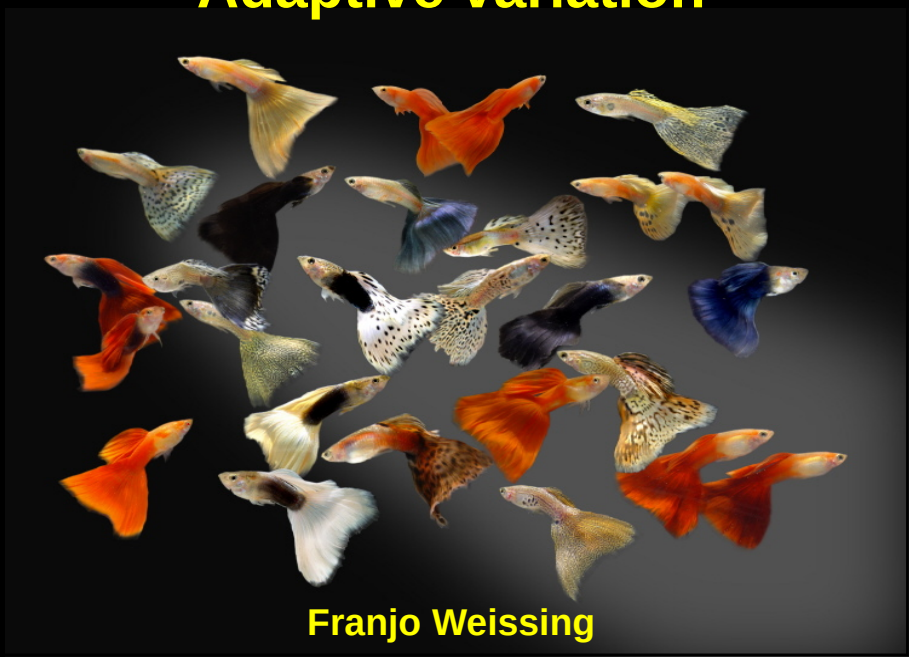
Adaptive variation

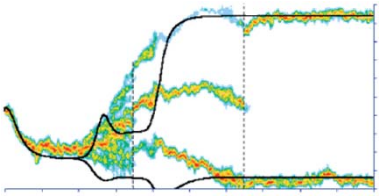


Franjo Weissing

'Adaptive' variation =
variation shaped by selection or competition

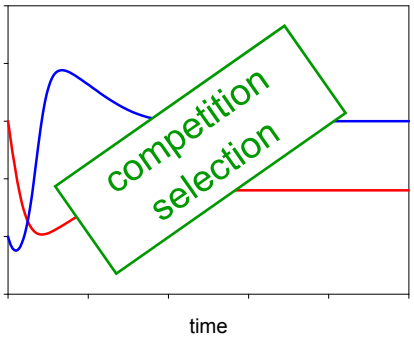
Research topics

- non-equilibrium processes
- sympatric speciation
- genetic polymorphisms
- differences between sexes
- individual differences
  (‘animal personalities’)

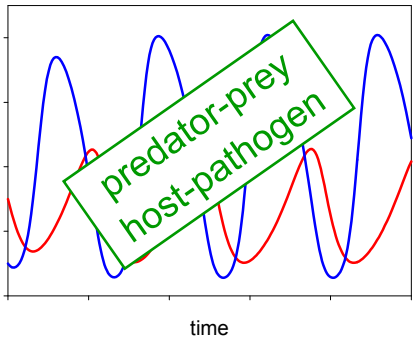


Equilibrium vs non-equilibrium dynamics

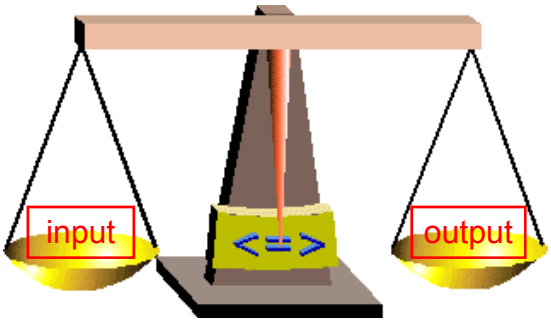
convergence to equilibrium:



non-equilibrium dynamics:



Equilibrium arguments in ecology & evolution



- Population ecology: birth rate = death rate
- Biogeography: immigration = emigration
- Behavioural ecology: benefits = costs

Advantages of an equilibrium analysis

Equilibrium arguments are supposed to be

- relatively simple
- rather robust (not depending on detail)
- rather general

▶ Is this really true?

Two examples

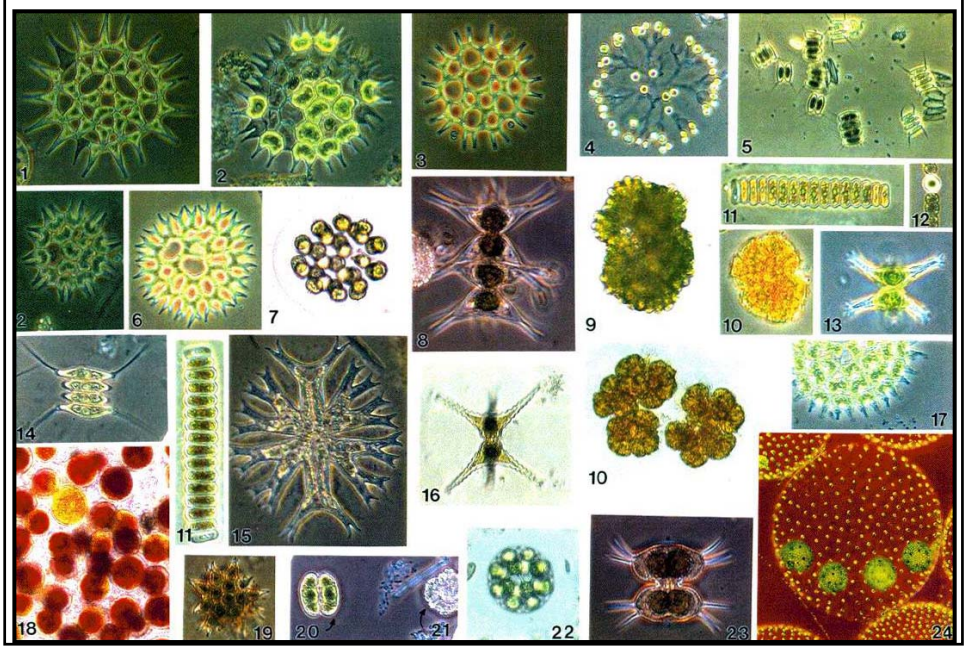
- Resource competition theory:
  "Principle of Competitive Exclusion"

Jef Huisman

- Sexual selection theory:
  "Handicap Principle"

Sander van Doorn

Part I: Explaining plankton diversity



Lotka-Volterra models

Interaction between 2 species:

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1(1 + aN_1 + bN_2)$$
$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2(1 + cN_1 + dN_2)$$

NB: per capita growth rate depends linearly on densities…
(phenomenological modeling approach)

r_1, r_2 :	intrinsic growth rates
a, b, c, d :	interaction coefficients

Lotka-Volterra competition models

Competition between 2 species:

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1(1 - \alpha_{11}N_1 - \alpha_{12}N_2)$$
$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2(1 - \alpha_{21}N_1 - \alpha_{22}N_2)$$

NB: per capita growth rate decreases linearly with densities…

α_{11}, α_{22} :	strength of intra-specific competition
α_{12}, α_{21} :	strength of inter-specific competition

Lotka-Volterra competition

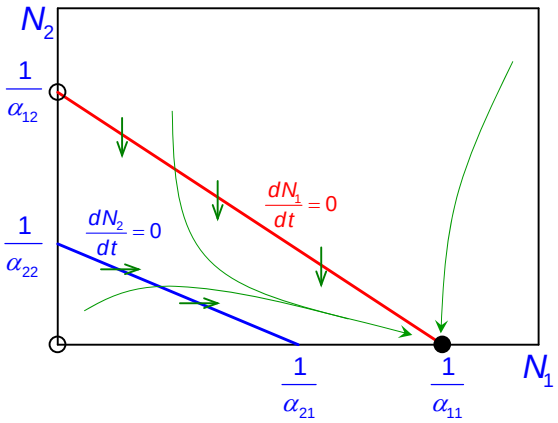
$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1(1-\alpha_{11}N_1-\alpha_{12}N_2)$$
$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2(1-\alpha_{21}N_1-\alpha_{22}N_2)$$

Scenario 1

$\alpha_{11} < \alpha_{21}$

$\alpha_{12} < \alpha_{22}$

1 wins



Lotka-Volterra competition

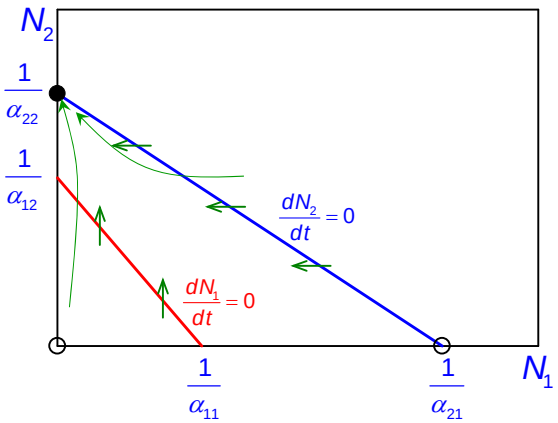
$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1(1-\alpha_{11}N_1-\alpha_{12}N_2)$$
$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2(1-\alpha_{21}N_1-\alpha_{22}N_2)$$

Scenario 2

$\alpha_{11} > \alpha_{21}$

$\alpha_{12} > \alpha_{22}$

2 wins



Lotka-Volterra competition

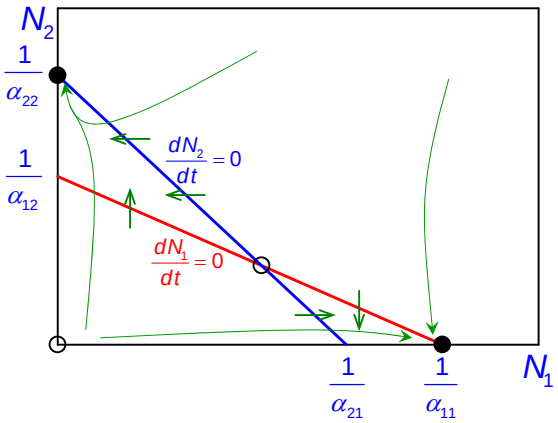
$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1(1-\alpha_{11}N_1-\alpha_{12}N_2)$$
$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2(1-\alpha_{21}N_1-\alpha_{22}N_2)$$

Scenario 3

$\alpha_{11} < \alpha_{21}$

$\alpha_{12} > \alpha_{22}$

1 or 2 wins



Lotka-Volterra competition

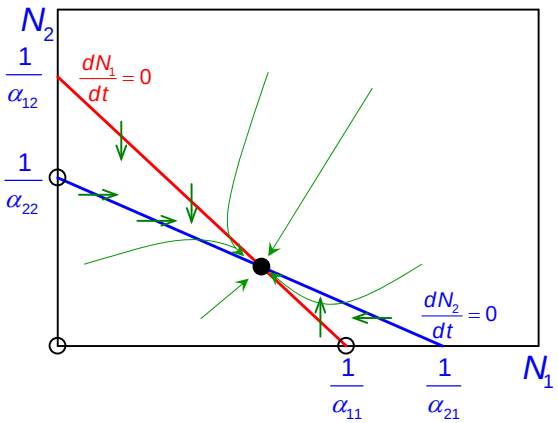
$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1(1-\alpha_{11}N_1-\alpha_{12}N_2)$$
$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2(1-\alpha_{21}N_1-\alpha_{22}N_2)$$

Scenario 4

$\alpha_{11} > \alpha_{21}$

$\alpha_{12} < \alpha_{22}$

coexistence



Lotka-Volterra competition models

Competition between 2 species:

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1(1-\alpha_{11}N_1-\alpha_{12}N_2)$$
$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2(1-\alpha_{21}N_1-\alpha_{22}N_2)$$

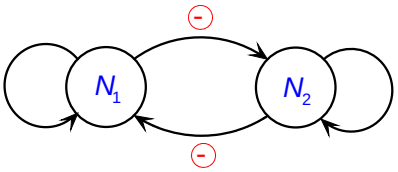
Main conclusion: coexistence if $\alpha_{12}\alpha_{21} < \alpha_{11}\alpha_{22}$

In words: intra-specific competition has to be stronger than inter-specific competition…

Mechanistic competition models

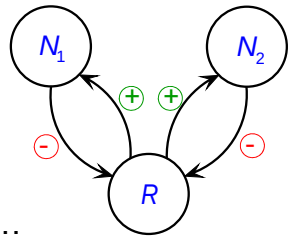
Lotka-Volterra competition models:

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i - \sum_j a_{ij}N_j$$



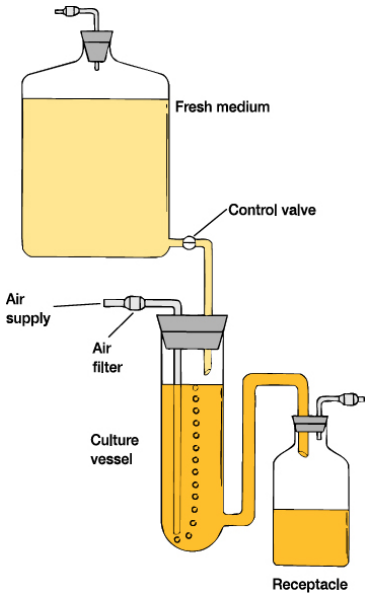
Mechanistic competition models:

$$\frac{1}{N_i}\frac{dN_i}{dt} = f_i(R)$$
$$\frac{dR}{dt} = i - o - c(N_1,\ldots,N_m)$$



resource dynamics modelled explicitly…

Growth and competition in a chemostat



N(t) algal density in chemostat

R(t) resource density in chemostat

S resource density in medium

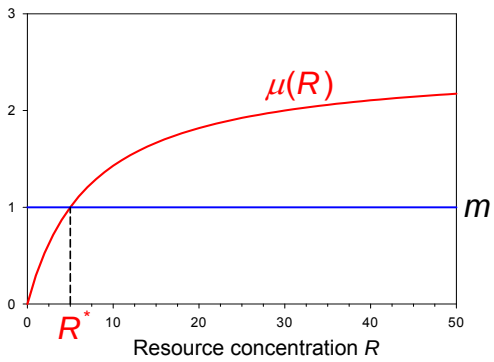
D flow rate

Growth on a single (abiotic) resource

$$\frac{dN}{dt} = N\left(\mu(R) - m\right)$$

$$\frac{dR}{dt} = D(S - R) - c \cdot \mu(R) N$$

Jacques Monod



Monod equation:

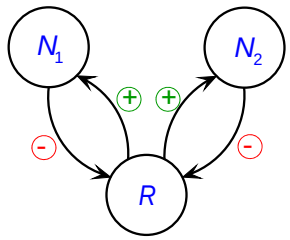
$$\mu(R) = \mu_{max} \frac{R}{R + K}$$

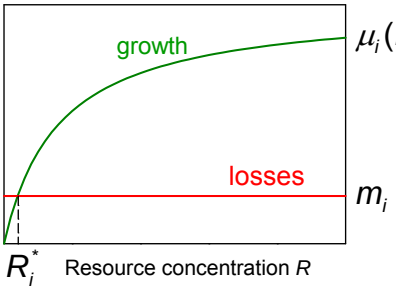
R^*: minimal resource requirement

Competition for a single (abiotic) resource

$$\frac{dN_i}{dt} = N_i\left(\mu_i(R) - m_i\right)$$

$$\frac{dR}{dt} = D(S-R) - \sum c_i \mu_i(R) N_i$$

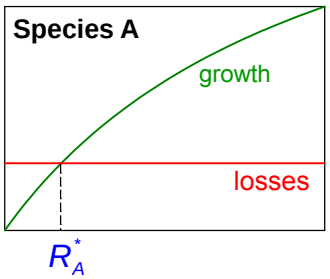


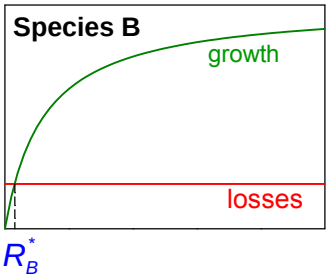


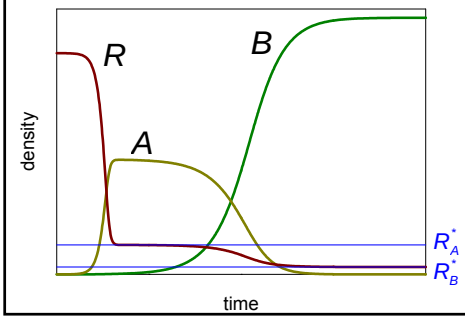
$$\mu_i(R) = r_i \frac{R}{K_i + R}$$

R_i^* : minimal resource requirement of species i

Predicting the outcome of competition





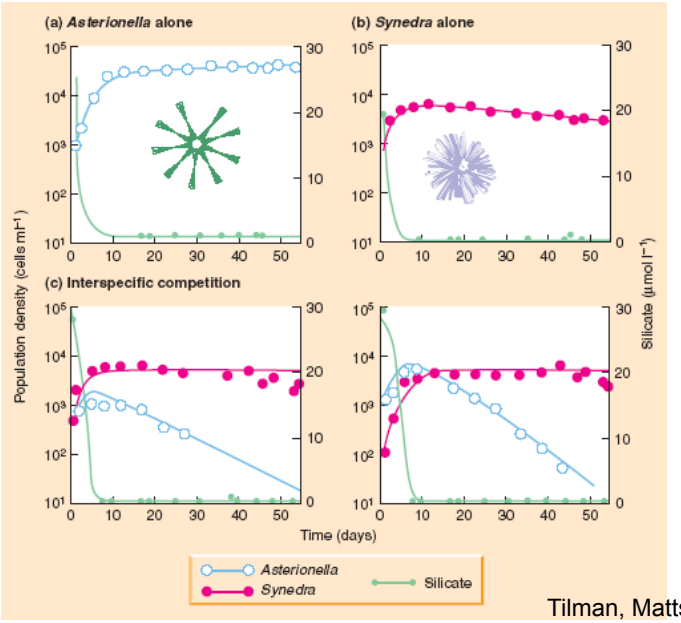


Q: Who will win?

$\Rightarrow$ species with lowest R^* wins!

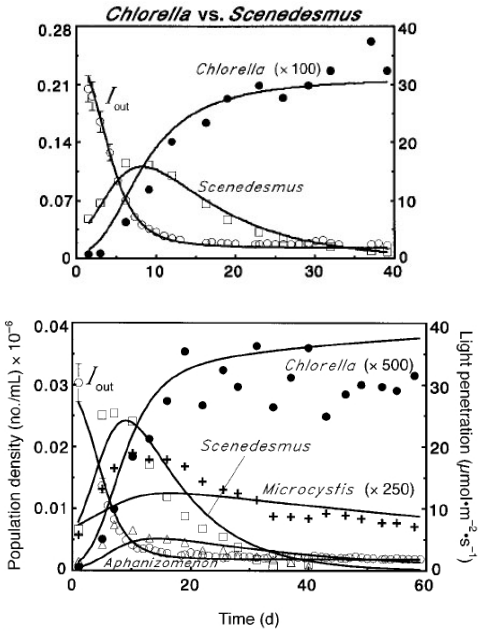
No coexistence!

Experimental confirmation



Tilman, Mattson & Langer 1981

Competition for light in a chemostat



Jef Huisman

- species with lowest R* does indeed win

Huisman, Jonker, Zonneveld & Weissing 1999

Competition for several limiting resources

$$\frac{dN_i}{dt} = N_i\left(\mu_i(R_1,\ldots,R_n) - m_i\right)$$

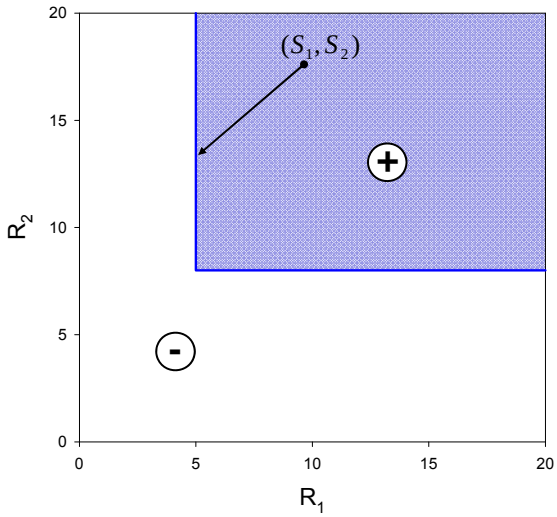
$$\frac{dR_k}{dt} = D(S_k - R_k) - \sum c_{ik}\,\mu_i(R_1,\ldots,R_n)N_i$$

Liebig's law of the minimum:

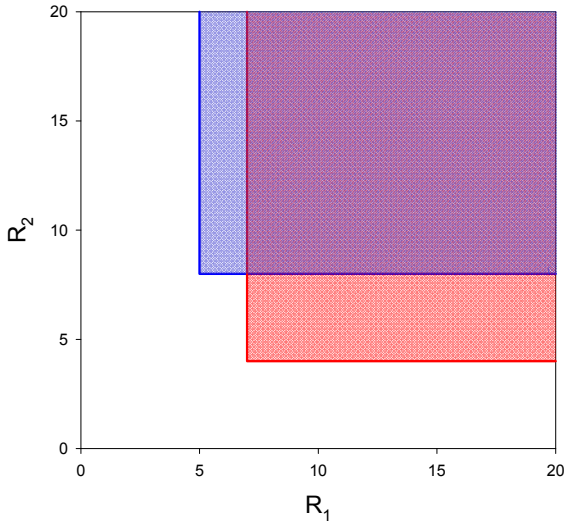
$$\mu_i(R_1,\ldots,R_n) = \mu_{i,\max}\cdot\min\left\{\frac{R_k}{R_k + K_{ik}}\right\}$$

Justus von Liebig

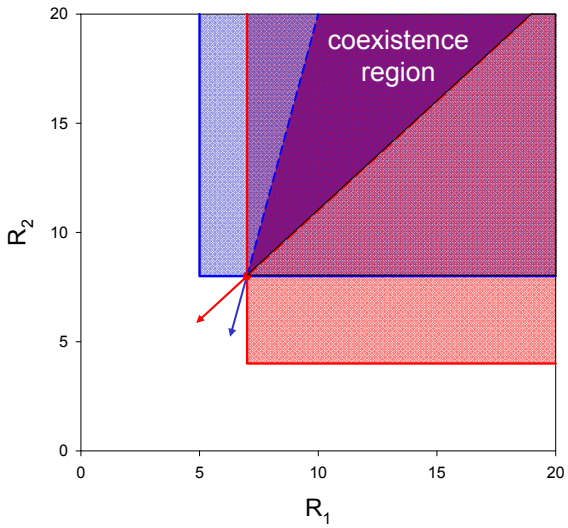
One species on two resources



Two species on two resources

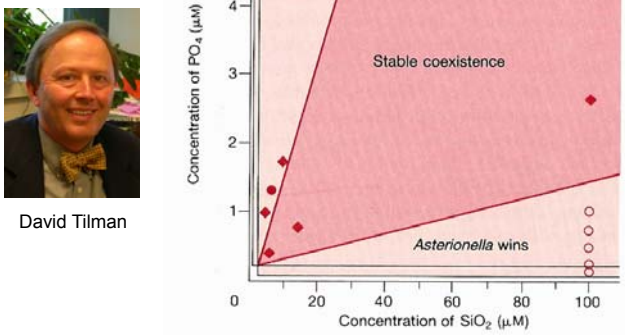


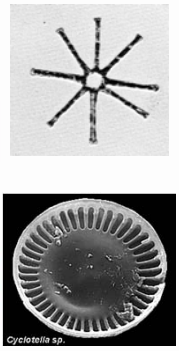
Two species on two resources



- convergence to equilibrium
- coexistence equilibrium, but often exclusion

Competition for two resources in a chemostat





David Tilman

- theory well confirmed experimentally…

The principle of competitive exclusion

- Gause's principle (1934): Species with identical requirements cannot coexist

Georgyi F. Gause

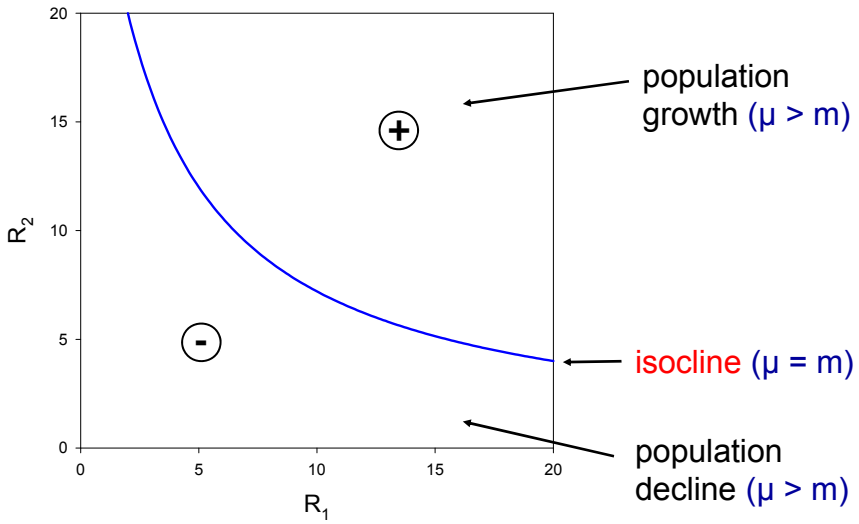
Resource competition models:

$$\frac{dN_i}{dt} = N_i\left(\mu_i(R_1,\ldots,R_n) - m_i\right)$$

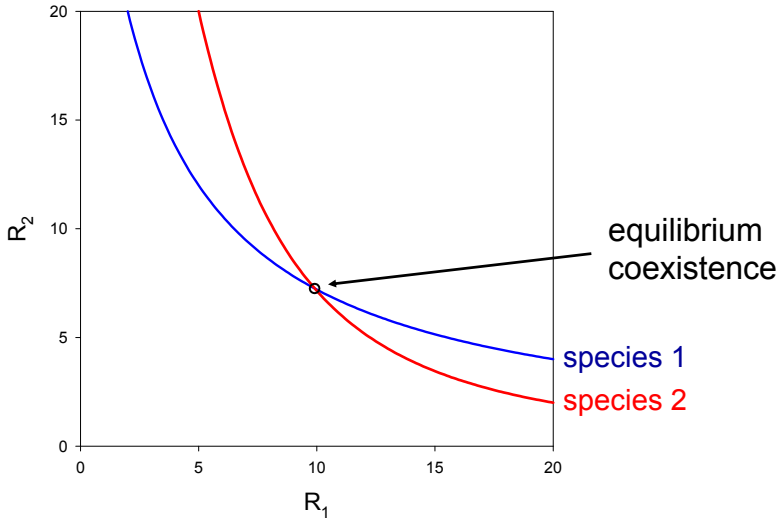
$$\frac{dR_k}{dt} = D(S_k - R_k) - \sum c_{ik}\,\mu_i(R_1,\ldots,R_n)N_i$$

- no more species than limiting resources…

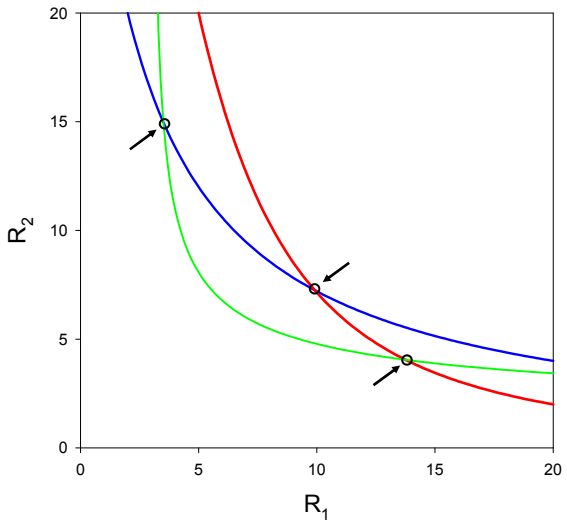
A simple graphical argument…



Competition for two resources



Competition for two resources



competition for 2 resources: not more than 2 species can coexist at equilibrium…

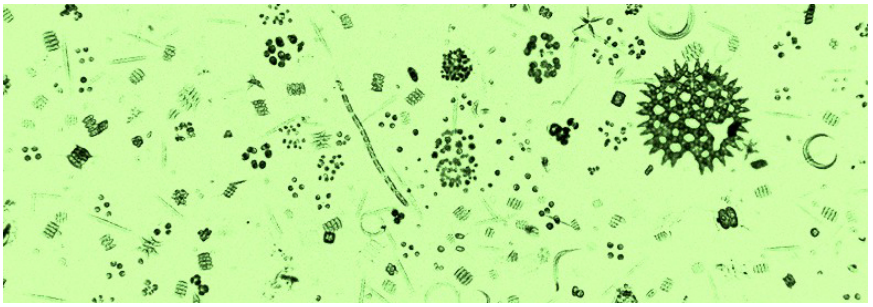
Huisman & Weissing 2001a

The principle of competitive exclusion

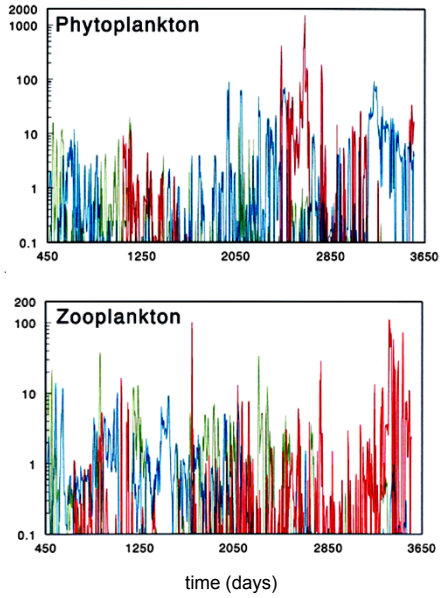
General result:

- no more species can stably coexist at equilibrium than there are limiting factors
- problem: "paradox of the plankton"

Hutchinson (1961)



Are ecological systems in equilibrium?



- What is the cause of non-equilibrium dynamics?

Heerkloss & Klinkenberg (1998)
Beninca et al. (2008)

Potential causes of non-equilibrium dynamics

- temporal variation (e.g. temperature fluctuations)
- spatial heterogeneity (e.g. vertical gradient; vortices)
- predation-induced oscillations
- chemical warfare among phytoplankton

George Evelyn Hutchinson

Question:

- Can competition itself cause oscillations?

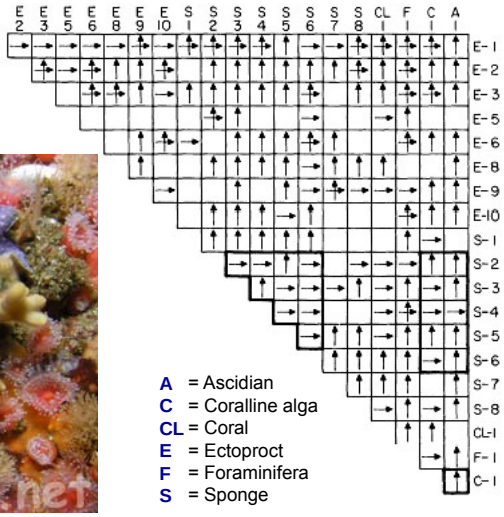
Can competition itself generate oscillations?

General belief:

- competitive dominance is transitive
  (sp1 $\rightarrow$ sp2 $\rightarrow$ sp3 implies sp1 $\rightarrow$ sp3)
- transitive species interactions lead to
  monotonic convergence ($\Rightarrow$ no cycling…)

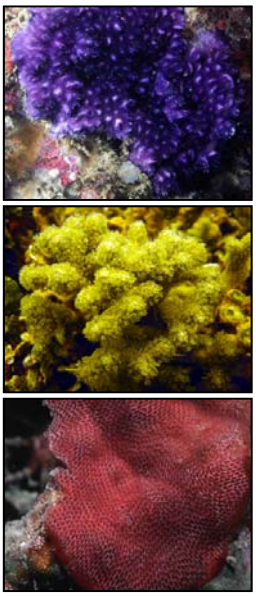
However …

Competitive relationships among reef species



Buss & Jackson 1979

Non-transitive interactions in reef species



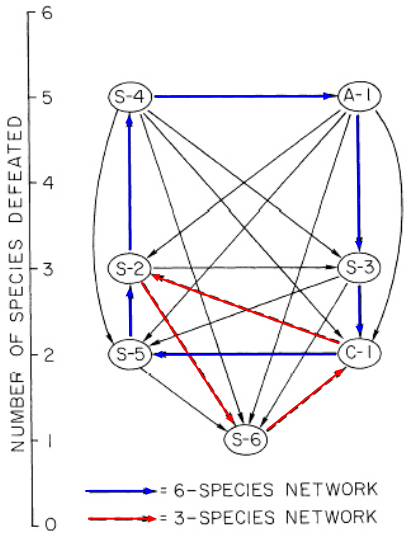


FIG. 3.—Flow diagram of the outcome of competitive interactions within the seven-species subset of the contact matrix illustrated in fig. 2. Two of the many networks are indicated by boldly drawn solid and dashed arrows.

The Rock-Scissors-Paper game

"Rock"

Rock beats scissors.

"Scissors"

Paper beats rock.

"Paper"

Scissors beats paper.

Resource competition: a possible scenario

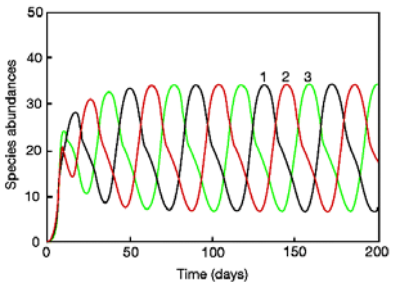
Example: 3 species competing for 3 resources

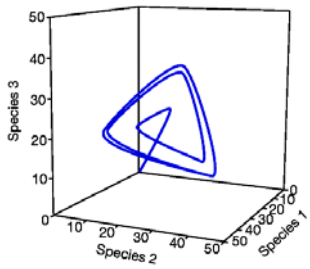
- species 1 is a strong competitor for resource 1, but consumes much of resource 2
- species 2 is a strong competitor for resource 2, but consumes much of resource 3
- species 3 is a strong competitor for resource 3, but consumes much of resource 1

Result:

- non-transitivity (sp1 → sp2 → sp3 → sp1 …)

Outcome of cyclic resource competition

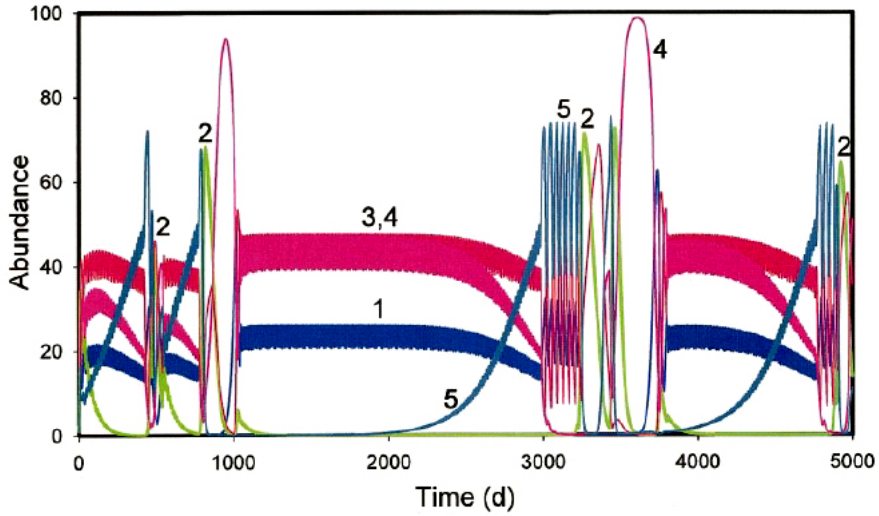




- competition does not necessarily lead to equilibrium
- competitive systems can oscillate forever…

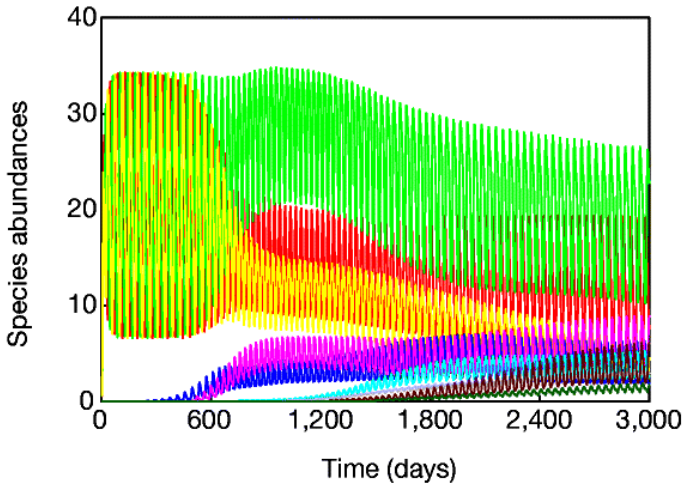
Huisman & Weissing 1999, 2002, Revilla & Weissing 2007

Complex dynamics of competition



Huisman & Weissing 2001a, Revilla & Weissing 2007

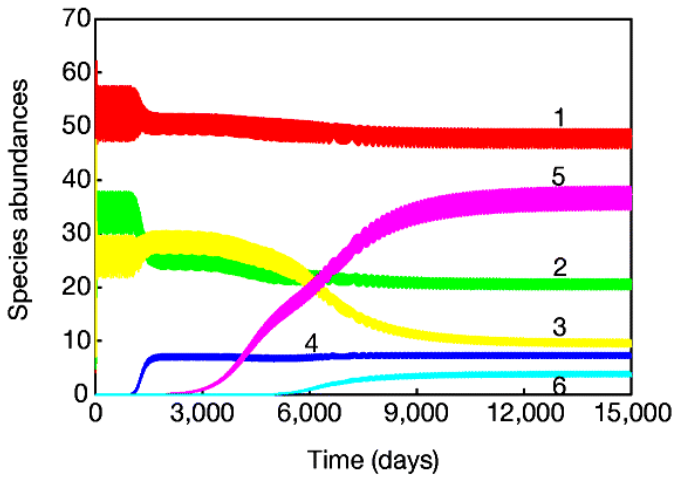
Consequences of non-equilibrium dynamics



- coexistence of 9 species on 3 limiting resources…

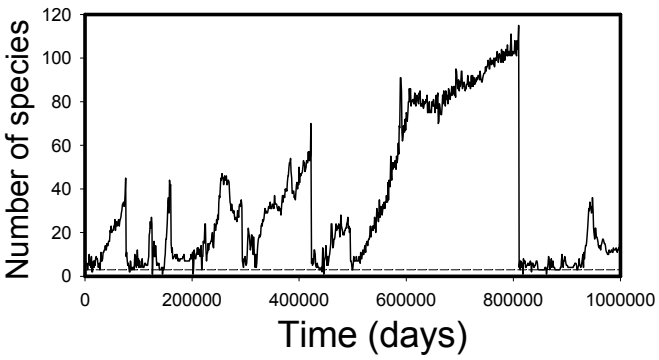
Huisman & Weissing 1999, Revilla & Weissing 2007

Consequences of non-equilibrium dynamics



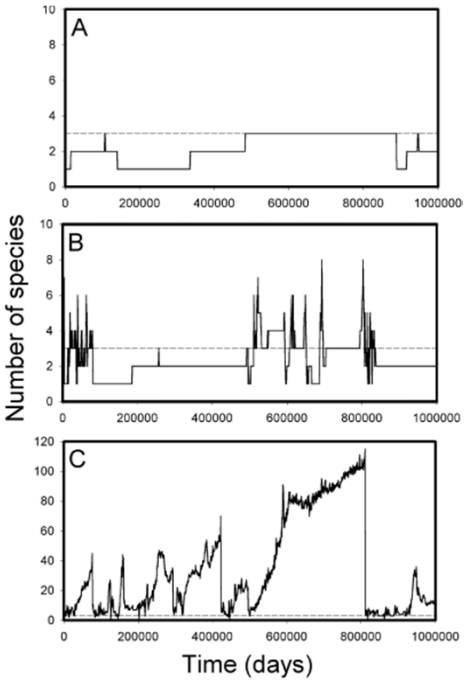
- ‘almost’ in equilibrium, but:
  coexistence of 6 species on 3 limiting resources…

Consequences of non-equilibrium dynamics



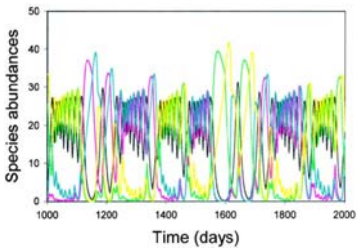
- cyclic dynamics may strongly enhance biodiversity
- catastrophic collapse of species-rich systems
- but…

Huisman, Johansson, Folmer & Weissing (2001)

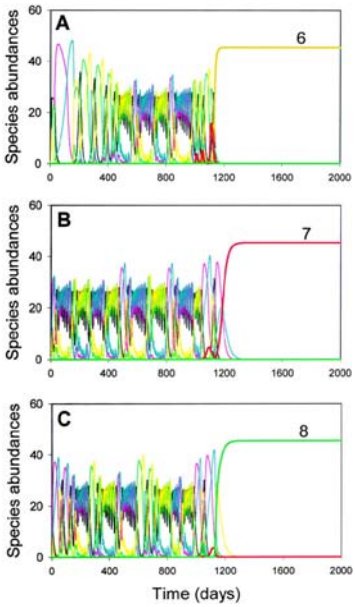


- outcome strongly dependent on physiological trade-offs and constraints…

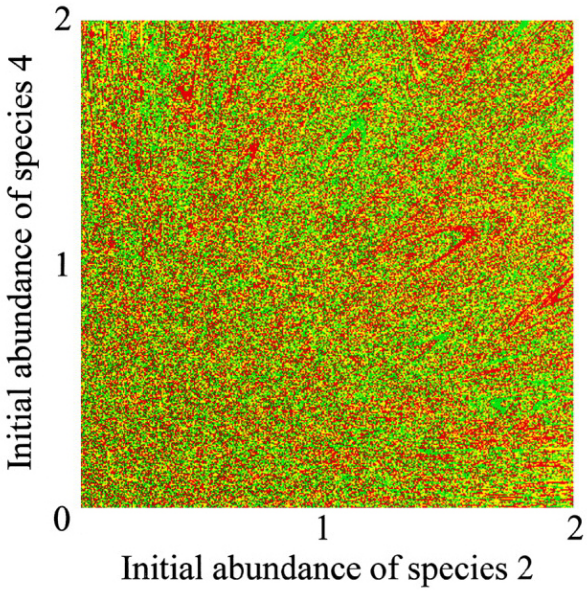
How predictable is the outcome?



- adding 3 specialist species to a chaotic 5-species system…
- one of the newcomers will win
- but which one?



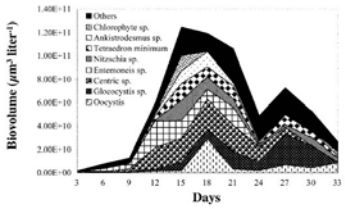
Fundamental unpredictability of competition

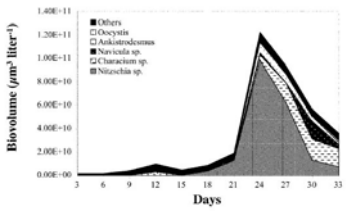


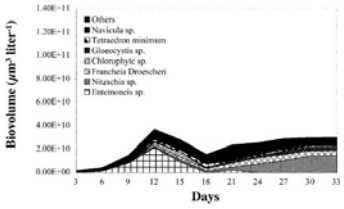
The outcome of competition can be as unpredictable as the throw of a dice…

Huisman & Weissing 2001b

How relevant are these conclusions?



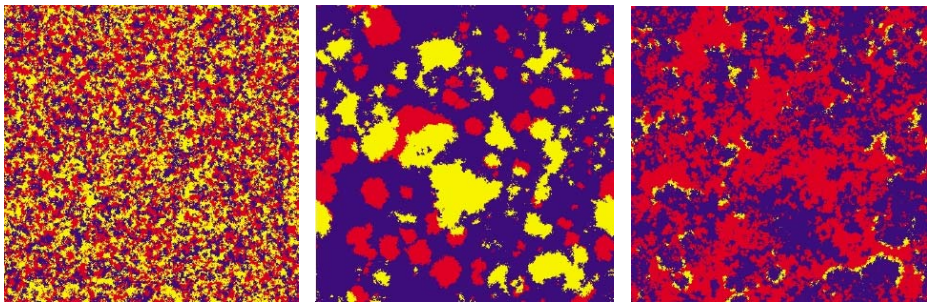




- several other examples since 2003…

Roelke, Augustine & Buyukates (2003)

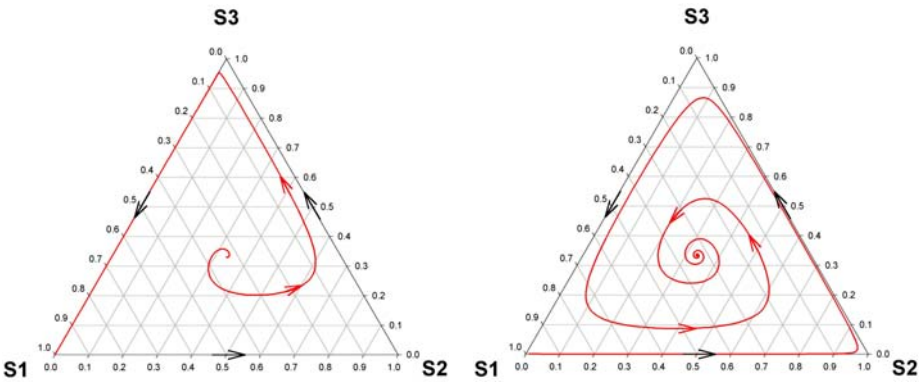
Competition in space



- spatial pattern formation…

Frean & Abraham (2001)

RSP–dynamics: spatial aspects



well-mixed system:
only one species survives

with spatial structure:
stable coexistence of types

Weissing 1990; Czárán et al. 2002

Example: chemical warfare among microbes

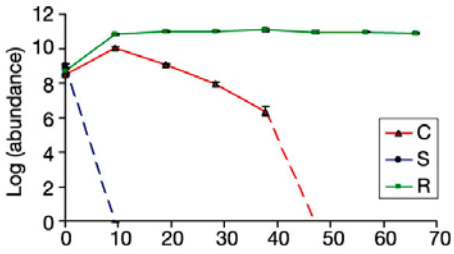
Scenario:

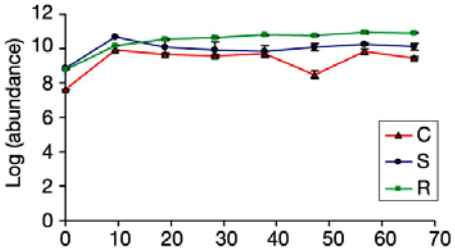
- wildtype strain, sensitive (S) to toxin
- mutant producing a toxin (T)
- new mutant resistant (R) to toxin

Expectation:

- non-transitive RSP interactions
  (S → T → R → S …)

Experiments with E. coli



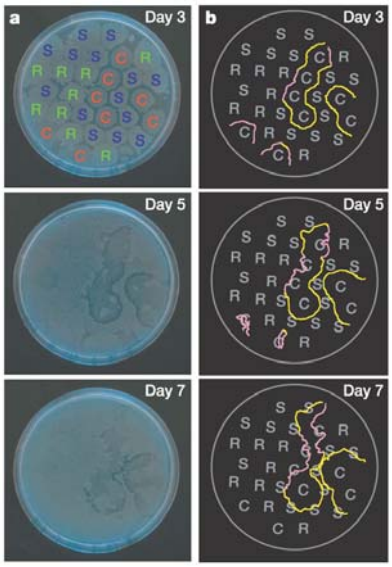


well-mixed flask:
only one species survives

petri dish:
stable coexistence

Kerr et al. (2002)

Experiments with E. coli



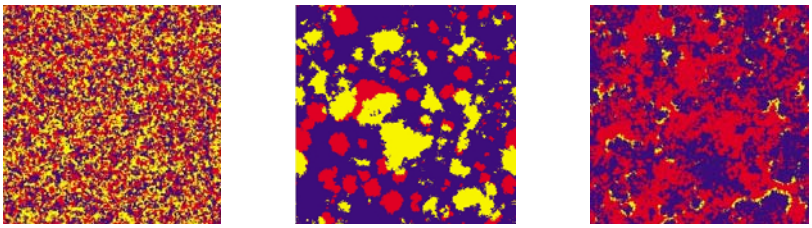
competition in a spatial environment:

cyclic chases on the agar plates…

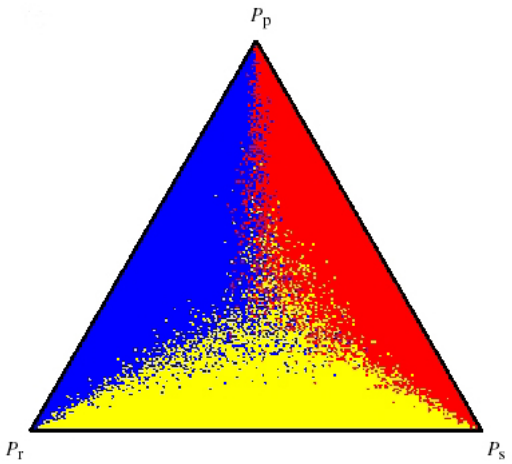
Kerr et al. (2002)

The unexpected complexity of competition

- competitive interactions are often intransitive ($R \rightarrow S \rightarrow P \rightarrow R \rightarrow \ldots$)
- outcome of competition unexpected and unpredictable
- the enemy of my enemy is my friend…
- hence: good competitors weaken their 'friends'



Survival of the weakest



- P_r: probability of R to invade in S
- P_s: probability of S to invade in P
- P_p: probability of P to invade in R

- red: R survives
- blue: S survives
- yellow: P survives

NB: Invasive strategies may succumb to their own success!

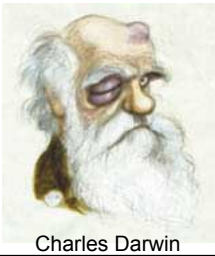
Frean & Abraham (2001)

Evolution of inefficiency

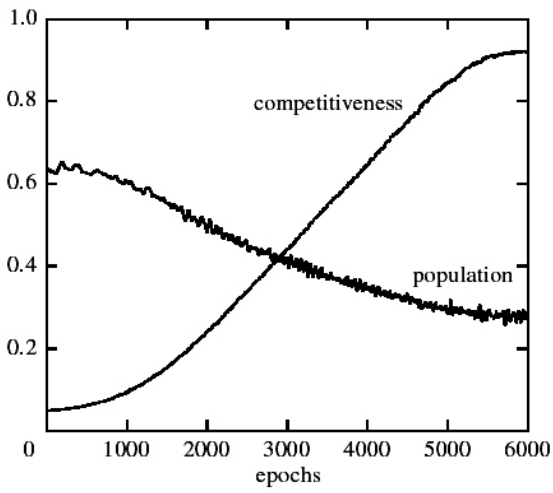
evolution towards enhanced invasiveness

⇓

evolution towards vulnerability...



Charles Darwin

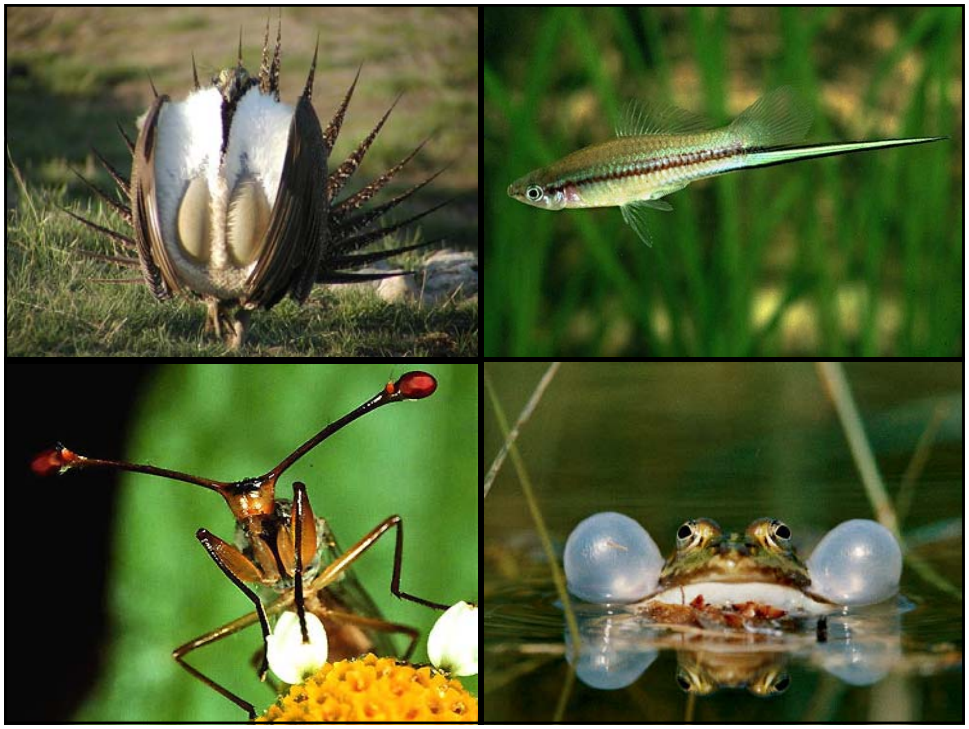


Huisman & Weissing 2000, Frean & Abraham 2001

Conclusions Part I

- The dynamics of competition is more complex than the textbooks suggest
- Equilibrium arguments are convenient, but they can be misleading
- The outcome of non-equilibrium dynamics can be highly unpredictable

Part II: Explaining ornament diversity



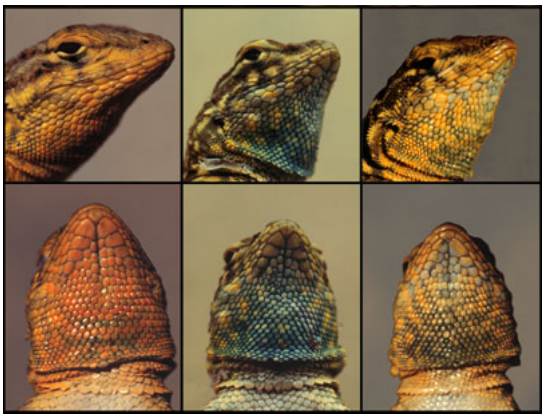
Sexual selection

- selection caused by differences in mating success

- intra-sexual selection
  (male-male competition)

- inter-sexual selection
  (female choice)

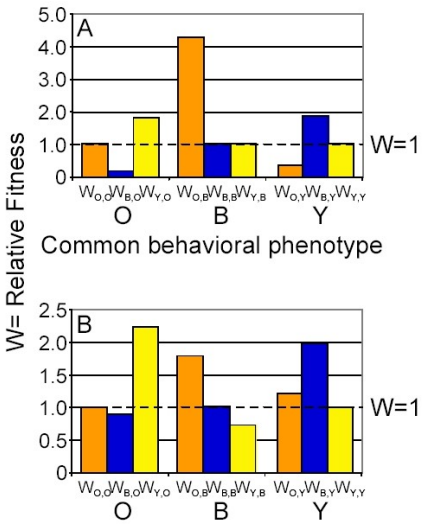
Example: the side-blotched lizard



- blue:
  small territories,
  mate guarding
- orange:
  large territories,
  highly aggressive
- yellow:
  no territories,
  'sneakers'

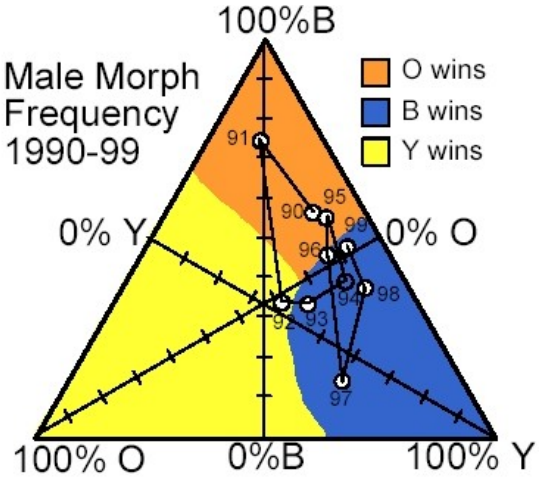
Sinervo & Lively (1996)

Frequency dependent fitness



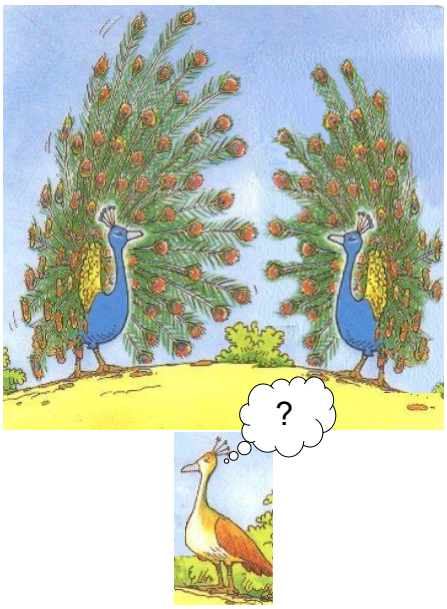
Sinervo & Lively (1996)
Sinervo (2001)

Oscillations of morph frequencies

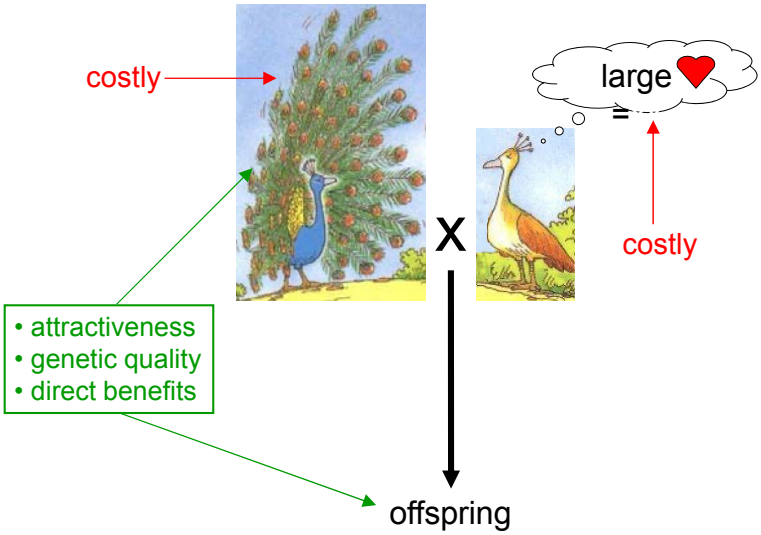


Sinervo & Lively (1996)
Sinervo (2001)

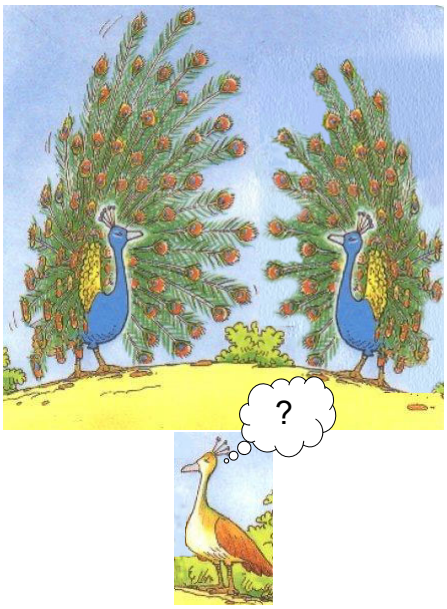
Why are females choosy?



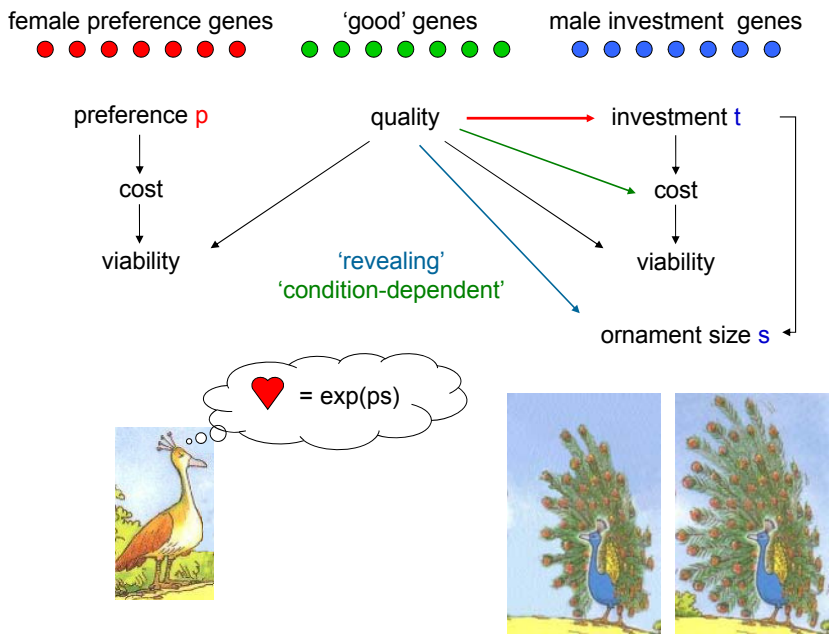
Why are females choosy?



Benefits of being choosy



- higher fecundity
  (direct benefits)
- sexy sons
  (Fisherian runaway)
- good genes
  (handicap principle)
- avoiding costs
  (sexual conflict)
- complementary genes
  (immunocompetence)

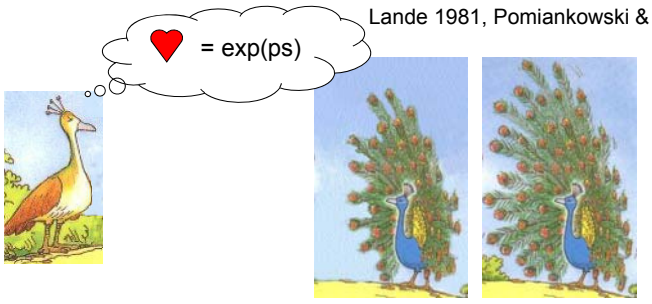


Sexual selection models

$$\begin{pmatrix} \Delta\bar{t} \\ \Delta\bar{p} \end{pmatrix} = \frac{1}{2} \cdot \begin{pmatrix} G_t & B_{tp} \\ B_{tp} & G_p \end{pmatrix} \cdot \begin{pmatrix} \beta_t \\ \beta_p \end{pmatrix}$$

$$\beta_t = \frac{\partial}{\partial t} \ln W_m(t, \bar{t}, \bar{p}), \quad \beta_p = \frac{\partial}{\partial p} \ln W_f(p)$$

Lande 1981, Pomiankowski & Iwasa 1991, 94, 99



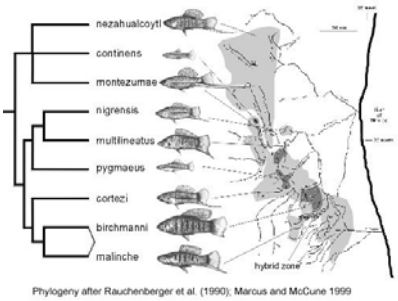
Equilibrium analysis of these models

- costly female preferences can only evolve if choosy female get direct or indirect benefits
- indicators of male genetic quality must be handicaps (either revealing or condition dependent)
- in case of multiple ornaments only few ornaments can have indicator function

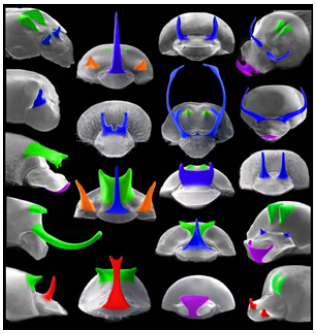
▶ Will process converge to equilibrium?

e.g. Iwasa, Pomiankowski et al. 1991, 94, 99

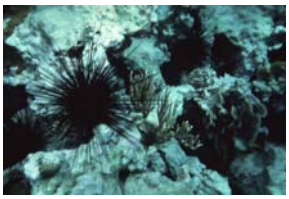
Phylogenetic lability of sexually selected traits



Meyer et al. 1994



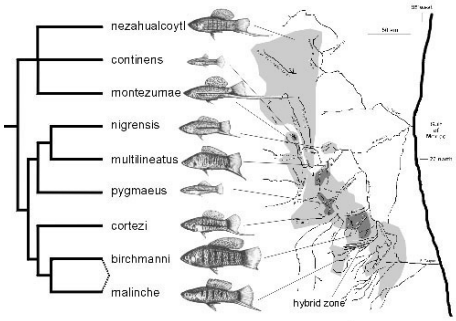
Emlen et al. 2005



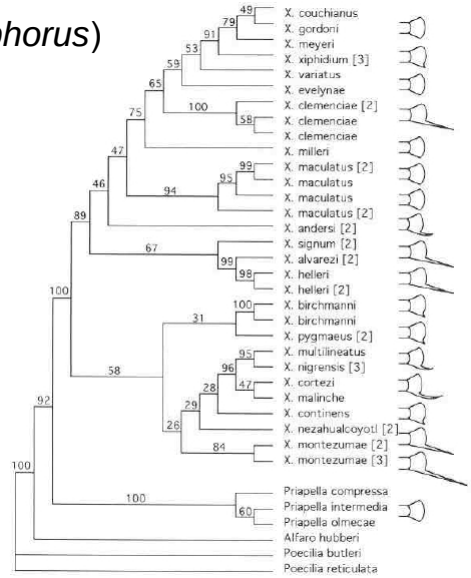
Vacquier 1998

Frequent loss and turnover of ornaments

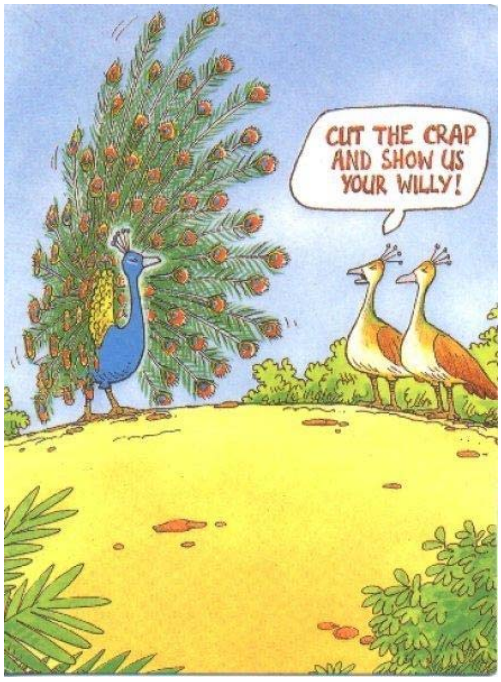
Example: swordtails (*Xiphophorus*)



Phylogeny after Rauchenberger et al. (1990); Marcus and McCune 1999



Meyer et al. (1994); Wiens (2001)



Sexual conflict on information content

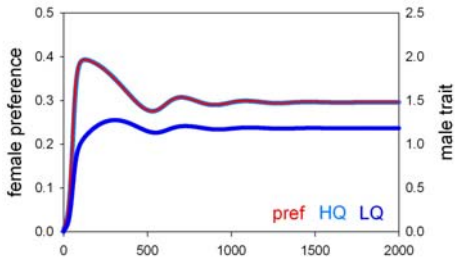
- females want honest information
- low-quality males want to hide this information

▶ arms race ??

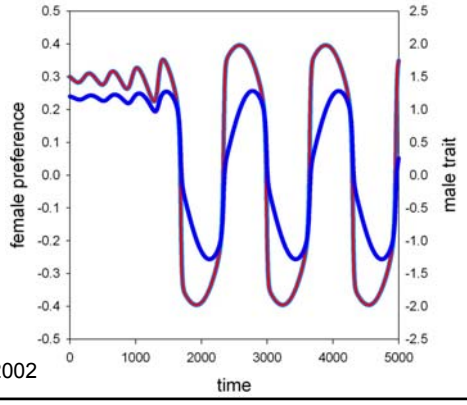
▶ explicitly model selection dynamics !!

Hill 1994

- evolutionary rate slower in females than in males: convergence to equilibrium

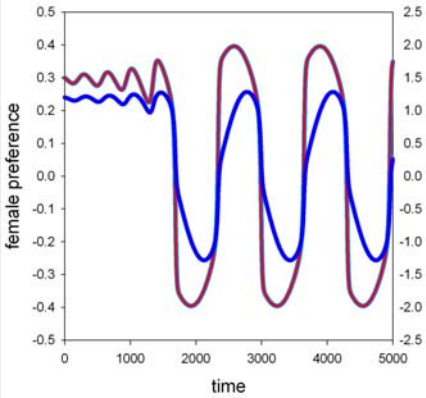


- evolutionary rate faster in females than in males: never ending arms race

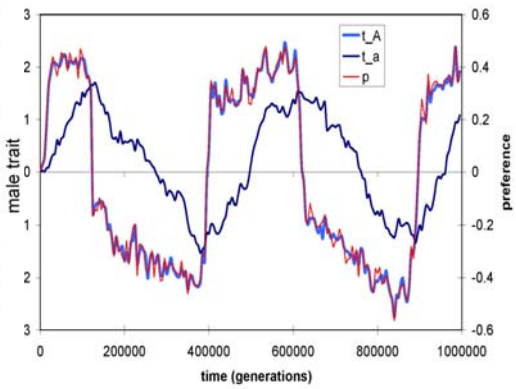


Van Doorn & Weissing 2006
cf. Iwasa & POM 1999, Houle & Kondrashov 2002

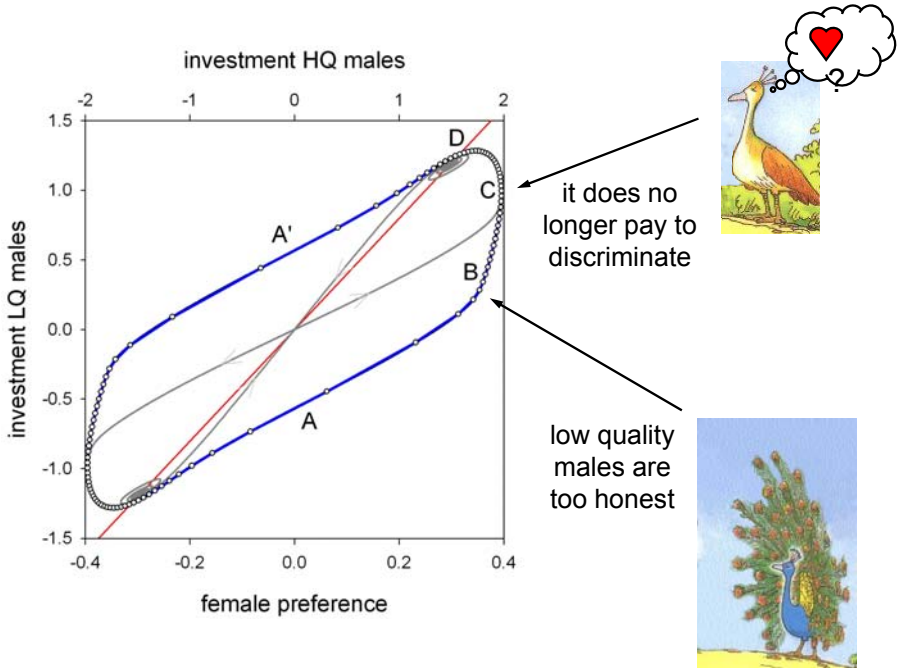
analytical model (adaptive dynamics):



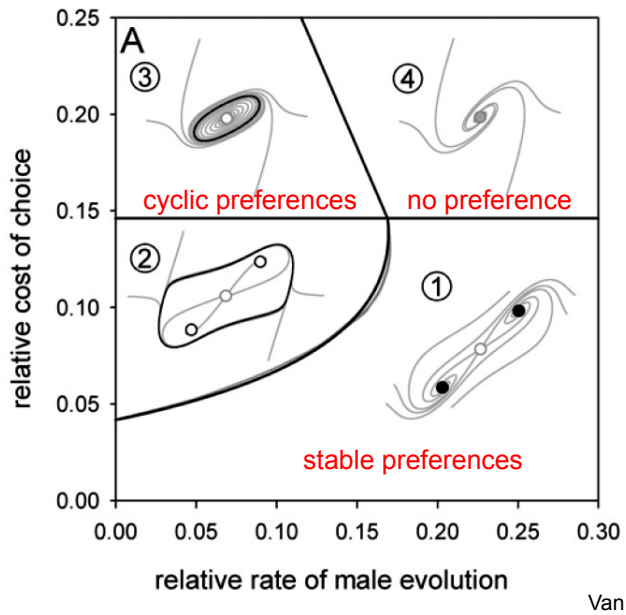
individual-based simulations:



Van Doorn & Weissing 2006



Classification of dynamic behaviour



textbooks:

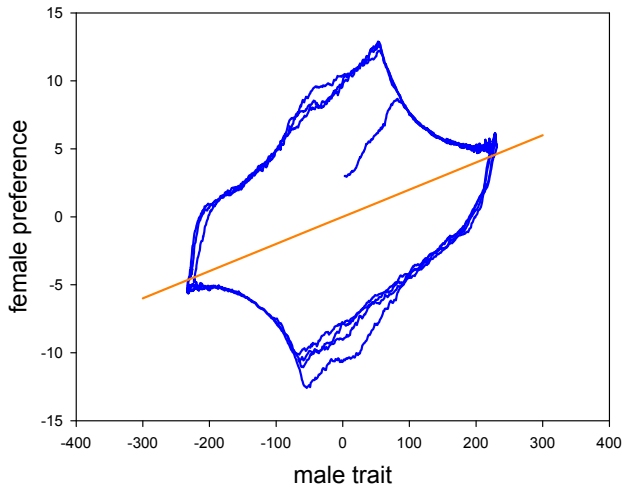
no preference

preference

Van Doorn & Weissing 2006

~~Equilibrium prediction: no costly preference if there are no direct or indirect benefits~~

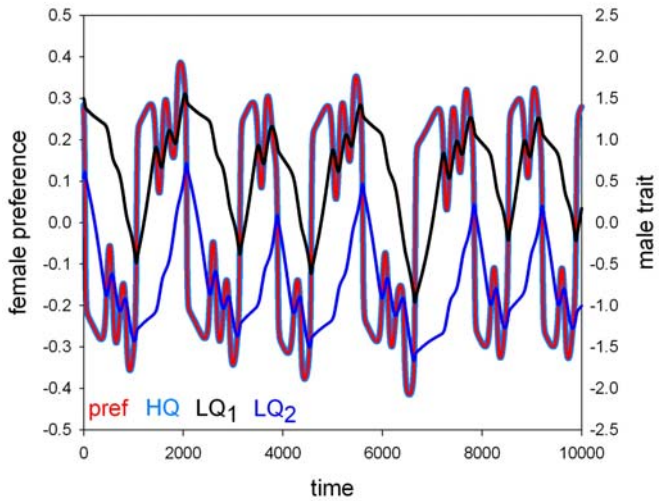
e.g. Iwasa et al. 1991



Kuijpers et al. 2010

~~Equilibrium prediction: no costly preference for a pure epistatic indicator~~

e.g. Iwasa et al. 1991



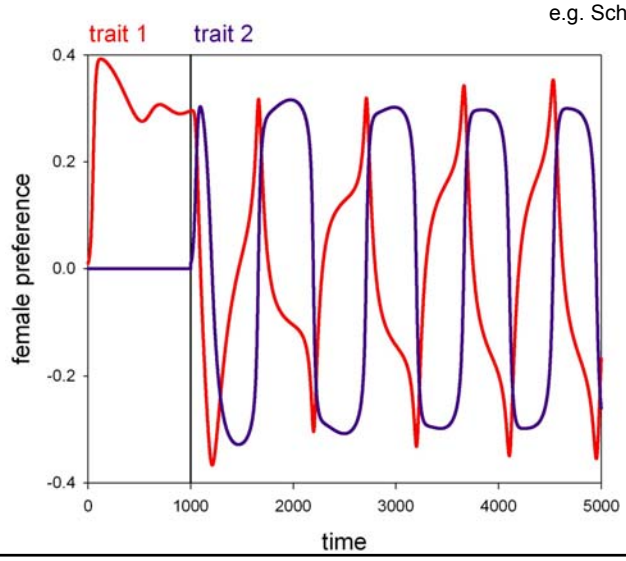
Equilibrium prediction: females should always evolve preference for most reliable indicator

e.g. Schluter & Price 1993

Pryke & Griffith 2006, 07

~~Equilibrium prediction: females should always evolve preference for most reliable indicator~~

e.g. Schluter & Price 1993

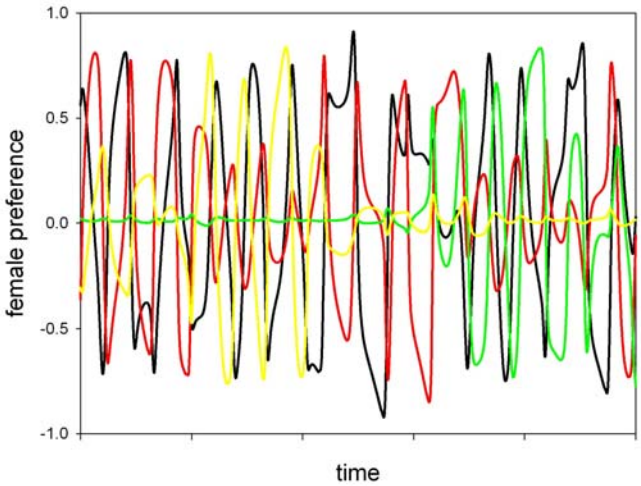


Eq prediction: in case of multiple ornaments only few ornaments can act as indicators

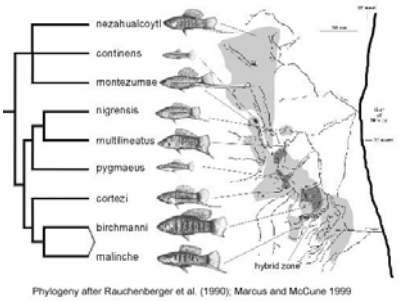
e.g. Van Doorn & Weissing 2004

~~Eq prediction: in case of multiple ornaments only few ornaments can act as indicators~~

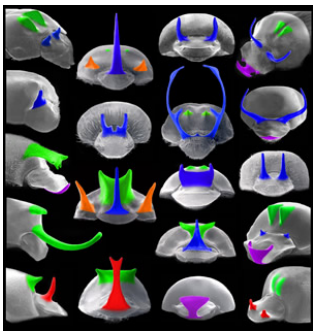
e.g. Van Doorn & Weissing 2004



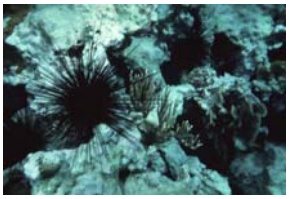
Frequent loss and turnover of ornaments



Meyer et al. 1994



Emlen et al. 2005



Vacquier 1998

Conclusions Part II

- Many results of sexual selection theory are implicitly based on equilibrium arguments
- The evolution of preferences may be much more dynamic than we used to think

▶ Explanation for phylogenetic lability of sexually selected traits…

General conclusion

- The dynamics of selection and competition is more complex than the textbooks suggest
- Equilibrium arguments are convenient, but they can be quite misleading