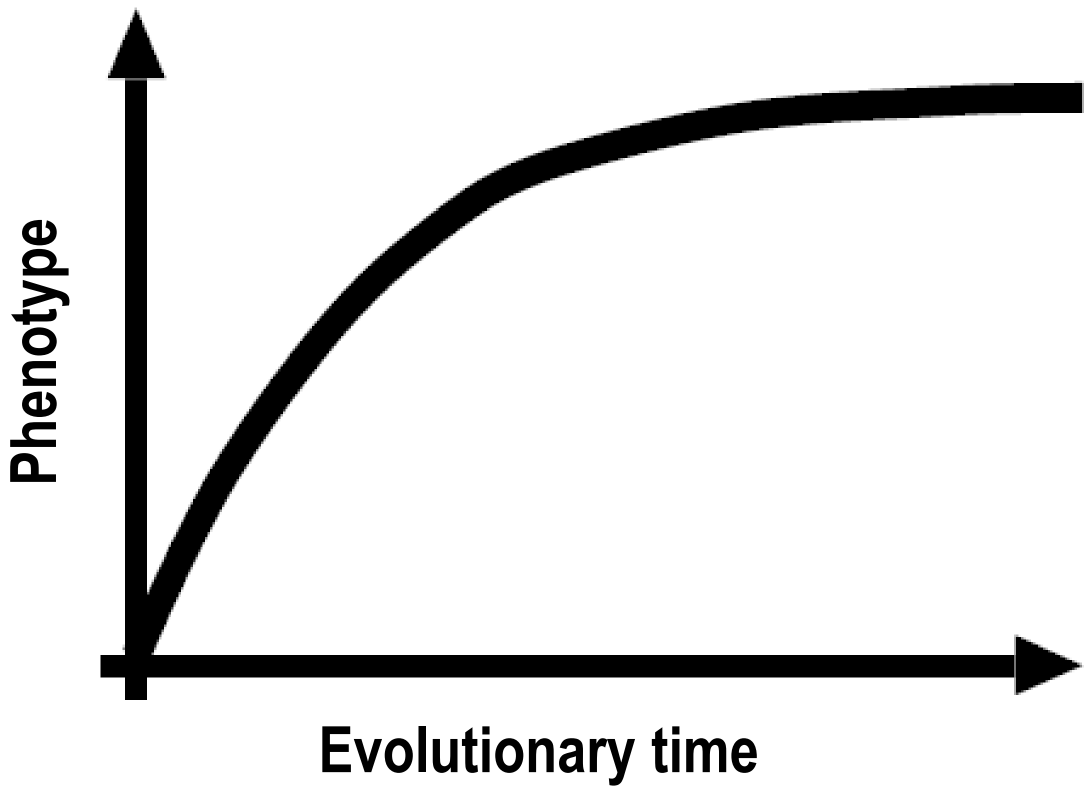
local selection gradient

fitness

Gradient-Ascent on Adaptive Landscapes

Monomorphic and Deterministic

Dieckmann & Law (1996)



Reaction-Diffusion Dynamics

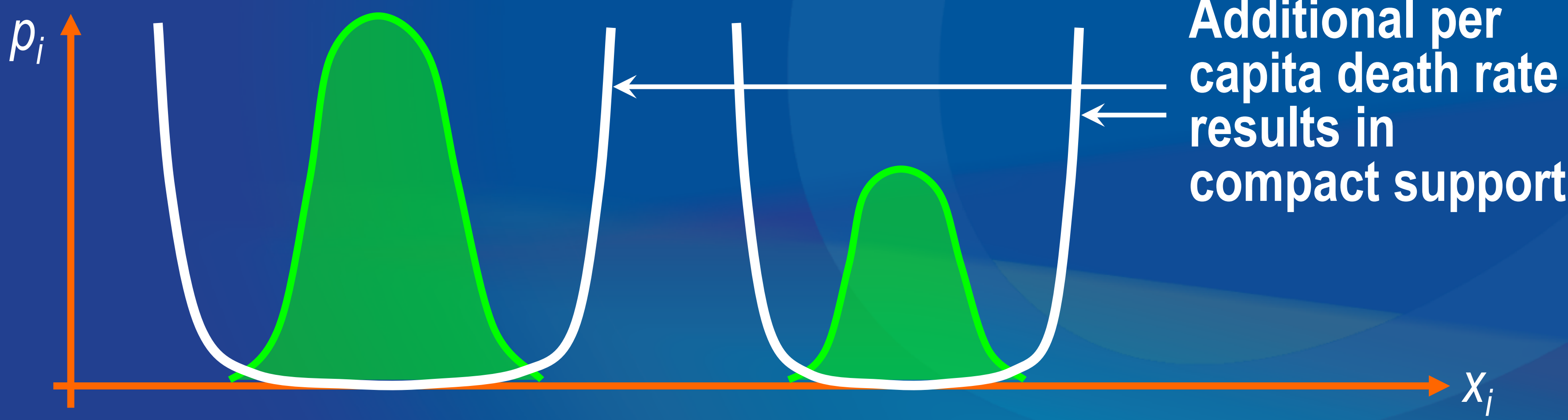
Polymorphic and Deterministic

Kimura (1965)
Dieckmann (unpublished)

- **Kimura limit**

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

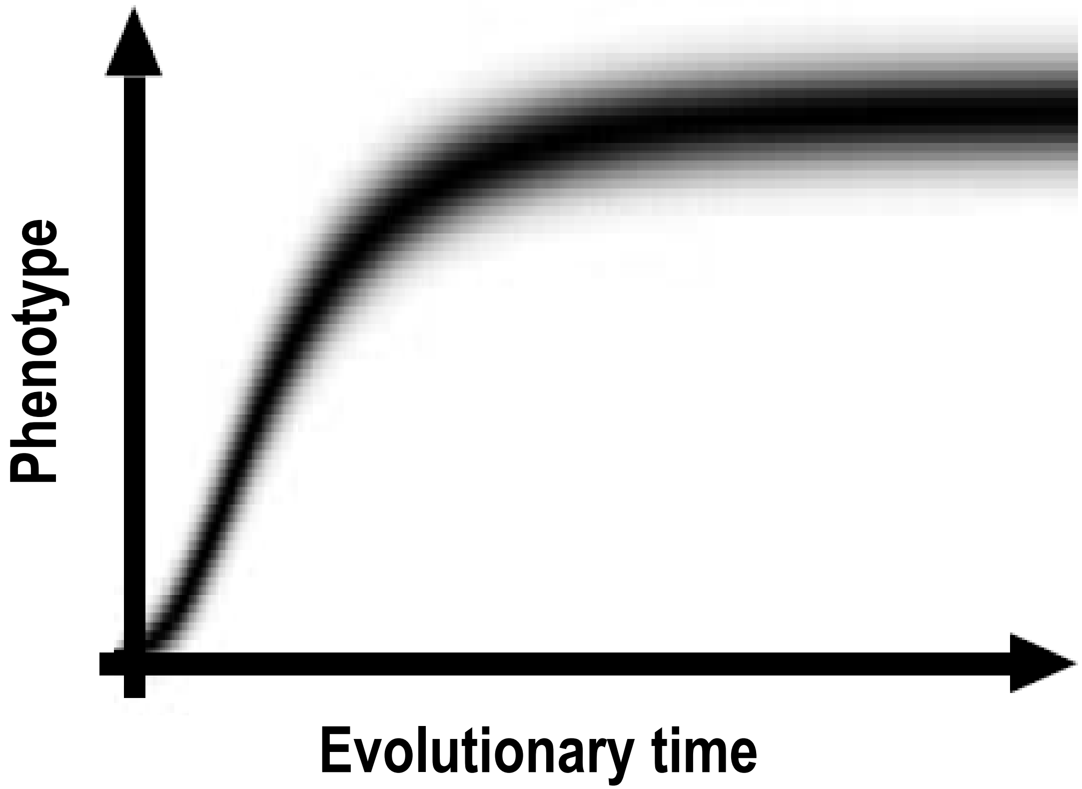
- **Finite-size corrections**



Reaction-Diffusion Dynamics

Polymorphic and Deterministic

Kimura (1965)

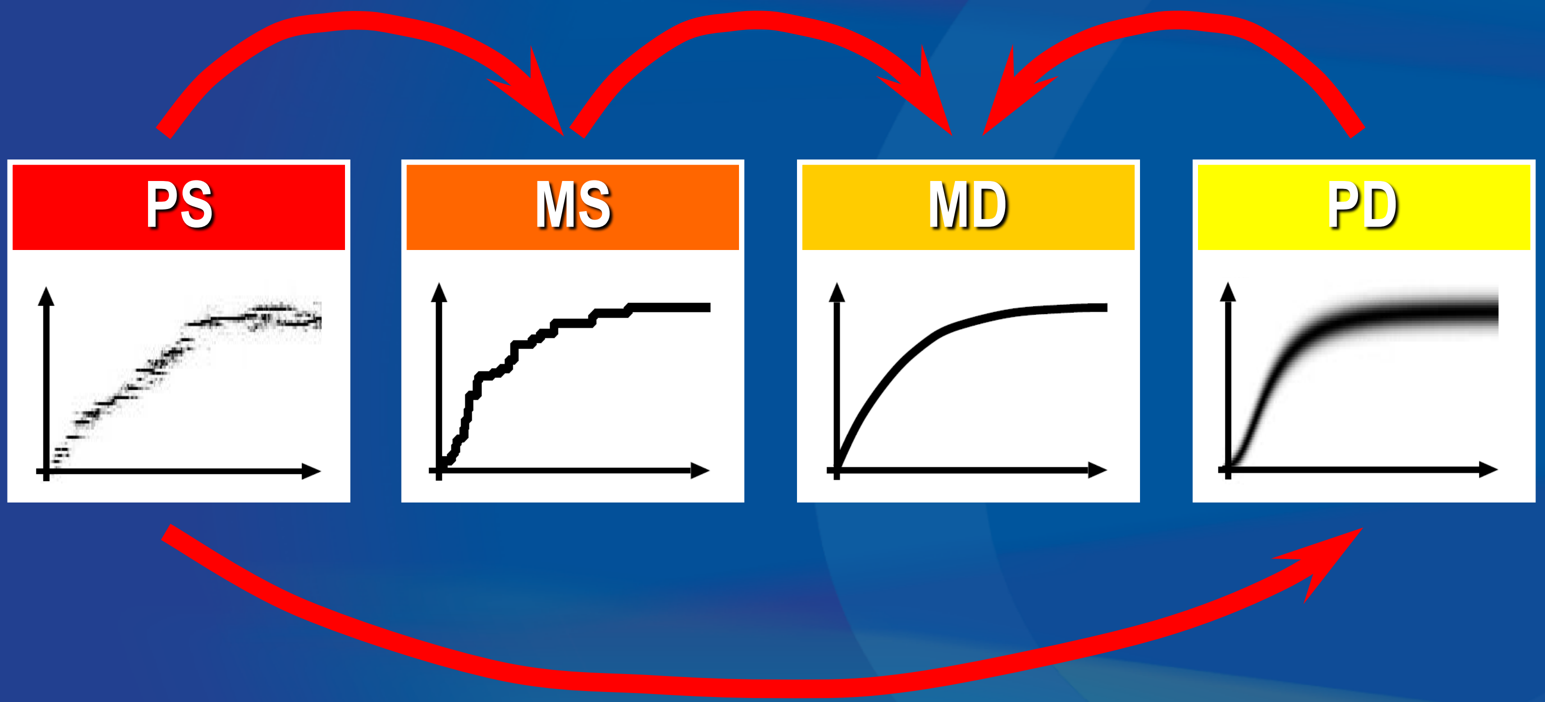


Summary of Connections

large population size
small mutation probability

small mutation variance

fixed standing variance



large population size
large mutation probability

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Eco-genetic models

Eco-Genetic Models

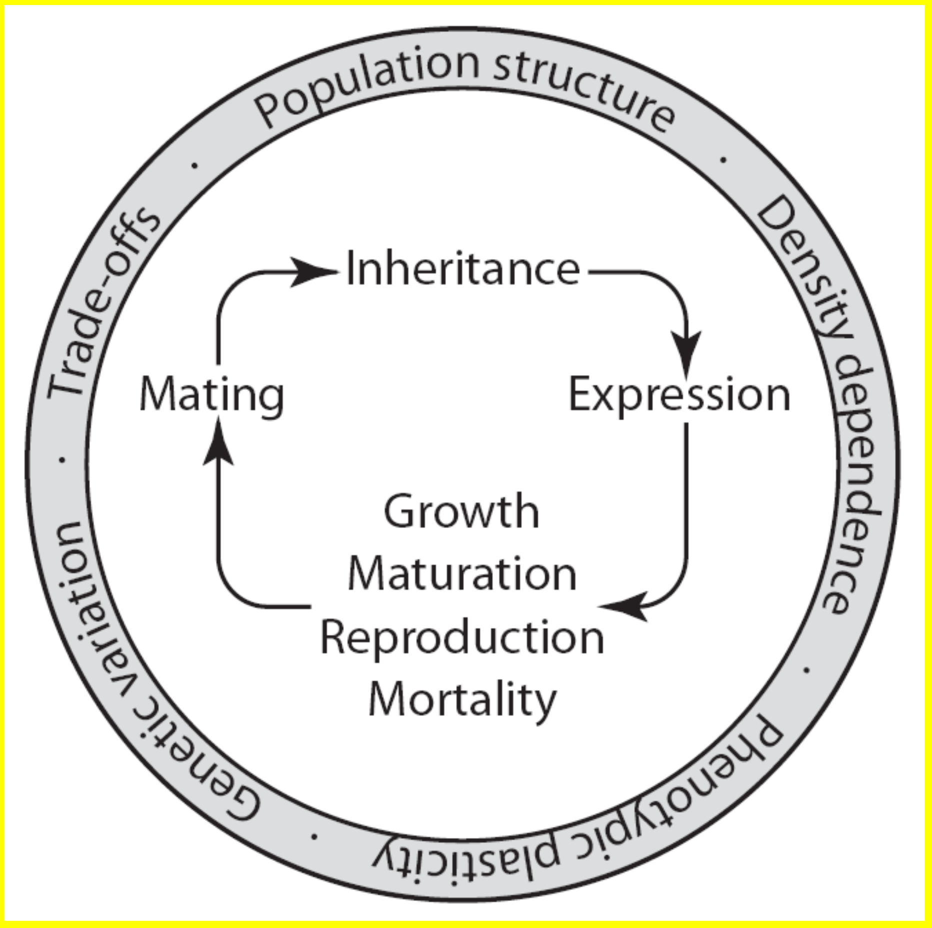
Eco-genetic models are process-based and designed to incorporate

Ecological detail

together with

Genetic detail

in the context of a stock's life cycle



Population Structure

- Individuals differ in physiological states and heritable traits; population structure thus arises from both

- Relevant physiological states may include
  (1) Age
  (2) Length
  (3) Weight
  (4) Condition
  (5) Maturity status
  (6) Sex
  (7) Stock component

Phenotypic Plasticity

- Phenotypes are not determined by genotypes alone, but also depend on environmental conditions
- Systematic effects of the latter kind are known as phenotypic plasticity
- Broader and narrower definitions exist: in a broader sense, learning and growth variation induced by resource availability are considered plastic responses
- The level and kind of phenotypic plasticity can itself evolve, and thus may be fine-tuned by selection

Genetic Variation

- Without genetic variation, selection pressures cannot elicit selection responses
- Without a correlation between the phenotypes of parents and their offspring (heritability), the effects of selection cannot be transmitted between generations
- Heritabilities are defined as the ratio between (additive) genetic variance and total phenotypic variance
- Genetic variances (and covariances) are insufficient for predicting selection responses when selection is strong, since genotypic distributions are then usually not normal

Purposes of Eco-Genetic Models

- **Evaluate** hypotheses advanced for explaining observed data
- **Understand** and quantify anthropogenic selection pressures
- **Forecast** the direction, speed, and outcome of evolutionary changes
- **Predict** the differential evolutionary vulnerability of species and populations
- **Investigate** the consequences of alternative management scenarios

Modelling Frameworks: Summary

	(1)	(2)
Game-theoretical models	No	No
Quantitative genetics models	No	Yes
Adaptive dynamics models	Yes	No
Eco-genetic models	Yes	Yes

(1) Ecological complexity, including both frequency- and density-dependent selection
(2) Genetic variation, enabling predicting the speed of evolution