Invasion

Evolution and Ecology

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology

Population Genetics

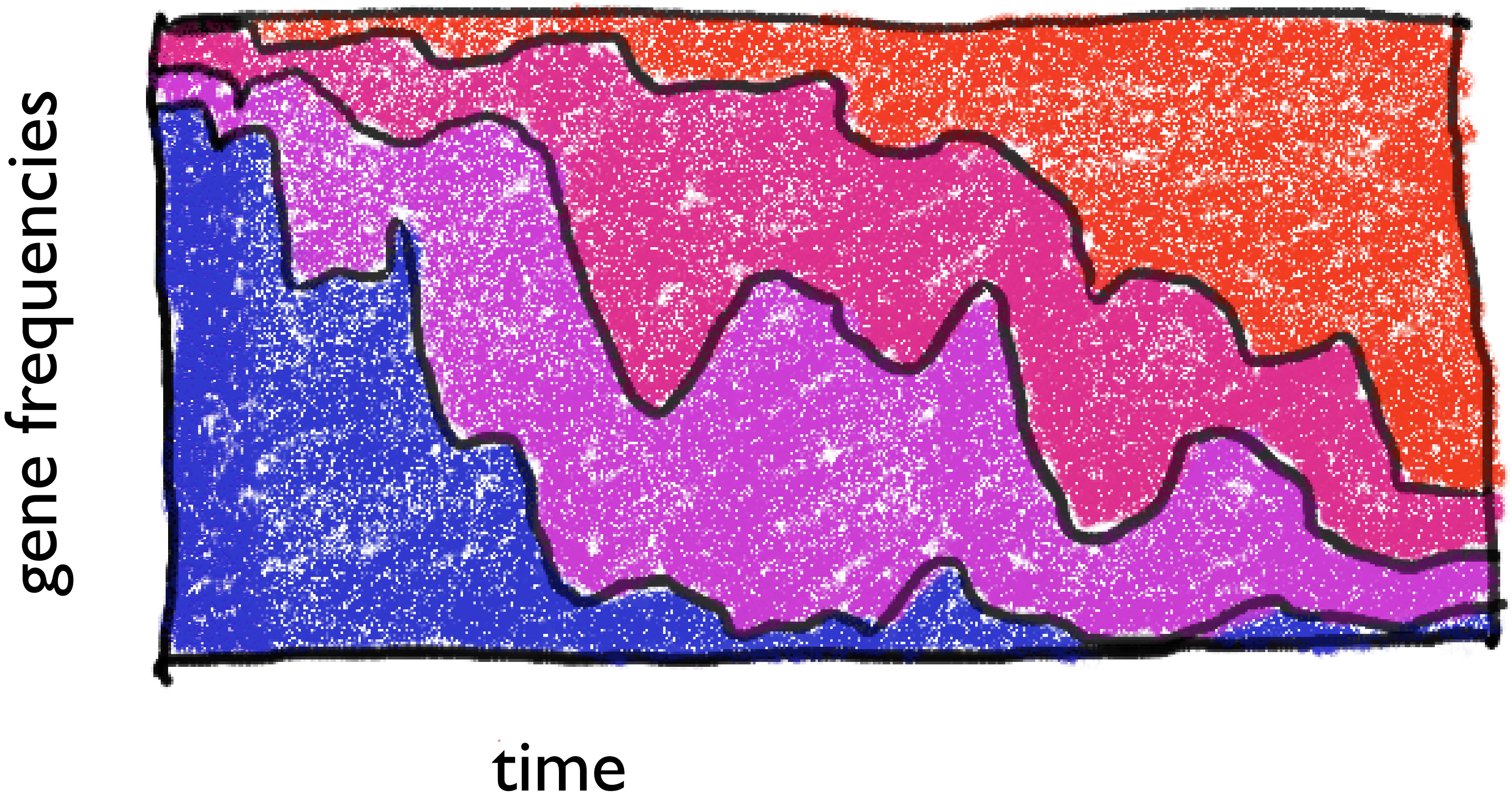
Population Genetics

Well-known standard case:

- Sexual reproduction
- Diploid genetics
- Two alleles (dominant/recessive)

Variables: gene frequencies

Gene frequencies



Population Genetics

Typical assumptions:

- single population
- simplified ecology
  - most ecological aspects are subsumed in 'frequency dependence'
- more realistic cases difficult to analyse
  - density dependence
  - population interactions

$$\frac{dx_i}{dt} = (b_i - d_i)\, x_i$$

$$= r_i x$$

may be density dependent!

$r_i = f_i(\dots, x_j, \dots)$

$i = a, A$

$$p_a = \frac{x_a}{x_a + x_A}$$

$$\frac{dp_a}{dt} = \frac{\frac{dx_a}{dt}(\cancel{x_a} + x_A) - x_a\left(\cancel{\frac{dx_a}{dt}} + \frac{dx_A}{dt}\right)}{(x_a + x_A)^2}$$

$$= \frac{\frac{dx_a}{dt}x_A - x_a\frac{dx_A}{dt}}{(x_a + x_A)^2}$$

$$= \frac{r_a x_a x_A - r_A x_A x_a}{(x_a + x_A)^2}$$

$$= \frac{x_a x_A}{(x_a + x_A)^2}(r_a - r_A)$$

$$= p_a(1 - p_a)(r_a - r_A)$$

<u>if</u> $r_a = r_A(1+s)$

then $$\frac{dp_a}{dt} = p_a(1-p_a)\,r_A\, s$$

"selection coefficient"

Measures of increase

Subtle differences

- λ rate of population increase
  - invasion continuous time : $\lambda > 0$
  - invasion discrete time : $\lambda > 1$
- R_0 basic reproduction ratio of individuals
  - invasion : $R_0 > 1$
- r net rate of reproduction of population
  - invasion : $r > 0$
- s selection coefficient
  - increase in frequency : $s > 0$

Population Genetics

Much attention to

- interaction among alleles and loci
  - dominance
  - modifiers
  - conditions that favour polymorphism
  - epistasis, linkage
  - links with developmental biology

Population Genetics

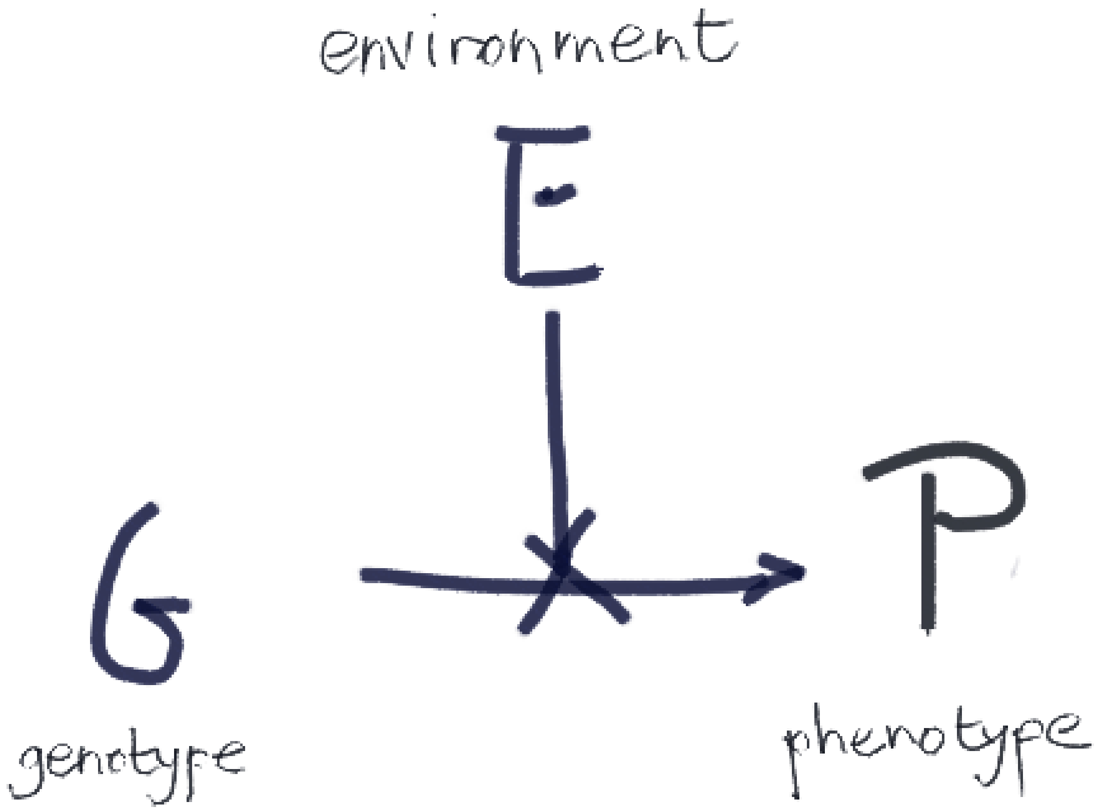
Little attention to

- Interactions among individuals
  - Population dynamics and ecology
  - Behaviour

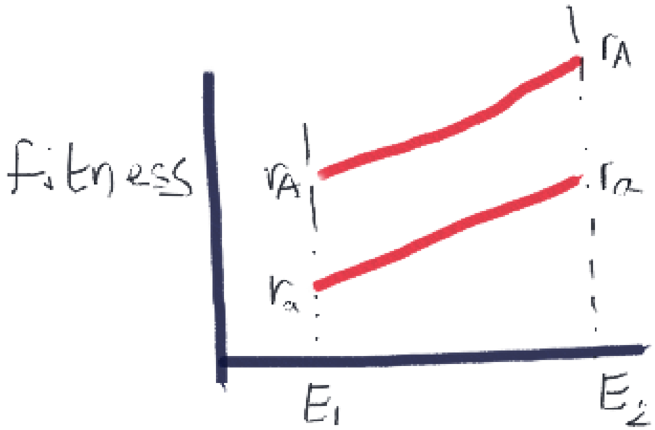
density dependence

phenotypic plasticity

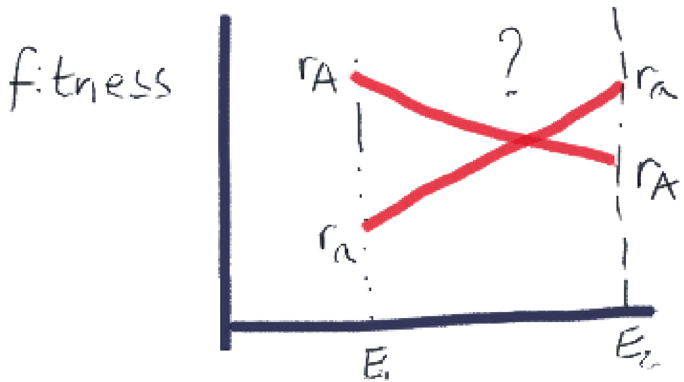
Phenotypic plasticity



Phenotypic plasticity

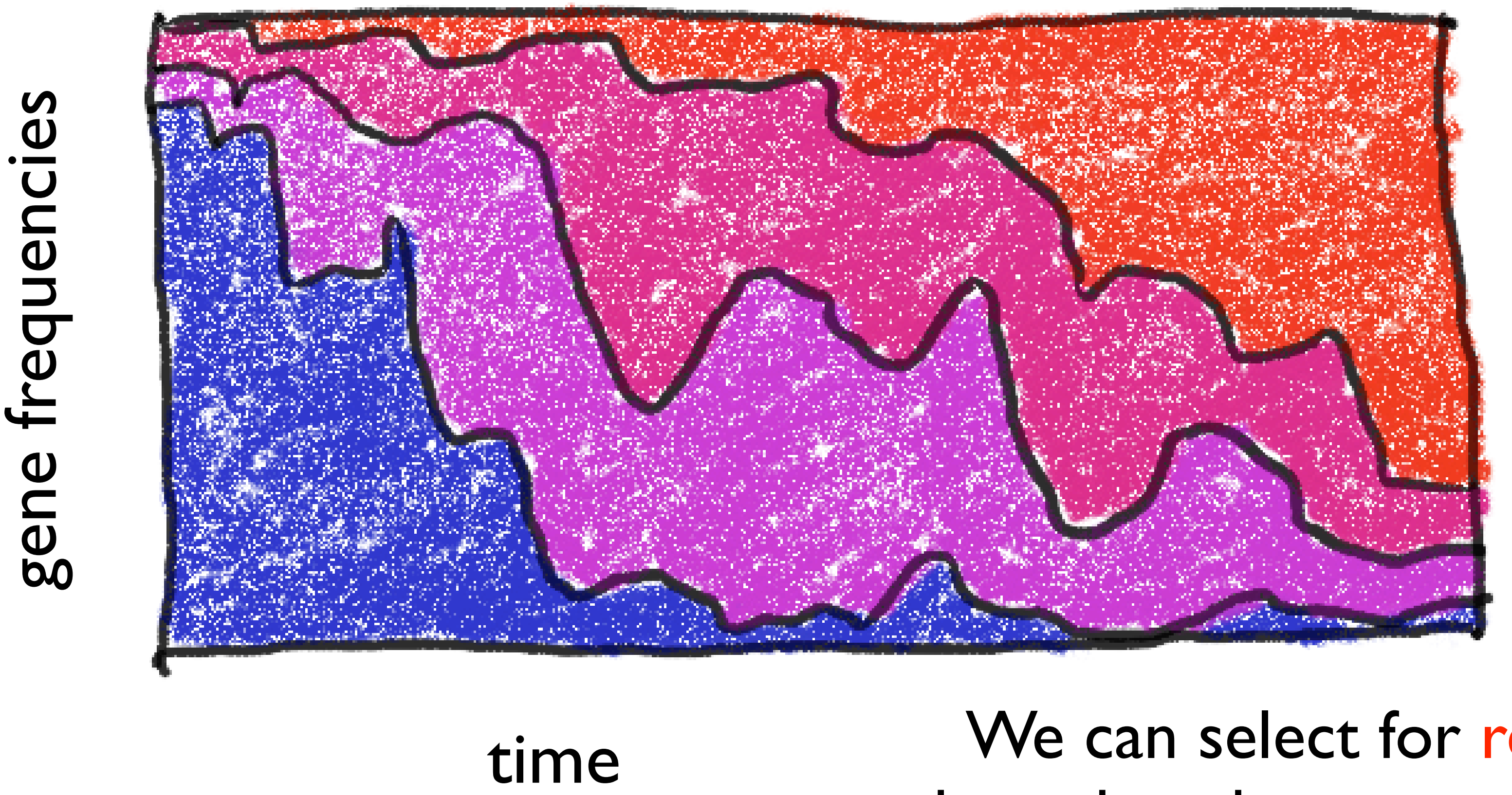


A dominates



it depends…

Gene frequencies



We can select for redness
but what about greenness???

Population Genetics

Caricature:

- 'Evolution is change in gene frequencies'
- 'That problem has been solved long ago'
- 'The big problem is to explain speciation'

Game Theory

Game Theory

First developments during 2nd World War

Then applied to Sociology

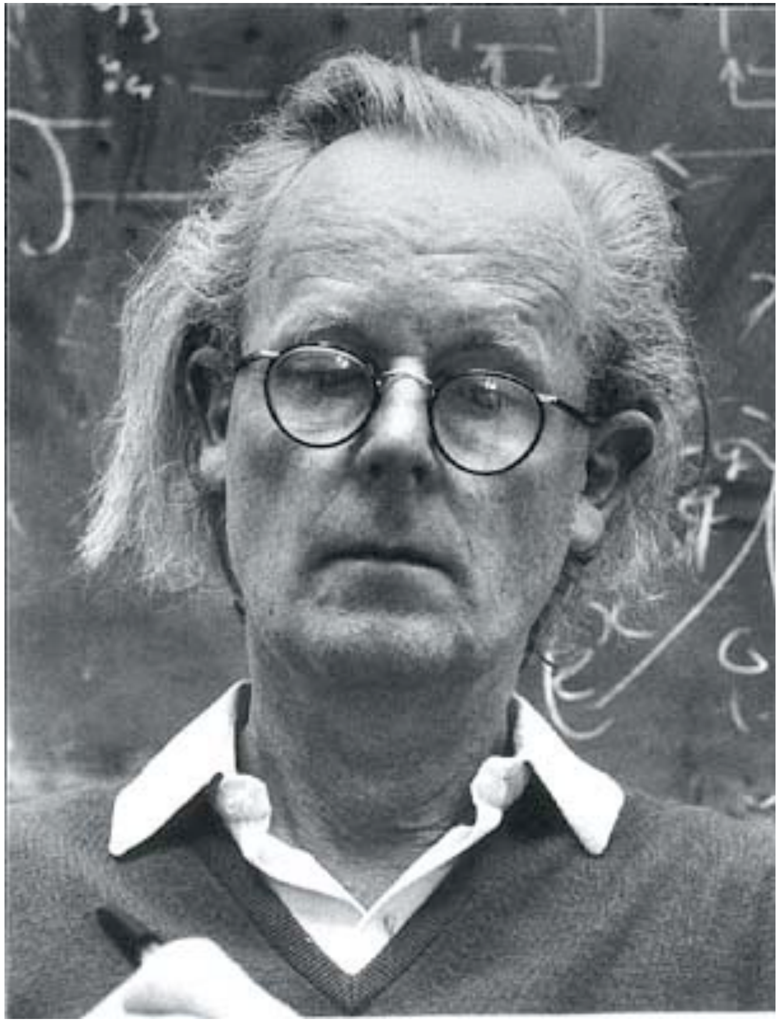
- Why do individuals cooperate?

Applied to Behavioural Ecology

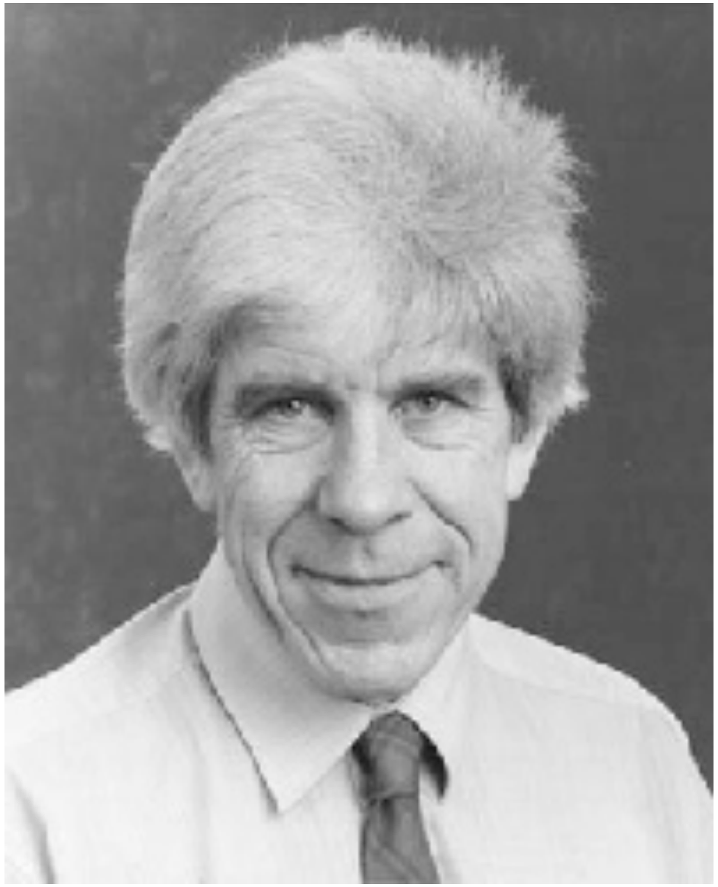
- Interactions among individuals

Bill Hamilton
John Maynard Smith

John Maynard Smith



Bill Hamilton



Evolutionary Game Theory

Observation: fighting animals rarely kill

Why such restraint?

Hawk-Dove Game

Maynard Smith & Price 1971

Game Theory

Individuals may choose among a range of strategies

Sometimes finding the optimum strategy is easy

Often, however, payoffs depend on what others do

The Hawk-Dove Game

		your opponent	
		H	D
you	H	$\frac{1}{2}(V-C)$	V
	D	0	$\frac{1}{2}V$

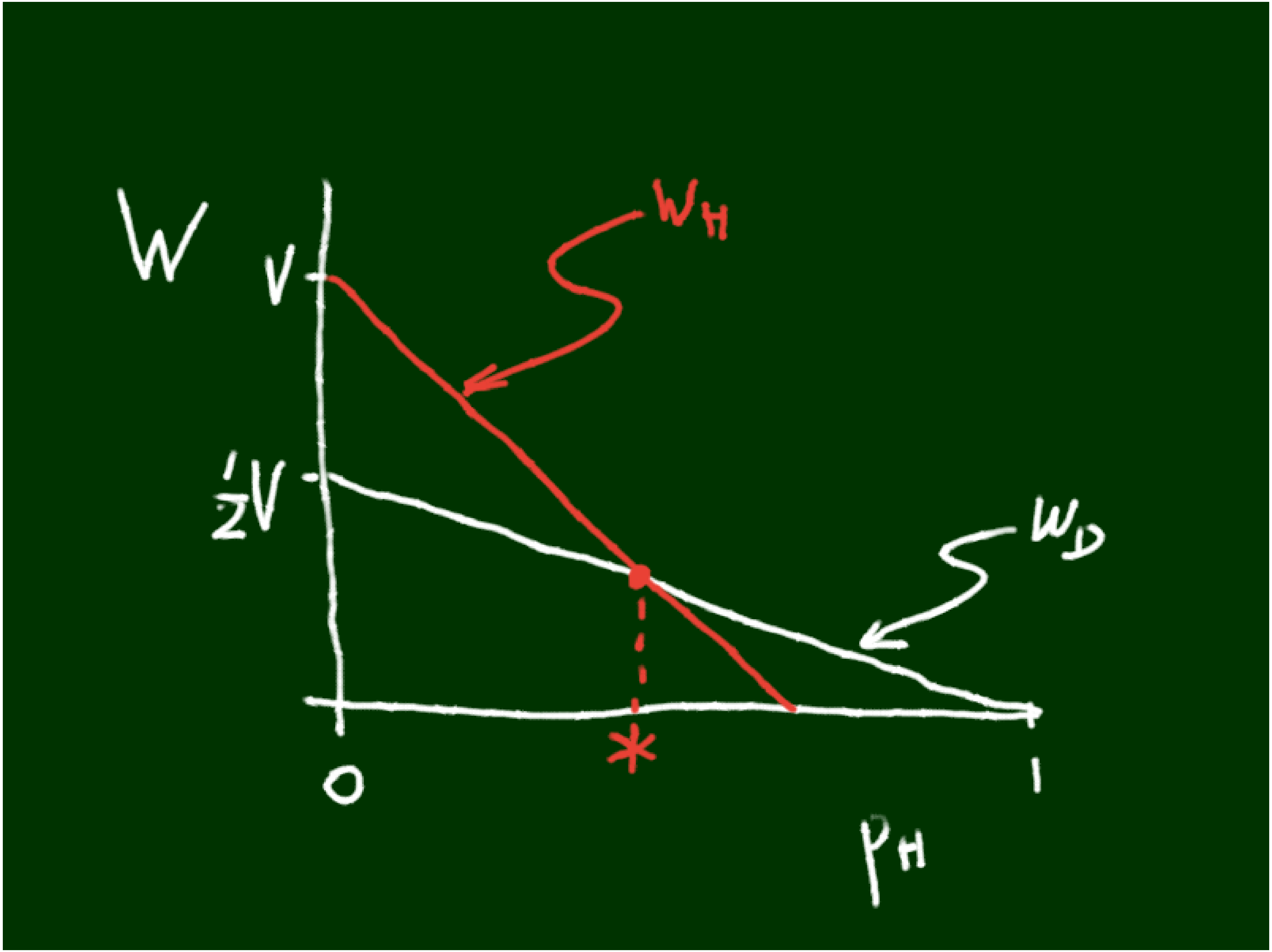
p_H : proportion Hawks

$$W_H = p_H \frac{1}{2}(V - C) + (1 - p_H)V$$

$$= V - \frac{1}{2}(V + C)\, p_H$$

$$W_D = p_H \cdot 0 + (1 - p_H)\frac{1}{2}V$$

$$= \frac{1}{2}V - \frac{1}{2}V p_H$$



W
V
½V
W_H
W_D
0
*
1
p_H

Evolutionarily Stable Strategies

If $p_H < p^*$ (few Hawks) then play ‘Hawk’

If $p_H > p^*$ (many Hawks) then play ‘Dove’

If $p_H = p^*$ both ‘Hawk’ and ‘Dove’ do equally well

A resident strategy that plays ‘Hawk’ with probability p^* cannot be beaten

Formalised in concept of ESS

John Maynard Smith,
Richard Dawkins

Evolutionary Stability

If for all strategies $J \neq I$

$$W(I|I) > W(J|I)$$

then strategy I is an ESS

If $W(I|I) = W(J|I)$ then I is ESS if $W(I|J) > W(J|J)$

- Maynard Smith & Price's second condition

convergence stability

Evolutionary Game Theory

Caricature:

- 'The fitness of an individual depends
- on the strategies it adopts
- (which can be either pure or mixed)
- but also depends on the resident strategies
- according to the payoff function'

Evolutionary Game Theory

Problems

- where do the strategies come from?
  - Physiology?
  - Developmental genetics?
  - Behaviour?
  - Life History Theory?
- where does the payoff function come from?

Example: Sex Allocation

In many species, mothers can decide the sex of their offspring

- Strategy = {% sons, % daughters}

Fischer in the 30s:

- produce 50% daughters

Hamilton in the 60s:

- depends on mating structure
- biased sex ratios

Ex: Habitat Selection

In many spatially heterogeneous environments, individuals can decide
where to go

Often, payoffs depend on where others go

Q1: where should you go ?

Q2 (knowing A1) where does everybody go?

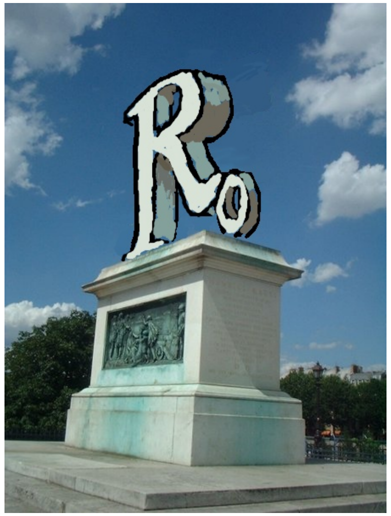
Prediction: Ideal Free Distribution

- nobody gains by moving to another place

Evolutionary Game Theory

Where does the payoff function come from?

- Fitness = Lifetime reproductive succces
- If Fitness > 1 $\Rightarrow$ Invasion
- Life History Theory



Important Insights

Population Genetics

- mutant genotypes may generate new phenotypes

Game Theory

- outcome of interaction depends on conditions

Life History Theory

- rare mutants will try to optimize their strategies

Ecosystem Dynamics

- invasion of rare species, density dependence

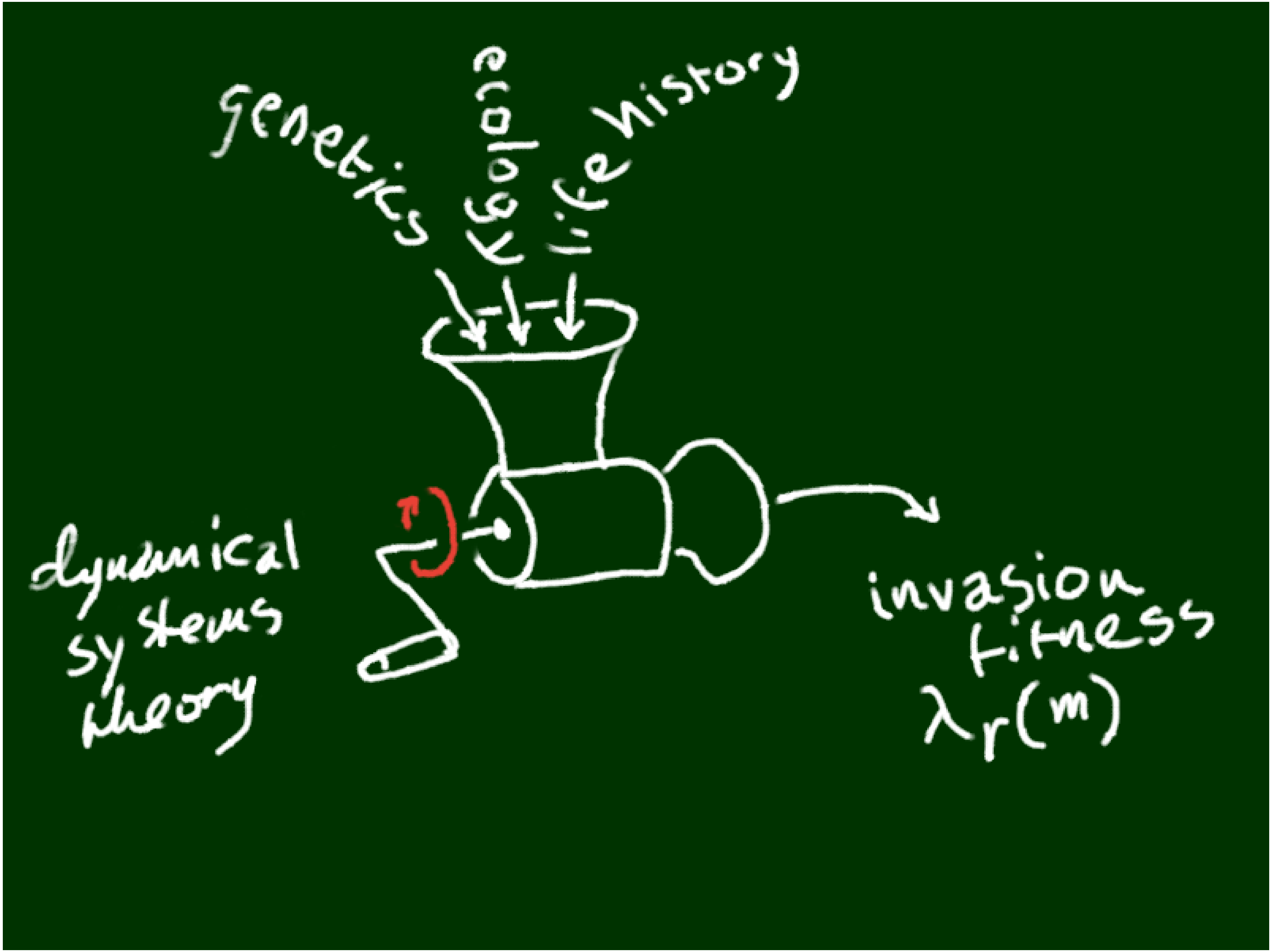
Adaptive Dynamics

Adaptive Dynamics

Caricature

- ‘New mutants may appear
- initially rare
- whose invasion fitness
- depends on the resident attractor’

Peter Hammerstein, Ilan Eshel, Hans Metz,
David Rand, Geza Meszena,
Ulf Dieckmann,
Stefan Geritz, Eva Kisdi.

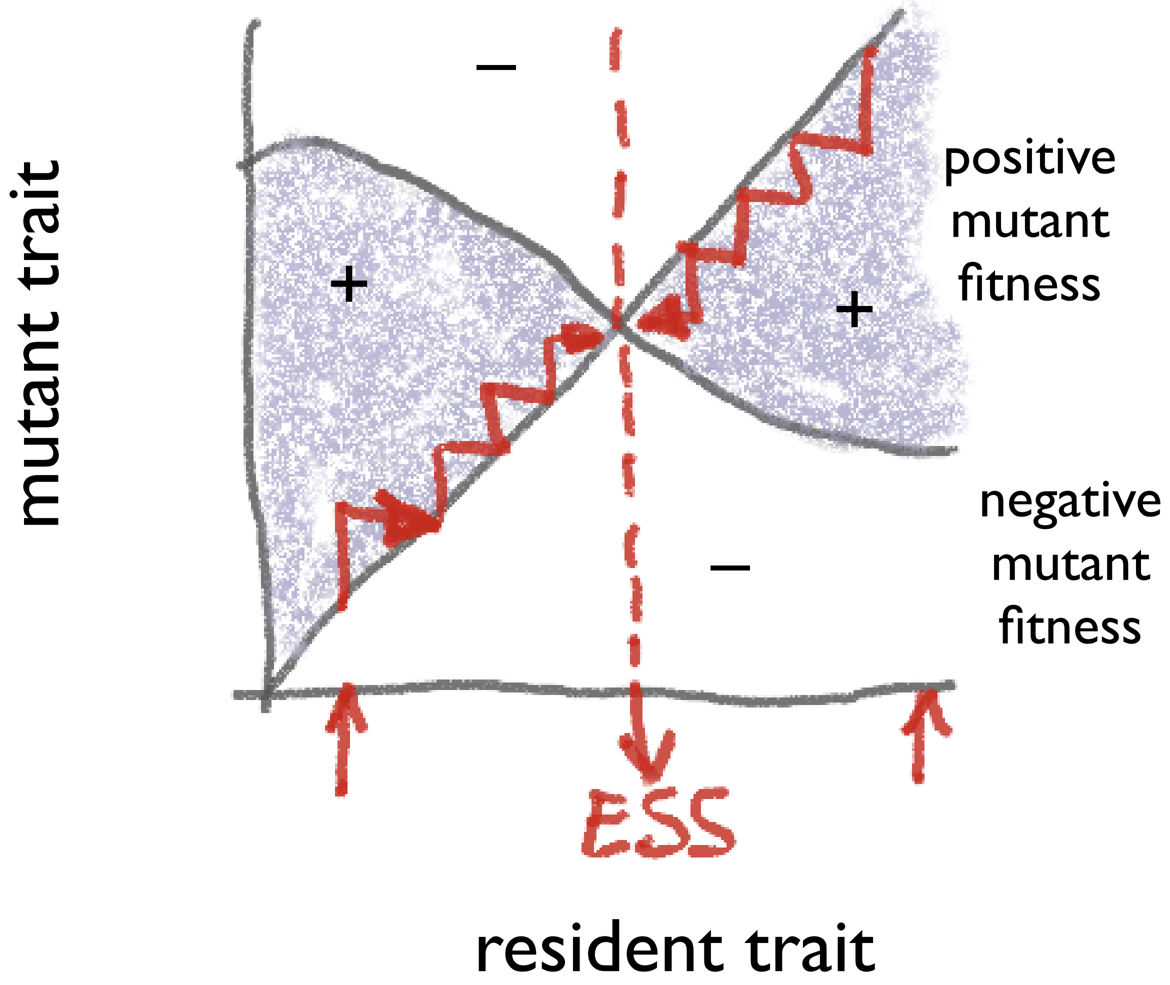

genetics
ecology
life history
dynamical systems theory
invasion fitness
$\lambda_r(m)$

Adaptive Dynamics

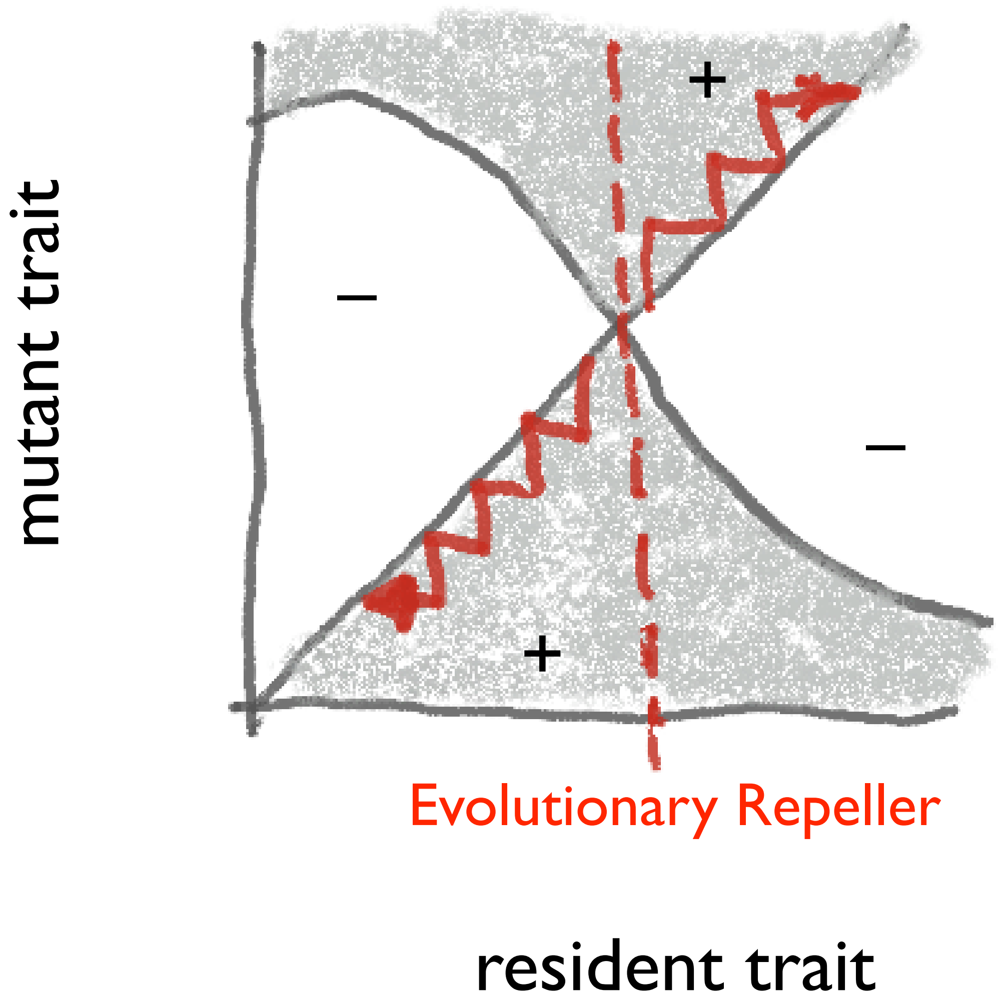
Practical Method

- monomorphic population trait a
- resident dynamics
- attractor
- mutant invasion
- pairwise invasibility plot (PIP)

Pairwise Invasibility Plot



Pairwise Invasibility Plot



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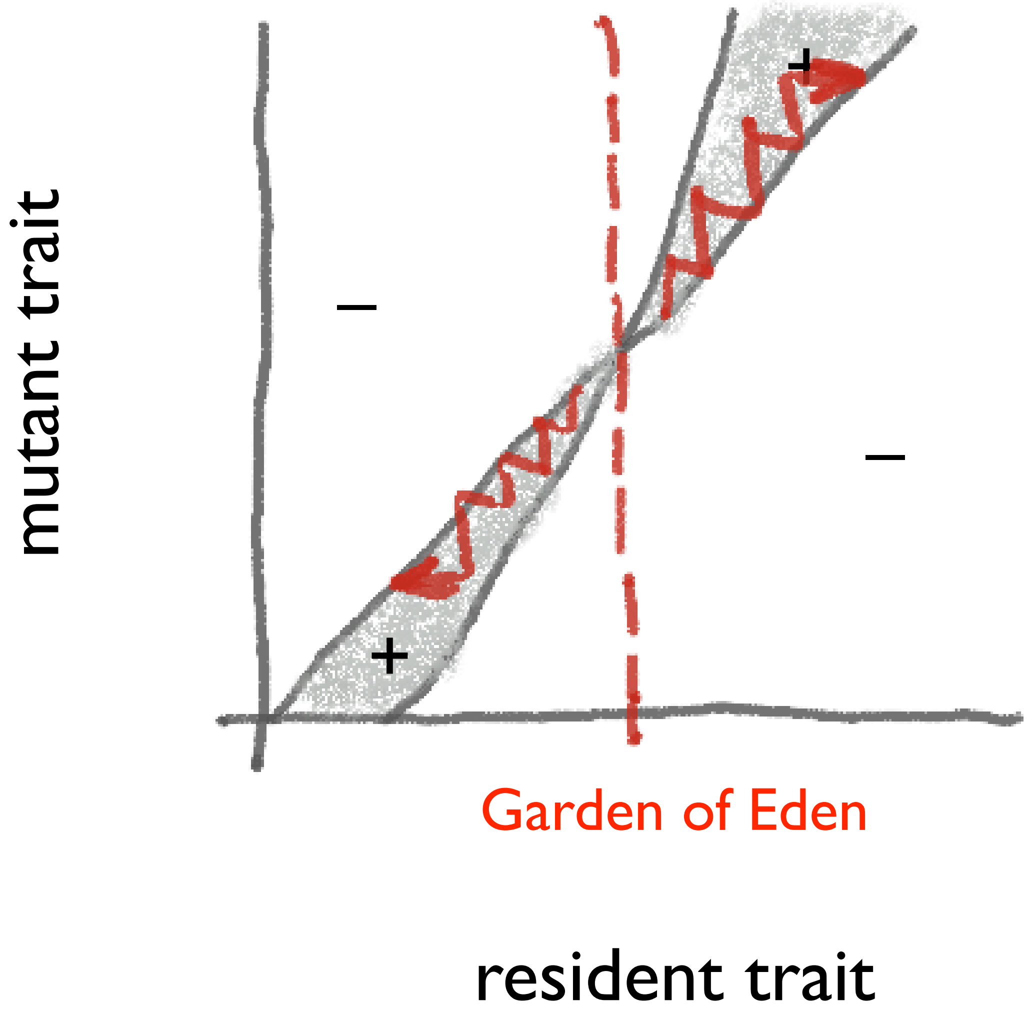

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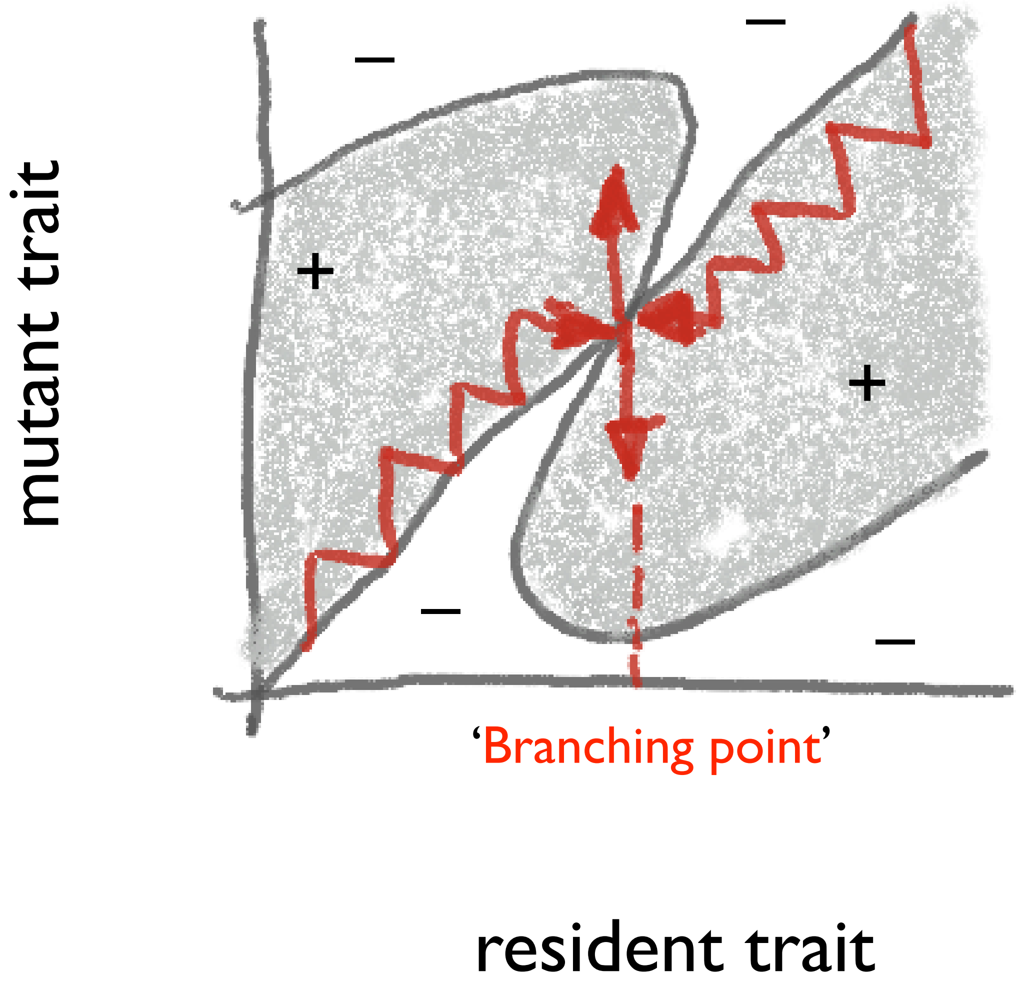
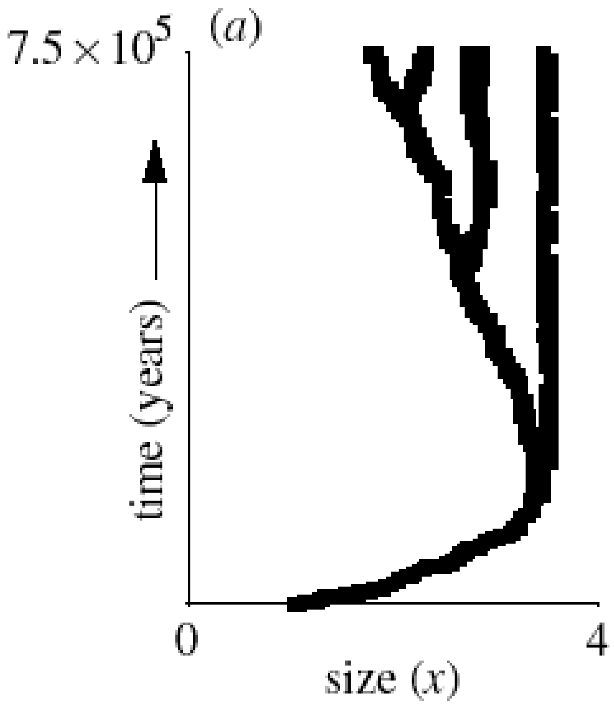
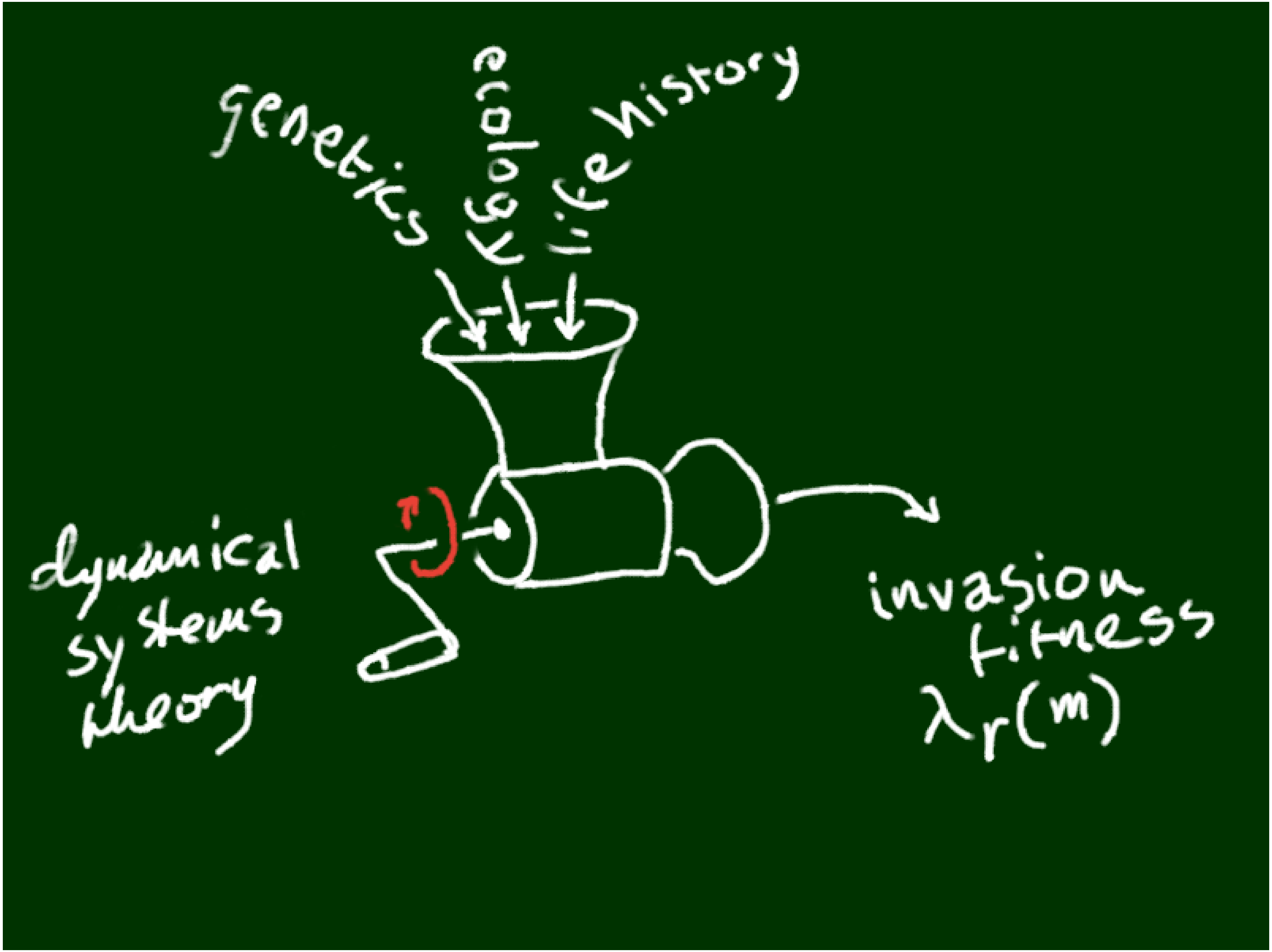


Kisdi & Geritz





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