The Adaptive Dynamics of Function-Valued Traits

A New Modeling Tool for Research in Evolutionary Ecology

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Outline

1 What Are Function-Valued Traits?

2 Adaptive Dynamics Theory

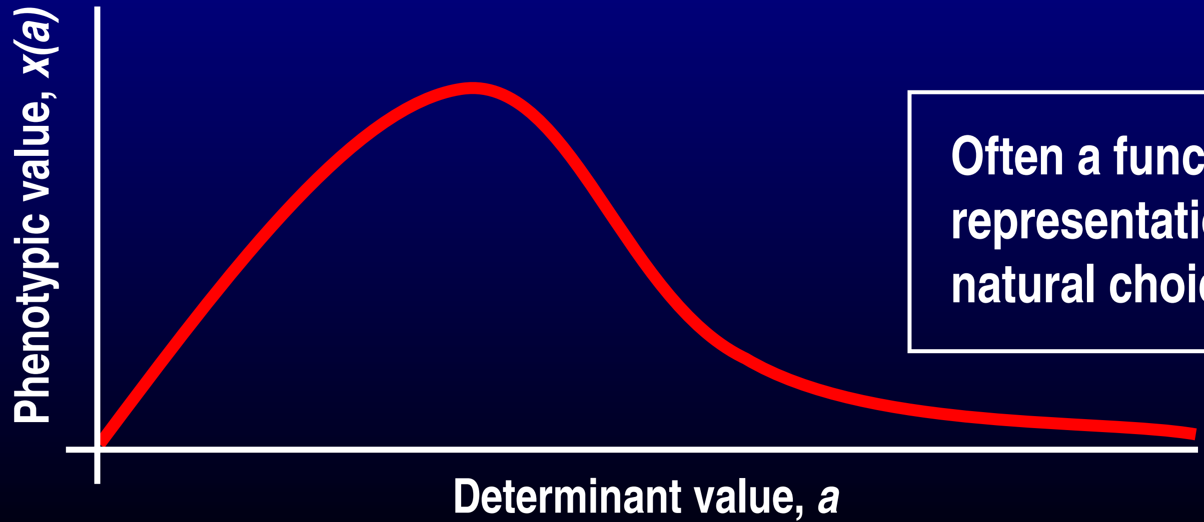
3 Achieving the Extension

4 & 5 Two Examples

1 What Are Function-Valued Traits?

Function-Valued Traits

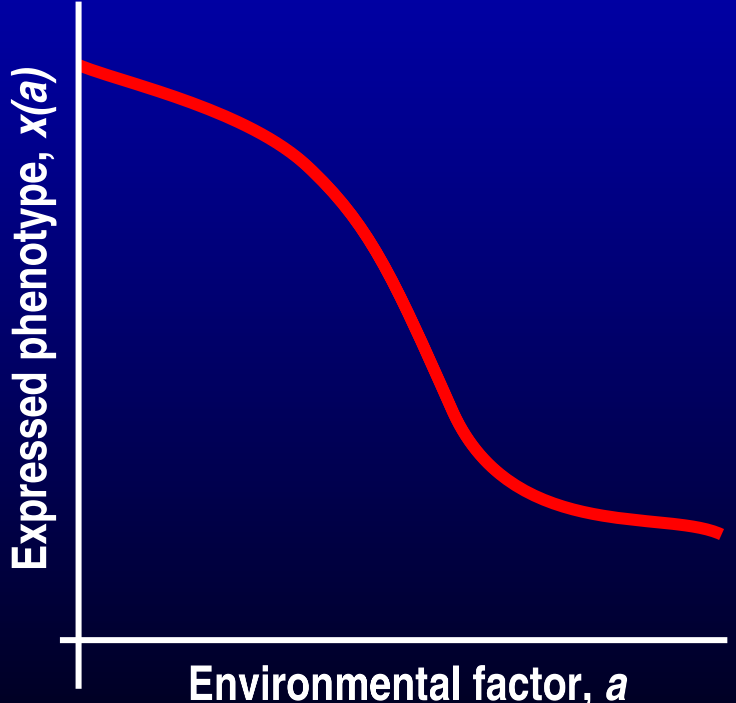
- Adaptive traits in evolutionary ecology can be
  - Scalar x
  - Vectorial $(x_1,x_2,...,x_n)$
  - Function-valued $x(a)$



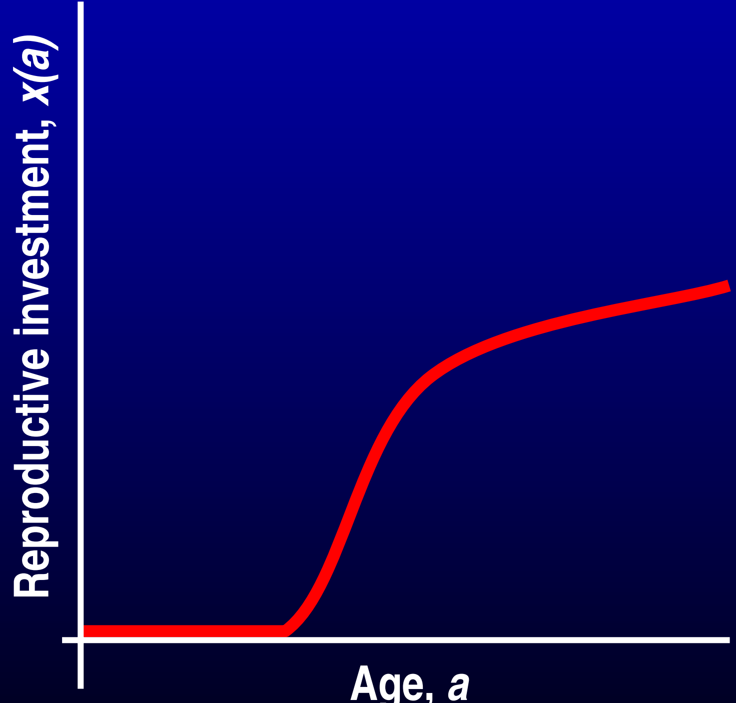
Often a function-valued representation is the natural choice.

Examples of Function-Valued Traits 1

- Reaction norms of phenotypic plasticity

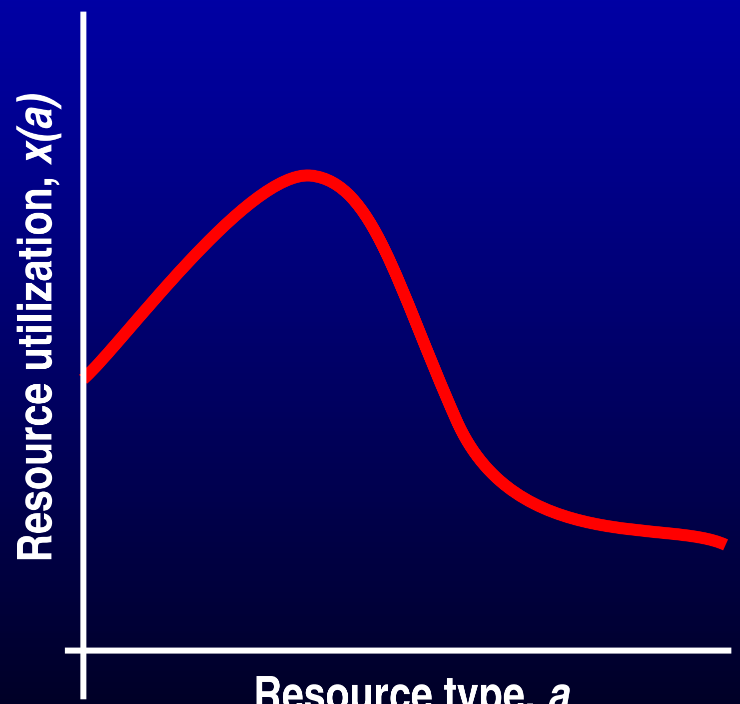


- Demographic traits in structured populations

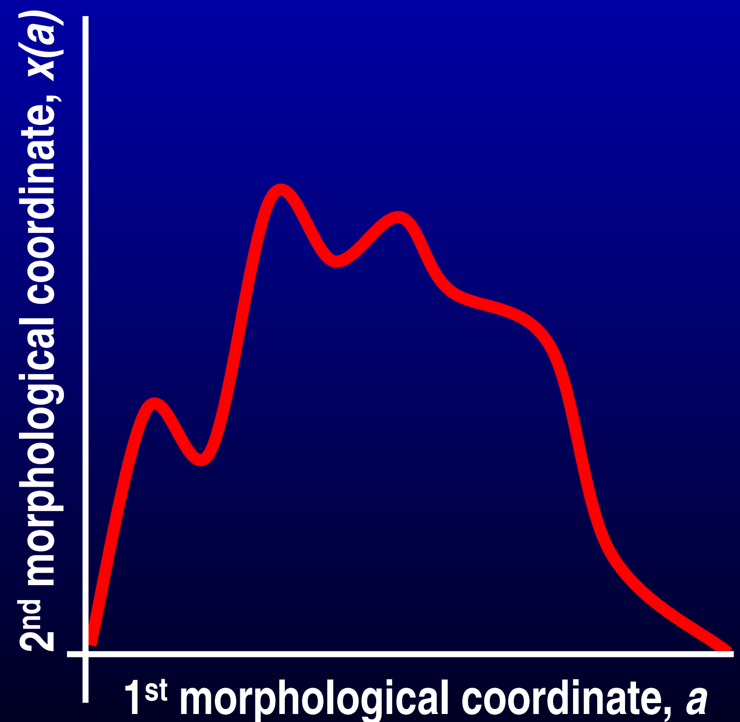


Examples of Function-Valued Traits 2

- **Resource utilization spectra**

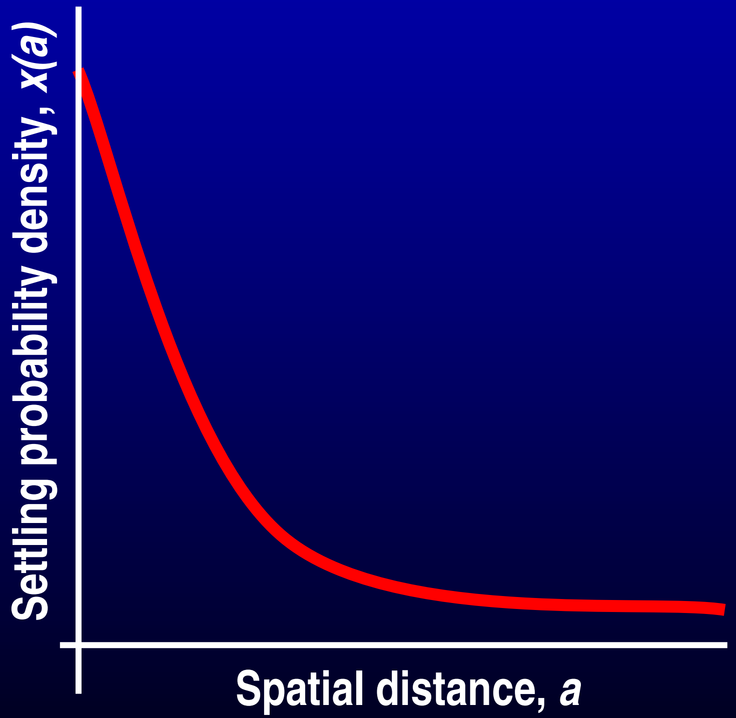


- **Morphological shapes**

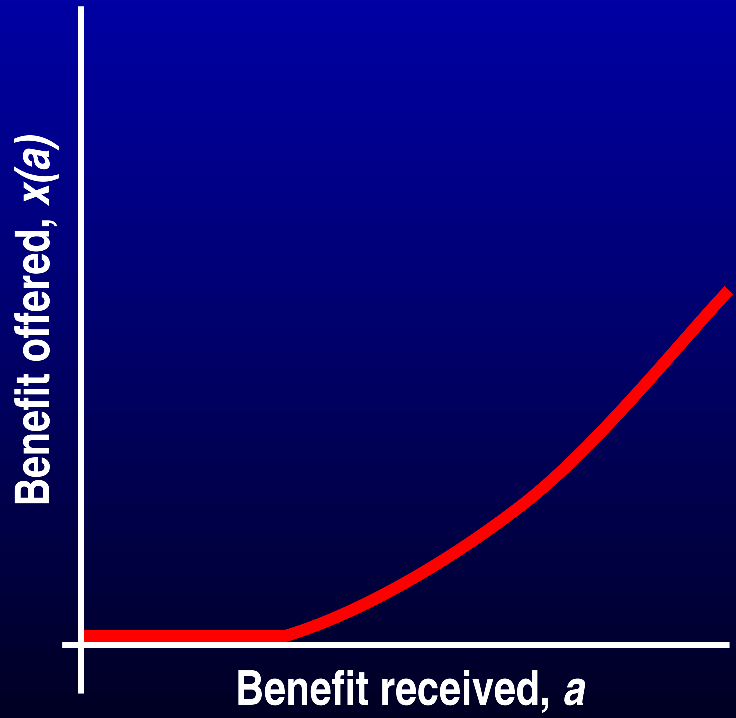


Examples of Function-Valued Traits 3

- Dispersal kernels



- Social interactions



2

Adaptive Dynamics Theory

Adaptive Dynamics Theory

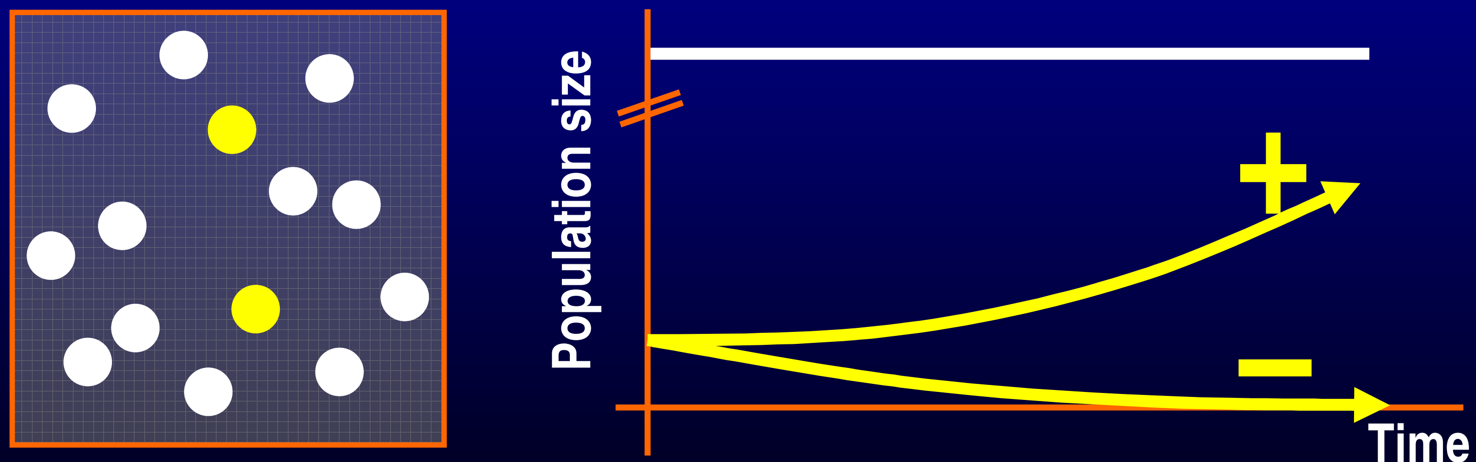
- Designed to address the implications of frequency-dependent selection.
- Intimately links ecological and evolutionary dynamics.
- Makes simplifying assumptions that differ from those of quantitative genetics.
- Relies on three key tools:
  - Invasion fitness
  - Pairwise invasibility plots
  - Canonical equation

Invasion Fitness

Metz *et al.* (1992)

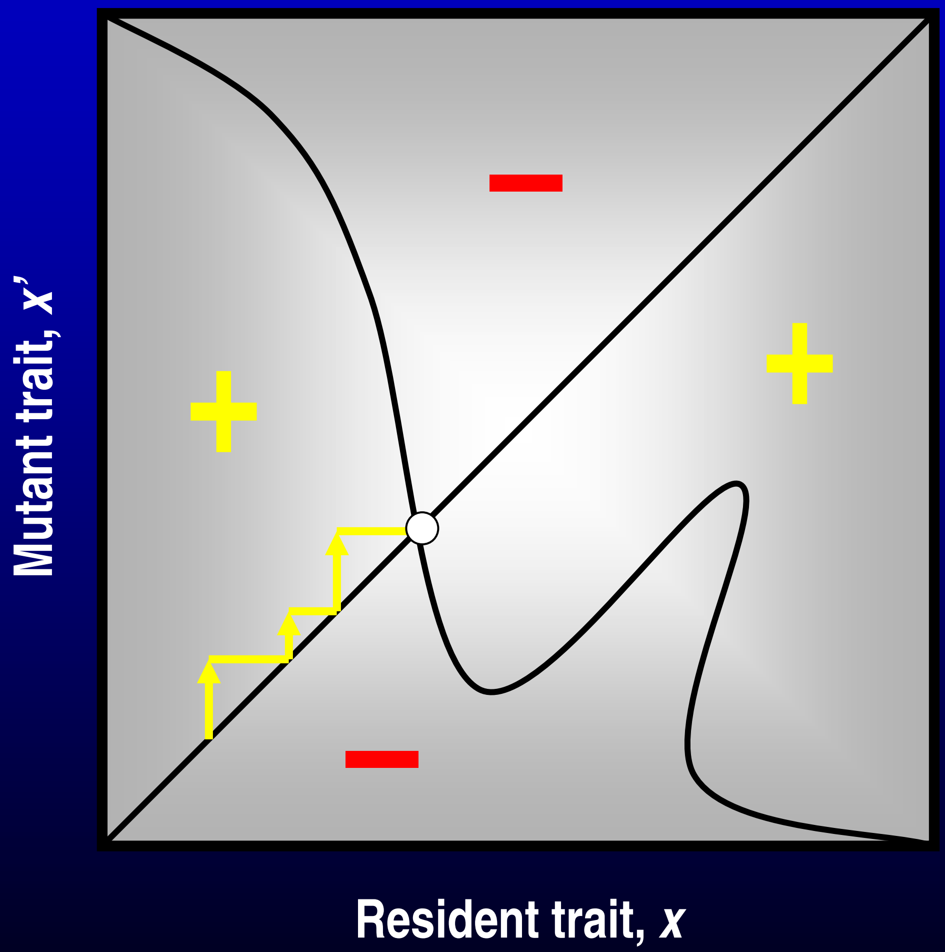
- **Definition**

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



Pairwise Invasibility Plots

Geritz *et al.* (1997)



Sign of invasion fitness:

+ Invasion of the mutant into the resident population is possible

− Invasion is impossible

Trait substitution sequence

Canonical Equation

Dieckmann and Law (1996)

$$\frac{d}{dt}x = \frac{1}{2}\mu\sigma^2 n(x)\frac{\partial}{\partial x'}f(x',x)\Big|_{x'=x}$$

Rate of adaptive change

Mutation probability

Mutation variance

Population size

Selection gradient

Invasion fitness

Dynamics amounts to hill-climbing on a variable adaptive landscape.

3

Adaptive Dynamics of FV Traits

Canonical Equation for FV Traits

$$\frac{d}{dt}x(a) = \frac{1}{2}\mu\, n_x \int \sigma_x^2(a', a)\, g_x(a')\, da'$$

Mutational variance-covariance function

Selection gradient

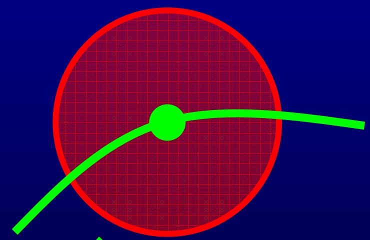
with

$$g_x(a) = \frac{\partial}{\partial \varepsilon} f(x + \varepsilon\delta_a, x)\Big|_{\varepsilon=0}$$

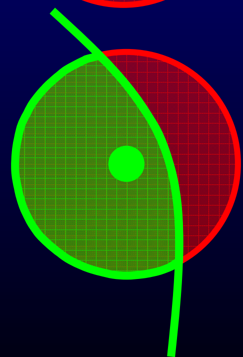
Epsilon perturbation at *a*

Adaptive Constraints on FV Traits

- Mutational variability may be unavailable, resulting in adaptive constraints.
- Two special cases are of particular interest. The mutation probability density $M_x(x')$ may be zero unless
  - $F(x') = 0$ (*equality* constraints):



  - $F(x') > 0$ (*inequality* constraints):



4 First Example

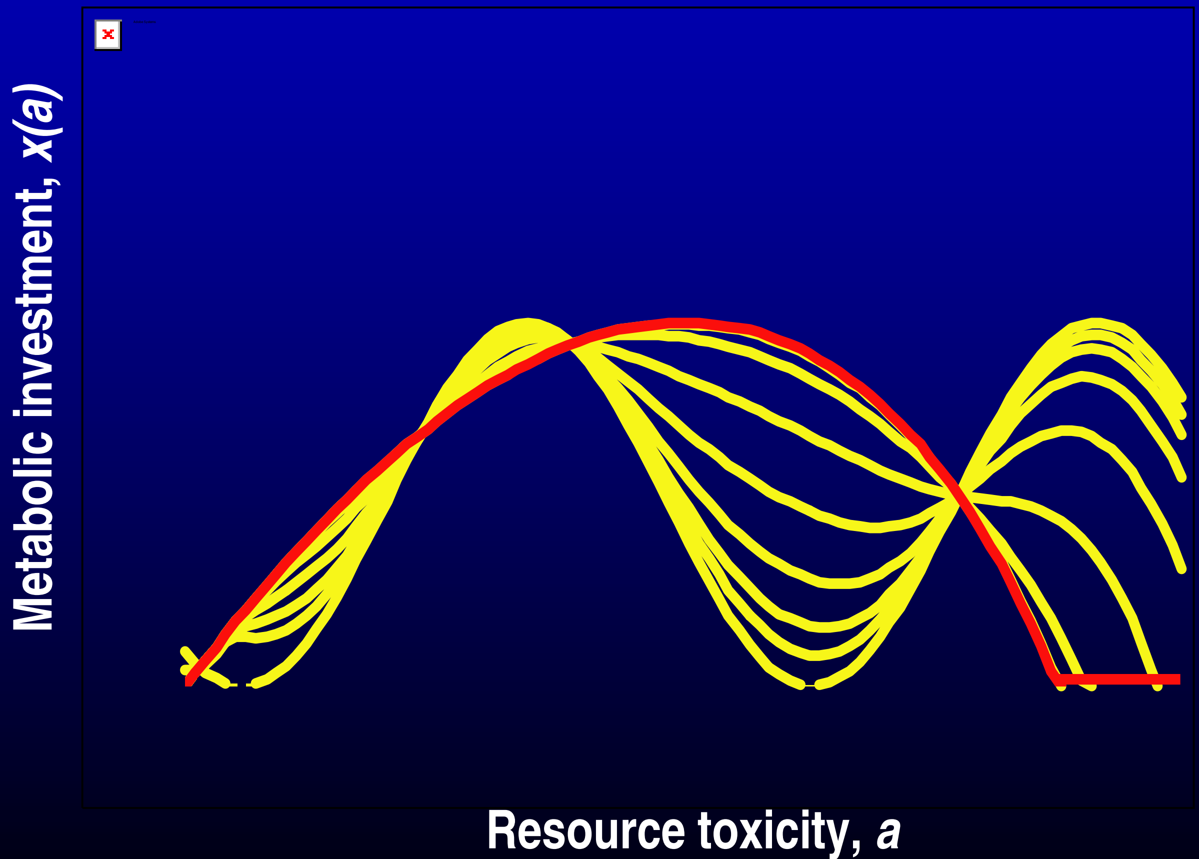
Evolution of a Metabolic Investment Strategy

First Example: Description

- We consider a consumer that harvests resources differing in toxicity a.
- The abundance of resources varies in proportion to, for instance, $r(a)=4a(1-a)$.
- The consumer's metabolic efficiency increases with its investment $x(a)$ according to $e(a)=x(a)/[x(a)+a]$.
- Total gain is given by integrating $r(a)e(a)$ and total costs are given by integrating $cx(a)$.
- Net gain is obtained as total gain minus total costs.

First Example: Result

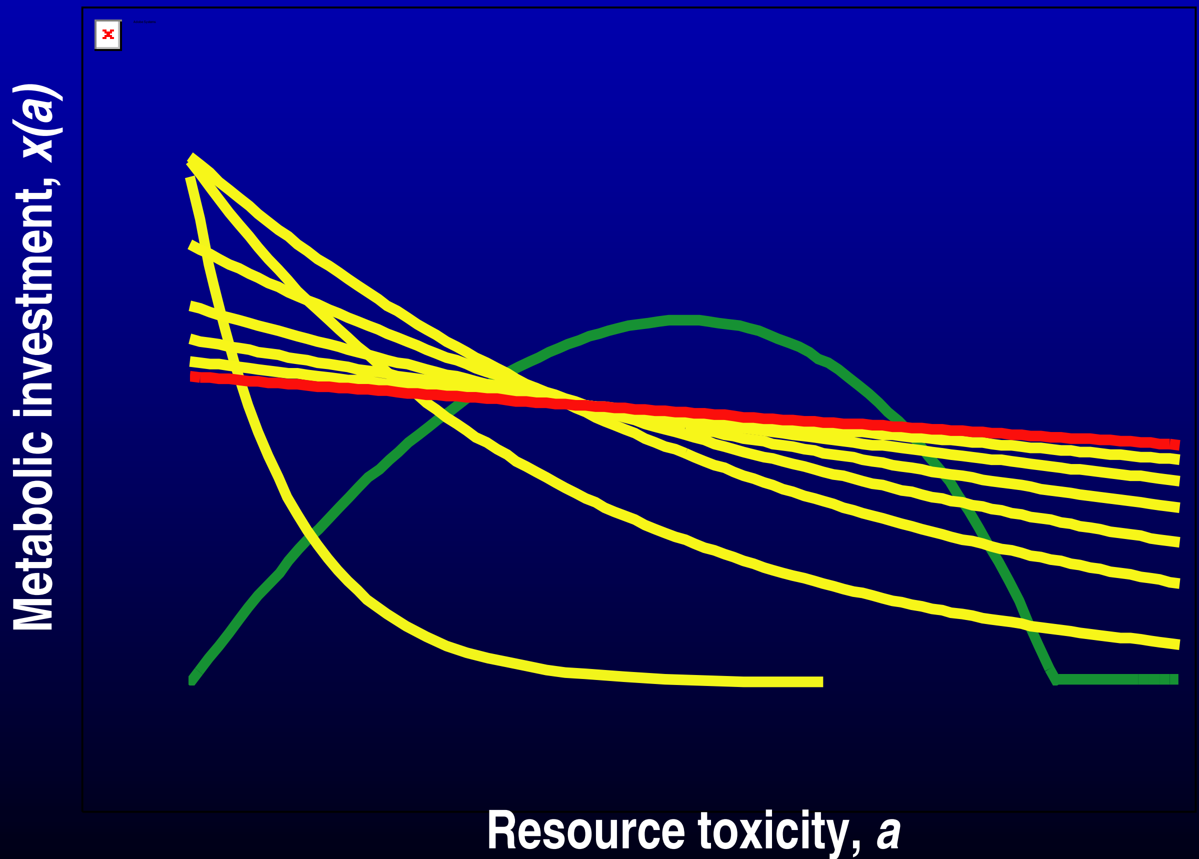
- Transient dynamics and evolutionary attractor



The shape of the evolutionary attractor can be determined analytically.

The Dangers of Parametrization 1

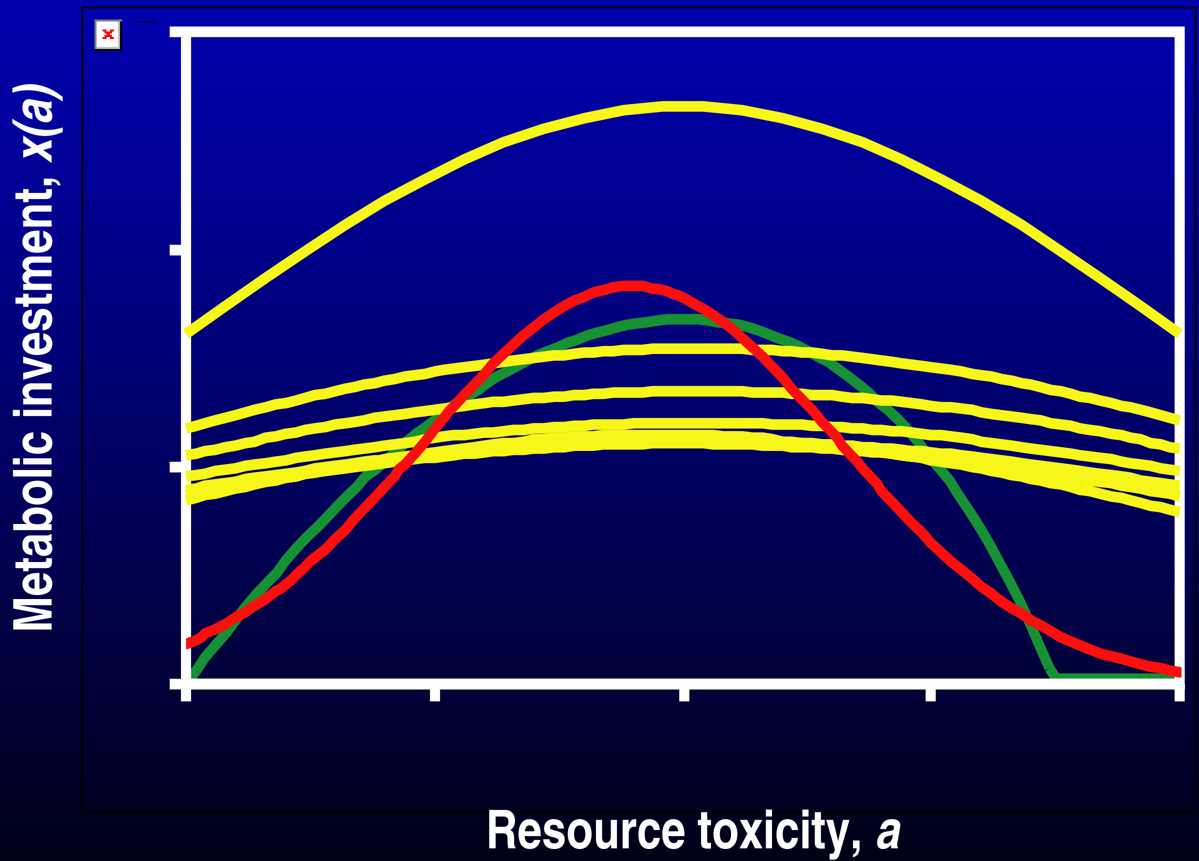
- Exponential ⇒ Irrelevant attractor



There is hardly any resemblance between the two evolutionary attractors.

The Dangers of Parametrization 2

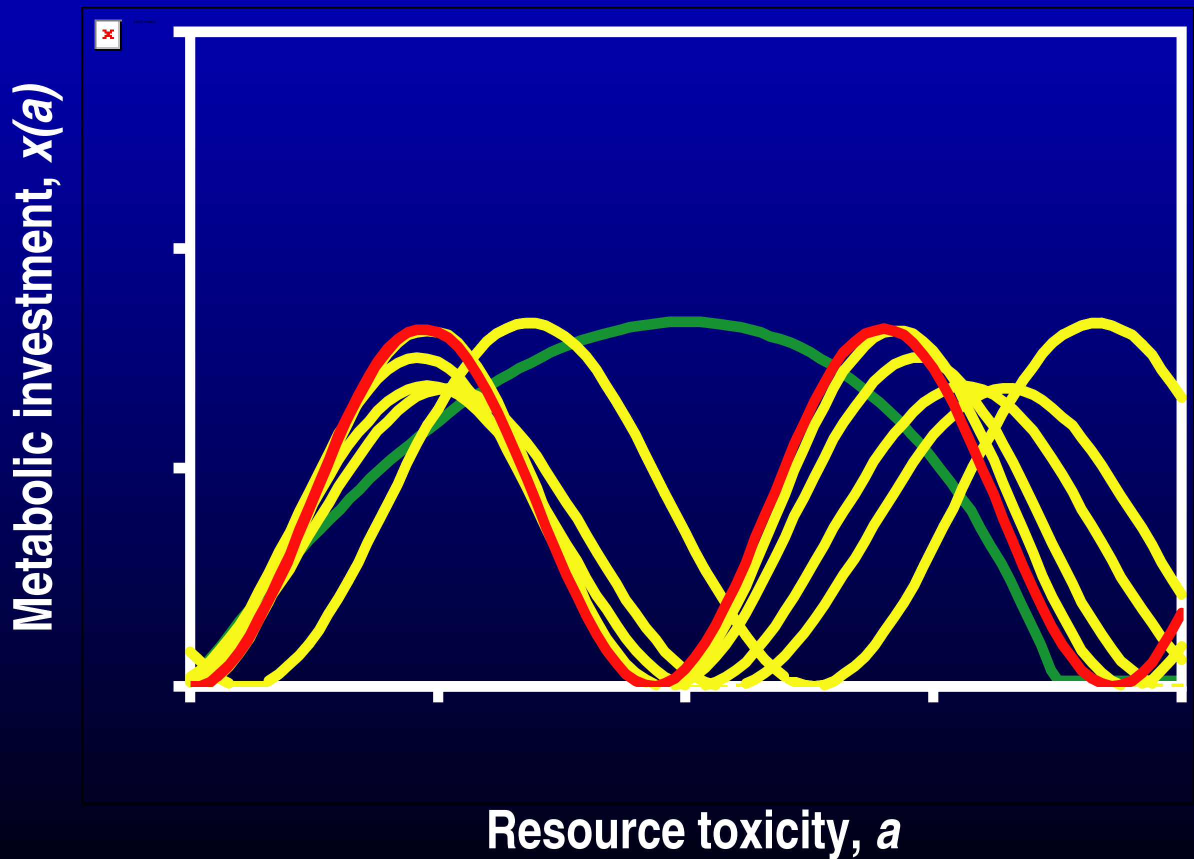
- Normal ✠ Qualitatively misleading attractor

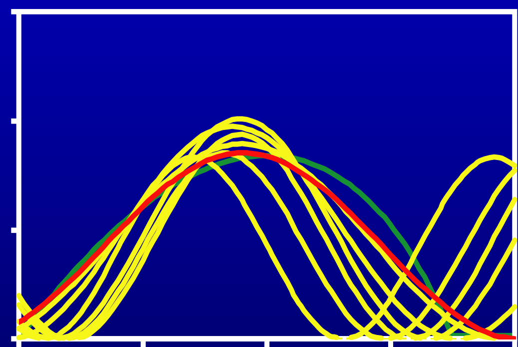


The asymmetry in the actual evolutionary outcome is missed.

The Dangers of Parametrization 3

- Sinusoidal ⇒ Meaningless evolutionary attractors





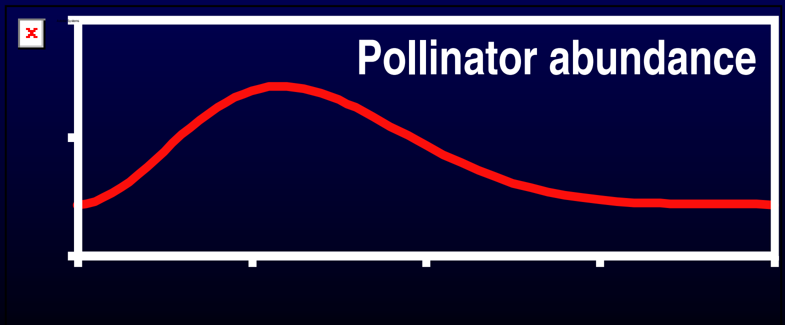
Spurious fitness valleys may stabilize spurious evolutionary attractors.

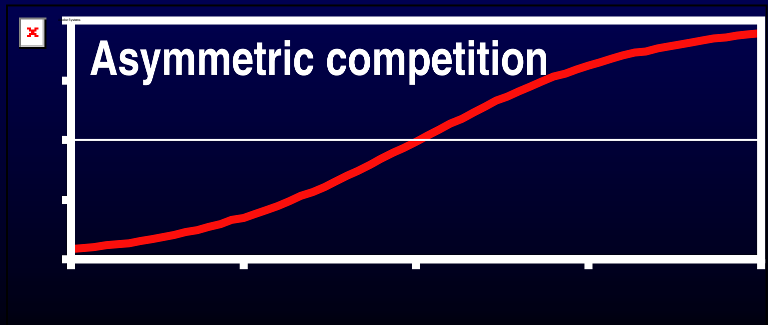
5 Second Example

Evolution of a Seasonal Flowering Schedule

Second Example: Description

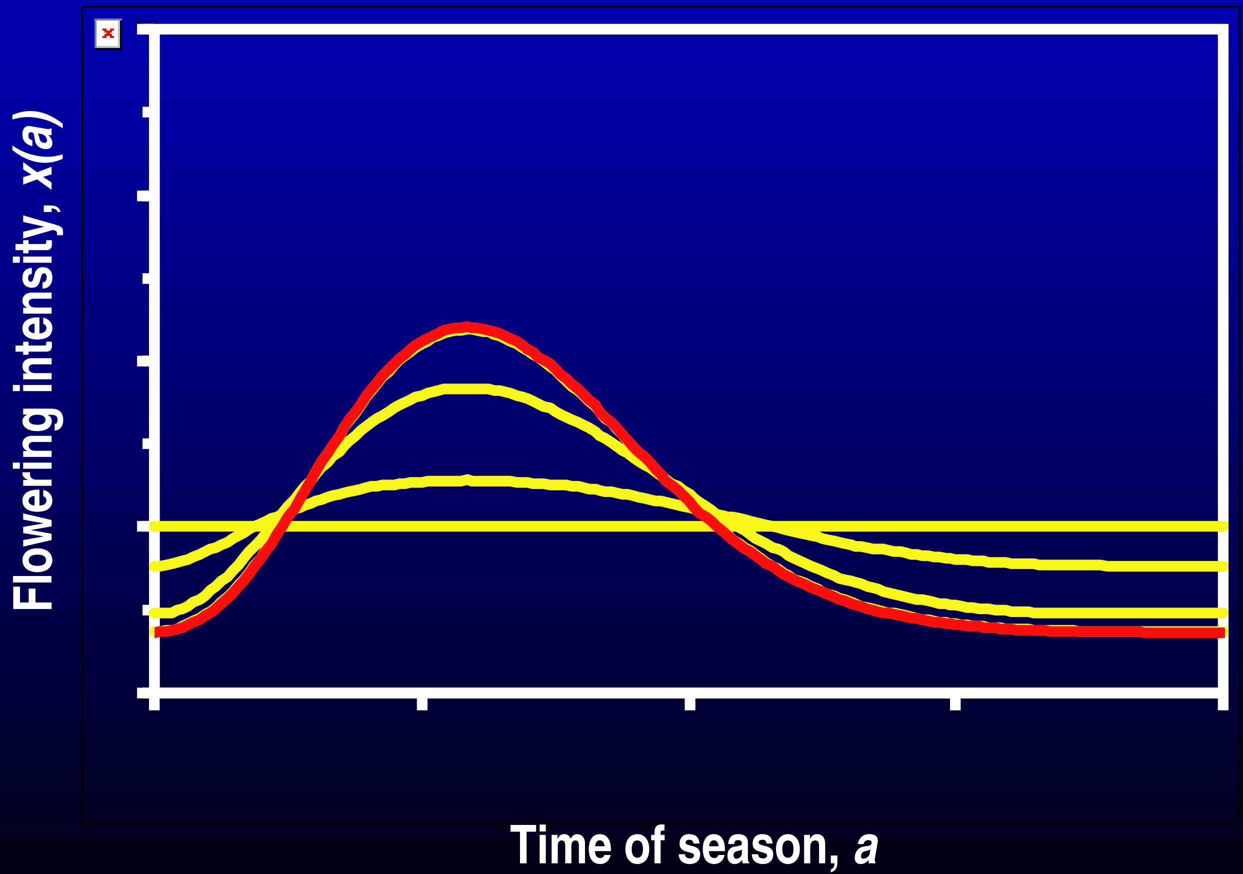
- We consider a plant that is exposed to a seasonally varying environment and at time *a* in the season exhibits a flowering intensity *x(a)*.
- A certain total flowering intensity cannot be exceeded.
- The abundance of pollinators varies over the year, and plants compete asymmetrically for attracting these pollinators.





Second Example: Results

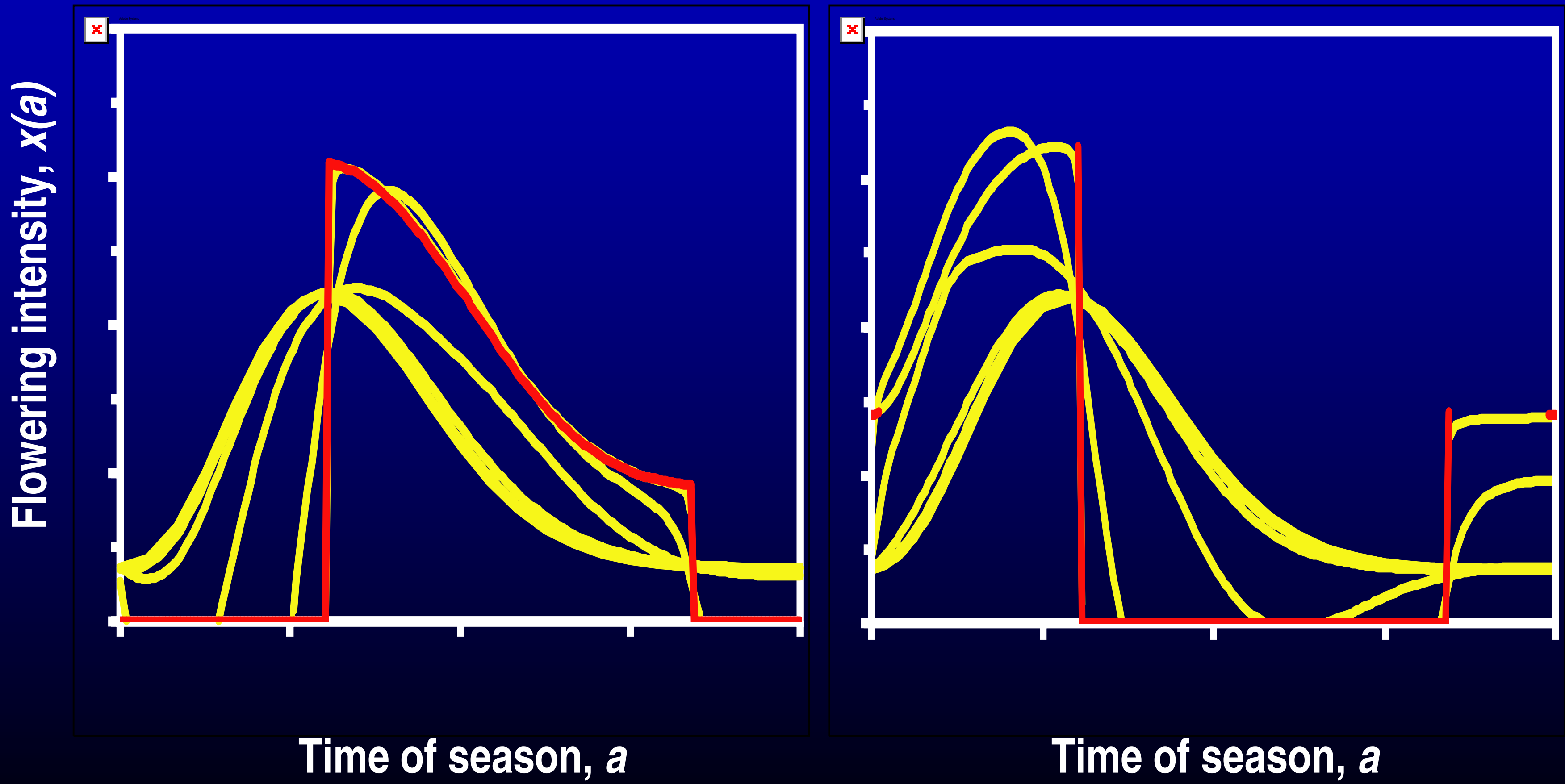
- Monomorphic seasonal flowering schedule



Interestingly, this evolutionary attractor corresponds to a fitness minimum.

Evolutionary Branching of FV Traits

- Dimorphic Seasonal Flowering Schedule



Summary

- Many phenotypes of interest in evolutionary ecology are best represented as function-valued traits.
- The long-term evolution of such traits can be studied using the canonical equation of adaptive dynamics theory.
- Frequency-dependent selection is readily encompassed.
- Equality and inequality constraints must receive particular attention.
- The evolutionary branching of function-valued traits opens up exciting opportunities for studying the interplay between individual-level plasticity and population-level diversity.