# Evolution and persistence of obligate mutualists and exploiters:

## competition for partners and evolutionary immunization

**Mathias Gauduchon    Régis Ferrière   Judith L Bronstein**

# Overview

1. Introduction
2. Adaptive Dynamics
3. Ecological and evolutionary persistence of obligate mutualism
4. Mutualism in face of exploiters invasion

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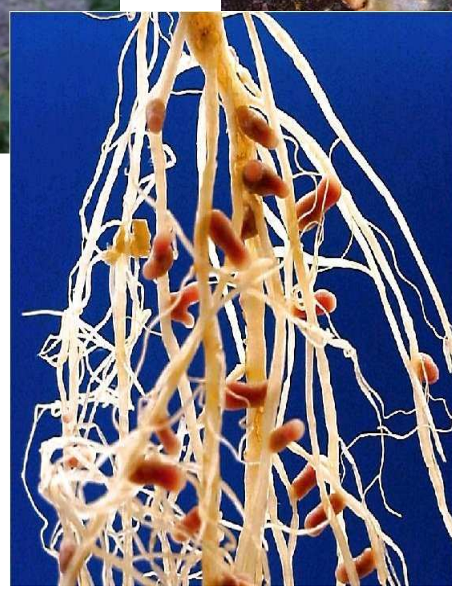
# Interspecific mutualisms

- Mutually beneficial interactions between species
- Great diversity of mecanisms and organisms involved

# Mutualisms



# Mutualisms

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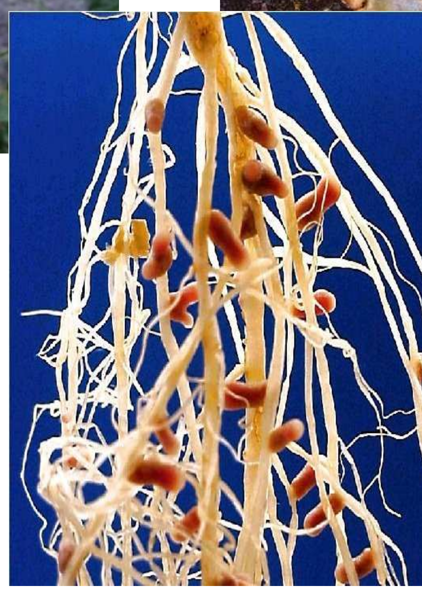


# Mutualisms

# Obligate mutualism

- Yucca-yucca moth
- Moth larvae feed on yucca seeds
- Yucca is pollinated
- Very specialized
- Each species cannot reproduce without its partner

# Cheaters

Nectar robbers

# Cheaters

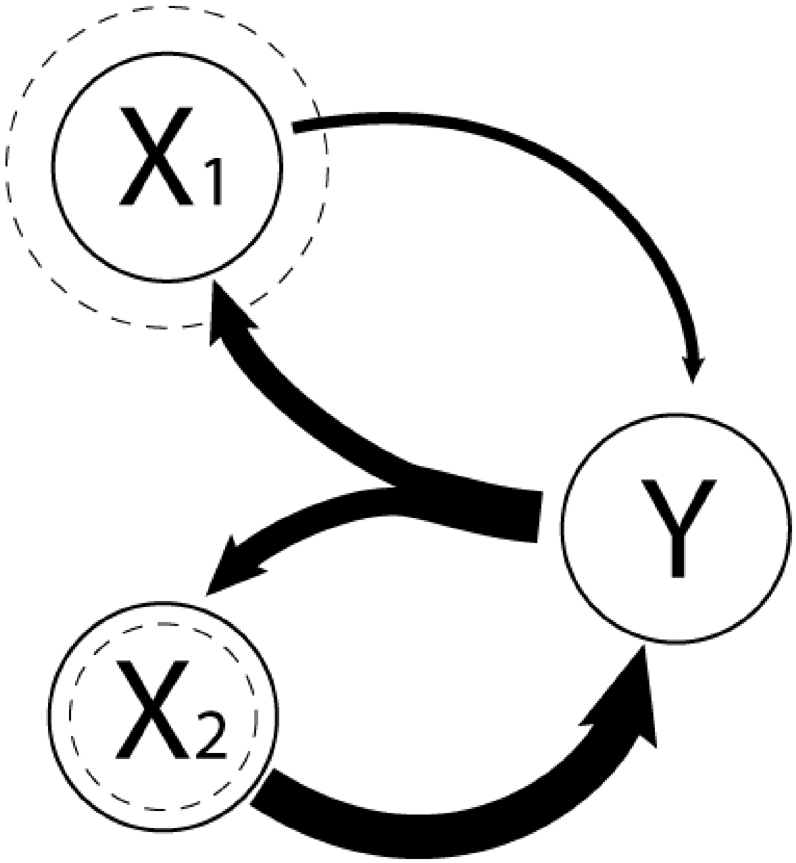
Deceipt orchids

# Cheaters

- Continuity between good mutualists and cheaters
- Exploiter = pure cheater

# Cheaters advantage

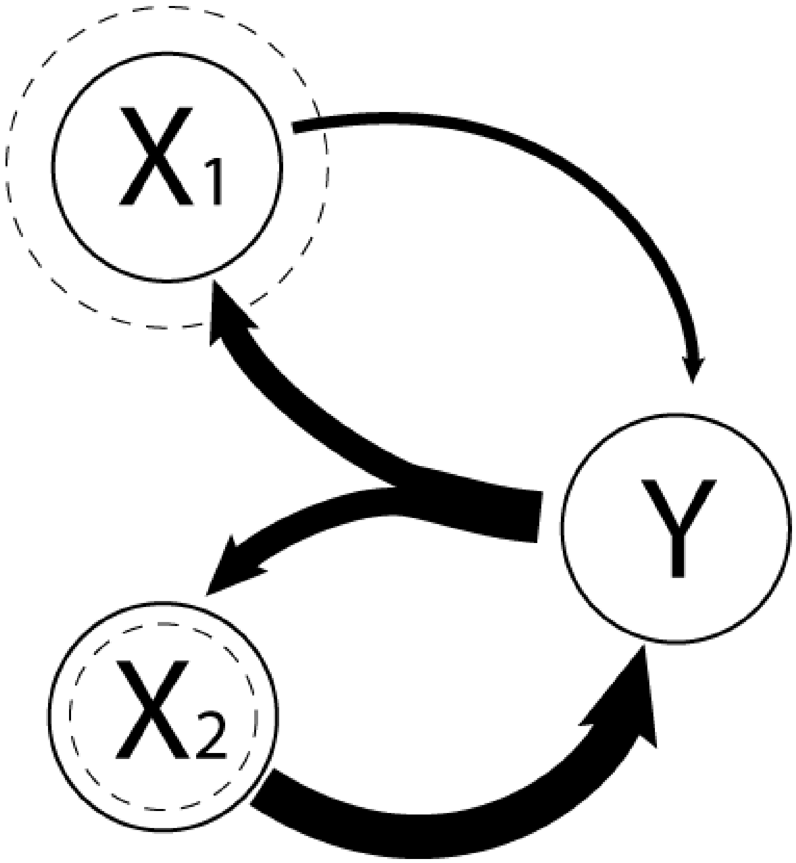
Mutualistic Investment → Cost




Cheaters should be selected by evolution

# Cheaters advantage

Mutualistic Investment → Cost




Cheaters should be selected by evolution

But long term coexistence:

ex: Yucca-Yucca moth

# Questions

- Evolutionary stability?
  - Threatened by cheaters
  - How is exploitation prevented?

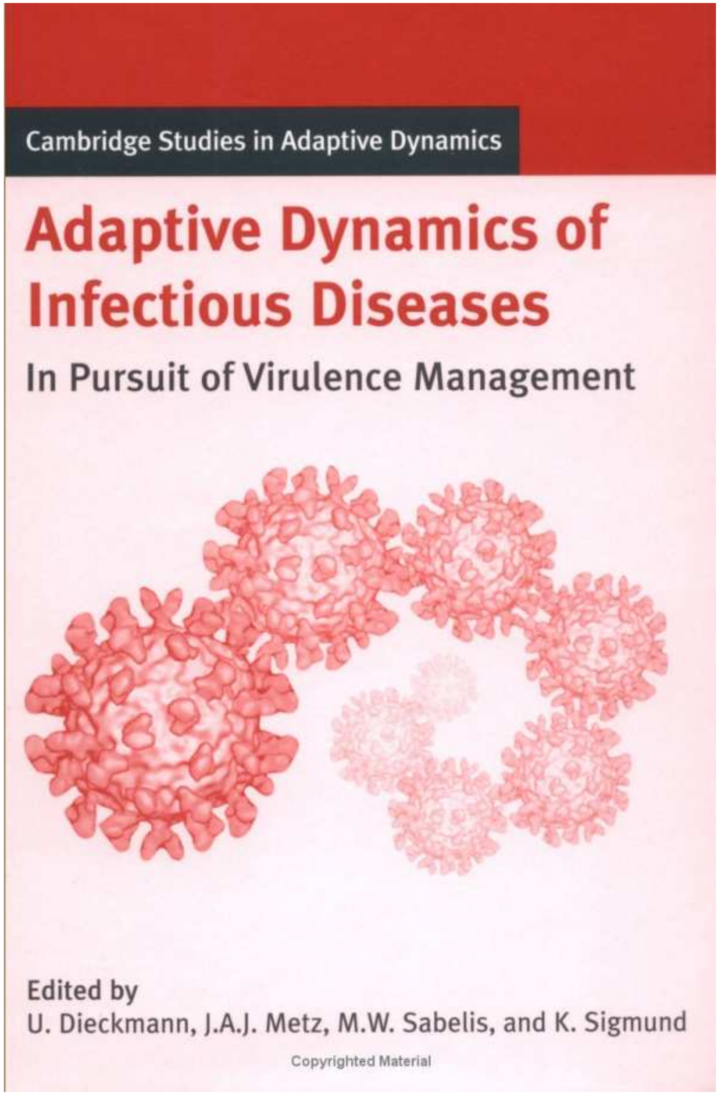
# Questions

- Evolutionary stability?
  - Threatened by cheaters
  - How is exploitation prevented?
- Evolutionarily stable and ecologically viable diversity?
  - Long-term coexistence with exploiters
  - How can exploitation be so ancient and widespread?

# Lack of evolutionary dynamic theories on mutualism

in comparison with …

# … host-parasite interactions



# … predator-prey interactions

## The Evolution of Predator-Prey Interactions: Theory and Evidence

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**Key Words** coevolution, predation, stability

■ **Abstract** Recent theories regarding the evolution of predator-prey interactions is reviewed. This includes theory about the dynamics and stability of both populations and traits, as well as theory predicting how predatory and anti-predator traits should respond to environmental changes. Evolution can stabilize or destabilize interactions; stability is most likely when only the predator evolves, or when traits in one or both species are under strong stabilizing selection. Stability seems least likely when there is coevolution and a bi-directional axis of prey vulnerability. When population cycles exist, adaptation may either increase or decrease the amplitude of those cycles. An increase in the defensive ability of prey is less likely to produce evolutionary countermeasures in its partner than is a comparable increase in attack ability of the predator. Increased productivity may increase or decrease offensive and defensive adaptations. The apparent predominance of evolutionary responses of prey to predators over those of predators to prey is in general accord with equilibrium theory, but theory on stability may be difficult to confirm or refute. Recent work on geographically structured populations promises to advance our understanding of the evolution of predator-prey interactions.

# Evolutionary process

- Mutants arise randomly

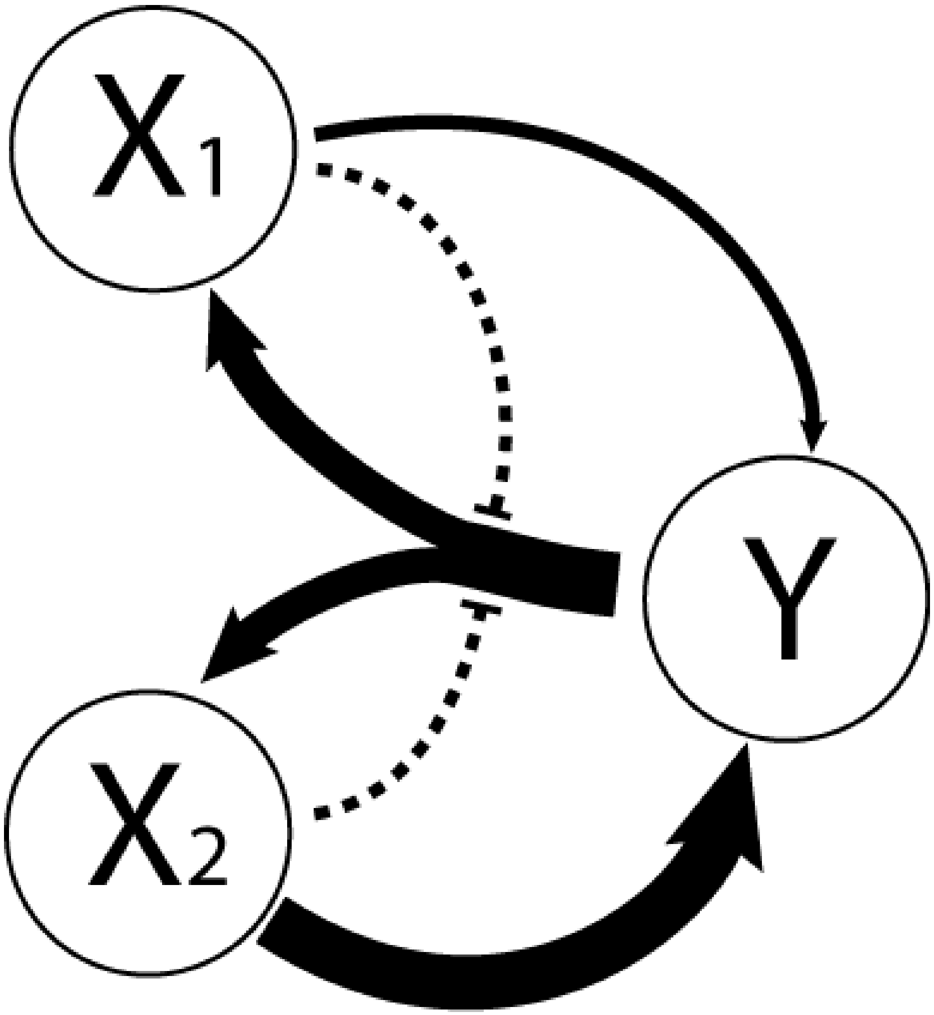
- They are selected for or against by natural selection

- Natural selection operates through ecological processes and mainly through competition

# In mutualistic interactions

Limiting resource is the access for partner

Competition is for partner



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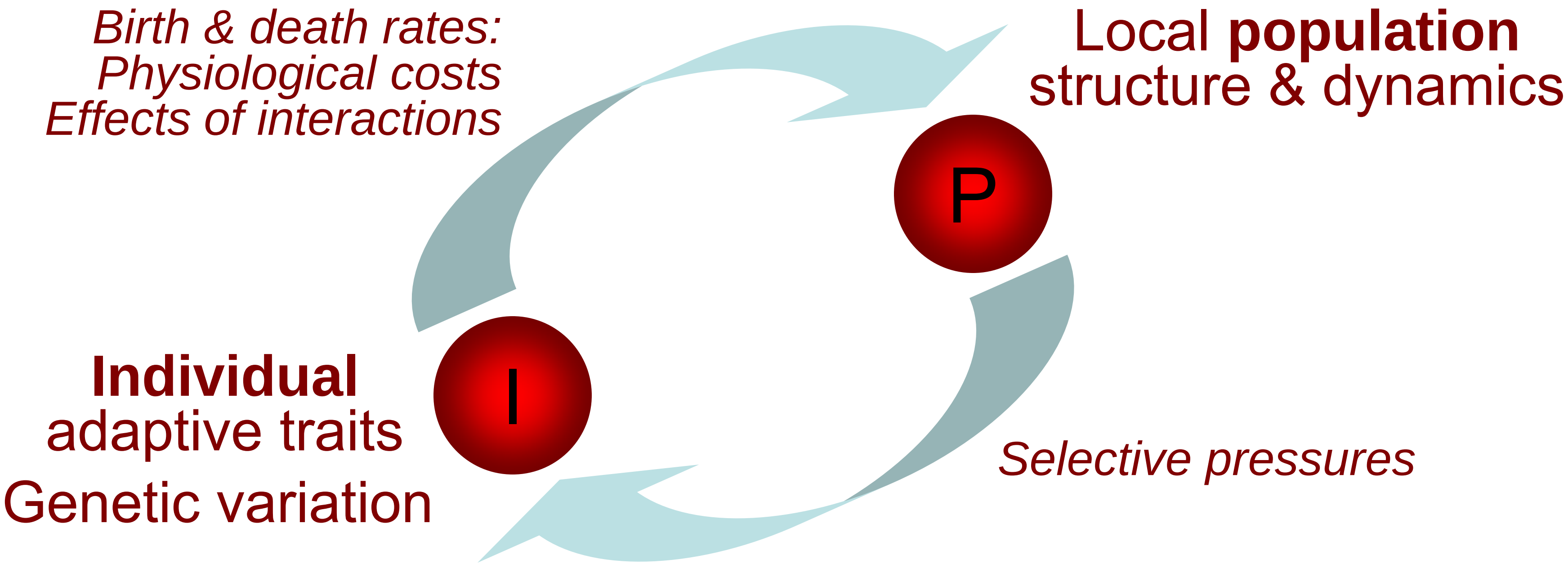
# Adaptive Dynamics

Theoretical framework for evolution

Particularly adapted to take into account ecological processes like competition for partners

# Closing the eco-evolutionary feedback loop




Ferriere, Le Galliard: in *Dispersal* (OUP, 2001)
Metz et al.: *TREE* 1992 – Day & Taylor: *JTB* 1998 – van Baalen & Rand: *JTB* 1998

# Adaptive Dynamics Hypothesis

- Simplified reproduction system:
  - Clonal reproduction
- Ecological and evolutionary timescales separation:
  - After mutant's invasion, ecological system stabilizes at equilibrium before next mutation arises
- Small mutations
- Large populations:
  - Only favorable mutants may invade

# Adaptive Dynamics Method

(1) Ecological equilibrium

(2) Mutant's invasion fitness

(3) Evolution of phenotypic trait

- Canonical equation

Environment with traits $s_1, s_2, \ldots, s_N$

$$\frac{ds_i}{d\tau} = k_i \hat{n}_i \left. \frac{\partial W_i(s_i', E(s))}{\partial s_i'} \right|_{s_i' = s_i}$$

change rate of phenotype trait $s_i$

Evolutionary rate of phenotypic trait $i$

density of individuals $s_i$

# Adaptive Dynamics Method

(4) Evolutionary singularities

- Rest points of the canonical equation
- Detection: bifurcation analysis
  - Especially attracting singularities
- Type of attractive singularity: $$\frac{\partial^2 W_i}{\partial s_i'^2}\left(s_i' = s_i, E(s)\right)$$
  - Stabilizing (ESS) ................................ $< 0$
  - Disruptive ........................................ $> 0$

    $\rightarrow$ Evolutionary branching

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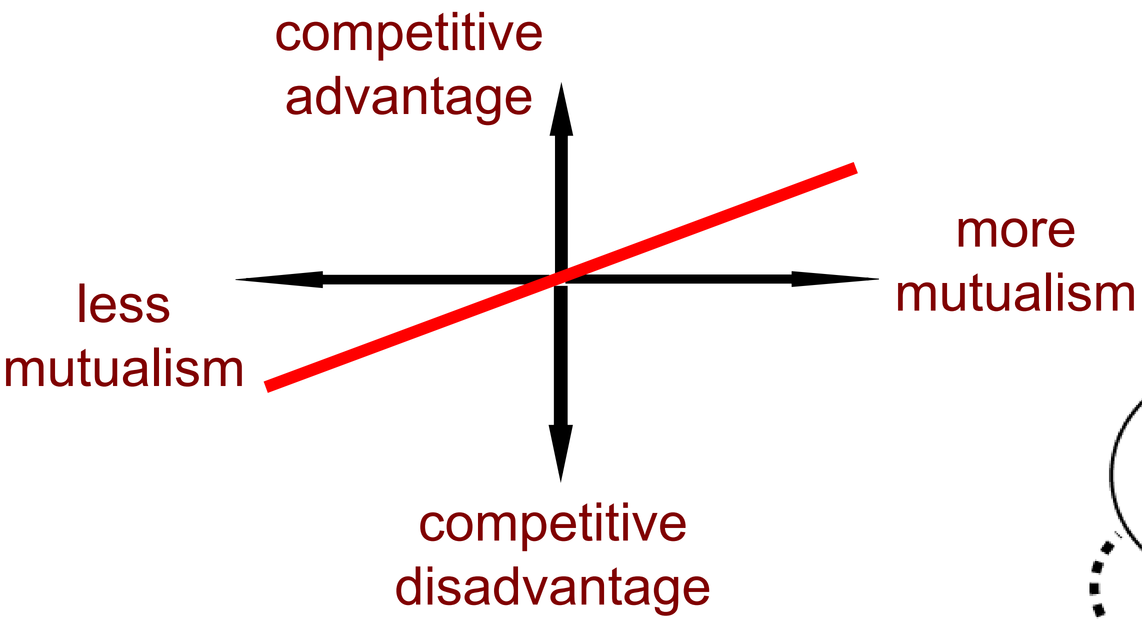
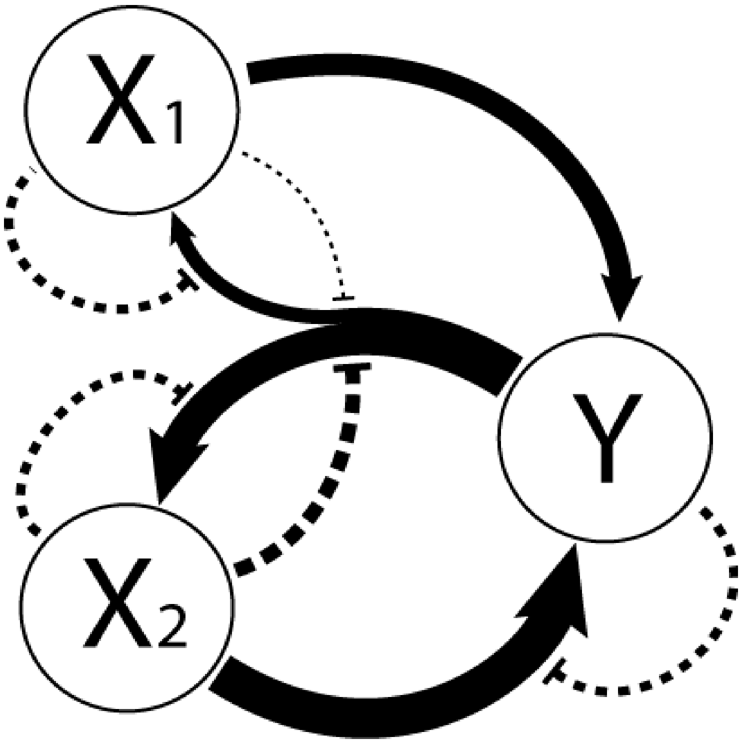
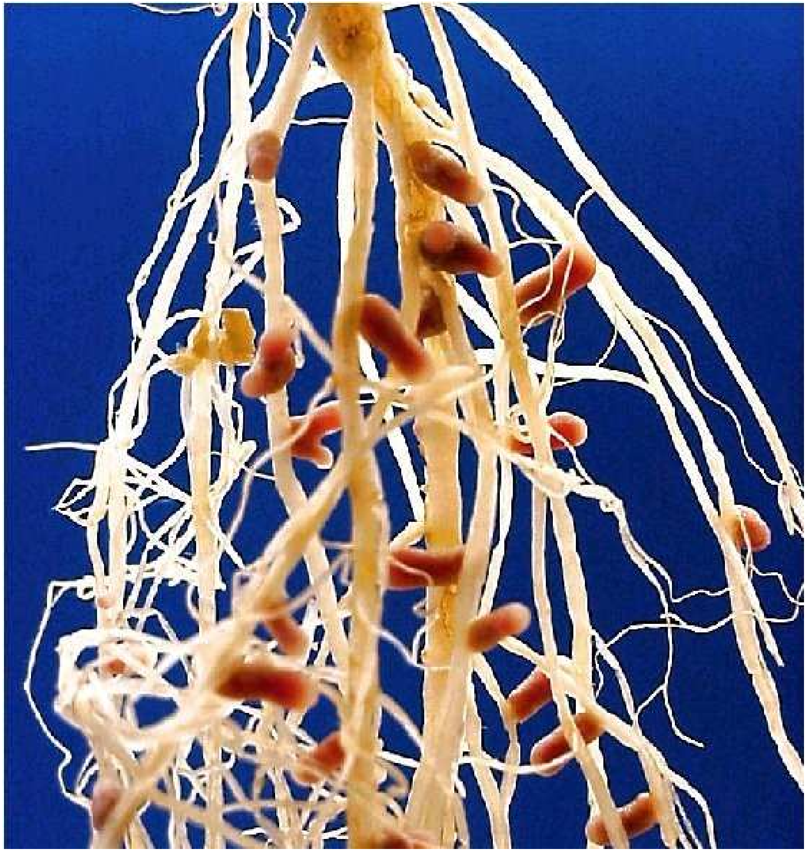
# Evolutionary stability of mutualisms:
## Partner Competition Asymmetry hypothesis



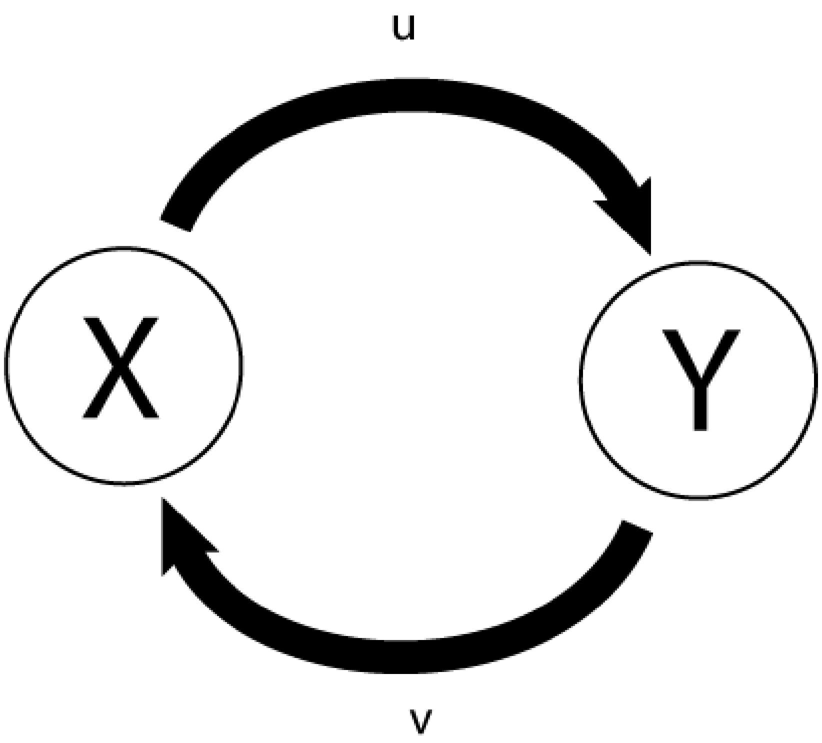
# Example of asymmetric competition

- Cheating rhizobia strains do not transform nitrogen
- Legumes reallocate resources toward ‘good mutualists’ nodules
- Or kill cheating nodules



# Model

- Obligate mutualism between two partners
- Evolutionary phenotypic traits *u* and *v* =quantitative measures of mutualistic investment



# Model

- Lotka-Volterra like model
- Mutualism cost associated with investment
- Density-dependant intraspecific competition
- Competition for the access to mutualistic resources

# Ecological equations

Density

$$\frac{dn_X}{dt} = \left[-R(u) - cn_X + vn_Y\left(1 - \alpha n_X\right)\right] n_X$$

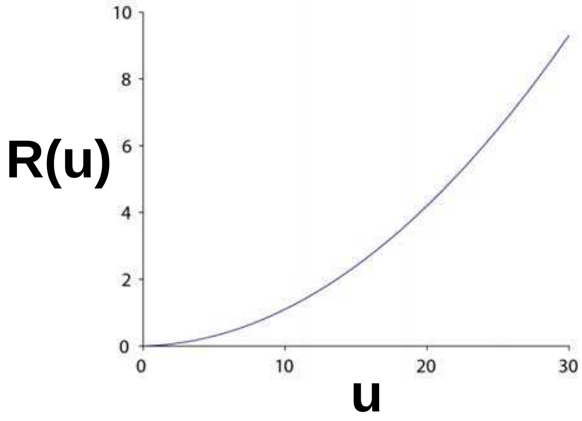
$$\frac{dn_Y}{dt} = \left[-S(v) - dn_Y + un_X\left(1 - \beta n_Y\right)\right] n_Y$$

# Ecological equations

Cost of mutualistic investment

$$\frac{dn_X}{dt} = \left[ -R(u) - cn_X + vn_Y\left(1 - \alpha n_X\right)\right] n_X$$

$$\frac{dn_Y}{dt} = \left[ -S(v) - dn_Y + un_X\left(1 - \beta n_Y\right)\right] n_Y$$



# Ecological equations

density-dependant competition

$$\frac{dn_X}{dt} = \left[ -R(u) - cn_X + vn_Y \left( 1 - \alpha n_X \right) \right] n_X$$

$$\frac{dn_Y}{dt} = \left[ -S(v) - dn_Y + un_X \left( 1 - \beta n_Y \right) \right] n_Y$$

# Ecological equations

Total amount of commodities provided by partner species

$$\frac{dn_X}{dt} = \left[ -R(u) - cn_X + vn_Y \left(1 - \alpha n_X\right) \right] n_X$$

$$\frac{dn_Y}{dt} = \left[ -S(v) - dn_Y + un_X \left(1 - \beta n_Y\right) \right] n_Y$$

# Ecological equations

Competition for mutualistic resources

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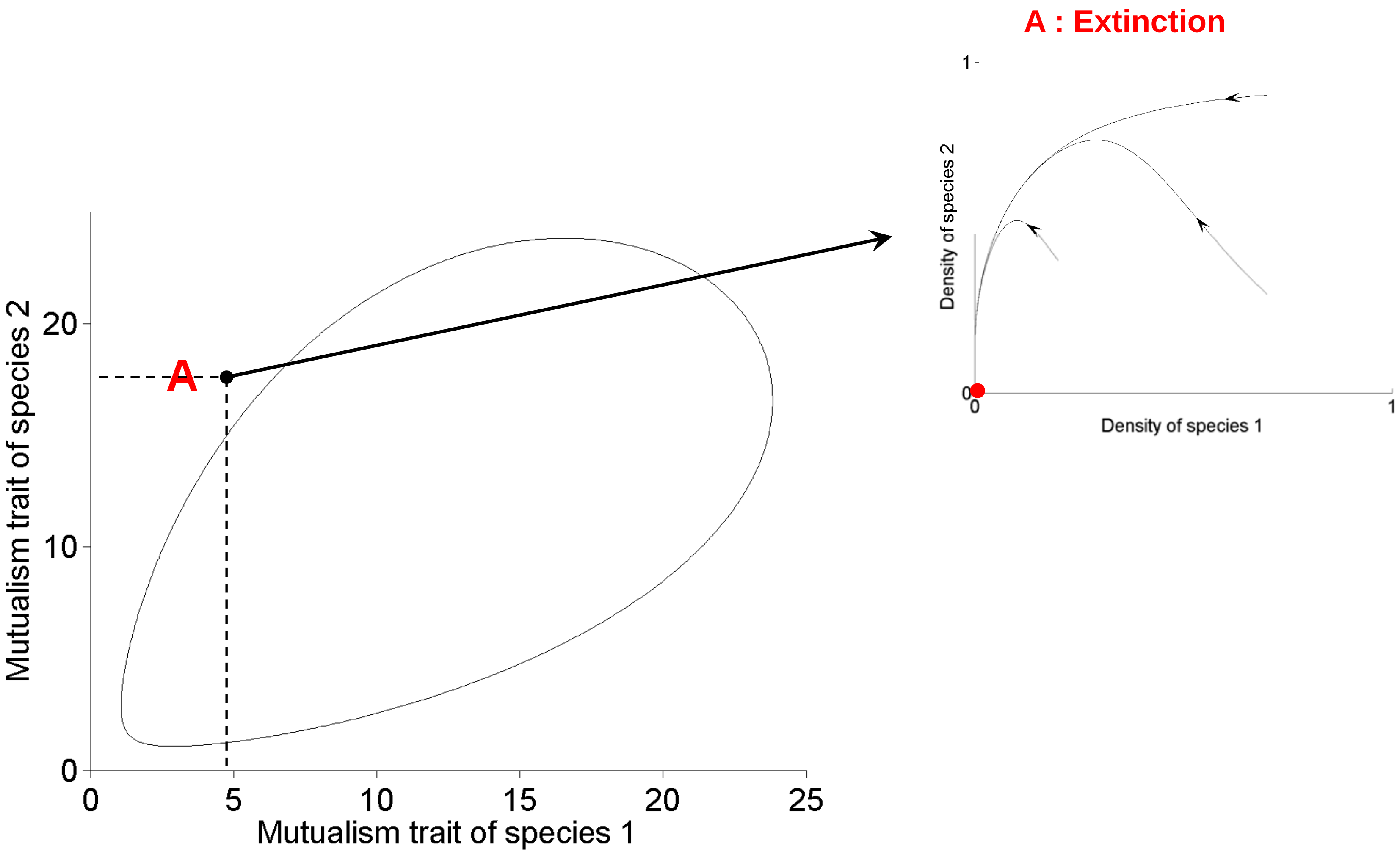
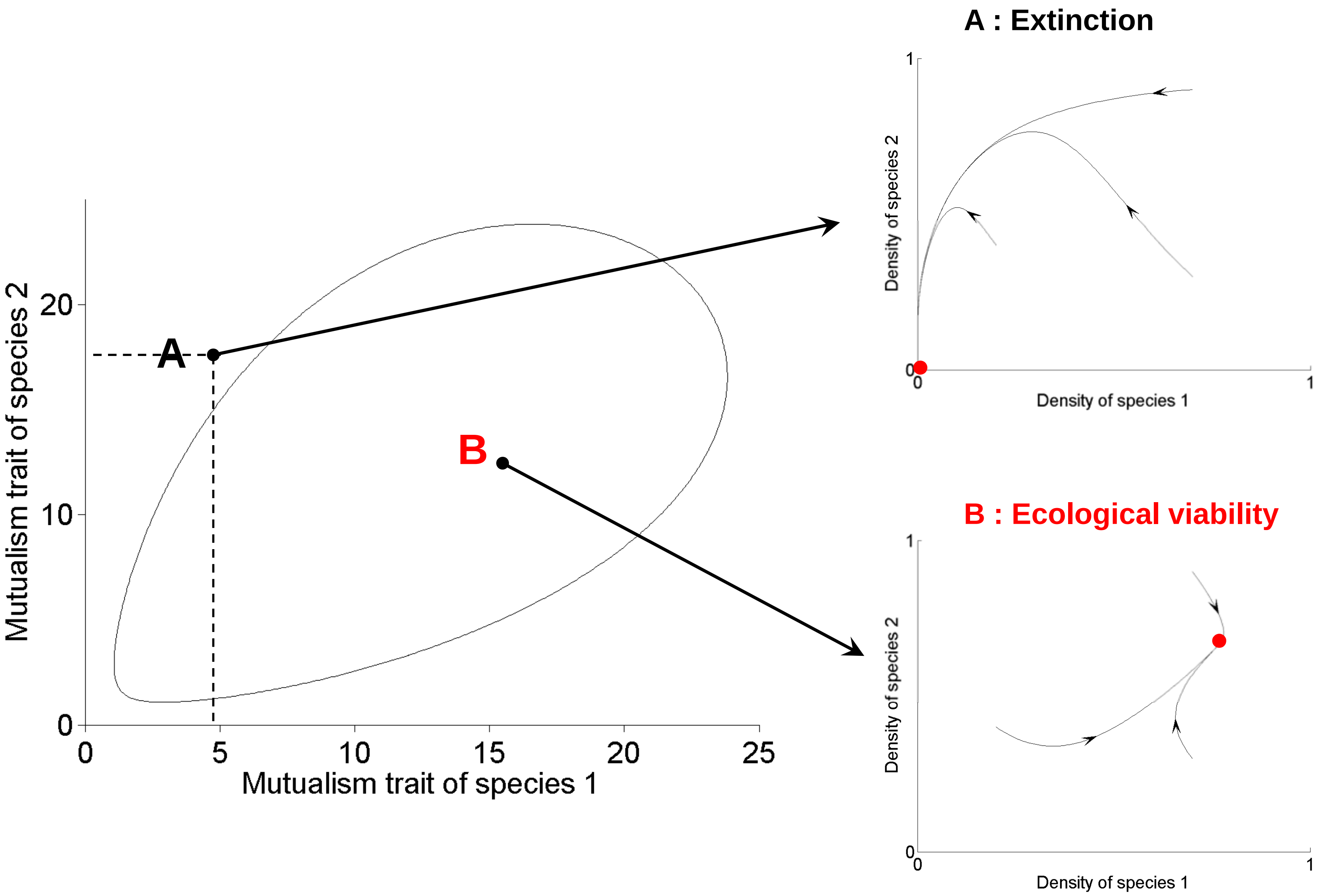
# Ecological viability domain



# Ecological viability domain



# Evolutionary model

- Consider a mutant e.g. in species X

- New phenotype $u_{mut}$ slightly different from parent's phenotype $u$.

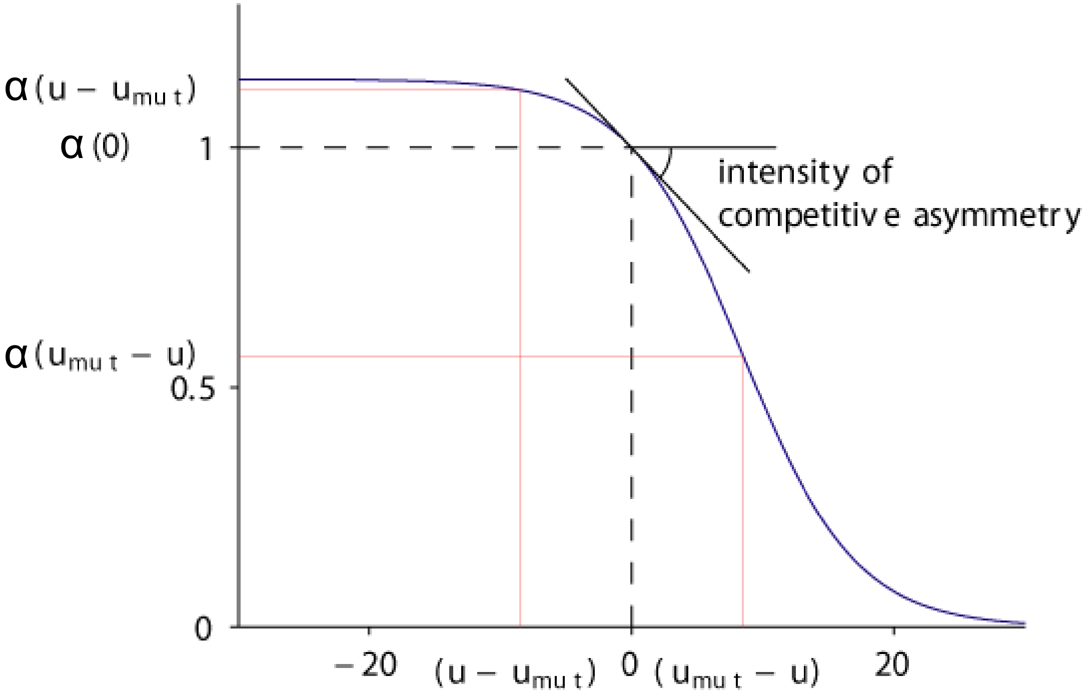
# Evolutionary model

- Consider a mutant e.g. in species X
- New phenotype $u_{mut}$ slightly different from parent's phenotype $u$.
- Intraspecific asymmetry arises between resident and mutant

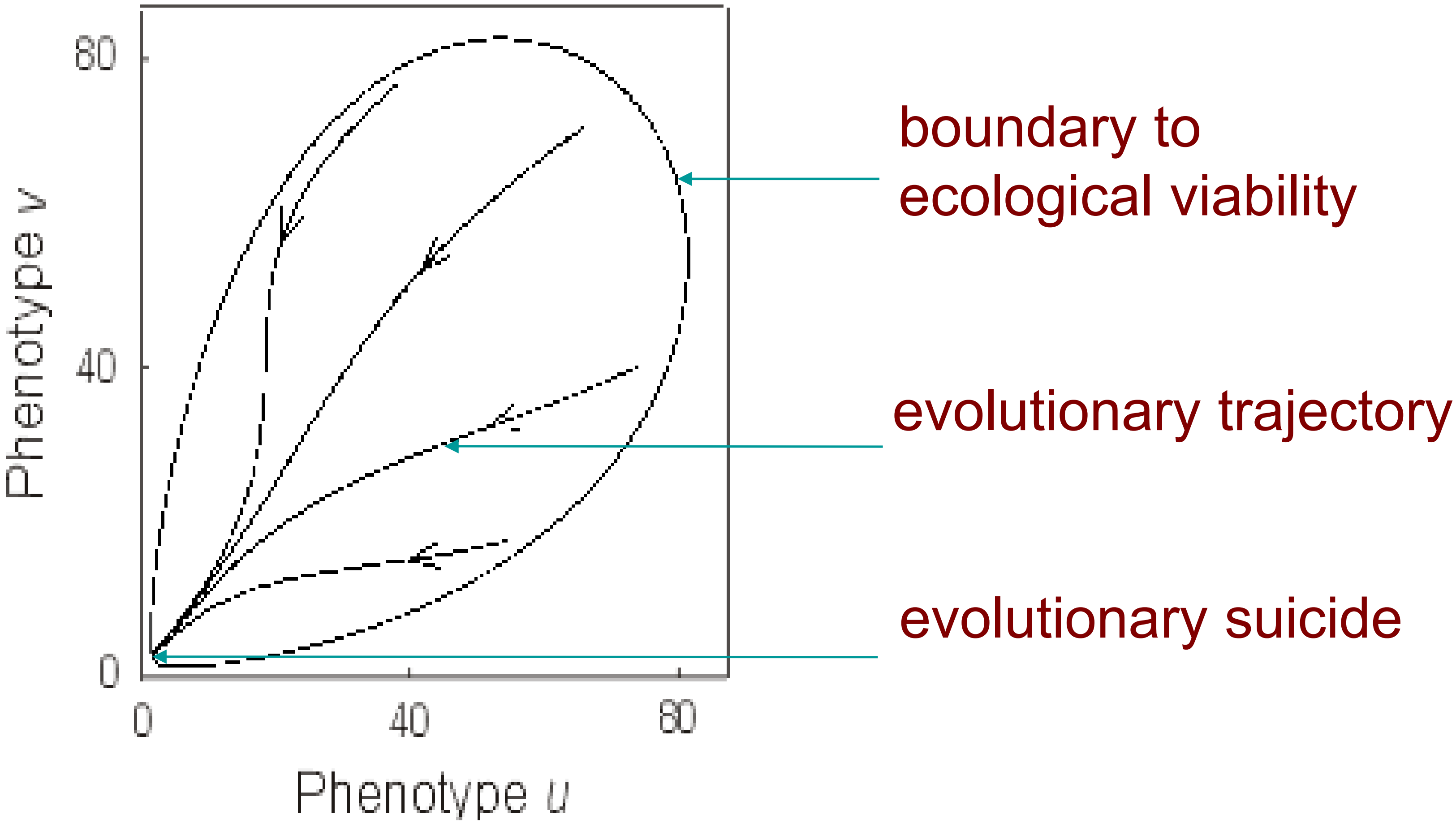
$$\frac{dn_X}{dt} = \left[-R(u) - c(n_X + n_{X'}) + vn_Y\left(1 - \alpha(0)n_X - \alpha(u - u_{mut})n_{X'}\right)\right]n_X$$

$$\frac{dn_{X'}}{dt} = \left[-R(u_{mut}) - c(n_X + n_{X'}) + vn_Y\left(1 - \alpha(0)n_{X'} - \alpha(u_{mut} - u)n_X\right)\right]n_{X'}$$

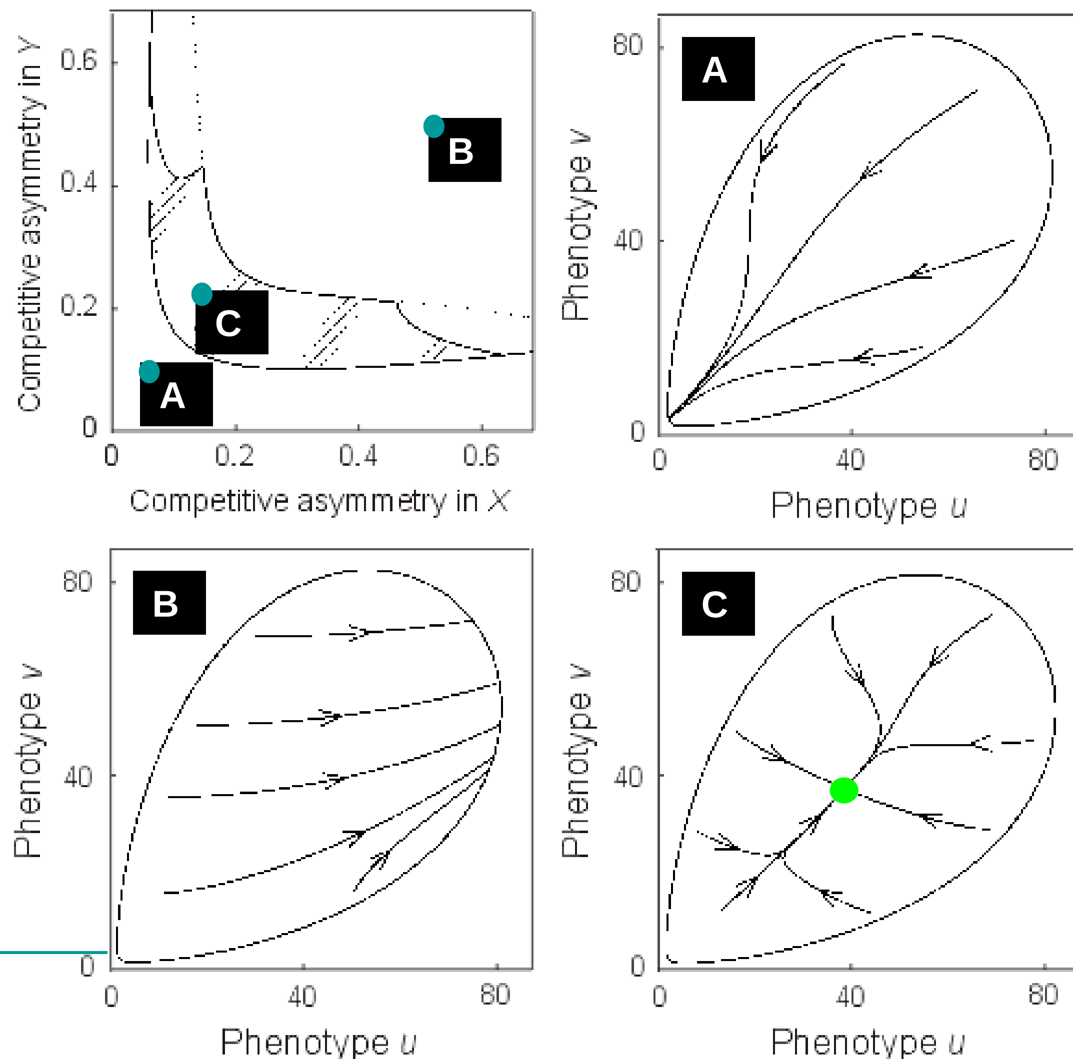
$$\frac{dn_Y}{dt} = \left[-S(v) - dn_Y + \left(un_X + u_{mut}n_{X'}\right)\left(1 - \beta n_Y\right)\right]n_Y$$



# Co-evolutionary trajectories



# Evolution of mutualism under asymmetric competition for partners

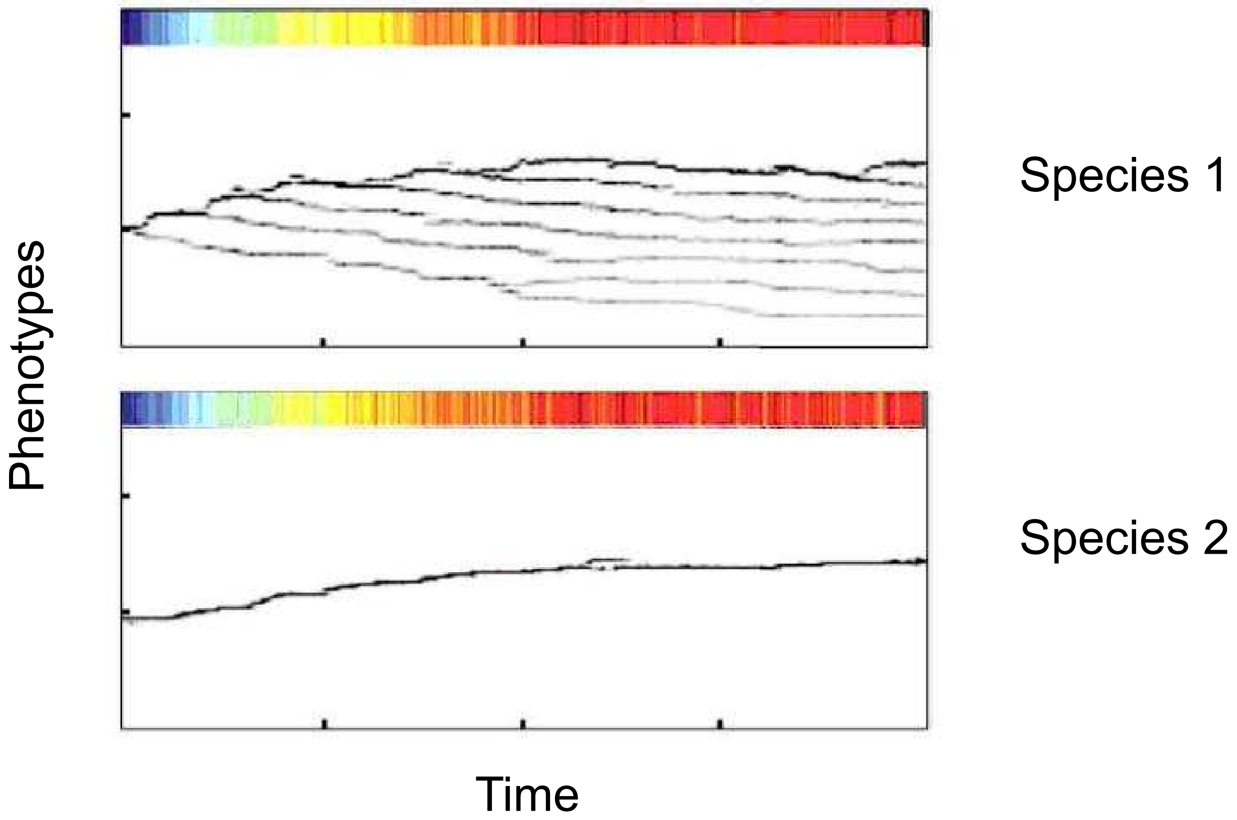



- marginal costs always exceed marginal benefits
- eventually costs exceed benefits

- marginal benefits always exceed marginal costs
- eventually costs exceed benefits

- marginal costs and marginal benefits balance at ecologically viable evolutionary attracting point

# Beyond evolutionary attractor




color code : total amount of exchanged commodities

minimum maximum

# Implications

(1) Evolutionary stabilisation of mutualism

— Through asymmetric competition for partners

(2) Evolutionary diversification

— Cheaters provide a support to better mutualists to express their competitive superiority

— A rewarding asymmetry is necessary for cheaters' persistence

# Implications

(3) Evolutionary benefit of ecological cheating

— Mutualistic associations that incorporate cheaters become more productive.

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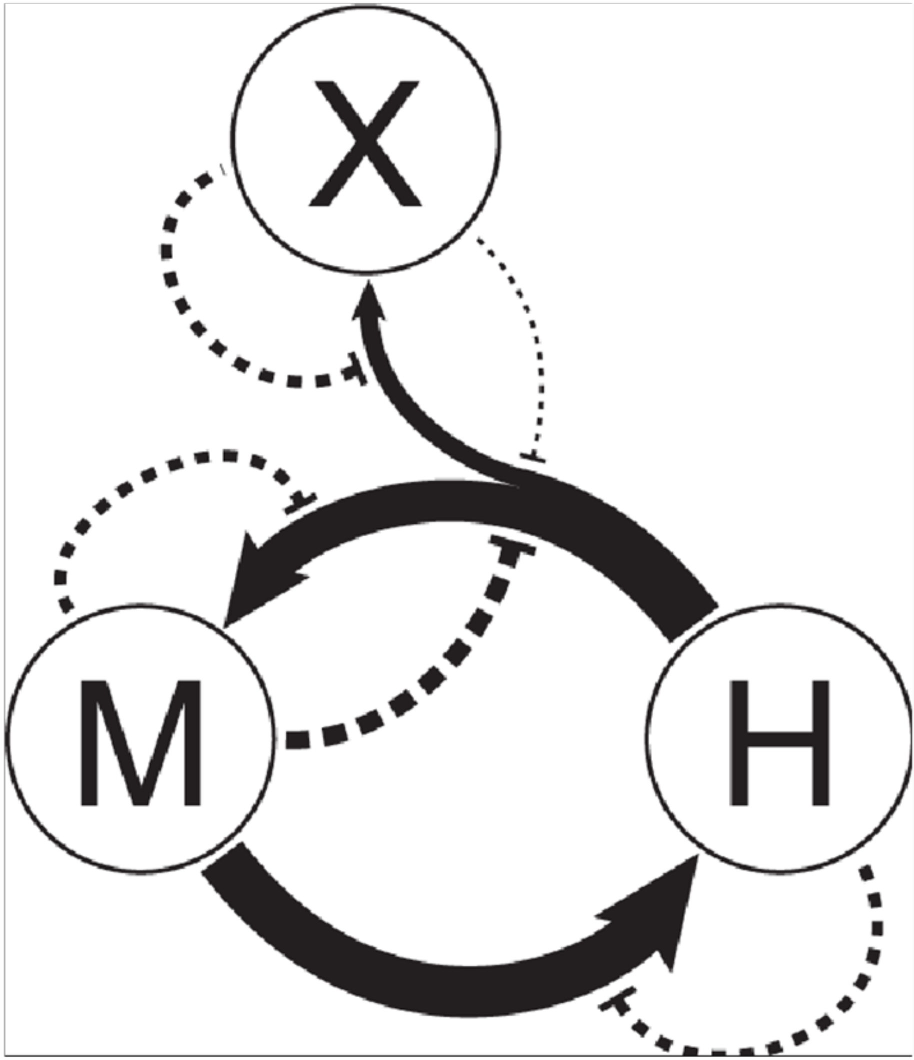
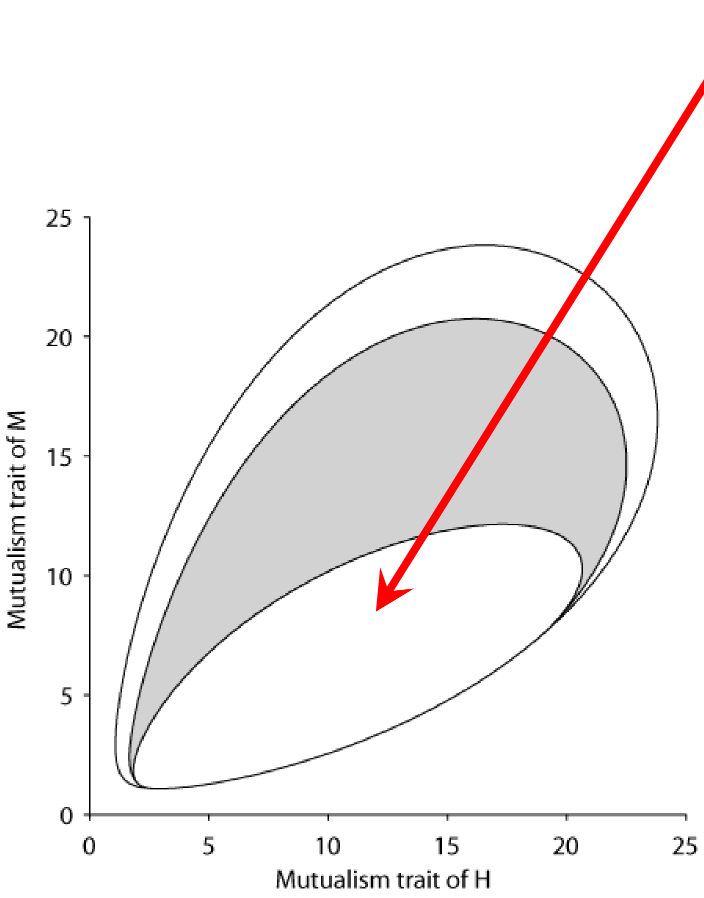
# Model

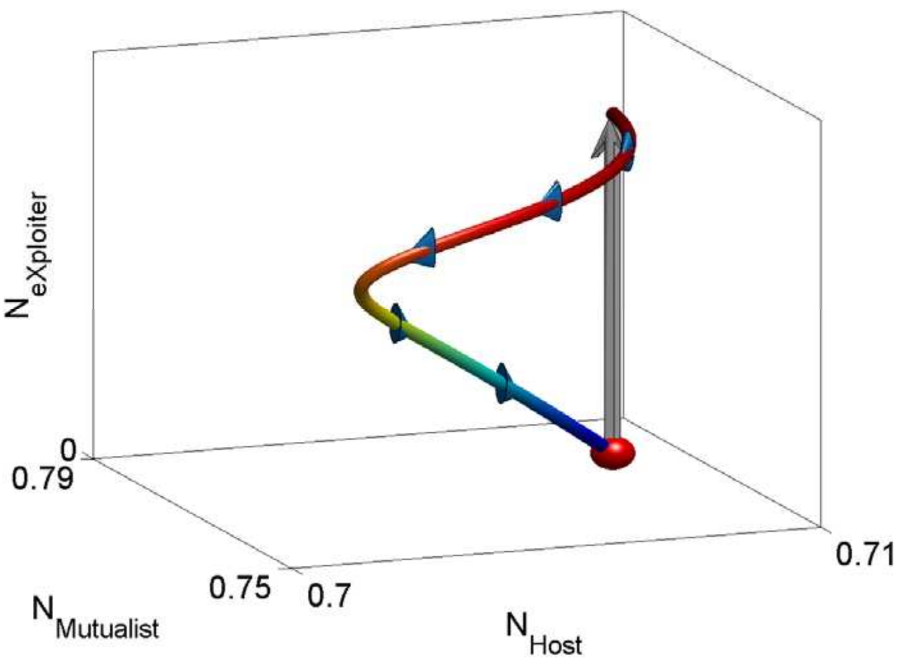
- Host and Mutualist association
- eXploiter is a pure cheater
  - Invasive species
  - Large mutant
- Simplifying hypothesis
  - Constant competitive asymmetry between X and M
  - The exploiter does not evolve



# Mutualism ecological dynamics in the face of exploitation

- Exploiters intruding mutualism evolutionary equilibrium
  - Weak mutualism: exclusion



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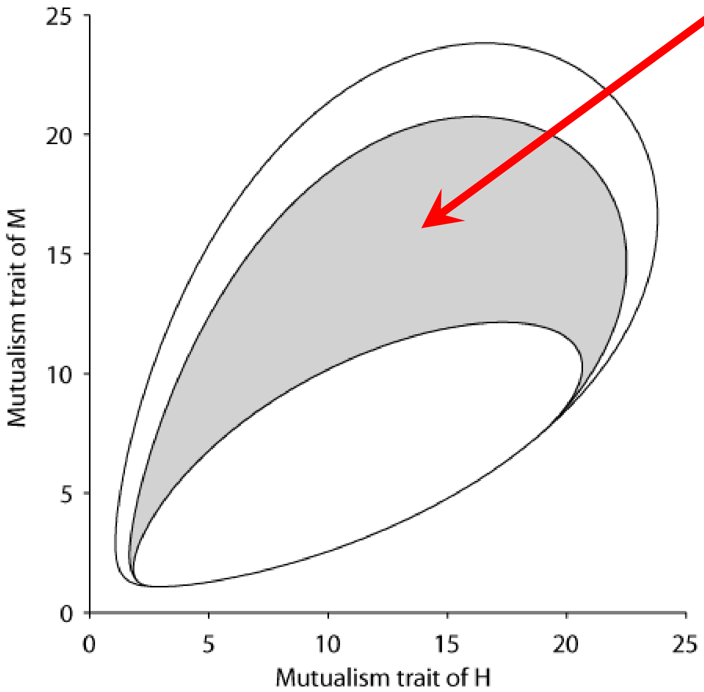
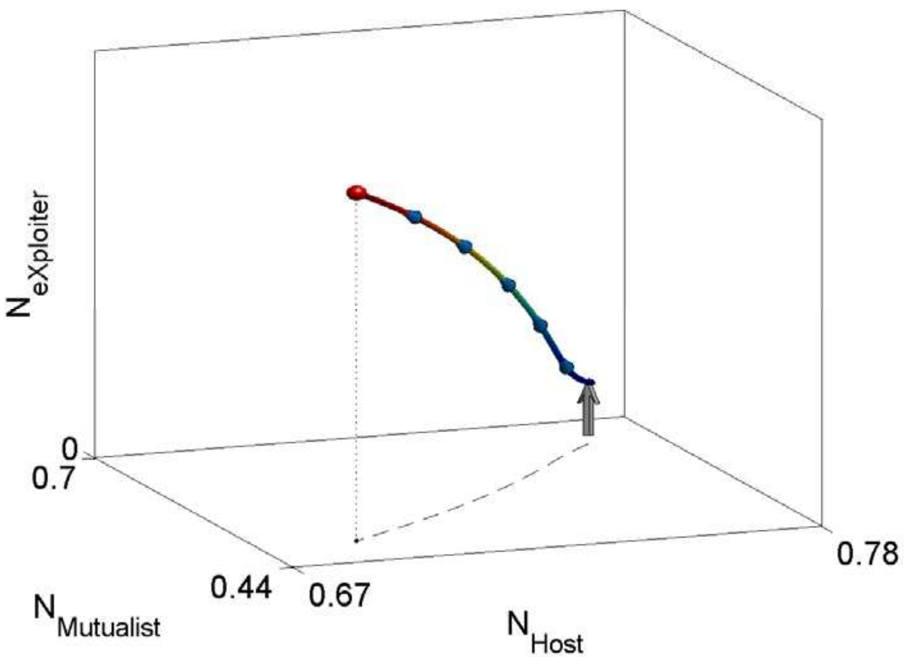
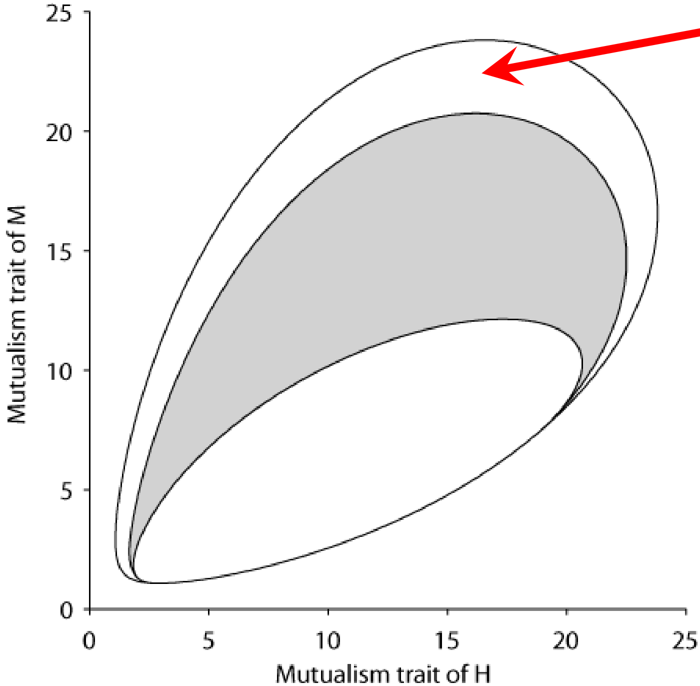
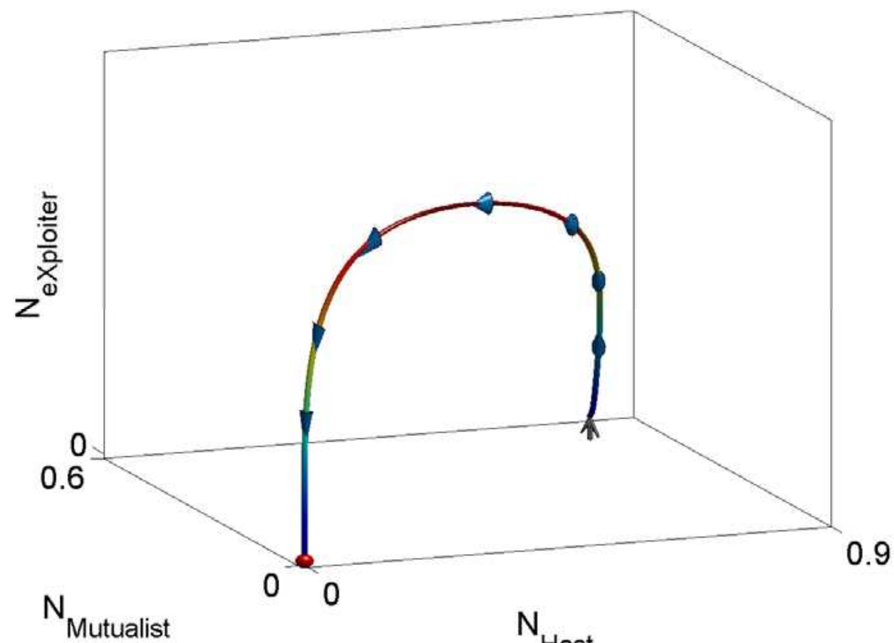


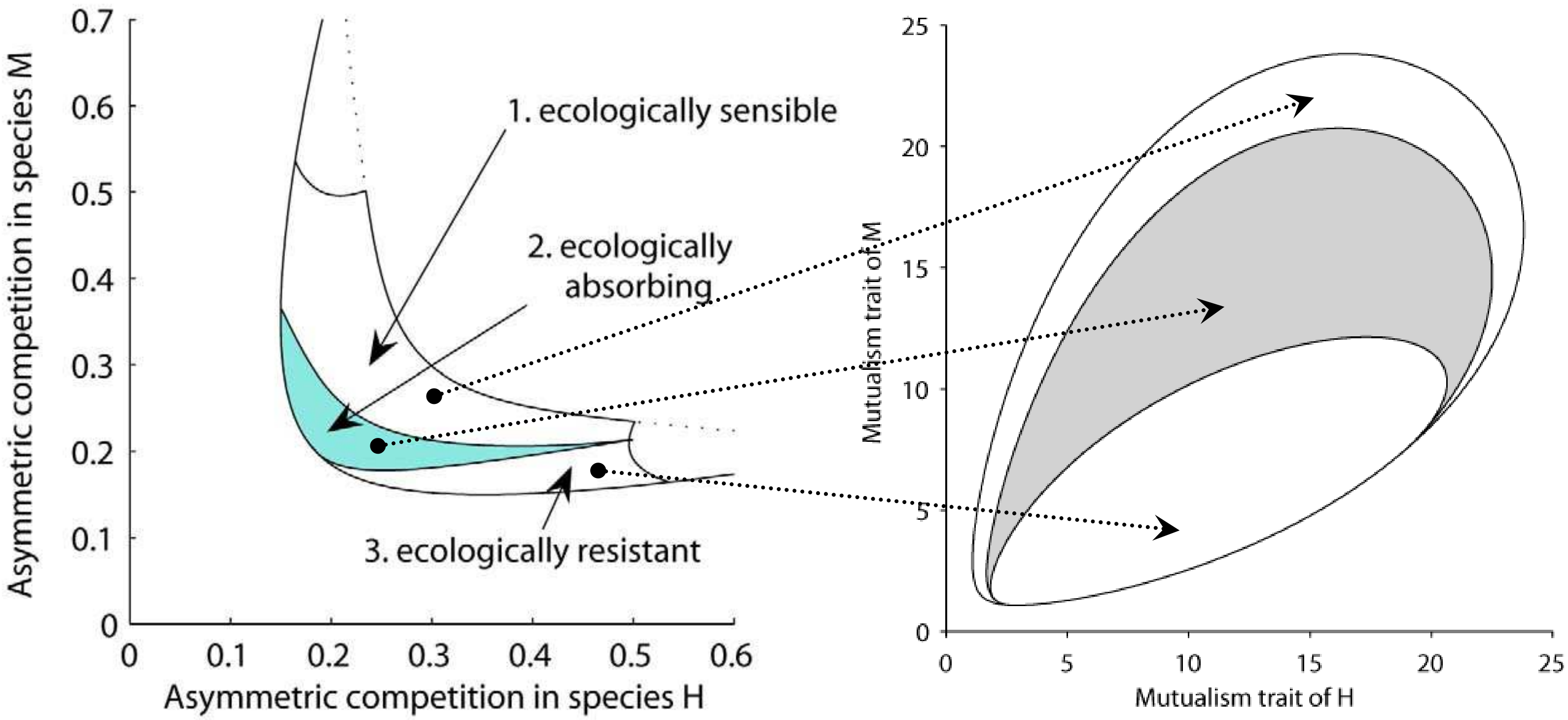
# Mutualism ecological dynamics in the face of exploitation

- Exploiters intruding mutualism evolutionary equilibrium
  - Weak mutualism: exclusion
  - Intermediate mutualism: coexistence
  - Strong mutualism: kamikaze invasion, global extinction



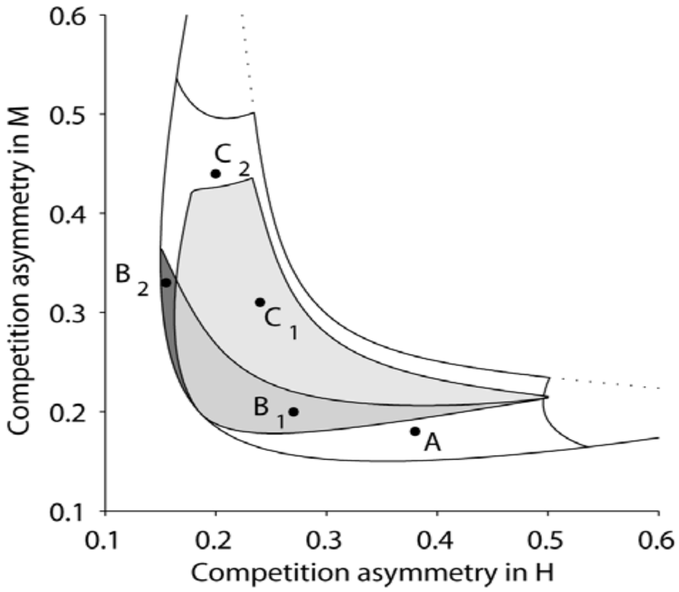
# Exploiter's effect on coevolved host-mutualist pair



# Evolution with the exploiter onboard

Exploiter's successful invasion causes:

- a shift in the coevolutionary equilibrium
- evolutionary murder
- alternatively
  - extinction if Host and Mutualist have already reached coevolutionary equilibrium
  - high-jacking toward a new coevolutionary equilibrium



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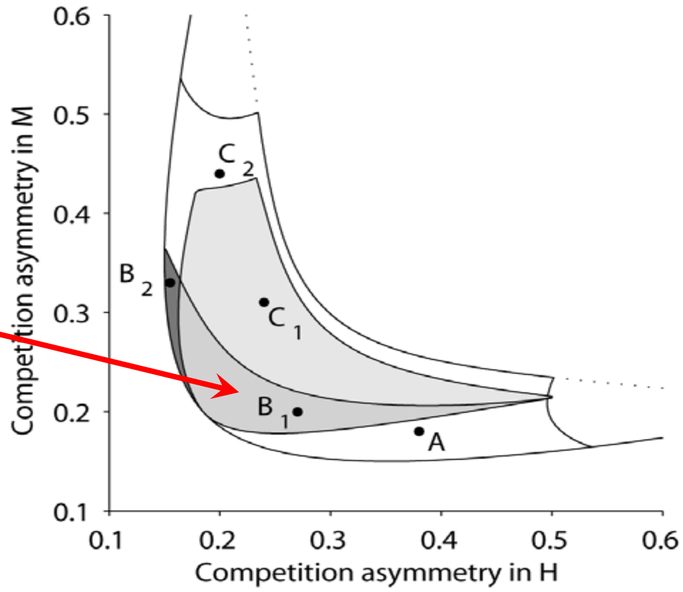

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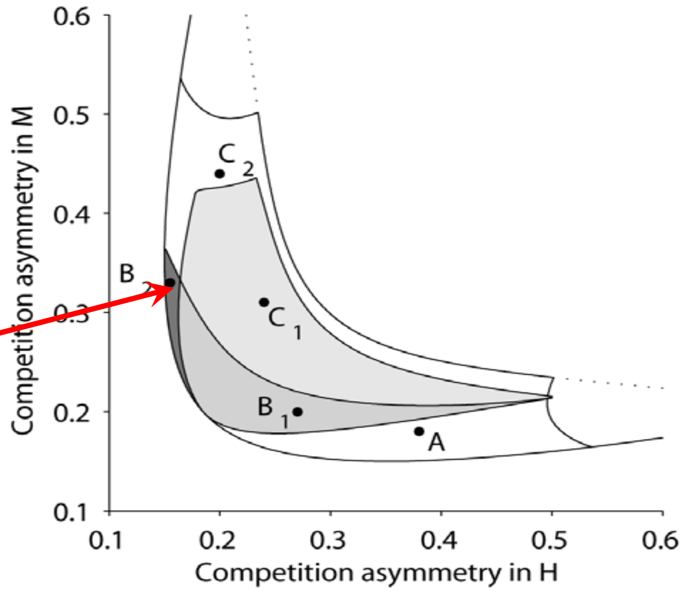

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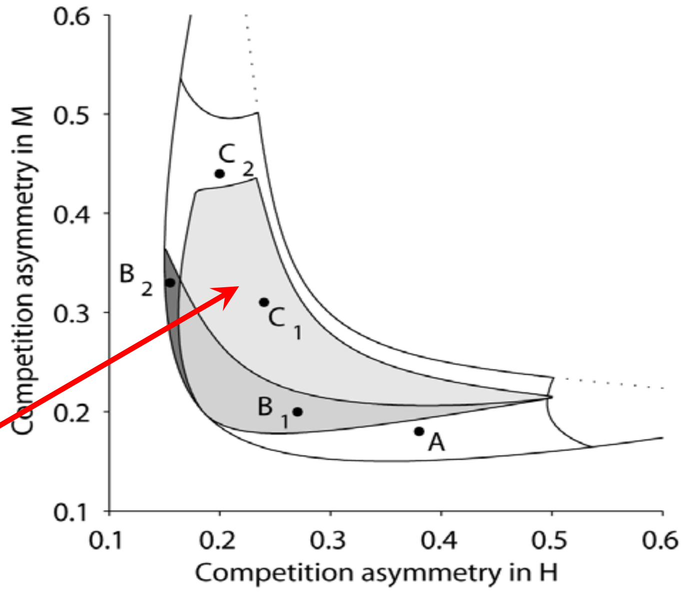

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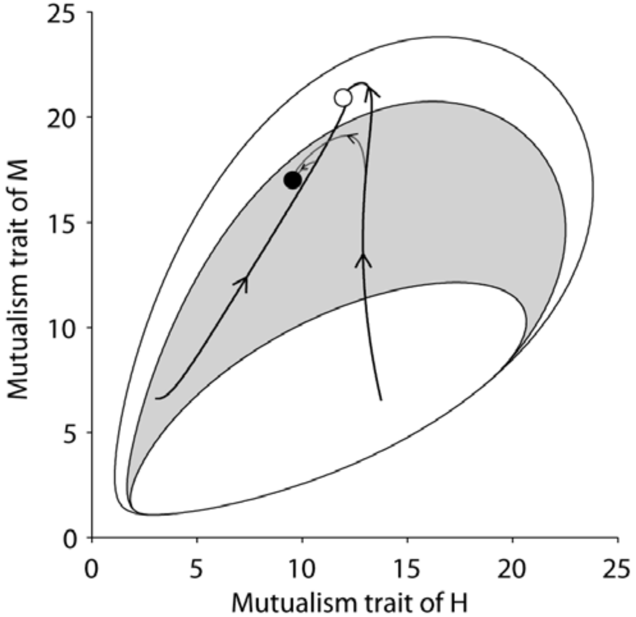
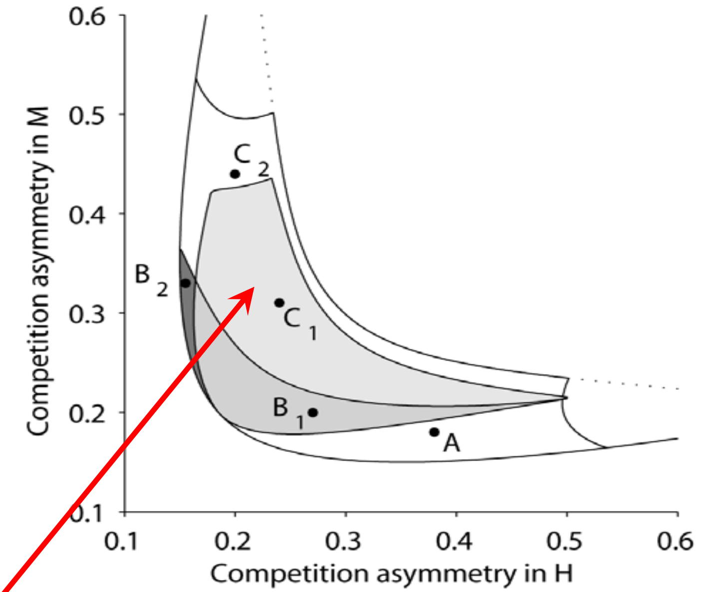



- Alternatively
  - extinction if Host and Mutualist have already reached coevolutionary equilibrium
  - high-jacking toward a new coevolutionary equilibrium

# Mutualism evolutionary dynamics in the face of exploitation

- Mutualisms that are best at evolutionarily policing internal cheaters, do worst against external exploiters, but…
- "**Evolutionary immunization**"
  - Exploiters intruding early in mutualism evolution can coexist
  - Sway coevolutionary trajectory towards mutualism evolutionary equilibrium stable against further invasion

# Persistence of mutualism in the face of invasion

- There exists a wide region of parameters for which mutualism can persist
  - It resists the exploiter's invasion
  - Exploiter's invasion has benign effects
  - Mutualism is 'immunized' by the early invasion of an exploiter

# Conclusions

# Mutualism persistence

- Competitive asymmetry is key
- In spite of exploiters invasions: ‘evolutionary immunization’

Evolution is a dynamical process !

# Perspectives

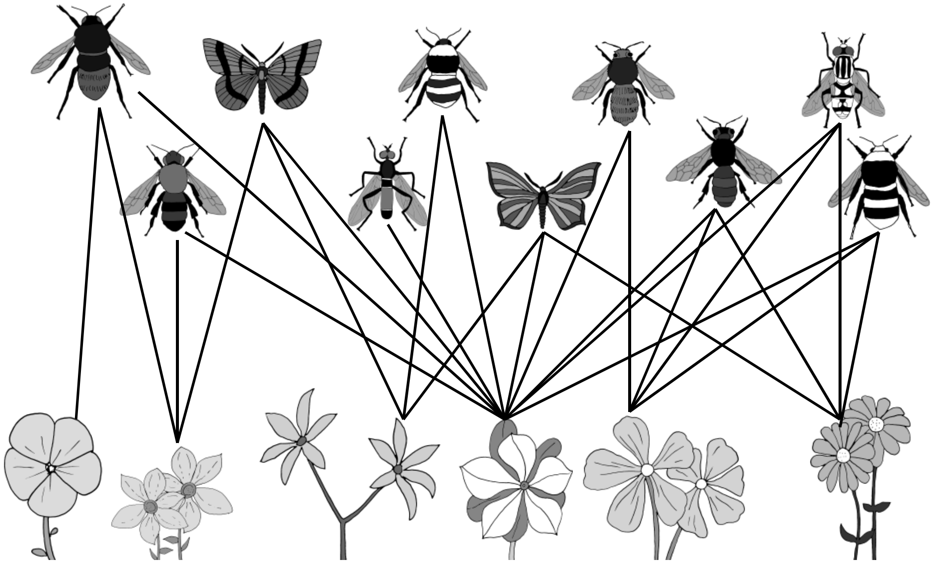
- **Evolution of exploiter after invasion**
  - Generalized coevolution
- **Facultative mutualism**
  - Importance of community context
- **Sexual models**
  - Importance of migration
- **Spatial structure**
  - Explaining mutualism variation in homogeneous habitat

# Mutualism and trophic context

- Mutualism ant – acacia
- Mutualistic interaction involves a third partner
- Impact of herbivores on
  - Mutualism costs and benefits
  - Competitive asymmetry

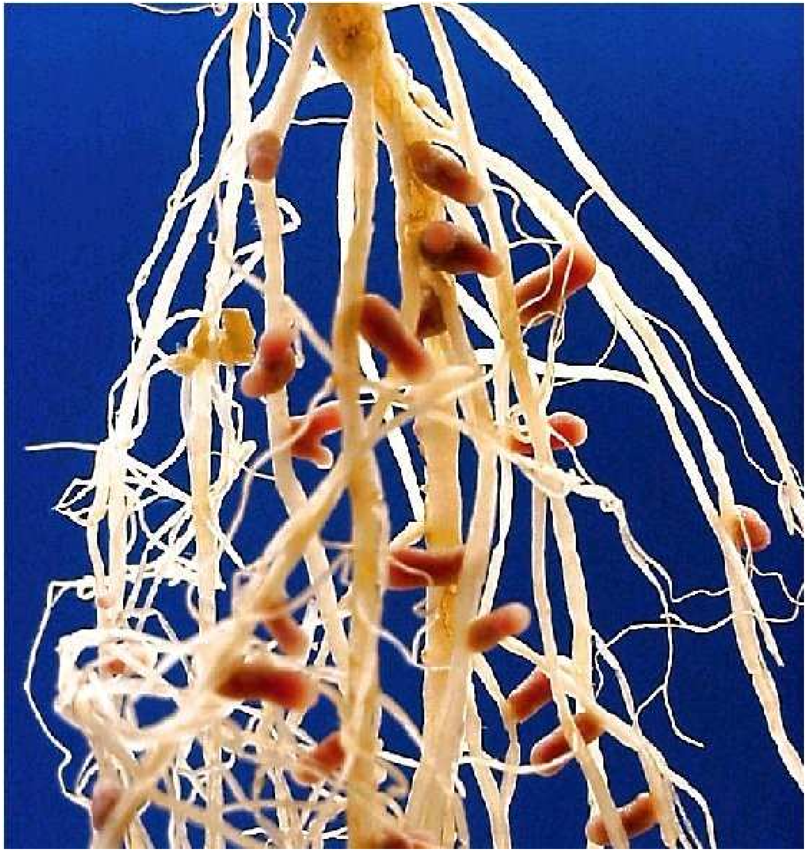
# Mutualism and community context

- Pollination networks
- Highly generalist system



# Evolution of discrimination and migration

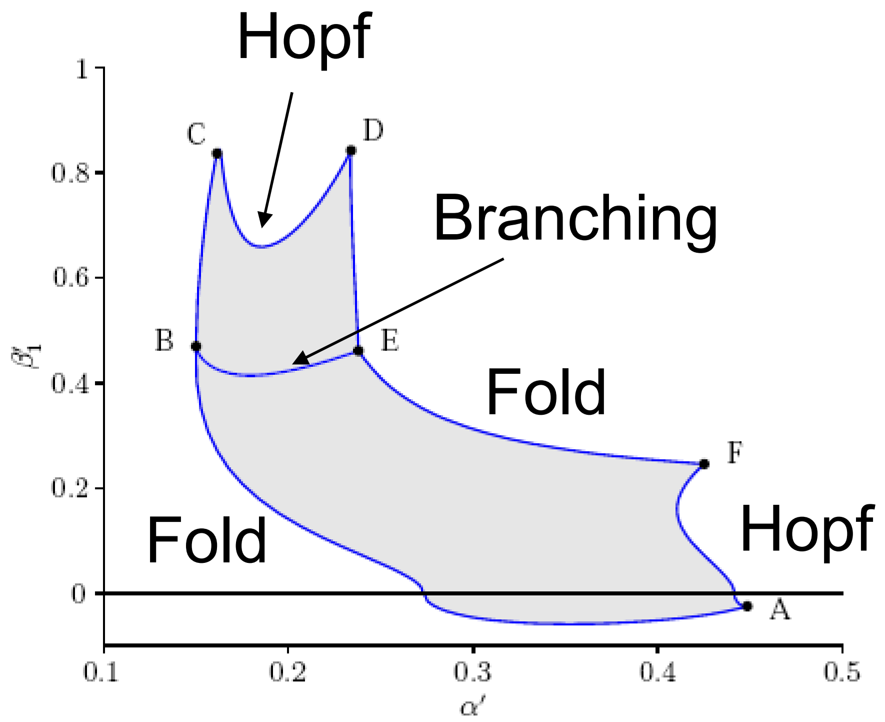
- Legume – rhizobium
- Discrimination evidences
- Spatial heterogeneity



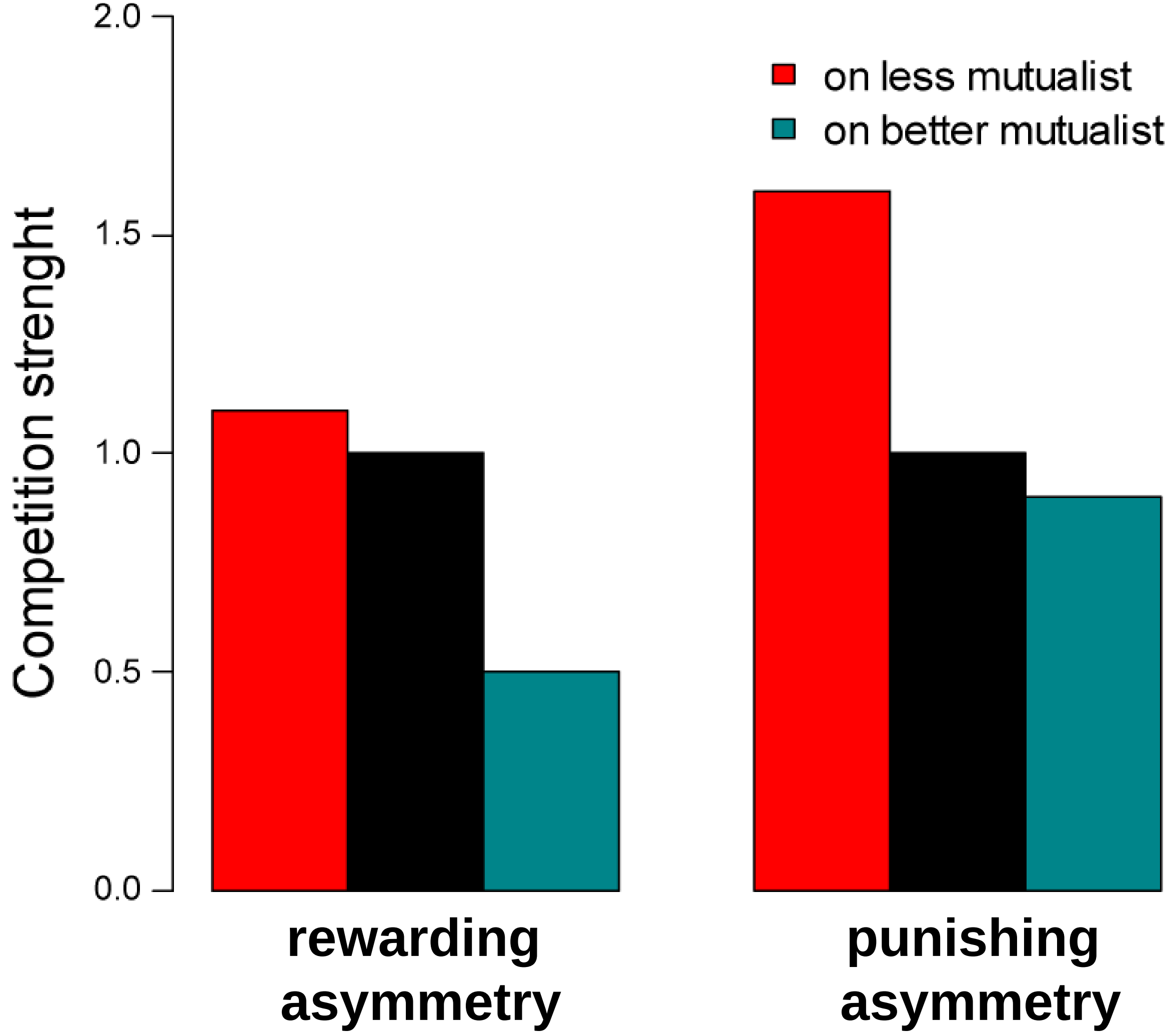
# Thank you for your attention

$$\mathbb{k}\sqrt{a^2+b^2}$$

# Bifurcation Analysis of Evolutionary Equilibria



# Punishing or rewarding asymmetry



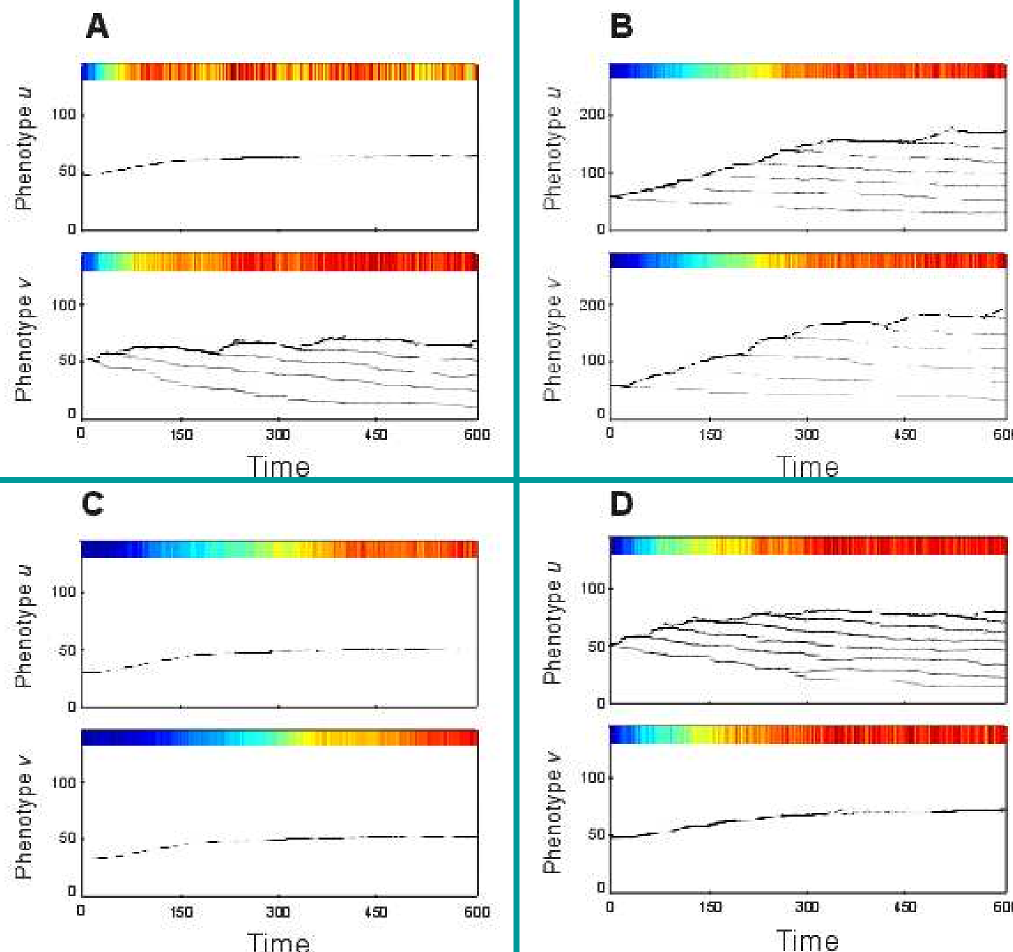
# Diversification scenarios

punishing asymmetry

rewarding asymmetry

rewarding asymmetry

rewarding asymmetry




punishing asymmetry

punishing asymmetry

rewarding asymmetry

punishing asymmetry

color code : total amount of exchanged commodities

minimum maximum