Introduction to Adaptive Dynamics

(also Evolutionary Invasion Analysis)

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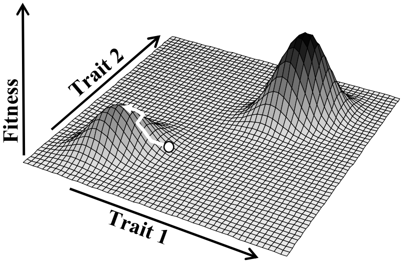
Optimizing selection (**static** fitness landscape)

- Fisher (1930)'s "fundamental theorem of natural selection": *"The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time."*
- Wright (1932): adaptive evolution as a hill-climbing process on a **static** landscape



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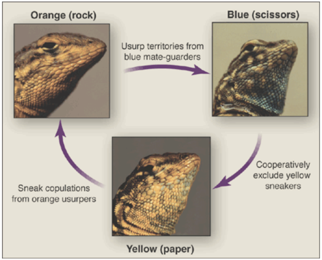
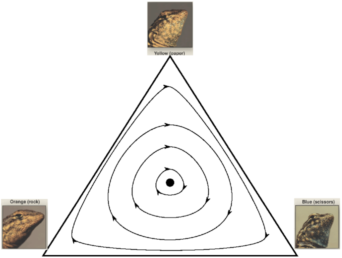
Frequency-dependent selection (**dynamic** fitness landscape)

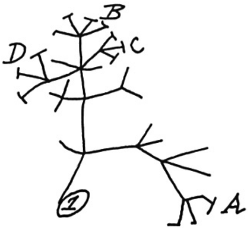
- Frequency-dependent selection occurs when fitness depends on the phenotype frequencies in the population
- Evolutionary Game Theory (Maynard-Smith, 1973)
- Trades genetical realism against ecological realism
- **No optimization principle in general**



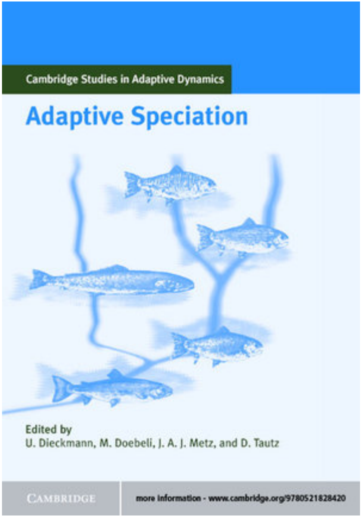


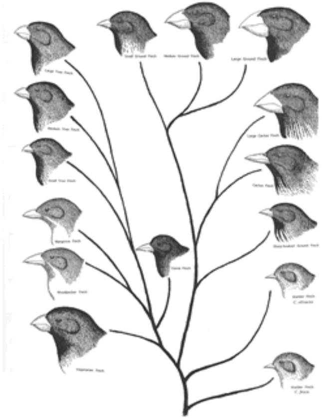
Adaptive dynamics

- A framework to model phenotypic evolution
- Based on ecological dynamics (includes density-dependence)
- Main assumption: mutation are rare (one at a time)
  - Fast ecological dynamics compared to evolutionary dynamics
  - Resident population challenged by small mutant sub-pop.
- Additional assumptions:
  - Mutations have small phenotypic effects
  - Reproduction is clonal (can be relaxed)



BIG QUESTION: EMERGENCE AND MAINTENANCE OF BIODIVERSITY





Darwin's finches
(Galápagos Islands)

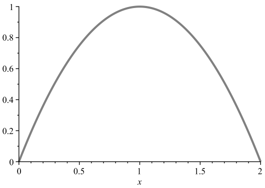
FROM ECOLOGY TO EVOLUTION: LOTKA-VOLTERRA COMPETITION

- N competing species: for $i, j = 1, 2, \ldots, N$

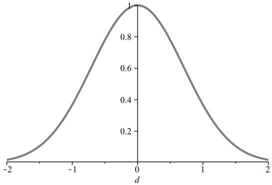
$$\frac{1}{n_i}\frac{\mathrm{d}n_i}{\mathrm{d}t} = r\left[1 - \frac{\sum_j a(x_i, x_j)n_j}{K(x_i)}\right]$$

  - n_i: species i's population density
  - x_i: species i's trait or phenotype (e.g. beak size)

- $K(x) = (K_0 - \lambda(x - x_0)^2)_+$
- $a(x_i, x_j) = \mathrm{e}^{-\frac{1}{2}(x_i - x_j)^2/\sigma_a^2}$



related to e.g. seed size distribution



competition function of distance $d = x_i - x_j$

From Ecology to Evolution: Lotka-Volterra competition

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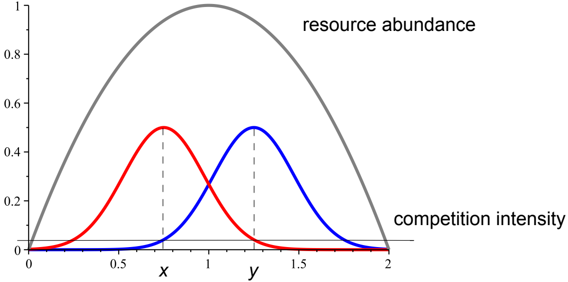


FROM ECOLOGY TO EVOLUTION: MUTANT INVASION

- Fast ecological dynamics compared to evolution
- Resident pop. at demographic attractor $(\hat{n}_1, \hat{n}_2, \ldots, \hat{n}_N)$
- Introduction of a mutant trait $\tilde{x}$ at very low density

$$\frac{1}{\tilde{n}}\frac{\mathrm{d}\tilde{n}}{\mathrm{d}t} = r\left[1 - \frac{\sum_i a(\tilde{x}, x_i)\hat{n}_i}{K(\tilde{x})}\right]$$

- For a monomorphic resident pop. with trait x: $\hat{n} = K(x)$
- The **invasion fitness** of a mutant trait y is

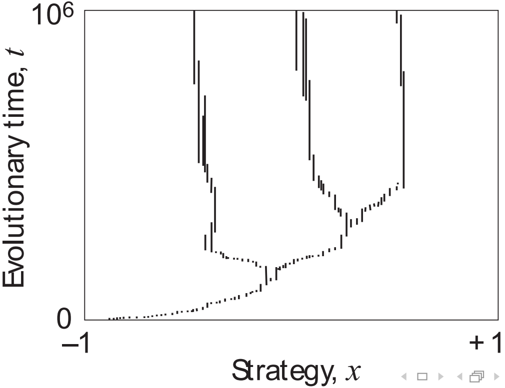
$$s(x,y) = r\left[1 - a(x,y)\frac{K(x)}{K(y)}\right]$$

- If $s(x,y) < 0$, the mutant goes extinct
- Necessarily, $s(x,x) = 0$ for all x (neutral case)

FROM ECOLOGY TO EVOLUTION: EVOLUTIONARY DYNAMICS

- Canonical equation of Adaptative Dynamics:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \underbrace{m(\hat{n}(x), x)}_{\text{mutation rate}} \times \underbrace{\left.\frac{\partial s(x,y)}{\partial y}\right|_{y=x}}_{\text{selection gradient}}$$

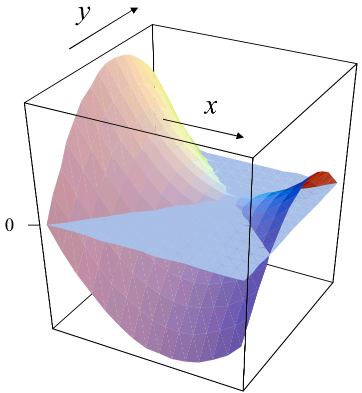


INVASION FITNESS

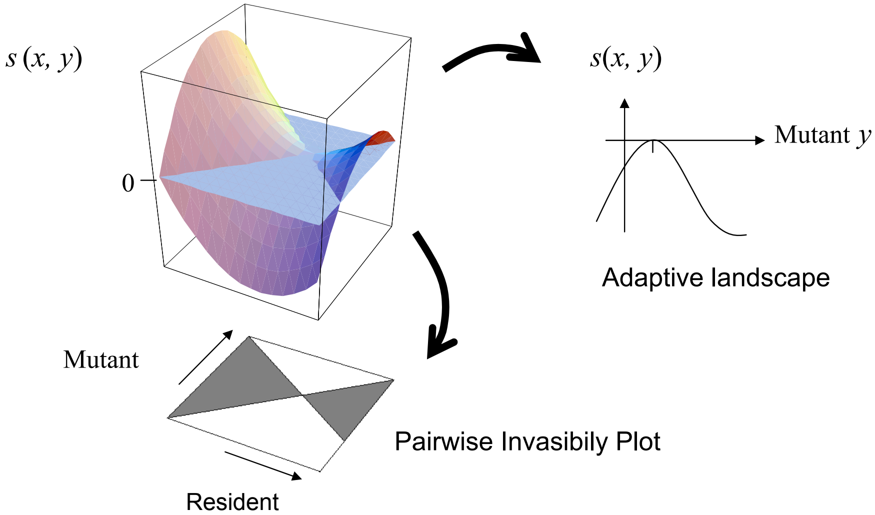
- Definition:

$$s(x,y) = \lim_{t\to\infty} \frac{1}{t} \ln \frac{\tilde{n}(t)}{\tilde{n}(0)}$$

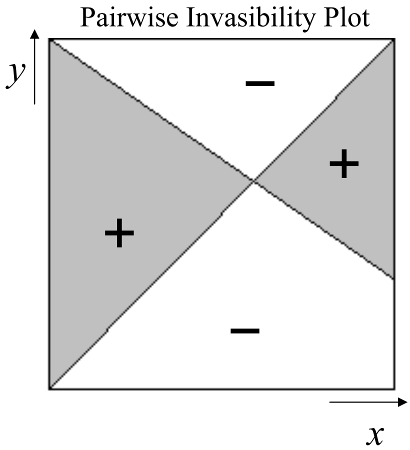
  intrinsic growth rate of **mutant** y against **resident** x (Lyapunov exponent)
- If $s(x,y) < 0$ the mutant is counter-selected
- If $s(x,y) > 0$ the mutant may invade

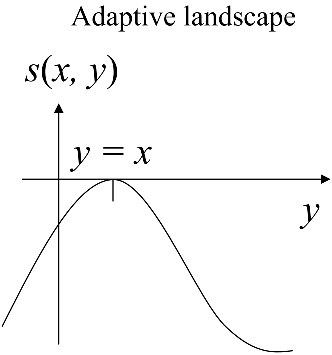


Adaptive landscape and Pairwise Invasibility Plot 1/2



ADAPTIVE LANDSCAPE AND PAIRWISE INVASIBILITY PLOT 2/2

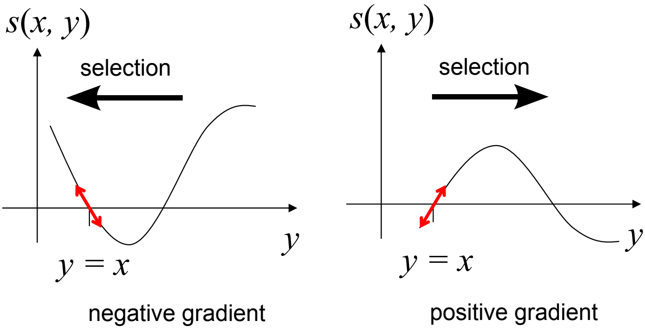




Selection gradient

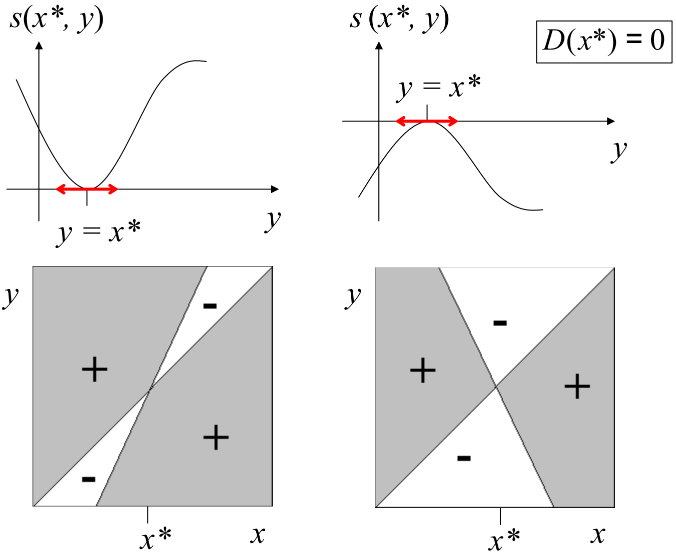
$$D(x) = \left.\frac{\partial s(x,y)}{\partial y}\right|_{y=x}$$

It's the slope of Invasion fitness in the vicinity of the resident trait

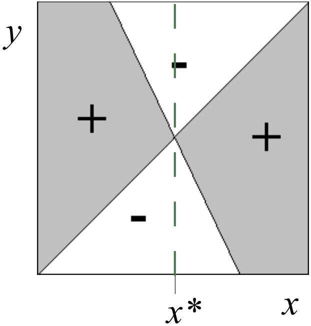


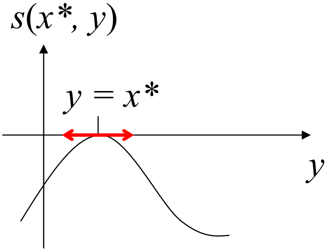
Its sign provides the direction of selection

EVOLUTIONARILY SINGULAR POINTS (SELECTION GRADIENT IS ZERO)



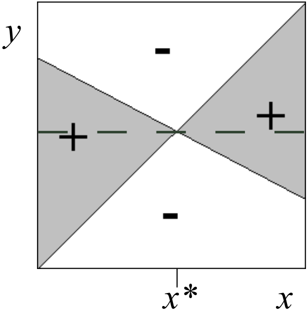
EVOLUTIONARY **STABILITY** OF A SINGULAR POINT

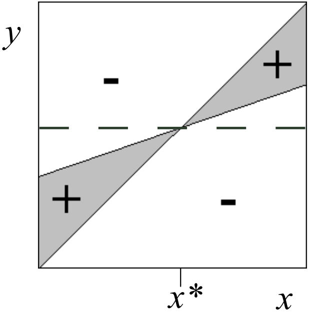




$$\left.\frac{\partial^2 s(x,y)}{\partial y^2}\right|_{y=x=x^*} < 0$$

CAPACITY OF A SINGULAR TRAIT TO INVADE WHEN INITIALLY RARE

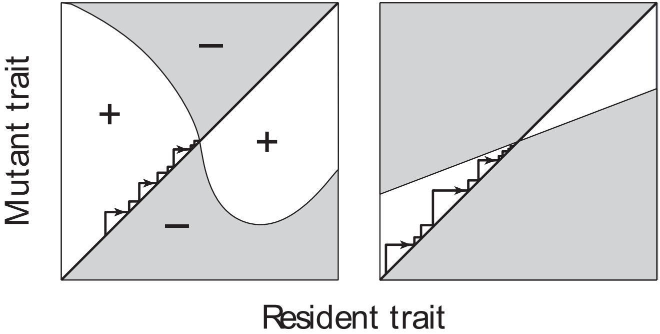




x^* can invade when rare $\qquad$ x^* cannot invade when rare

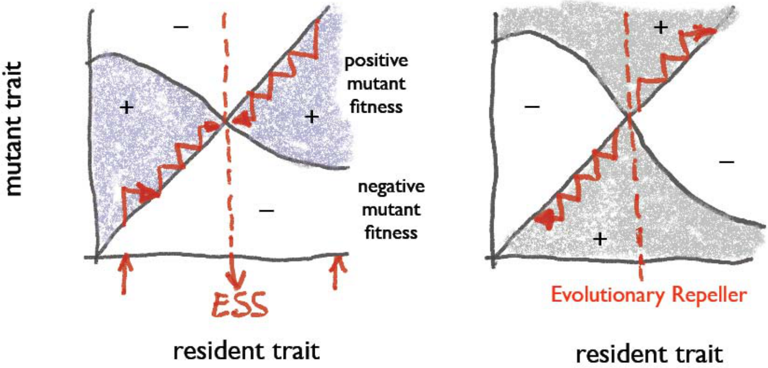
$$\left.\frac{\partial^2 s(x,y)}{\partial x^2}\right|_{y=x=x^*} > 0$$

Evolution may converge to a trait unable to invade

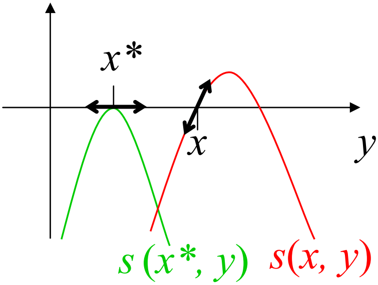


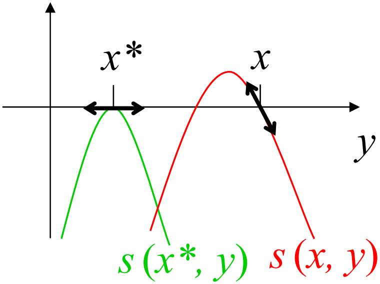
A point that can be reached through small mutational jumps is an attractor of the evolutionary dynamics

Evolutionary **Attractiveness** of a singular point 1/2



EVOLUTIONARY ATTRACTIVENESS OF A SINGULAR POINT 2/2



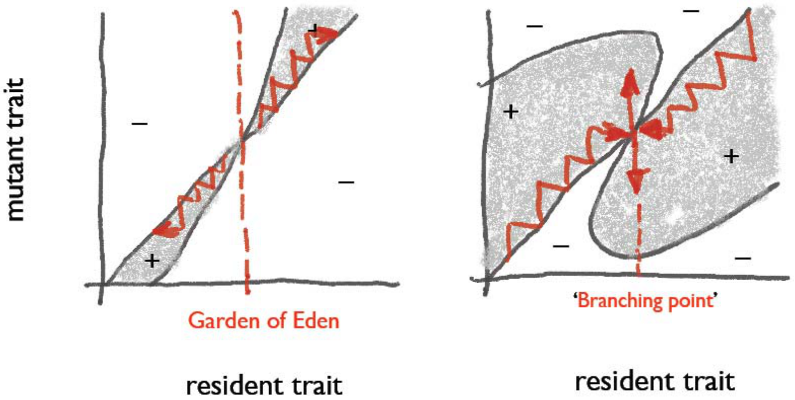


x^* is a repellor

x^* is an attractor

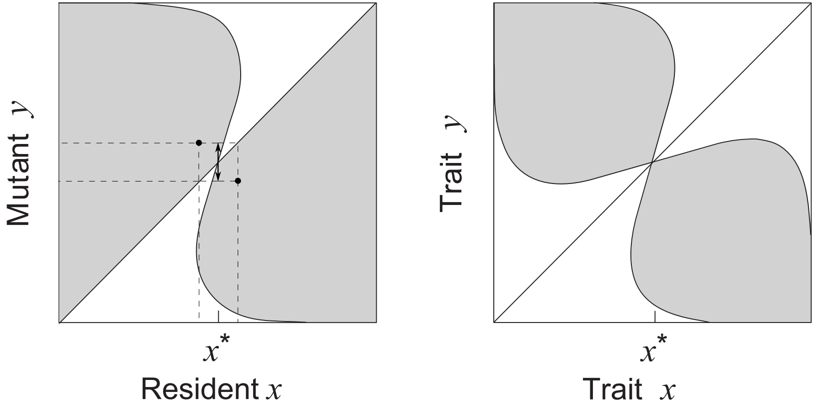
$$\left.\frac{\mathrm{d}D(x)}{\mathrm{d}x}\right|_{x=x^*} = \left.\frac{\partial^2 s(x,y)}{\partial x \partial y} + \frac{\partial^2 s(x,y)}{\partial y^2}\right|_{y=x=x^*} < 0$$

ATTRACTIVENESS DOES NOT IMPLY STABILITY!



MUTUAL INVASION AND POLYMORPHISM MAINTENANCE

2 traits x, y can coexist if $s(x, y) > 0$ **and** $s(y, x) > 0$



$$\left.\frac{\partial^2 s(x,y)}{\partial x^2} + \frac{\partial^2 s(x,y)}{\partial y^2}\right|_{y=x=x^*} > 0$$

CONDITIONS FOR **EVOLUTIONARY BRANCHING** TO OCCUR

1. selection gradient is zero at the branching point x^*:

$$\left.\frac{\partial s(x,y)}{\partial y}\right|_{y=x=x^*} = 0$$

2. x^* is an evolutionarily attracting point:

$$\left.\frac{\partial^2 s(x,y)}{\partial x \partial y} + \frac{\partial^2 s(x,y)}{\partial y^2}\right|_{y=x=x^*} < 0$$

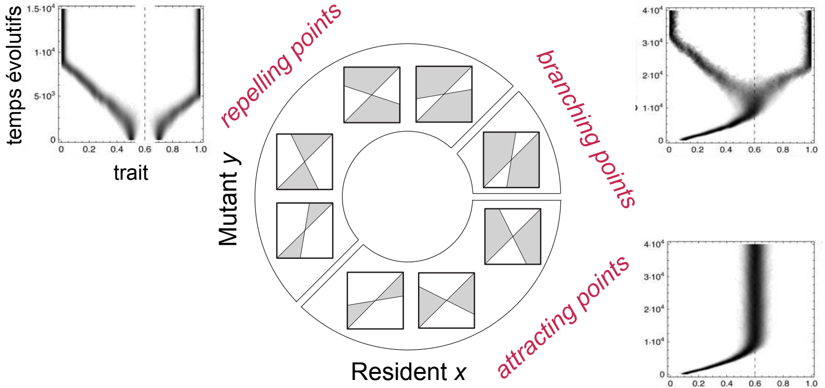
3. x^* is evolutionarily **un**stable:

$$\left.\frac{\partial^2 s(x,y)}{\partial y^2}\right|_{y=x=x^*} > 0$$

4. Traits on both sides of (and close to) x^* can coexist:

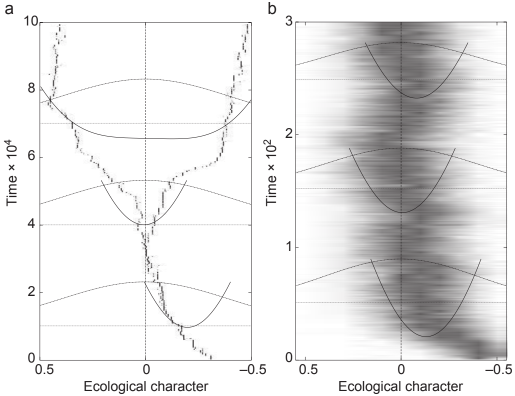
$$\left.\frac{\partial^2 s(x,y)}{\partial x^2} + \frac{\partial^2 s(x,y)}{\partial y^2}\right|_{y=x=x^*} > 0$$

Graphical overview of the possible dynamics



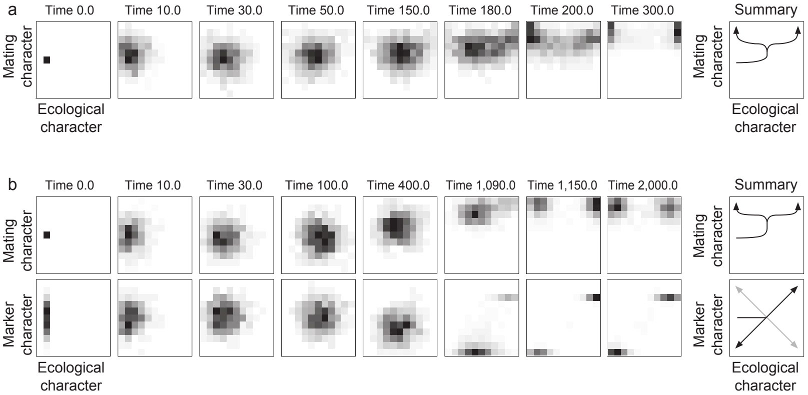
A FAMOUS (AND CONTROVERSIAL) PAPER 1/3

Dieckmann U, Doebeli M (1999) On the origin of species by sympatric speciation **Nature** 400:354–357.



A famous (and controversial) paper 2/3

Dieckmann U, Doebeli M (1999) On the origin of species by sympatric speciation **Nature** 400:354–357.



A FAMOUS (AND CONTROVERSIAL) PAPER 3/3

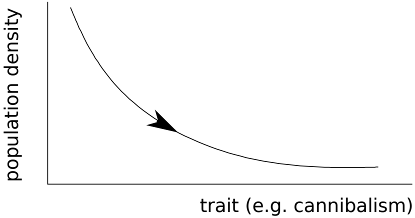
Dieckmann U, Doebeli M (1999) On the origin of species by sympatric speciation **Nature** 400:354–357.

> *Our results extend and contrast previous insights by showing that competition for unimodal resources can initiate sympatric speciation even if assortative mating depends on an ecologically neutral marker trait. [...] Evidence is accumulating that ecology is important for speciation and our theory may provide an integrative framework for understanding otherwise puzzling evidence for monophyletic origins of many sympatric species, including cichlids, sticklebacks, snails, giant senecios and anolis lizards. In all these cases, it is likely that frequency-dependent mechanisms are important determinants of the species' ecologies.*

The controversy: population geneticists *versus* evolutionary ecologists, see the target review by Waxman & Gavrilets (2005) in J. Evol. Biol. and the 15 associated commentary papers.

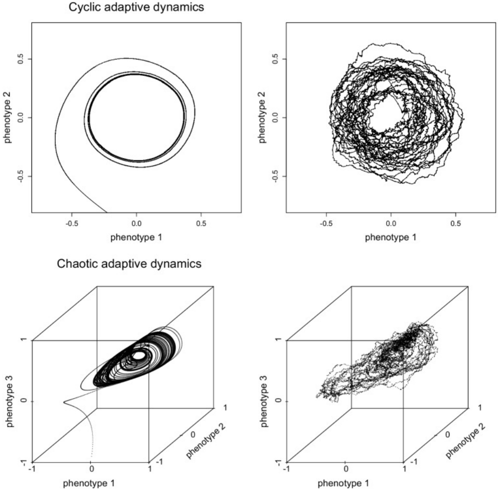
Evolution can lead the population to extinction

- Example: the evolution of cannibalism



- Short-sighted selection for selfish behavior can lead to sub-optimal outcomes for the population
- Analogy with the tragedy of the commons in Economics

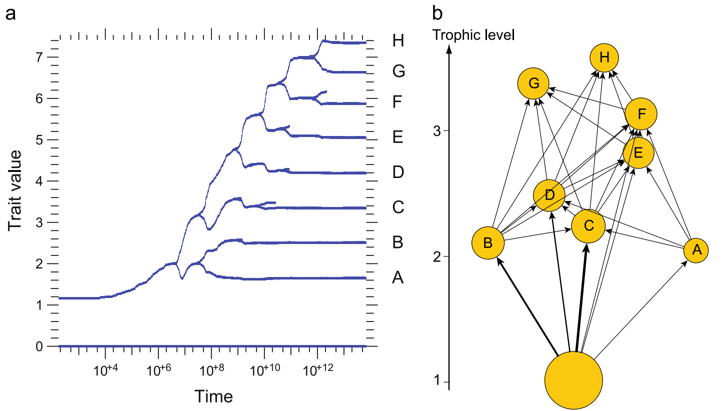
EVOLUTIONARY DYNAMICS CAN BE CYCLIC OR CHAOTIC*



*Doebeli et al (2017) eLife.

Recent developments

Theor Ecol



Brännström A, Loeuille N, Loreau M, Dieckmann U (2011) Emergence and maintenance of biodiversity in an evolutionary food web model. *Theor. Ecol.*

Resources and references

1. Lecture slides by Virginie Ravigné:
   `fr.slideshare.net/seminairemee/ravign-2010`
2. Lecture slides by Minus van Baalen:
   `ecologie.snv.jussieu.fr/minus/courses/Gulbenkian2007.pdf`
3. Lectures notes by Odo Diekmann (with exercises):
   `www.math.ens.fr/equipes/edp/biomath/diekmann14012003.pdf`
4. Book 'Adaptive Speciation' by Ulf Dieckmann *et al.*:
   `www.cambridge.org/fr/knowledge/isbn/item6796485/AdaptiveSpeciation`
5. Book 'Adaptive Diversification' by Michael Doebeli:
   `http://press.princeton.edu/titles/9484.html`
6. Bibliographical resources by Eva Kisdi:
   `http://www.mv.helsinki.fi/home/kisdi/addyn.htm`
7. Mini-projects prepared by Eva Kisdi:
   `http://mathstat.helsinki.fi/~kisdi/AD-Oslo/`