Invasion as a unifying conceptual tool in ecological and evolutionary theory

(and theoretical immunology)

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Invasion

Evolution and Ecology

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

} Adaptive Dynamics

Evolution and Ecology

History

Before 1800

- various theories of evolution
- species evolve

Lamarck, Erasmus Darwin

After 1800

- mechanism: natural selection

Charles Darwin, Alfred R. Wallace

On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life

by

Charles Darwin, M.A.,
Fellow of the Royal, Geological, Linnæan, etc. societies;

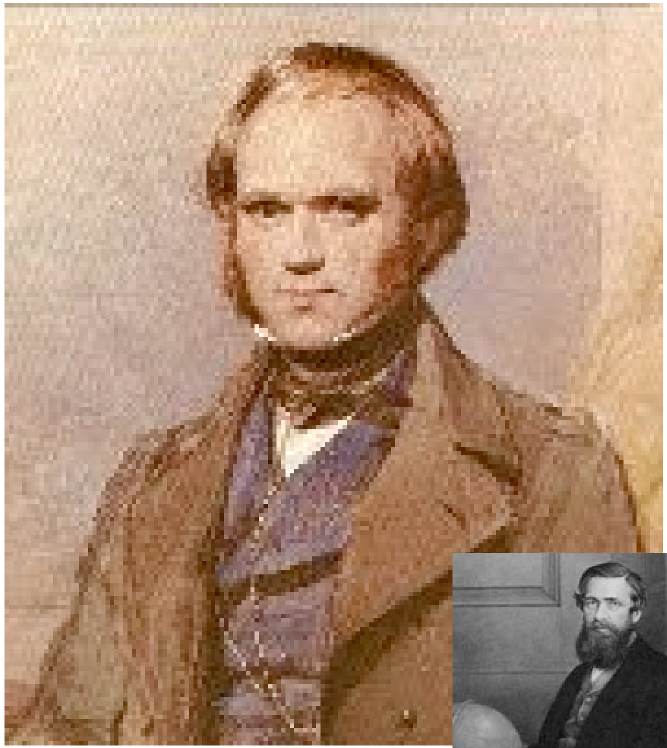
Author of *Journal of researches during H. M. S. Beagle's Voyage round the world.*

London: John Murray, Albemarle Street, 1859

Darwin's Insight
(& Wallace's)

+ Reproduction generates variation
+ Individuals compete
+ Traits affect individuals' differential survival

= 'Evolution by Natural Selection'



Rediscovery of Mendel

Early 1900s

- rediscovery of Mendel's work
- phenotypes change because genotypes change
- genes remain the same
  - no evolutionary change

!?!

Synthesis

Genes are not fixed

- rare mutations modify genes

Hugo de Vries

'Neo-Darwinian Synthesis'

- fixation of mutations

Ronald A. Fischer

Population Genetics

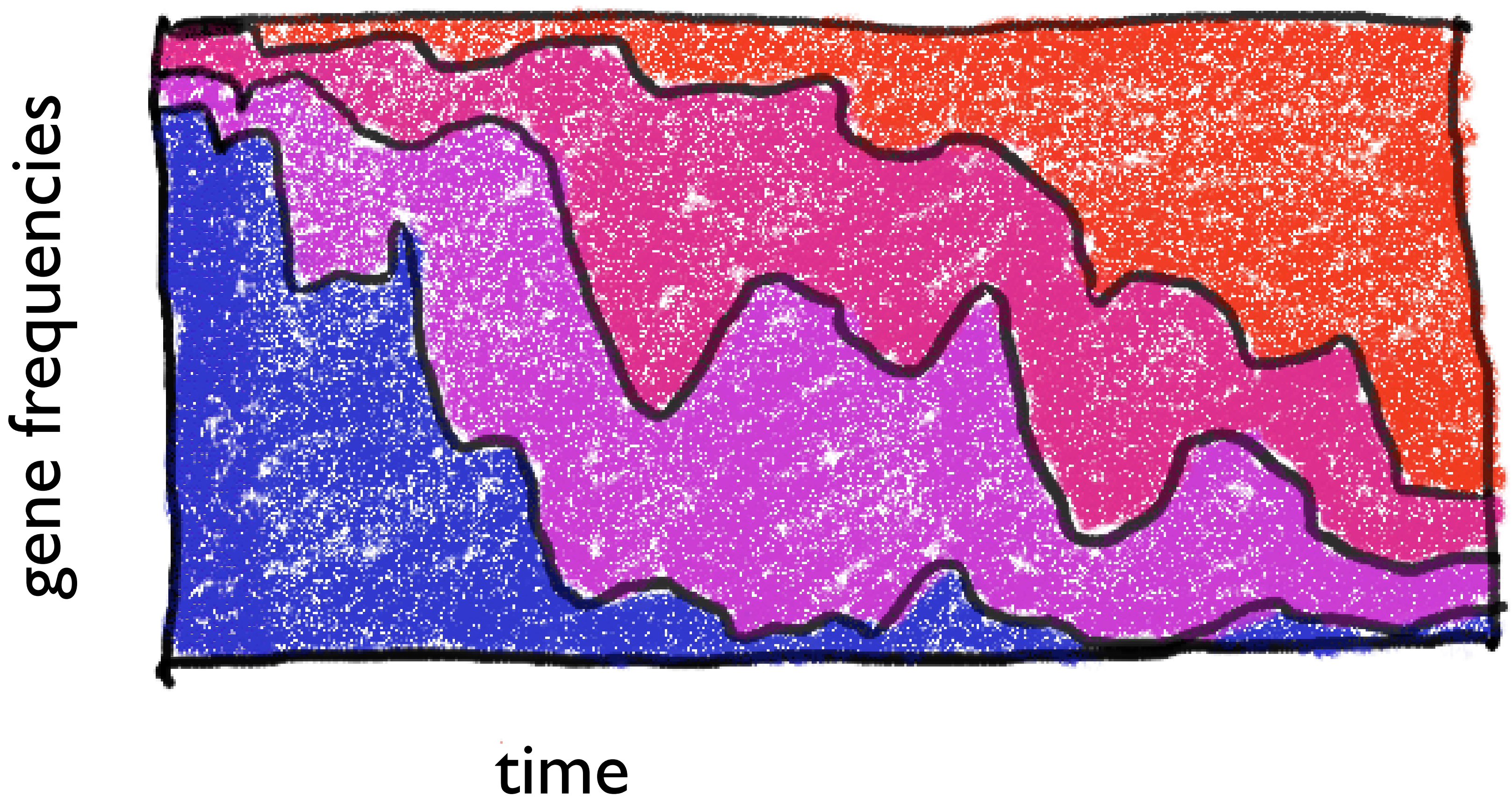
Population Genetics

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!

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

$i = a, A$

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

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

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

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

then $\frac{dp_a}{dt} = p_a(1-p_a) r_A s$ ← "selection coefficient"

Population Genetics

Much attention to

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

Population Genetics

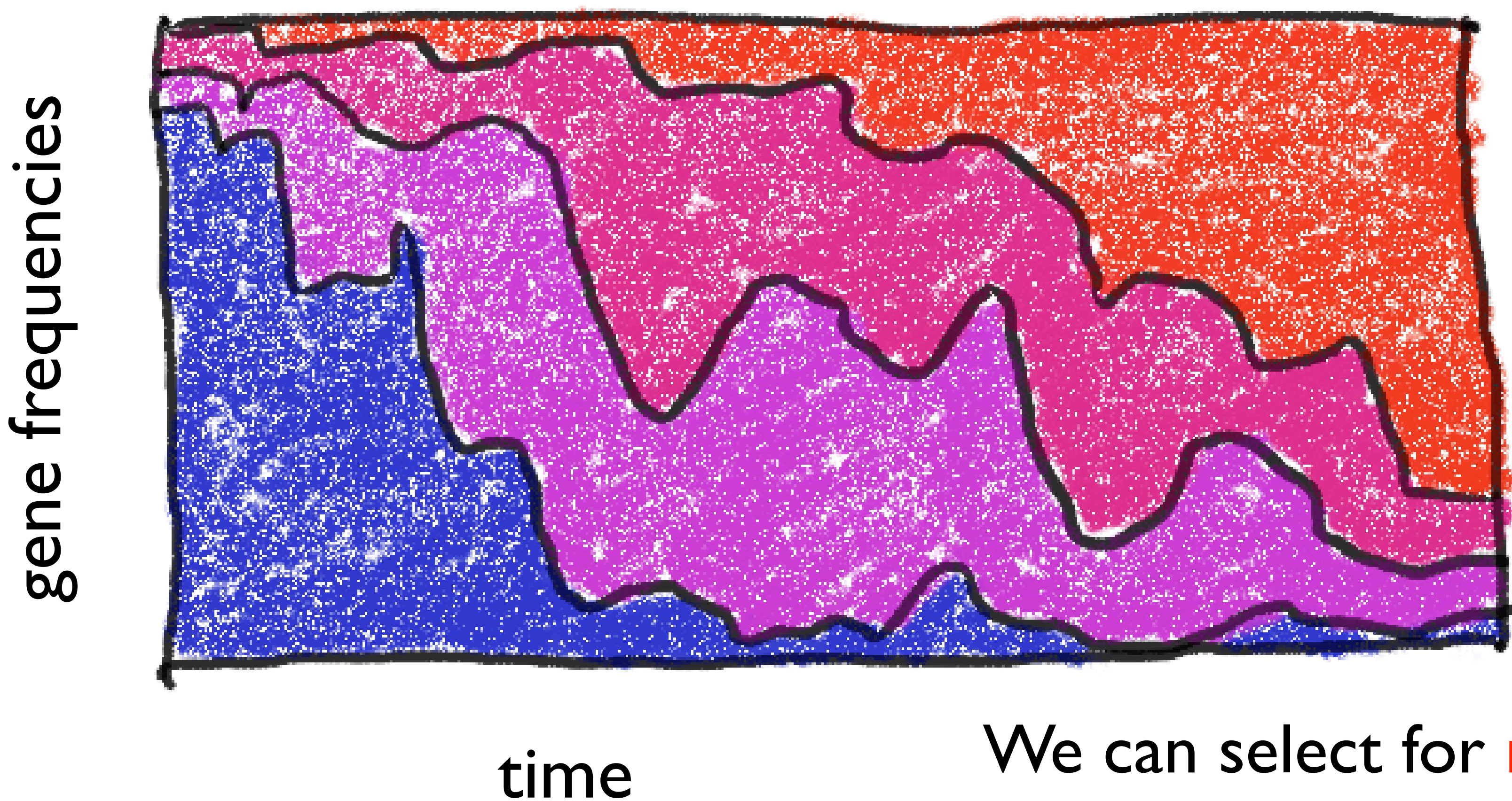
Little attention to

- Interactions among individuals
  - Population dynamics and ecology
  - Behaviour

density dependence

phenotypic plasticity

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

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	$\frac{1}{2}V$

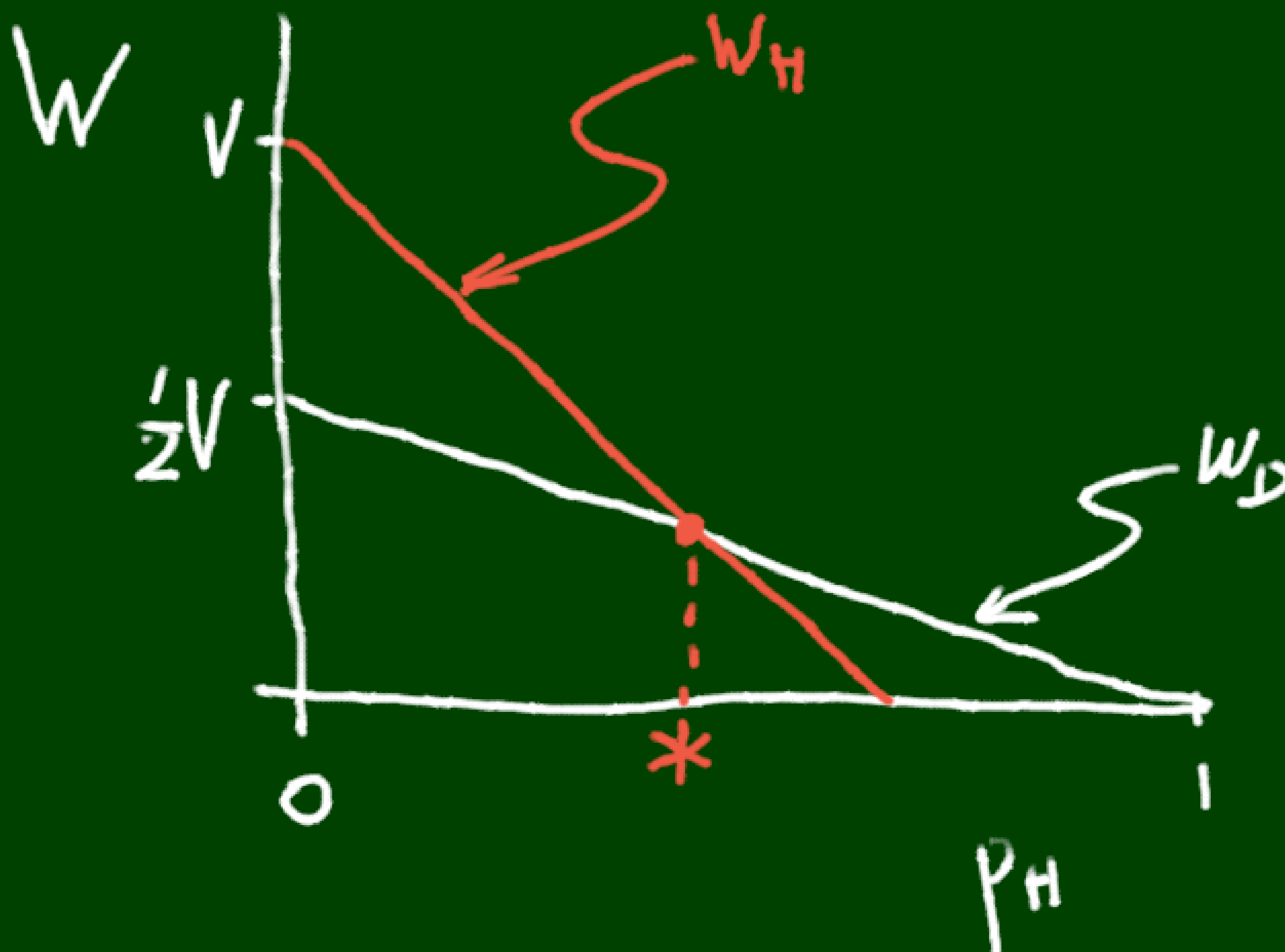
p_H : proportion Hawks

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

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

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

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


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?

Evolutionary Game Theory

Where does the payoff function come from?

Fitness = Lifetime reproductive succces

If Fitness > 1 $\Rightarrow$ Invasion

Life History Theory

Life History Theory

All organisms grow, reproduce and eventually die

Given finite resources, how should an individual invest in growth, reproduction and survival

Kooijman

Since 1960s : Evolutionary Life History Theory

Eric Charnov, Steve Stearns

Life History Theory

Population-level view:

- Net rate of reproduction: $r = b - d$
  - where the rates of reproduction b and mortality d may depend on environmental conditions
- A population invades if (and only if) r is positive

Life History Theory

Individual-level view

- A population increases on average an individual has more than one offspring
- Average lifetime: $1/d$
- Expected lifetime reproductive success or 'Basic Reproduction Ratio' $R = b/d$

Life History Theory

Hypothesis

- Natural Selection maximizes $R_0 = b/d$
- Basic Reproduction Ratio

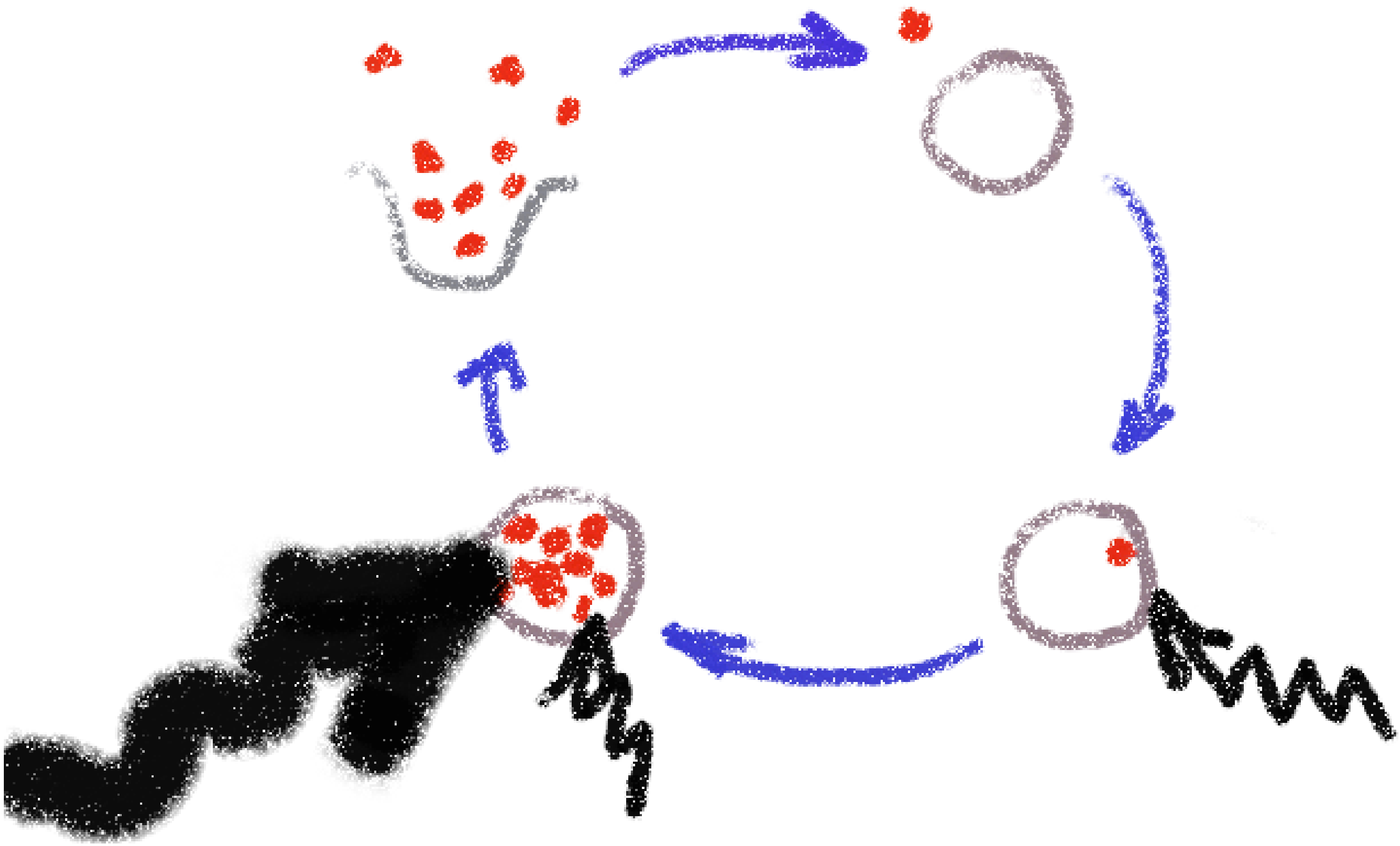
Most theory is about how individuals might achieve this

Life History Theory

Caricature

- ‘Individuals try to maximize their lifetime reproductive success by adopting the optimal allocation of resources into reproduction and survival.’

Medical Application: HIV



Medical Application: HIV

$$\frac{dE}{dt} = \beta C v - mE \quad -aE$$

$$\frac{dL}{dt} = mE - bL \quad -aL$$

$$\frac{dv}{dt} = cbL - \delta v$$

Medical Application: HIV

$$\frac{dE}{dt} = \beta C v - mE$$

$$\frac{dL}{dt} = mE - bL - AL$$

$$\frac{dv}{dt} = cbL - \delta v$$

Medical Application: HIV

$$\frac{d}{dt}\begin{pmatrix} E \\ L \\ V \end{pmatrix} = \begin{pmatrix} -m & 0 & \beta C \\ m & -b-A & 0 \\ 0 & cb & -\delta \end{pmatrix}\begin{pmatrix} E \\ L \\ V \end{pmatrix}$$

Medical Application: HIV

$$\frac{dx}{dt} = Mx$$

Medical Application: HIV

$$\frac{dx}{dt} = Mx$$

Linear model

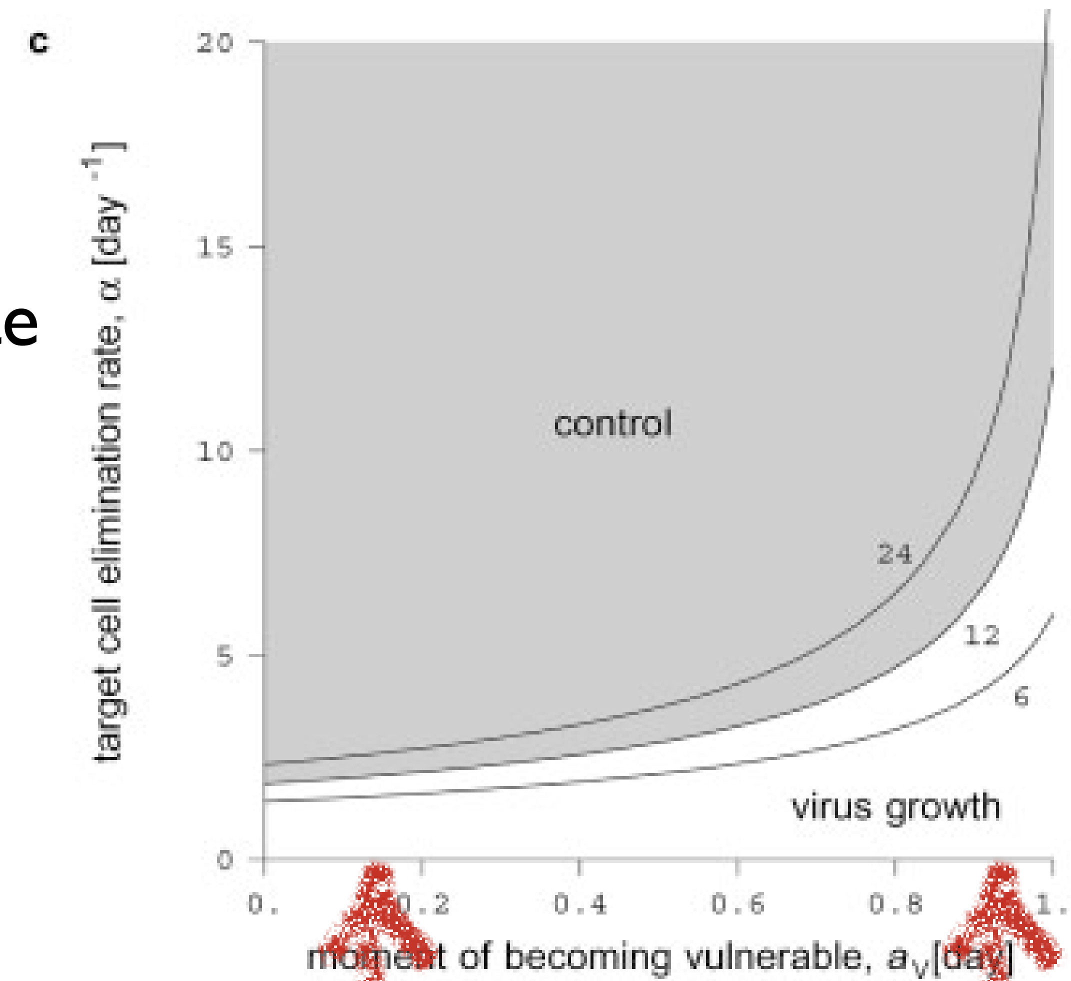
Dominant eigenvalue λ

Solution converges to $x(t) = ue^{\lambda t}$

Virus increases if $\lambda > 0$, decreases if $\lambda < 0$

Medical Application: HIV

Killing rate



Age at which cells become vulnerable

Life History Theory

Generally

- environment is usually taken to be constant
- whereas in reality demographic rates are likely to be density dependent:

$$b = b(x,y,\ldots),\ d = d(x,y,\ldots)$$

Need to incorporate feedback

Life History Theory

Invasion in a dynamically changing environment

Realm of…

Ecosystem Dynamics

Ecosystem Dynamics

Species are fixed entities

But there are potentially many of them

Which of these can coexist?

How does it depend on their ecology?

How does it depend on external parameters?

Ecosystem Dynamics

Without ecological feedback

- only one species will dominate!
- species with the highest net rate of reproduction (r)

So how do we explain biodiversity?

Coexistence

Every species needs resources

- nutrients, light, space…
- species compete for these resources

Mathematical result:

- Number of species $\leq$ Number of resources
- if populations in ecological equilibrium

  (MacArthur in the 60s, Tilman 90s)

Coexistence

Nobody really knows how many different physical and chemical resources there are

But 100000000 different resources?

Nonequilibrium Coexistence

Many if not most ecosystems are

- not in equilibrium
- but fluctuate

Fluctuating systems allow more species

Armstrong & McGehee 1980s, Weissing & Huisman

Attractors

Every combination of species is represented by a dynamical system

Every dynamical system has its attractor(s)

- equilibrium/periodic orbit/chaos

Hofbauer & Sigmund, Rinaldi

Permanence

In a permanent ecosystem no species will go extinct

Every participating species will invade when rare

(ignoring 'Humpty Dumpty' effects)

Therefore to work out which species coexist we have to calculate their invasion exponent

Hofbauer & Sigmund, Rand

Invasion exponent

If a species' invasion exponent is positive
it will invade the ecosystem

Invasion exponents can (in principle)
be derived from the dynamical system

- work out attractor without species
- calculate long-term average growth rate

Ecosystem Dynamics

Caricature

- ‘Species dynamics depends on other species directly or indirectly
- Biodiversity is given by how many species from a given species pool can invade the community
- If no new species can invade, the community is saturated’

Jonathan (Joan) Roughgarden, Stuart Pimm

Important Insights

Population Genetics

- new mutants 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

Adaptive Dynamics

Adaptive Dynamics

Caricature

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

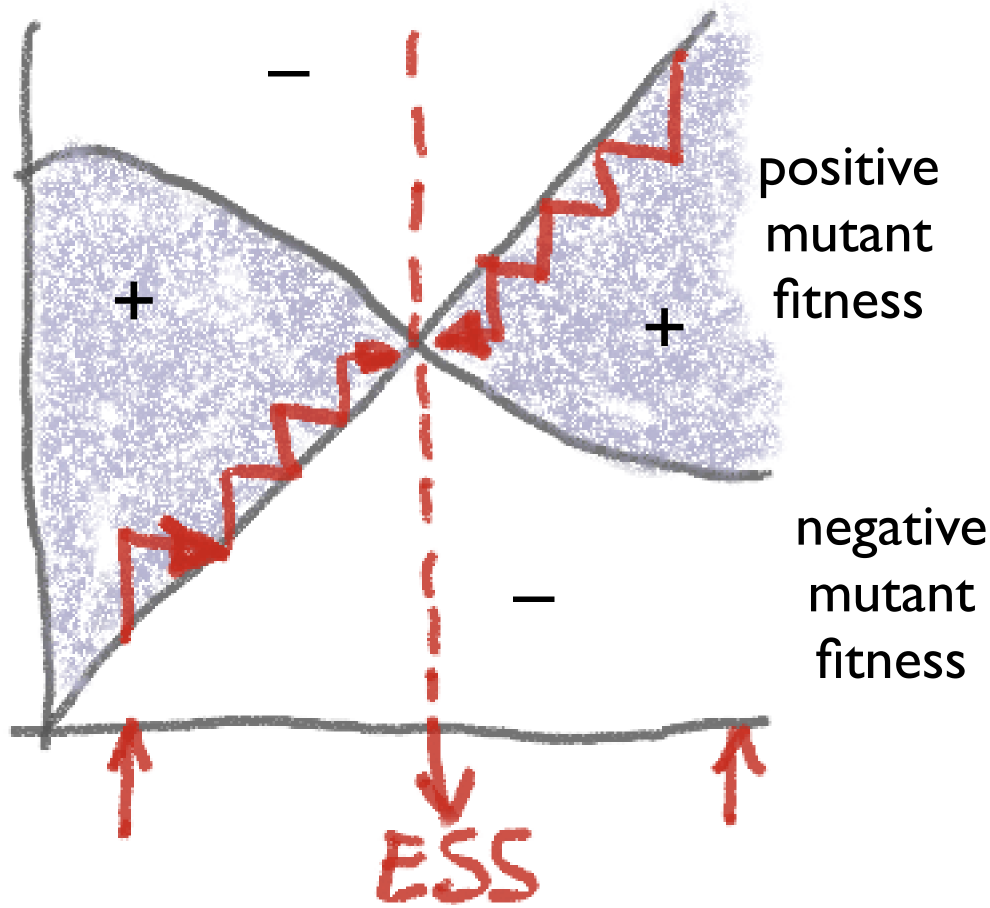
Peter Hammerstein, Ilan Eshel, Hans Metz,
David Rand, Geza Meszena,
Ulf Dieckmann,
Stefan Geritz, Eva Kisdi,

Adaptive Dynamics

Practical Method

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

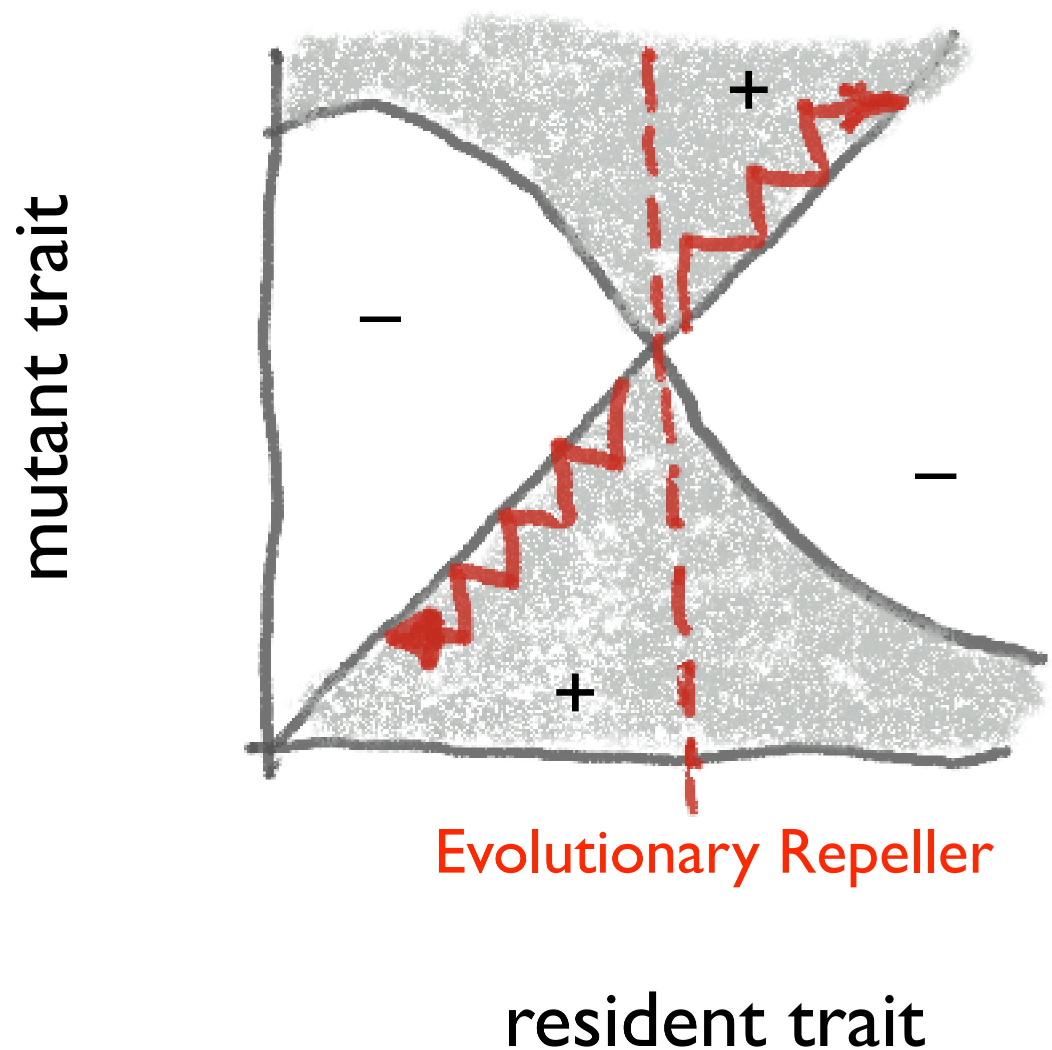
Pairwise Invasibility Plot



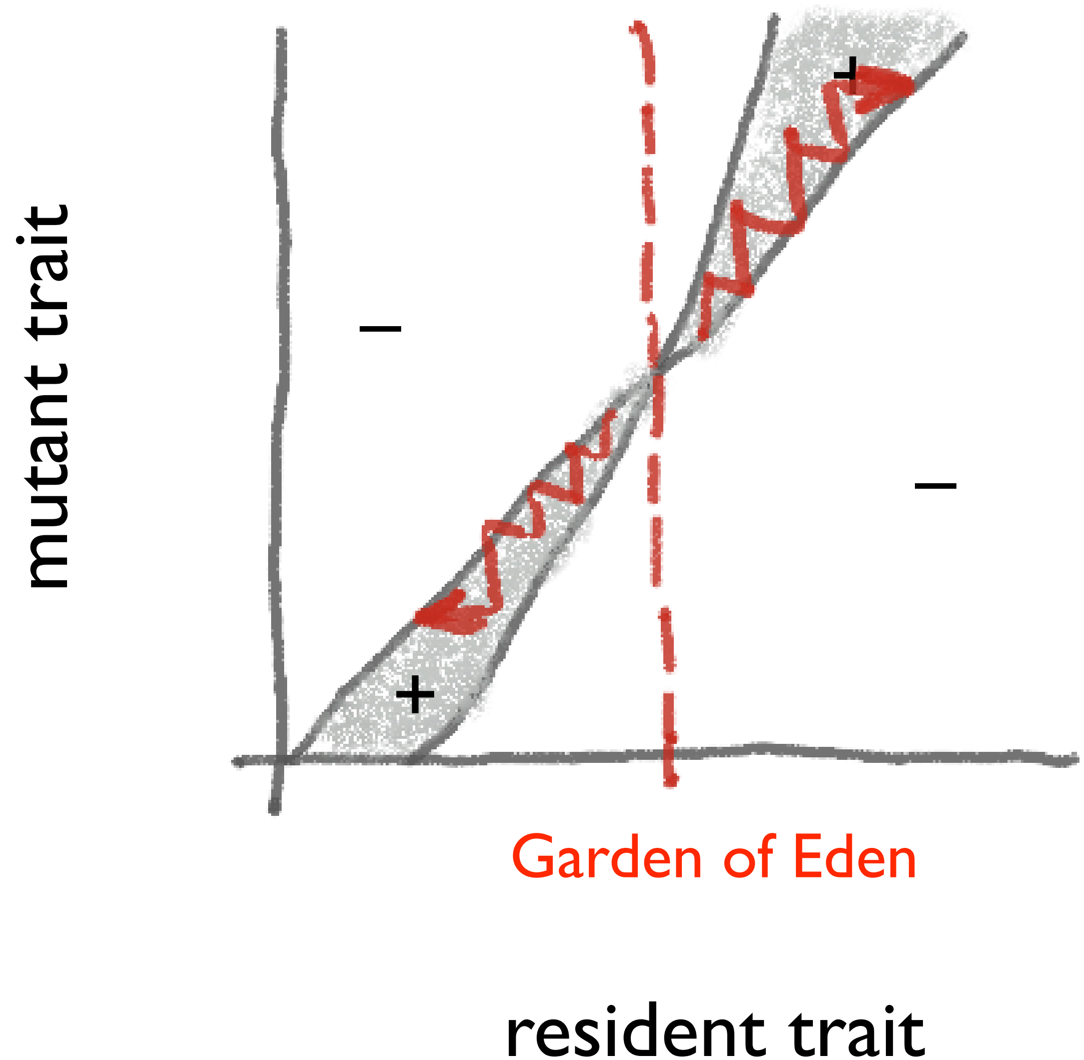
mutant trait

resident trait

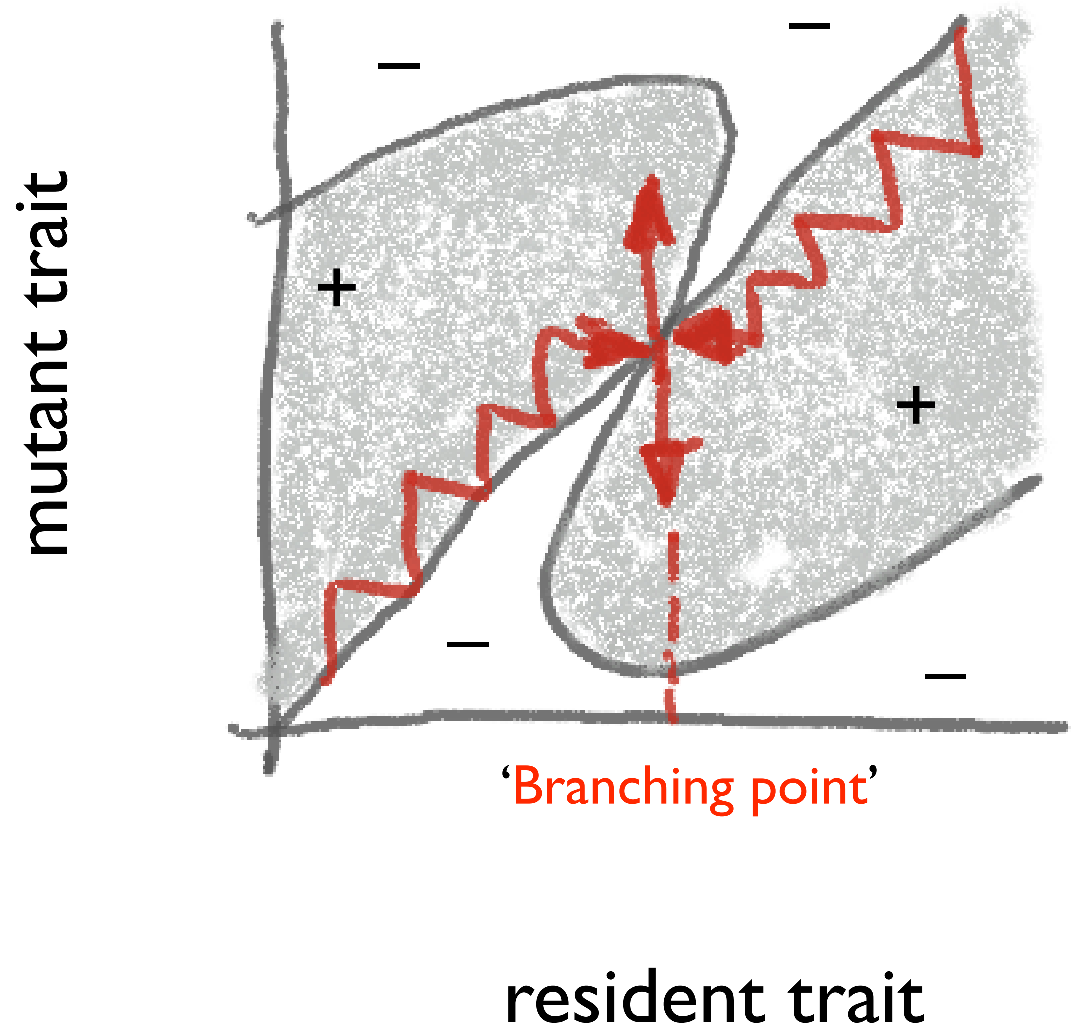
Pairwise Invasibility Plot



Pairwise Invasibility Plot



Pairwise Invasibility Plot

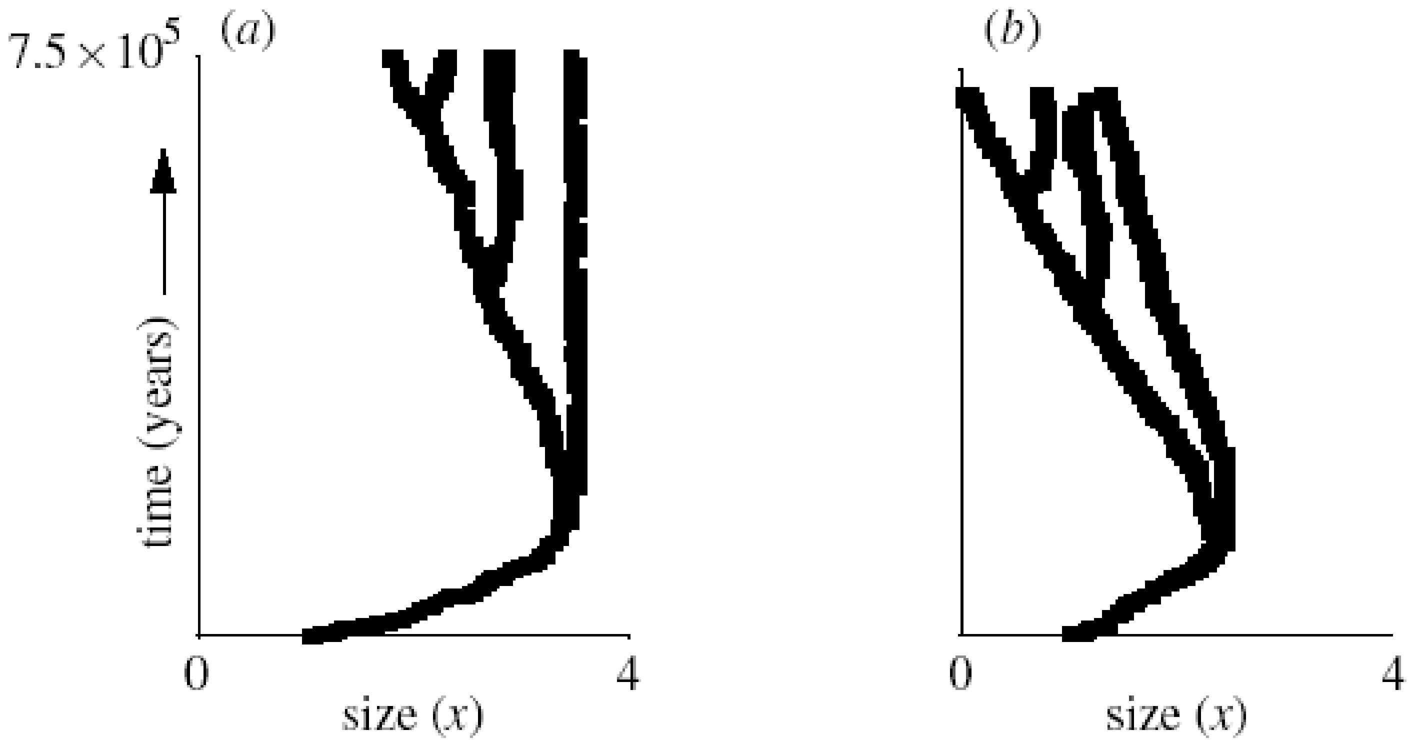


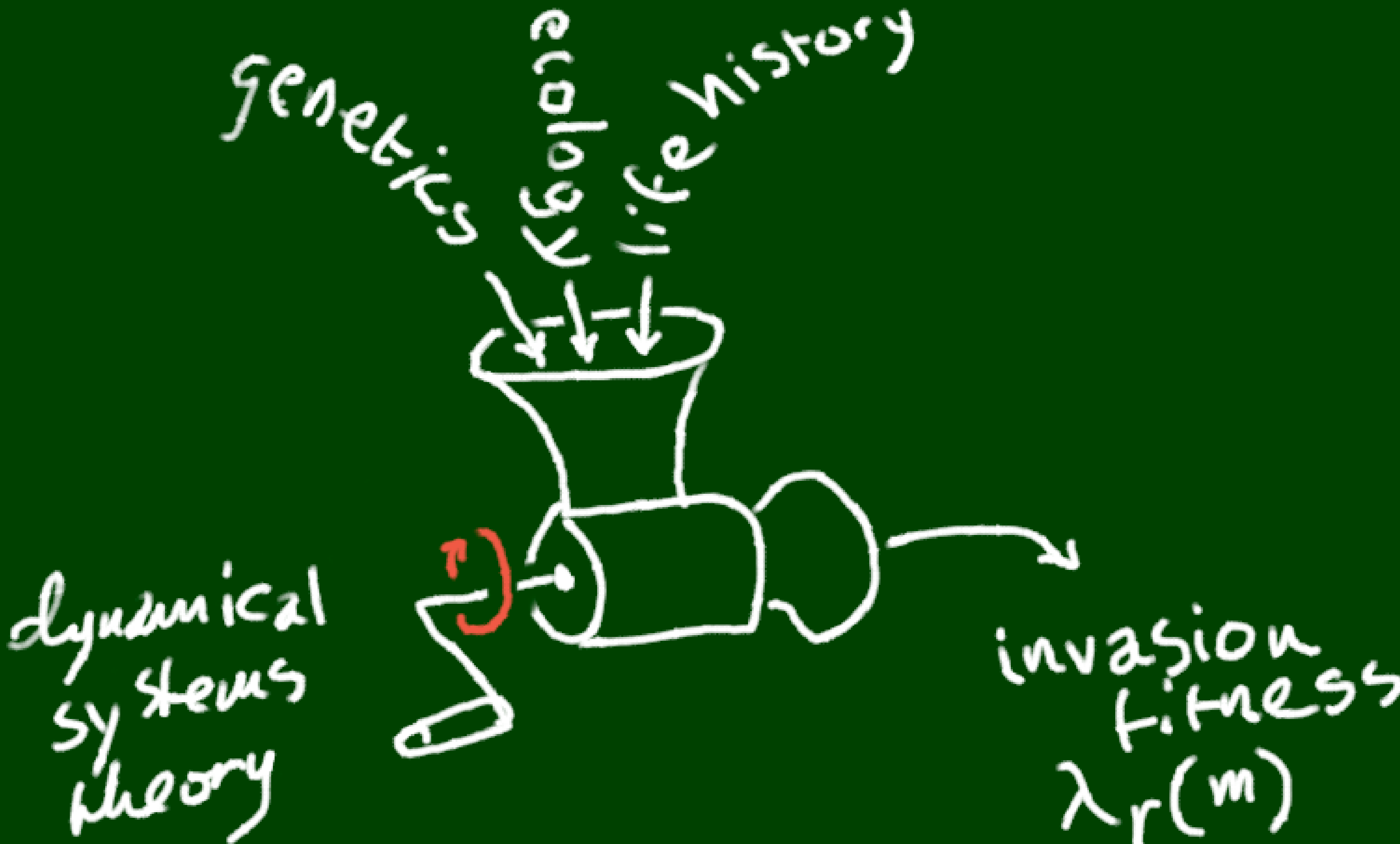
Asymmetric Competition

model by Éva Kisdi & Stefan Geritz (2001)

- complicated mechanistic model
- simplified caricature

Kisdi & Geritz




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

Adaptive Dynamics

Singular points may be

- Evolutionarily Stable
  - when no mutant can invade
- Convergence Stable
  - when the population will evolve *towards* it

ES points not necessarily CS and *vice versa*

Hans Metz,
David Rand,
Richard Law.
Ulf Dieckmann,
Stefan Geritz, Eva Kisdi

$$P = \frac{\partial^2 \lambda}{\partial a_m^2}$$

$$Q = \frac{\partial^2 \lambda}{\partial a_r^2}$$

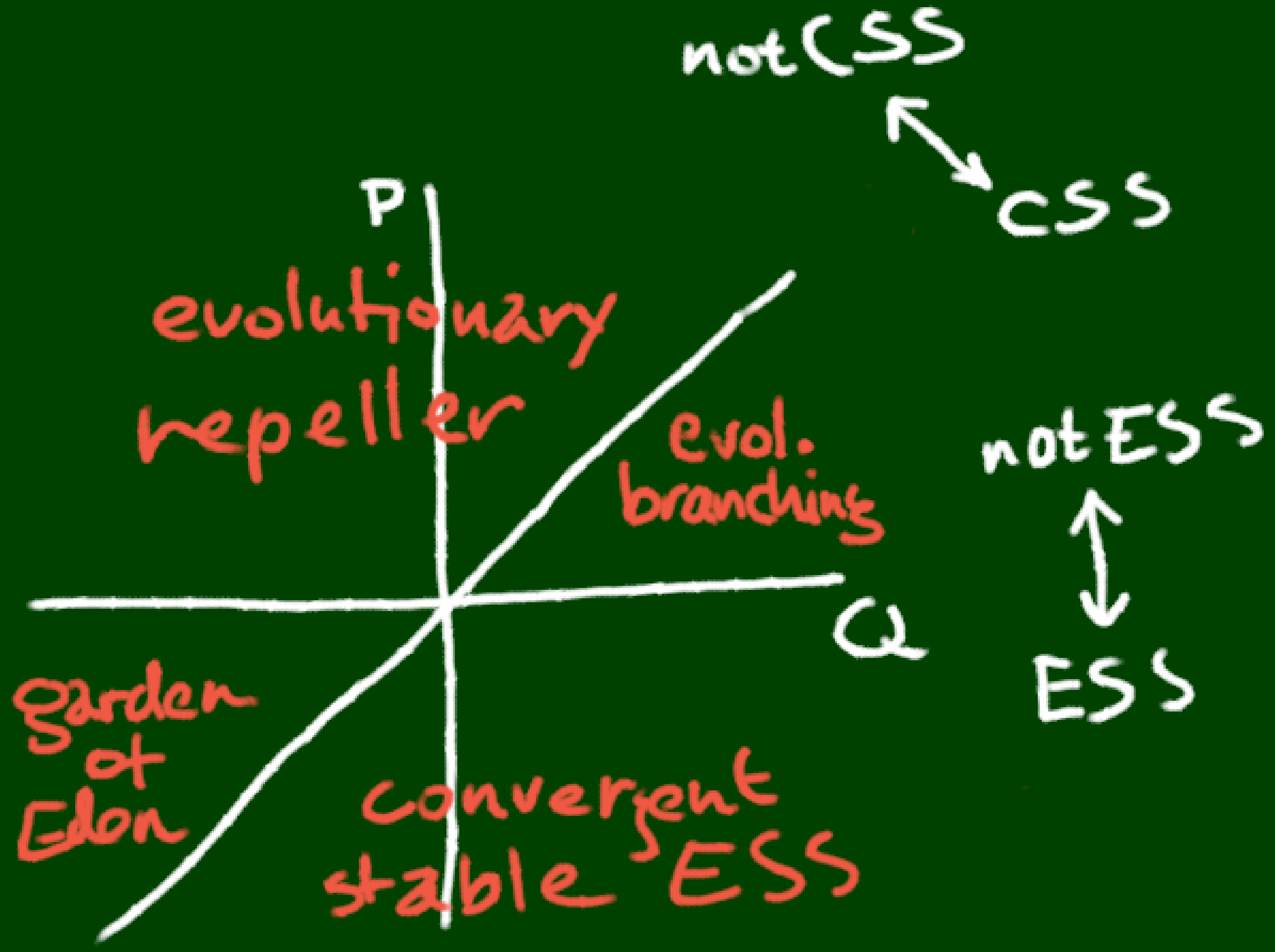
both evaluated at singular point

evolutionary stability:

$P < 0$ ESS

convergence stability:

$Q < P$ CSS



not CSS
CSS
not ESS
ESS
P
Q
evolutionary repeller
evol. branching
garden of Eden
convergent stable ESS