Evolution of ecosystem properties

Simon Levin

Trieste 2010

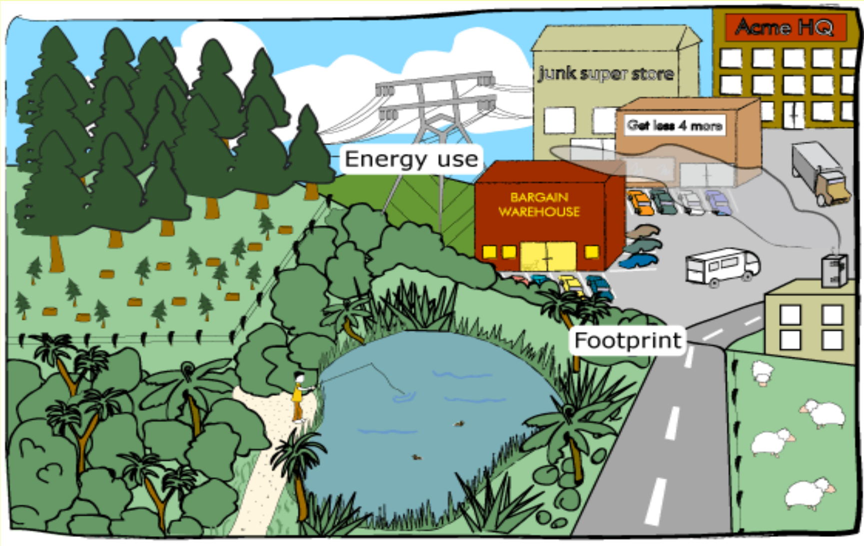
members.home.nl/pamali/schilderen

The central problem facing societies is achieving a sustainable future

farm3.static.flickr.com

Sustainability means many things

- Financial markets and economic security
- Energy and other natural resources
- Biological and cultural diversity
- Ecosystem services



www.waikato.govt.nz/enviroinfo

Challenges

- How do *ecosystem services* depend on biological diversity and ecosystem functioning?
- What sustains those essential aspects of ecosystem structure?

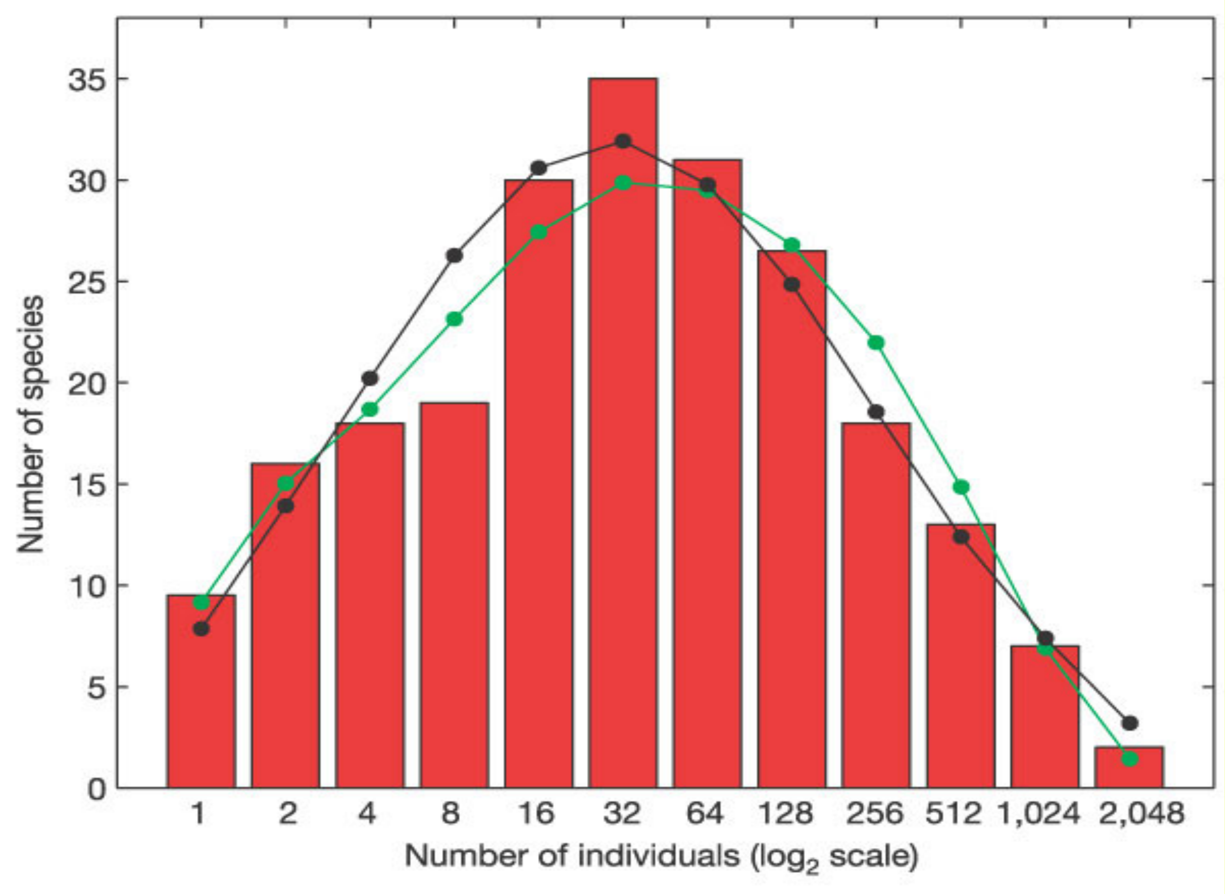
In any ecosystem, there are characteristic macroscopic patterns that sustain ecosystem services

www.bio.unc.edu

www.yale.edu/yibs

www.csiro.au

There are striking regularities in such macroscopic patterns, independent of much microscopic detail



Volkov, Banavar, Hubbell and Maritan
Nature 424, 1035-1037

In marine systems, characteristic regularities include

- Distribution of phytoplankton
- Nutrient use patterns
- Size-structure spectra
- Patchiness of zooplankton and fish

2.bp.blogspot.com

Marine ecosystems show remarkable constancy in element ratios, although absolute levels may vary considerably

- Water column
- Primary producers
- Consumers

Redfield ratios

(in marine organic matter)

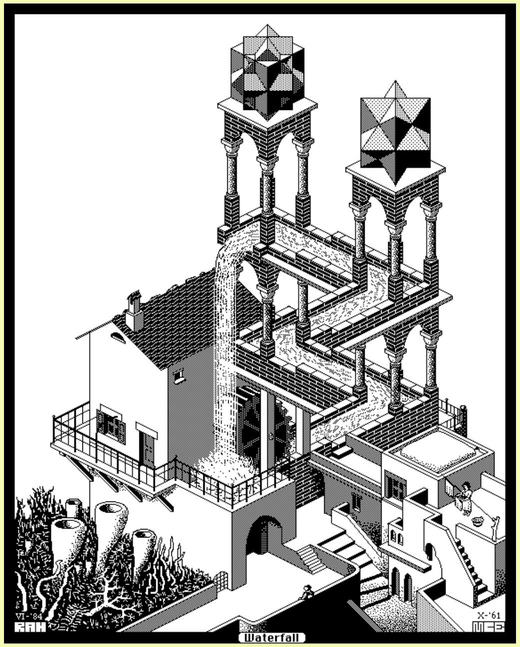
P : N : C: $-O_2$

(oxygen required to respire marine organic matter)

1 : 16 : 106 : 138

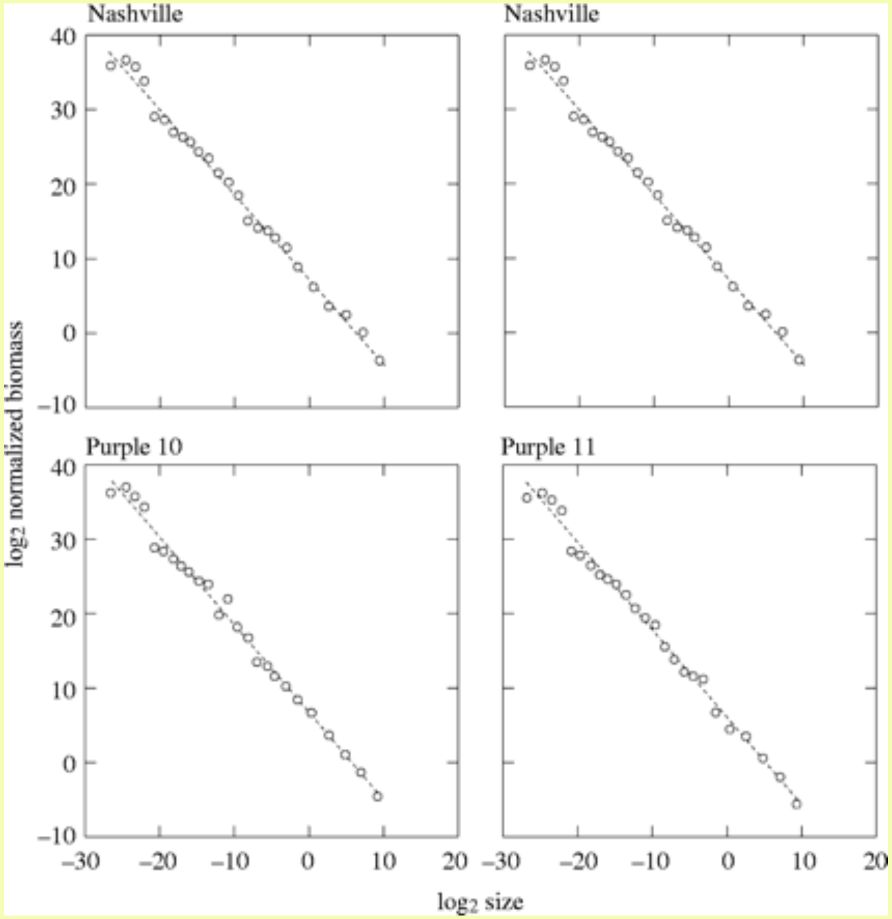
(subject to some debate)

Stoichiometry provides just one set of robust patterns



Sheldon’s particle size spectrum is a remarkable constant across broad scales in marine ecosystems

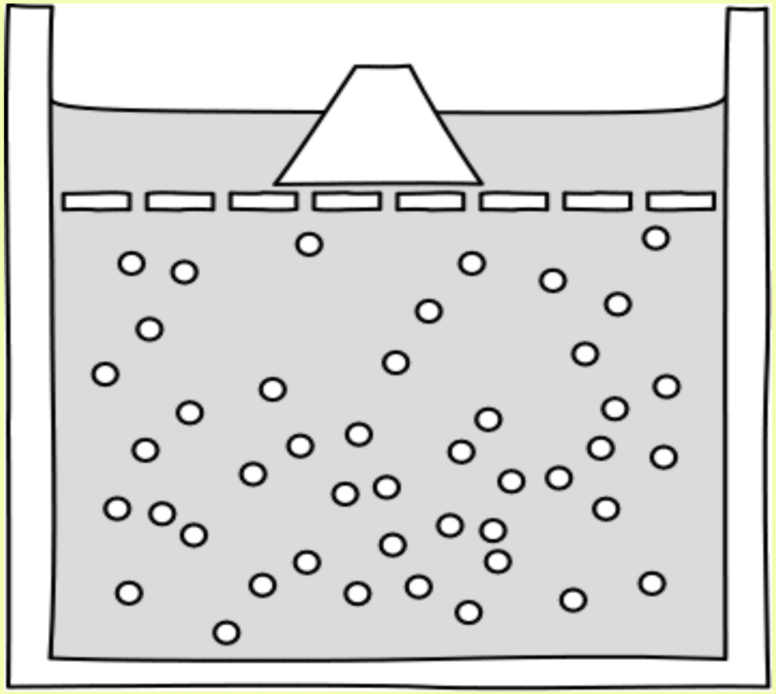
Particle Size Spectrum (Sheldon)



Normalized biomass size-spectra in carbon units from several stations in the New England Seamounts Area (Northwest Atlantic). (Marquet et al, after Quiñones et al., 2003.)

How can we understand the emergence of such regularities from evolutionary forces at lower levels of organization?

Sustainability must focus on these macroscopic regularities, while recognizing that control of those rests at lower levels of organization



What maintains the robustness of macroscopic patterns, and nutrient cycling?

Lovelock proposed the GAIA Hypothesis:

Elsie Russell

Lovelock : the GAIA Hypothesis:

- Biota controls physico-chemical environment at just the right conditions for its survival

Elsie Russell

Lovelock : the GAIA Hypothesis:

- Biota controls physico-chemical environment at just the right conditions for its survival
- In extreme form, the biosphere is a superorganism, selected for its macroscopic properties

Problems with Gaia

- Gaia describes macroscopic regularities

Problems with Gaia

- Gaia describes macroscopic regularities
- Evolution operates at lower levels, and not for “benefit” of whole system

Ecosystems and the Biosphere are Complex Adaptive Systems

Heterogeneous collections of individual units (agents) that interact locally, and evolve based on the outcomes of those interactions.

Levin 1999: Fragile Dominion

Patterns emerge, to large extent from phenomena at much lower levels of organization

- Individual agents

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- Individual agents
- Small spatial scales

Patterns emerge, to large extent from phenomena at much lower levels of organization

- Individual agents
- Small spatial scales
- Short temporal scales

We need a theoretical foundation

- Resting on our understanding of the principles of evolution, at the level of genomes and populations
- Explaining the features that underlie the robustness of the services we derive from ecosystems

There is a long and rich history of the application of mathematics to ecology

Vito Volterra
1860-1940

Fluctuations of the
Adriatic Fisheries

Evolutionary theory also has a rich mathematical history

$$dp/dt = s(pq/\overline{w})(d\overline{w}/dp)$$

Sewall Wright

R.A.Fisher

J.B.S.Haldane

The challenge remains to meld these two scales

Place ecological interactions within an evolutionary framework

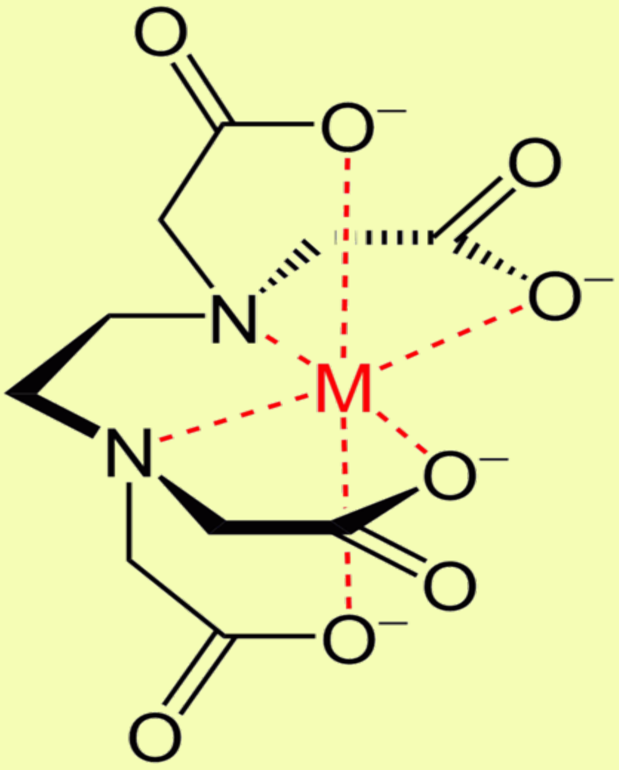
$dx/dt = f(x;\alpha,E)$	Ecological
$d\alpha/dt = \varepsilon g(x;\alpha,E)$	Evolutionary

Sample applications

- Evolution of dispersal and successional patterns
- Stoichiometry
- Species distributions
- Resource use in nutrient-limited environments
- N-fixation

Many problems involve public goods

- Water use in arid lands
- Chelation and siderophores
- N fixation
- Antibiotics
- Extracellular proteins



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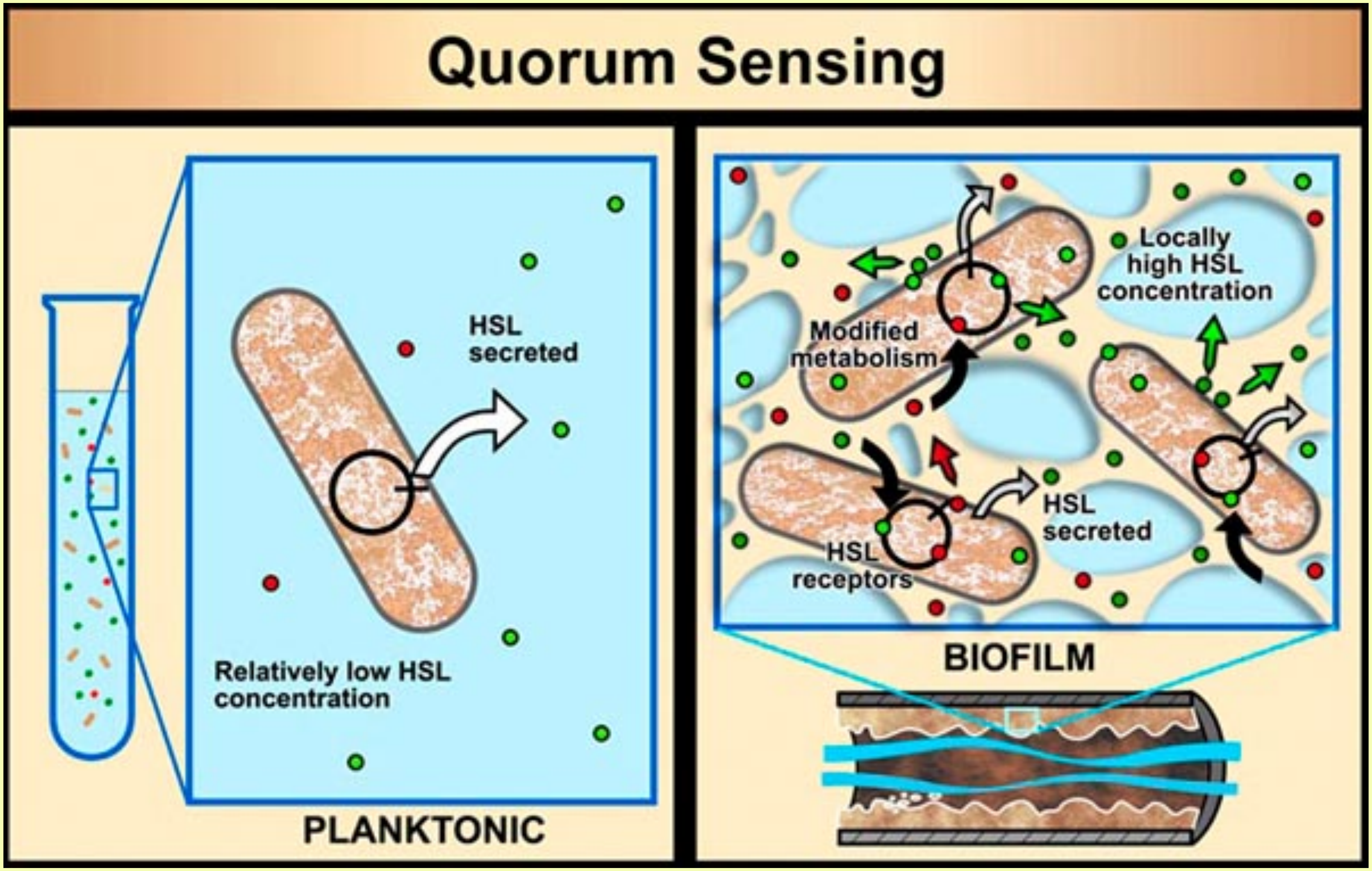
Even bacteria cooperate



www.cs.montana.edu/~ross

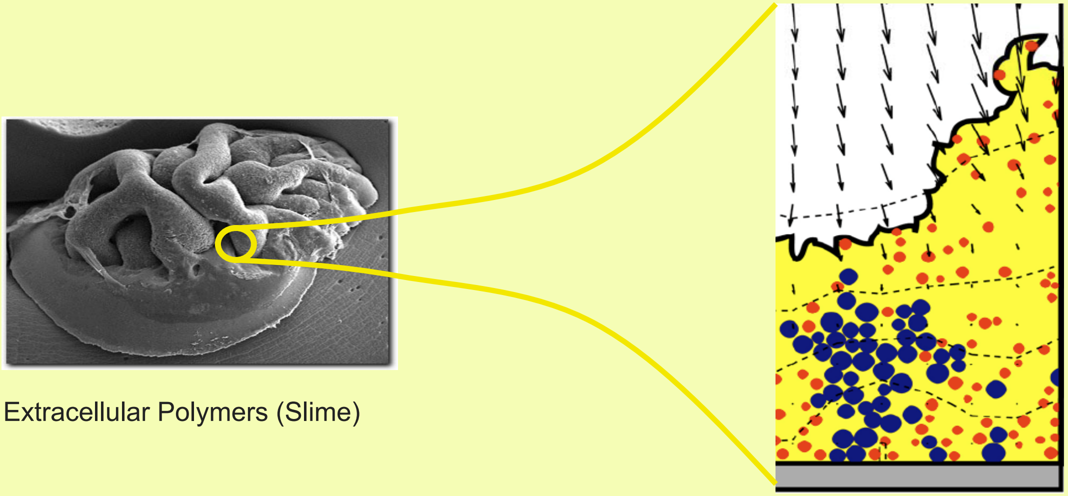
Even bacteria cooperate

www.scharfphoto.com

Link between group living and communication

Nadell, Xavier, Levin, Foster

Quorum Sensing ↔ **Slime** ↔ **Biofilms**



Extracellular Polymers (Slime)

Key

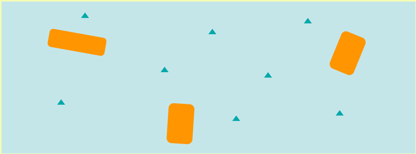
● Cell that cannot make polymer

● Cell that makes polymer

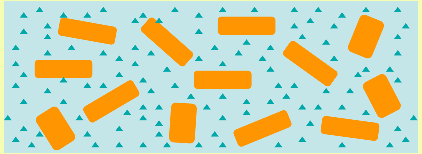
● Extracellular polymer

→ Nutrient Diffusion

Low cell density

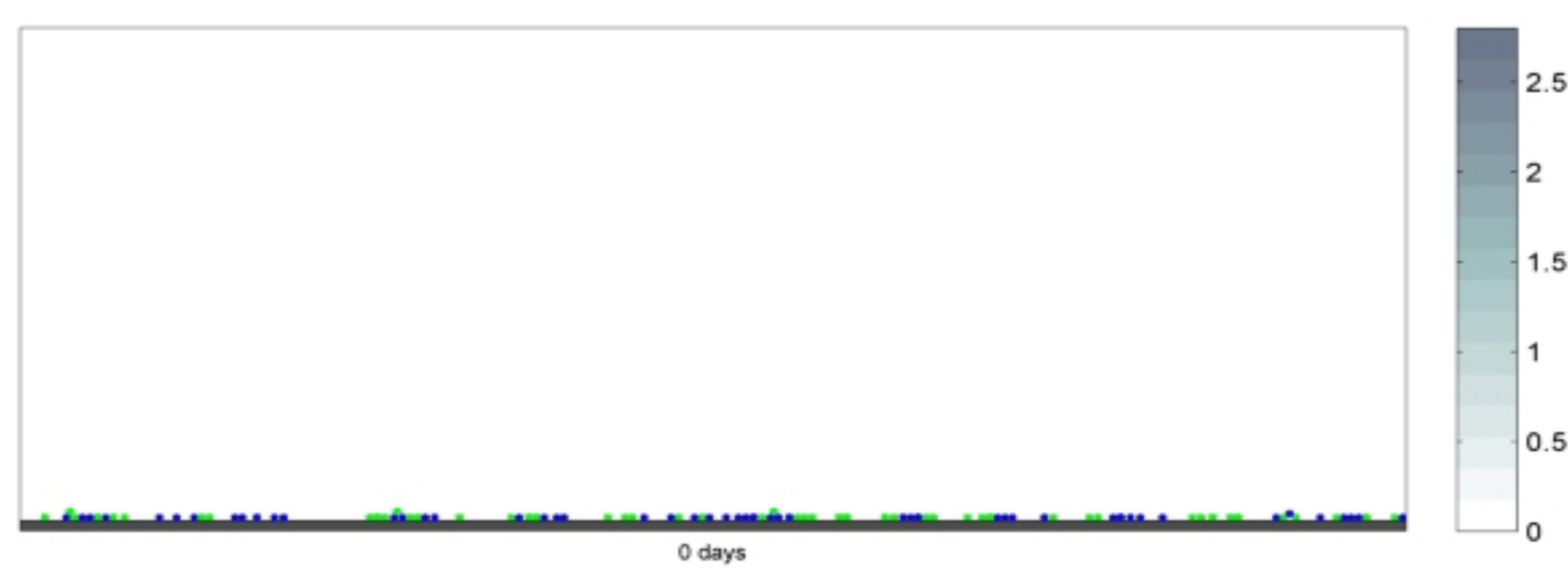


High cell density



	Low cell density	High cell density
Pseudomonas aeruginosa	Slime OFF	Slime ON
Vibrio cholerae	Slime ON	Slime OFF

Biofilm formation and quorum sensing



🔵 Constitutive Slime-producer

🟢 QS Strain (below quorum)

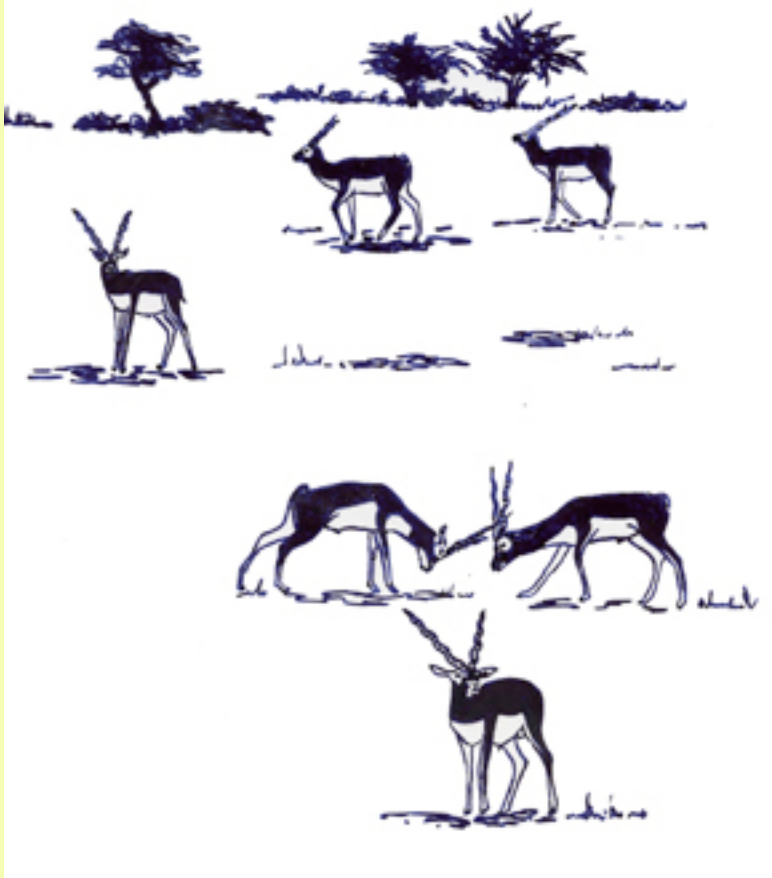
🟡 Slime

🔴 QS Strain (above quorum)

Nadell, Xavier, Levin, Foster

Approaches to evolutionary ecology

- Optimization
- Game theory
- Dynamic games
- Collective phenomena
- Coevolution



ces.iisc.ernet.in

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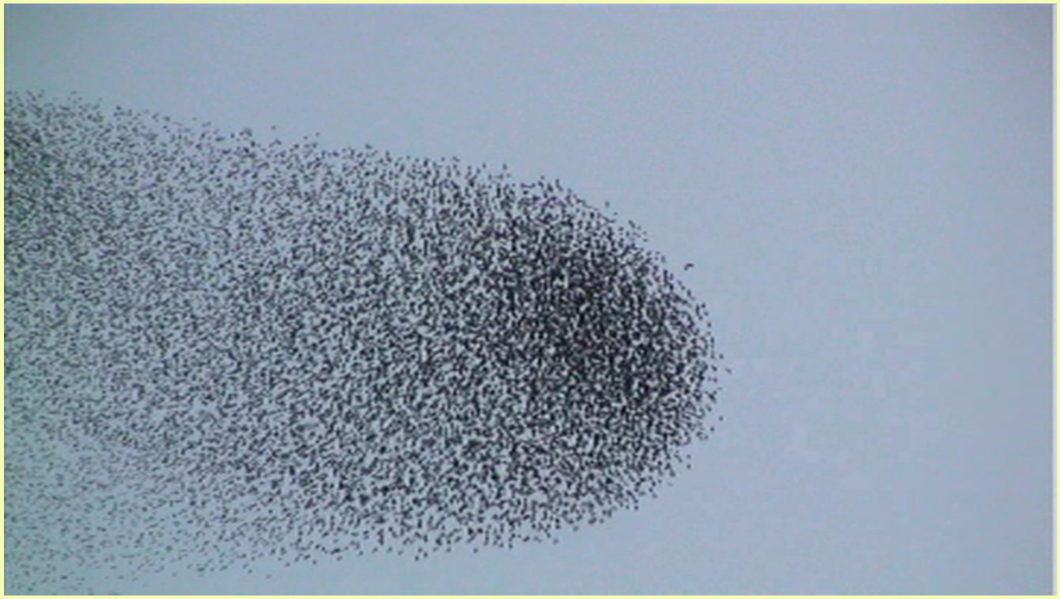
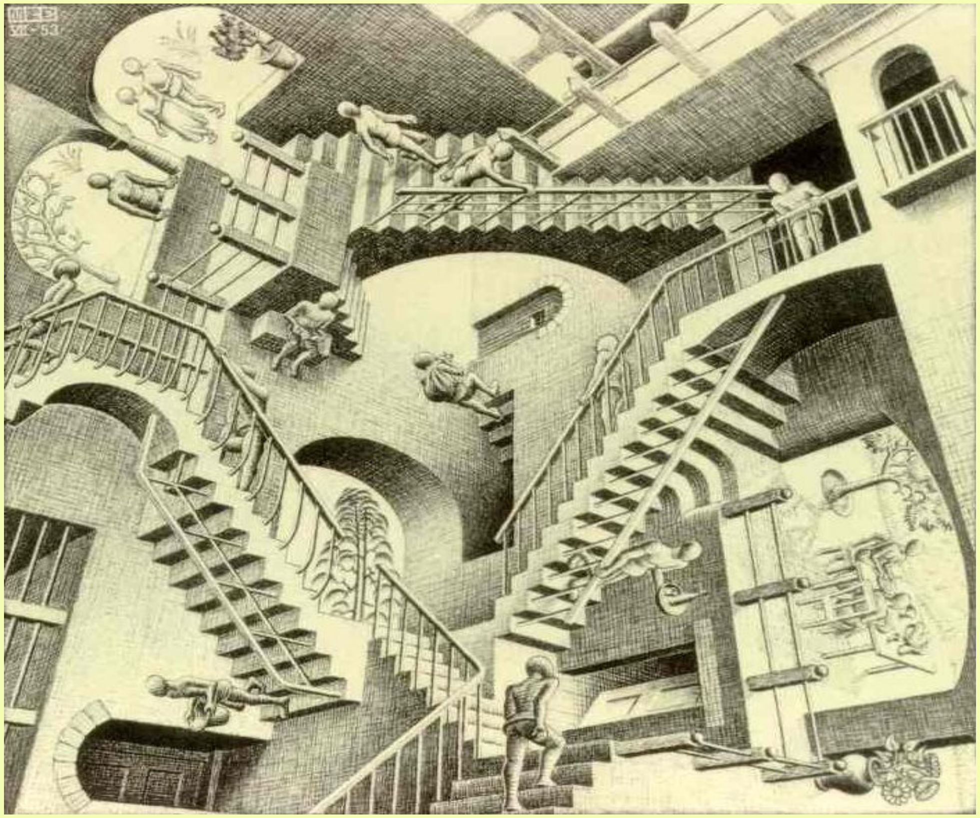
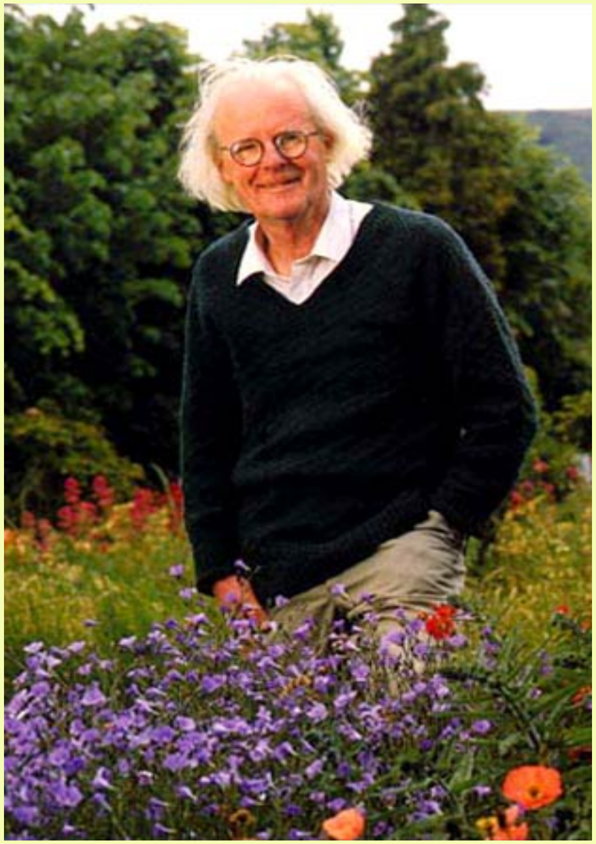


Because of frequency-dependence

- Optimization must give way to game theory



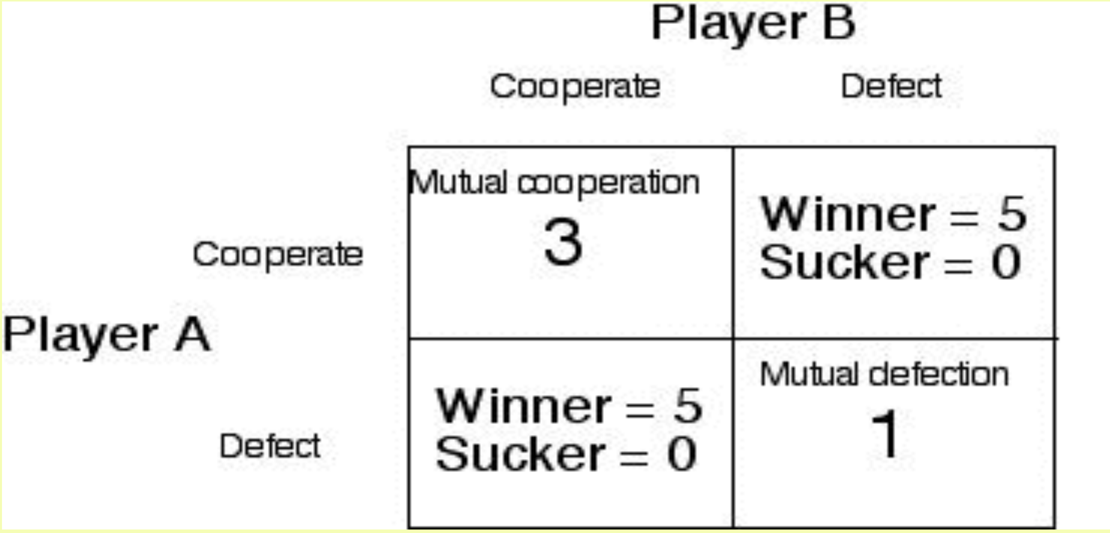
Maynard Smith introduced the notion of the evolutionarily stable strategy



www.pbs.org

Evolutionarily stable strategy (ESS)

- Type that, once established, cannot be displaced
- Prisoner’s dilemma…Nash equilibrium

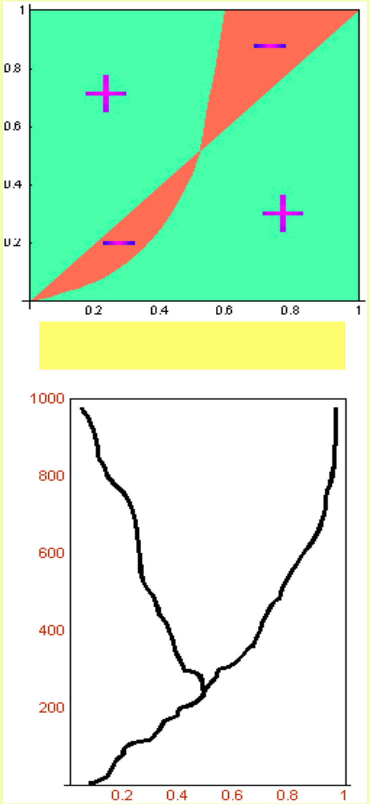


		Player B	
		Cooperate	Defect
Player A	Cooperate	Mutual cooperation 3	Winner = 5 Sucker = 0
	Defect	Winner = 5 Sucker = 0	Mutual defection 1

www.animalbehavioronline.com

Problems with ESS

- Not a dynamic concept
- ESS may not be achievable
- More general theory has developed
  - *Neighborhood invader strategy*
  - *Convergence stable strategy*
  - *Continuously stable strategy*
  - *Evolutionary branching*



Game theory and evolution

- Sex ratio (R.A.Fisher)

Game theory and evolution

- Sex ratio
- Sequential hermaphroditism

animal-world.com

Game theory and evolution

- Sex ratio
- Sequential hermaphroditism
- Helpers at the nest (*Emlen, Emlen, Levin*)

www.birdnature.com

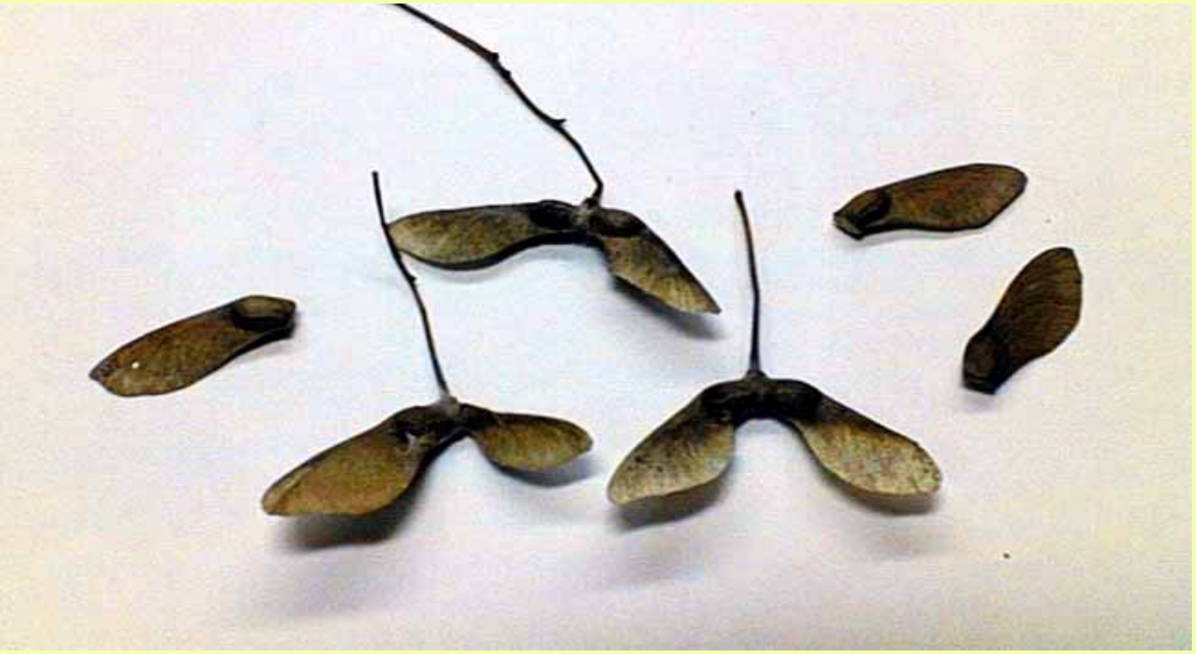
Game theory and evolution

- Parent-offspring conflict *(Trivers)*

www.stud.ntnu.no/groups/humgru/lise

Parent -offspring conflict

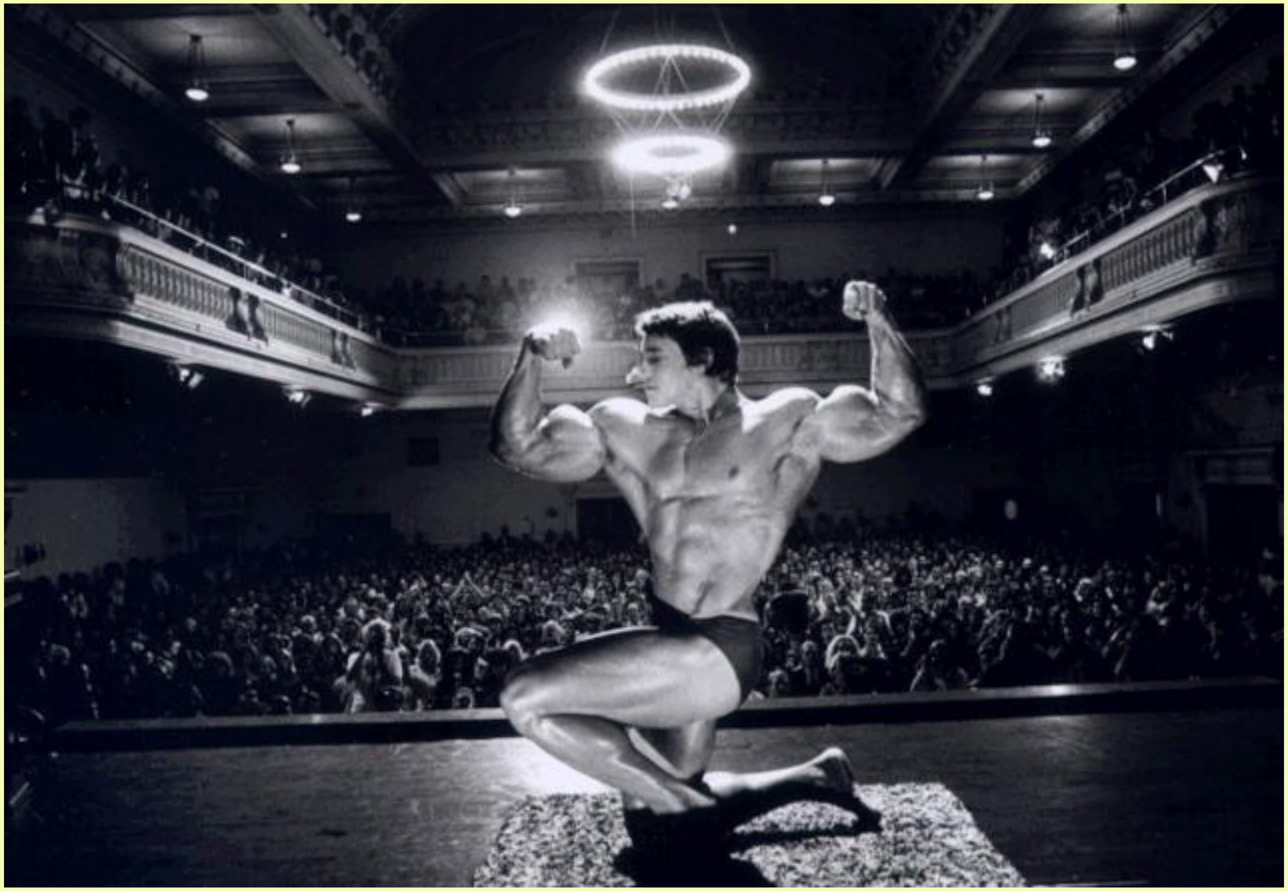
- Seed dispersal



General quantitative theory:

Adaptive dynamics of phenotypes

- Let r be the measure of the *fitness* of a phenotype u (a vector)



http://www.geektimes.com/michael

Evolutionary dynamics of phenotypes

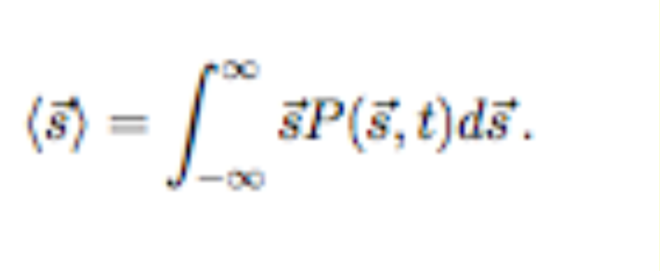
- *$r(v,u)$ is the fitness of a rare phenotype v invading a population in which u is established*
- *$r(v,u)$ typically is the linearized growth rate of the v-phenotype population near $(0, u^*)$*
- *More generally, dominant eigenvalue or Floquet exponent*

Henceforth, assume scalar phenotypes

Adaptive dynamics

(Metz and Dieckmann)

Trait *s* is distributed in population



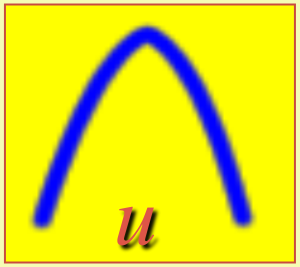
$$\langle \vec{s} \rangle = \int_{-\infty}^{\infty} \vec{s} P(\vec{s}, t) d\vec{s} \, .$$

Controversial

- Asexual
- Separation of time scales
- Ignores genetic variation within phenotypic class
- But approach can be generalized to address first two points

Focus just on invasion dynamics at critical points

Piotr Zacny



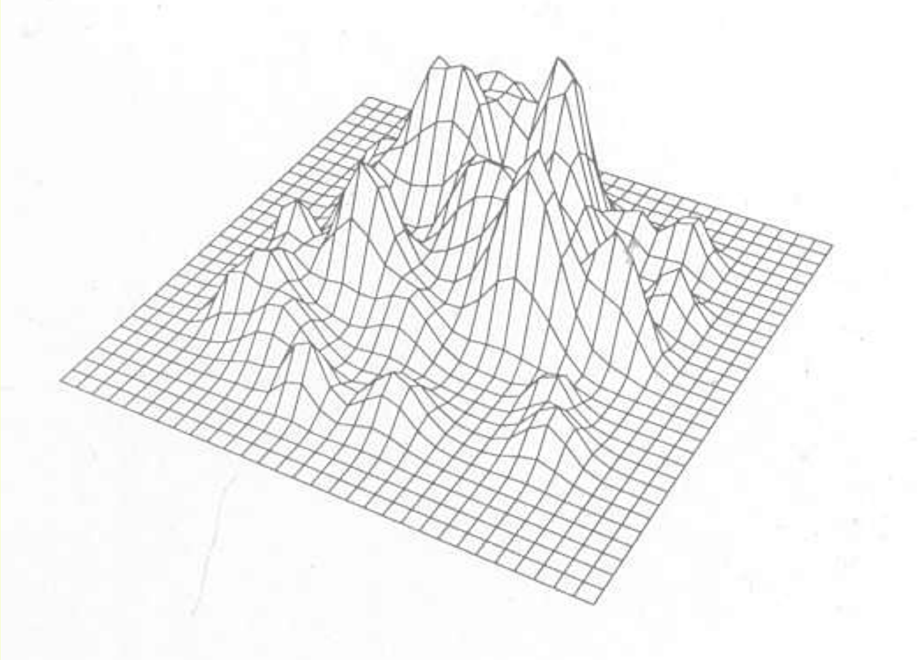
ESS *(evolutionarily stable strategy)*

$r\,(v, u)$ is maximized as a function of v at $v = u$

$$\frac{\partial r}{\partial v} = 0, \quad \frac{\partial^2 r}{\partial v^2} \leq 0$$

But the notion of ESS turns out to be just a beginning

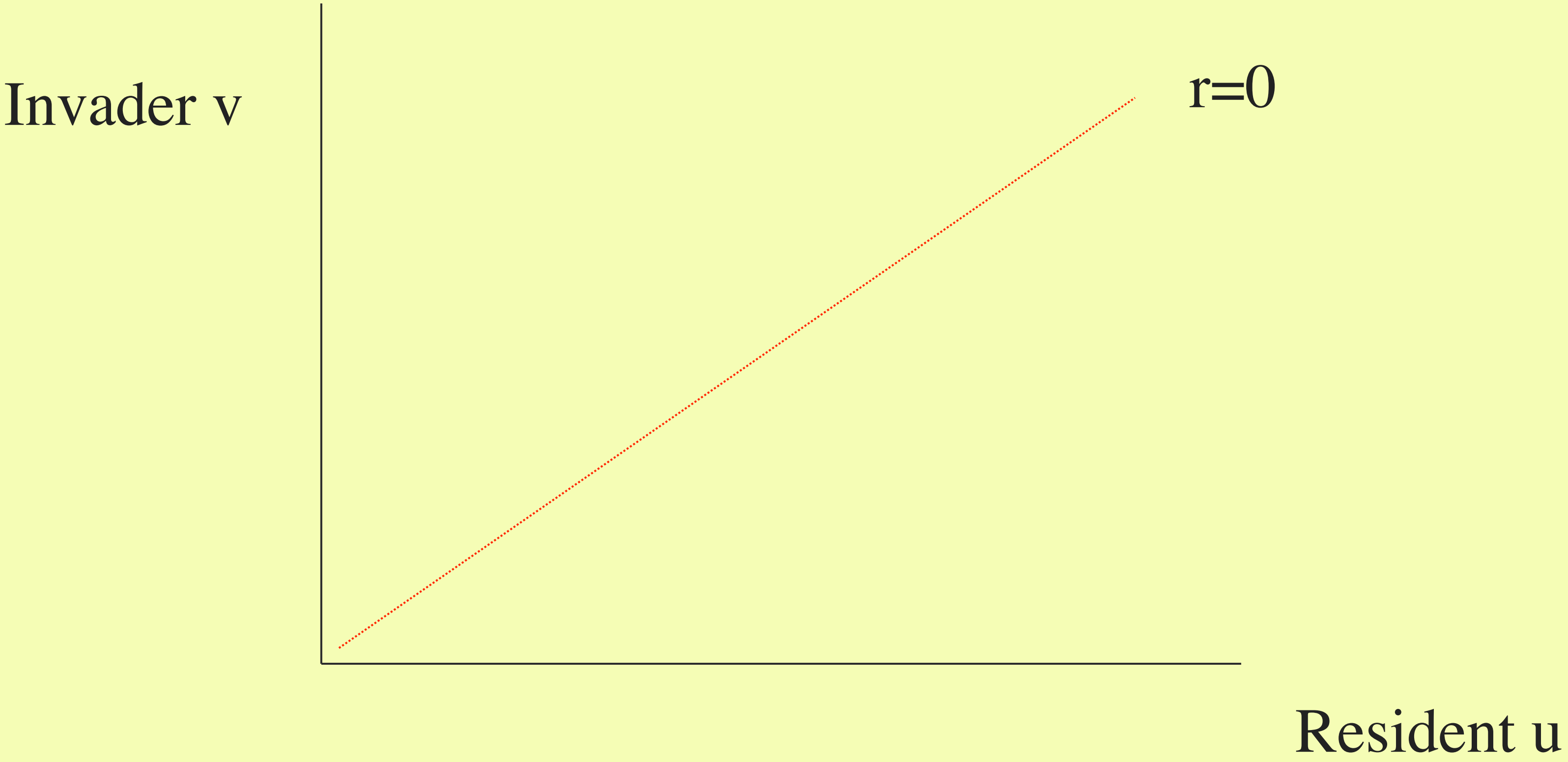
- *There may be several ESSes*



But the notion of ESS turns out to be just a beginning

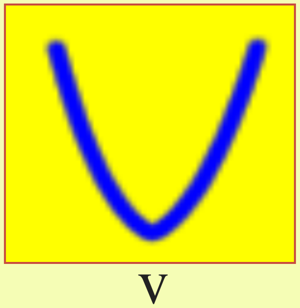
- There may be several ESSes
- An ESS may not be reachable

Need complementary notions



Along diagonal, $\partial r / \partial u + \partial r / \partial v = 0$

So critical points wrt u are critical points wrt v



Need complementary notions

- Neighborhood invader strategy (NIS)
  - *r is minimized as a function of u*

$$\frac{\partial r}{\partial u} = \frac{\partial r}{\partial v} = 0, \ \frac{\partial^2 r}{\partial u^2} \geq 0$$

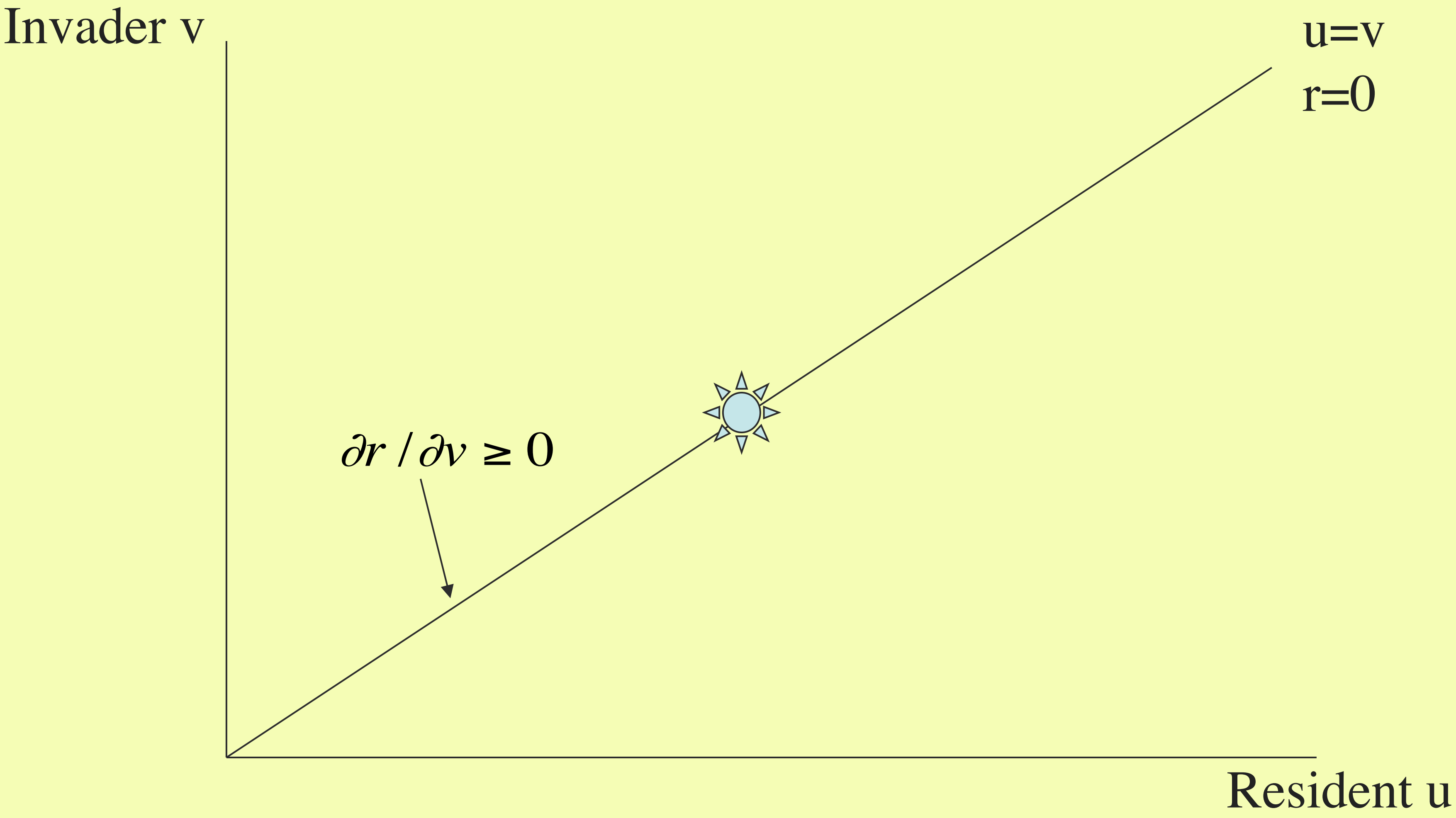
www.neighbourhoodwatch.net

ESS
NIS

Need complementary notions

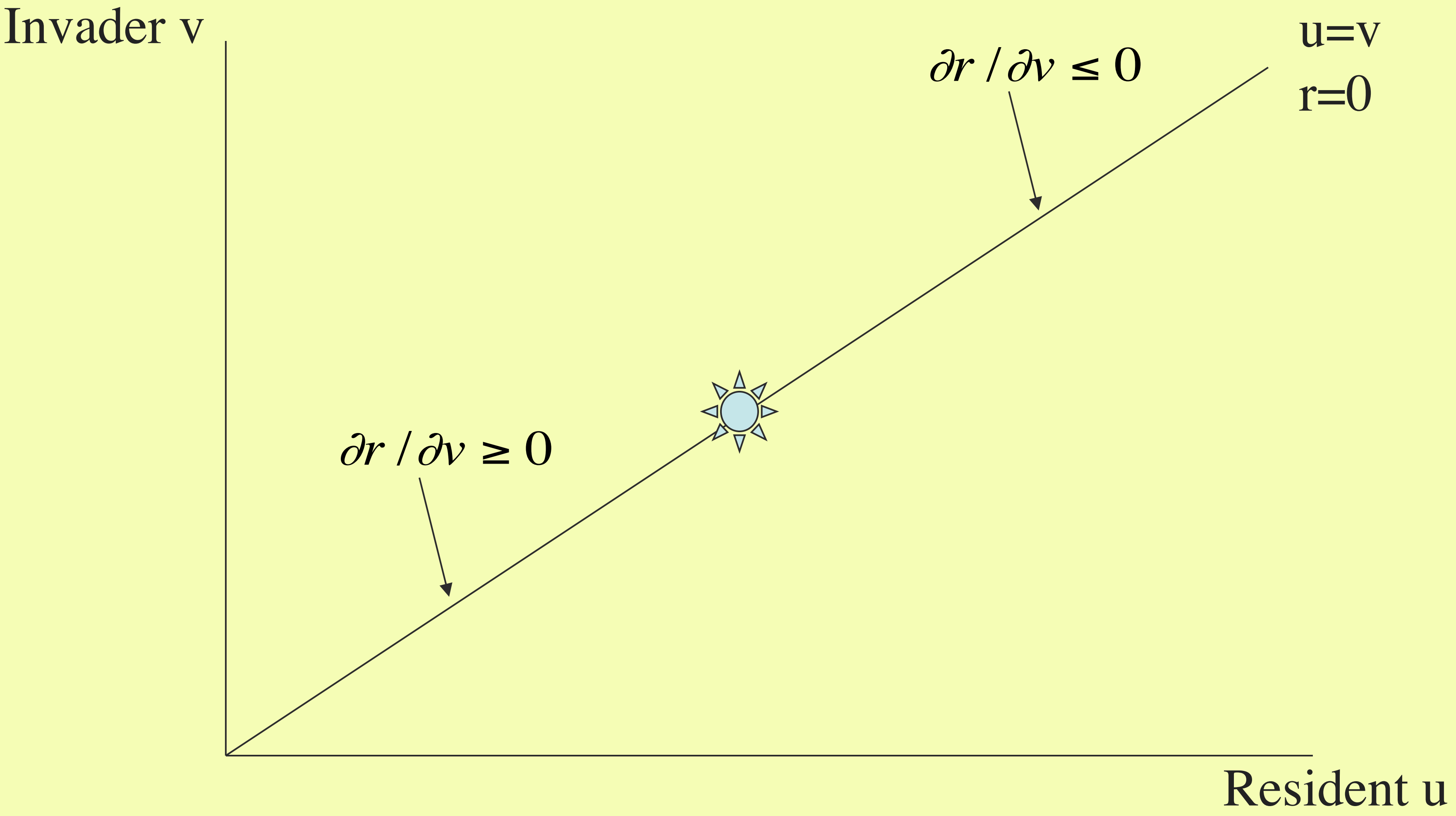
- Convergence stable strategy
  - Strategy that is evolutionarily attracting

Convergence-stable



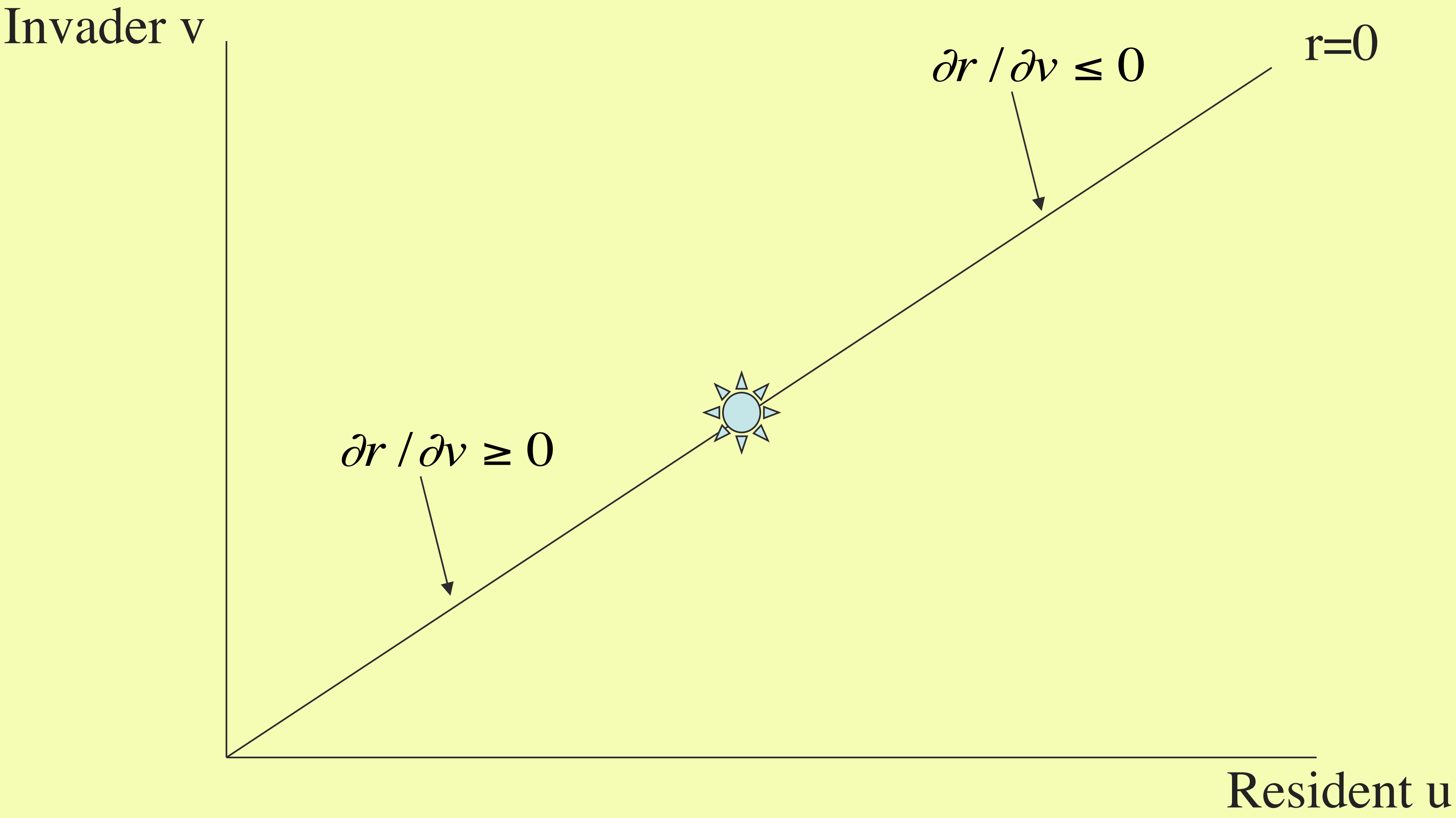
A resident to the left can be invaded from the right

Convergence-stable



A resident to the right can be invaded from the left

Convergence-stable



$$\partial^2 r / \partial u \partial v + \partial^2 r / \partial v^2 \leq 0$$

Convergence-stable condition can be rewritten

$$\partial^2 r / \partial u \partial v \leq -\partial^2 r / \partial v^2$$

But

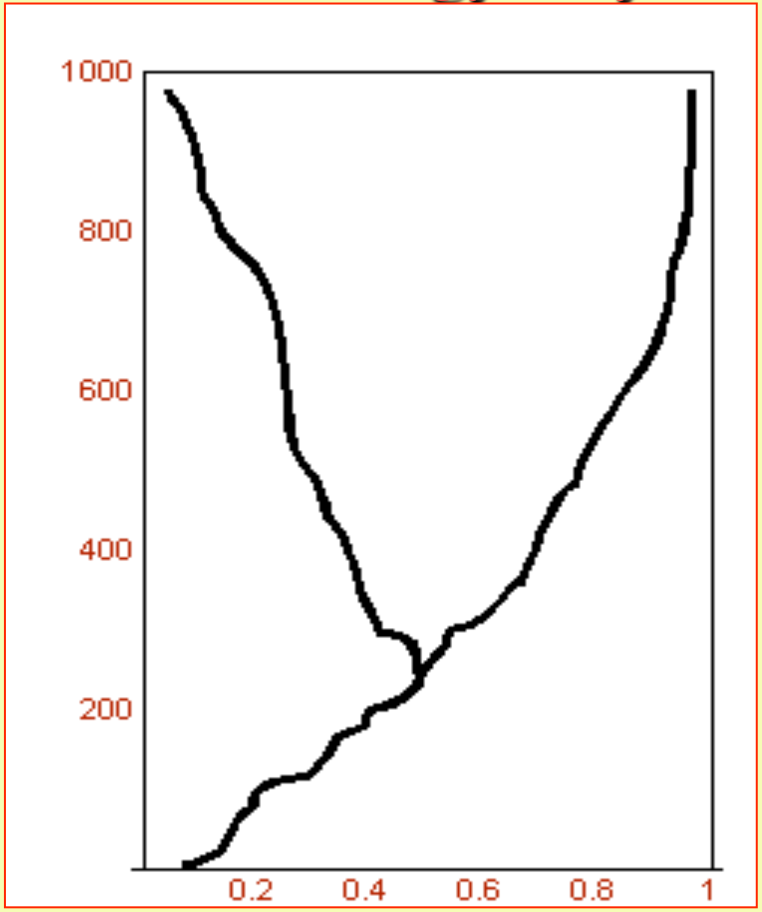
$$\partial^2 r / \partial u^2 + 2\partial^2 r / \partial u \partial v + \partial^2 r / \partial v^2 = 0$$

Therefore

$$\partial^2 r / \partial u^2 \geq \partial^2 r / \partial v^2$$

So ESS + NIS sufficient, not necessary

- So a convergence-stable strategy may not be an ESS

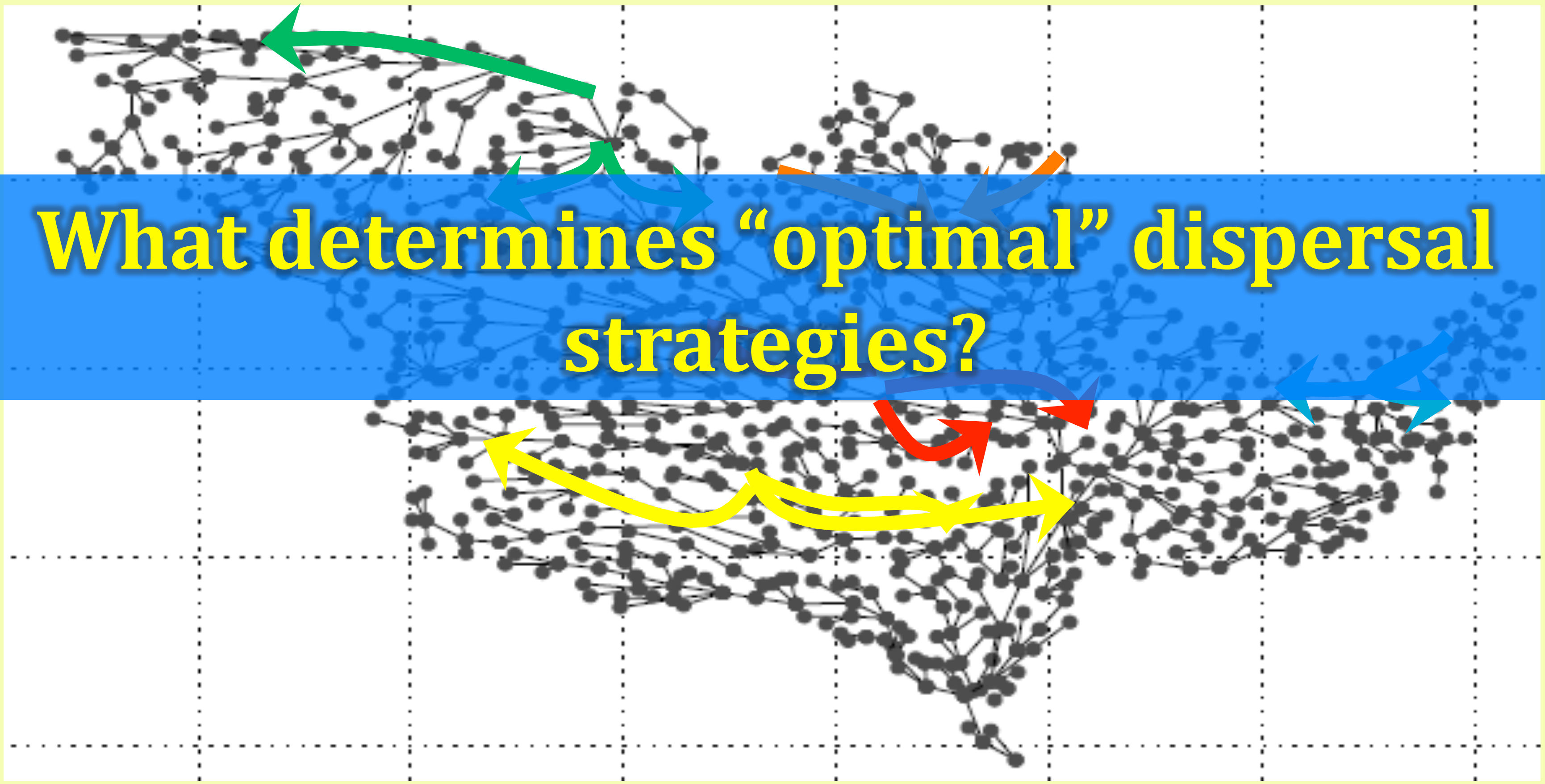


- Ma and Levin introduce “doubled-dimension” method to study bifurcations

This leads to a powerful way to understand ecological interactions

- *Begin with a basic dynamical model*
- *Allow heritable variation in the traits of interacting individuals*
- *Explore the adaptive dynamics of such systems, including evolutionary branching and coexistence of types*
- *Find continuously stable strategies*
- *Plasticity can be incorporated*

Evolution of dispersal in spatial landscapes

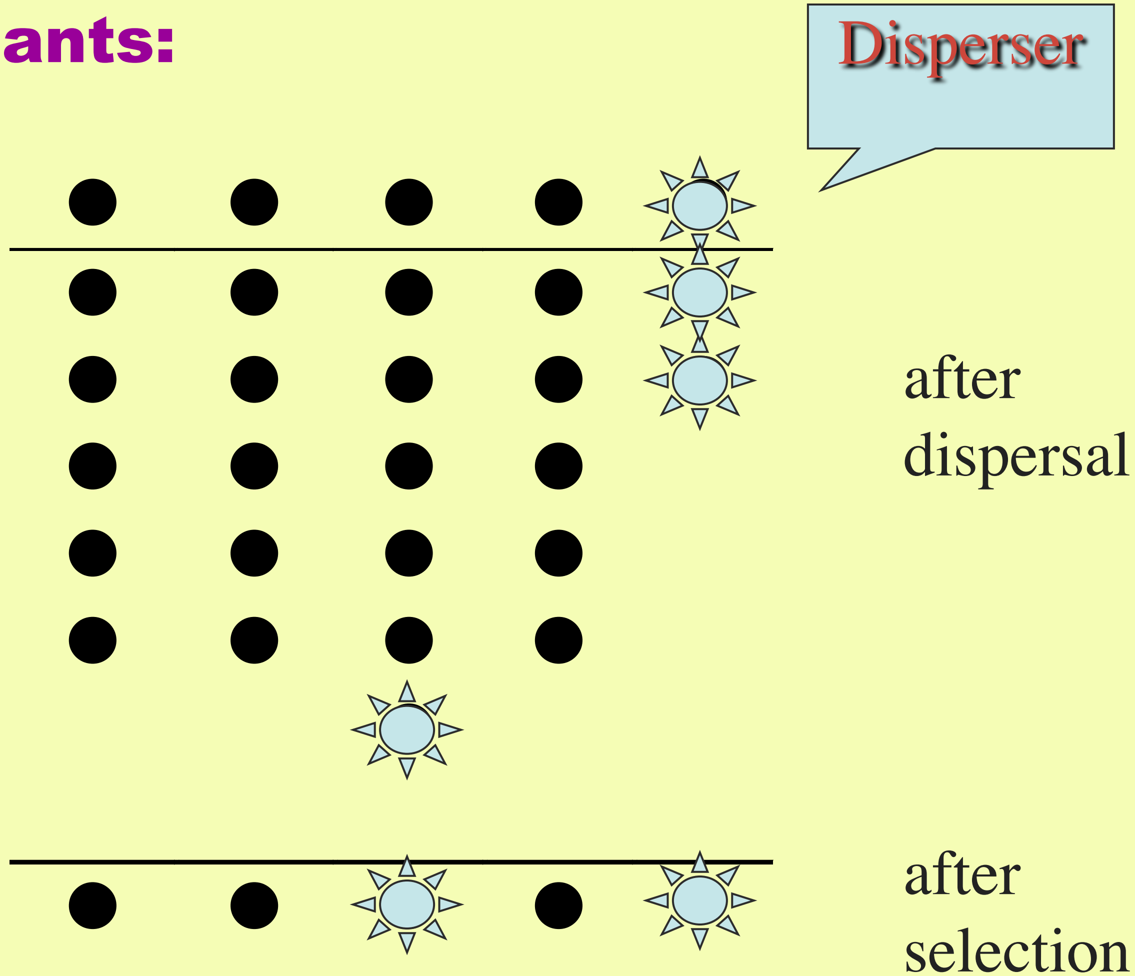


What determines "optimal" dispersal strategies?

Muneepeerakul, Rodriguez-Iturbe, Rinaldo, Levin, …

Why do organisms disperse?

Annual Plants:



Disperser

after
dispersal

after
selection

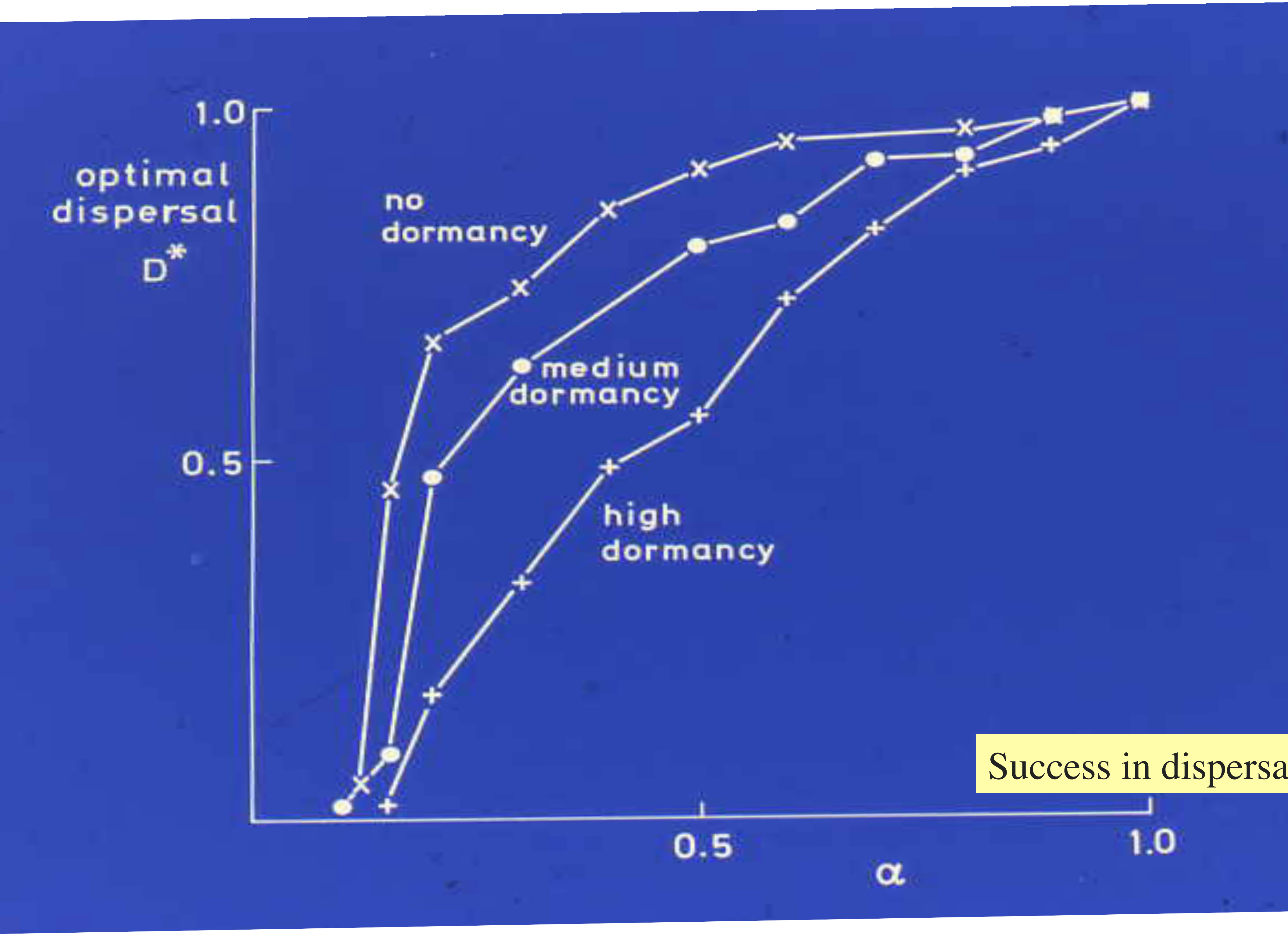
Hamilton and May, 1977

If p is the probability of successfully finding a site to settle, the evolutionarily stable strategy is to disperse a fraction

$$1/(2-p)$$

Levin, Cohen and Hastings (1983): Dispersal in annual plants

- Sites can support more than one individual
- Local yield depends on number of seeds competing
- Scramble competition
- Dormancy also allowed



Success in dispersa

Spatial- and temporally-correlated environments

- ESS may not exist, or may not be achieveable
- “Evolutionarily compatible strategies” may lead to coexistence and coalitions

Ezoe; Levin and Muller-Landau; Geritz

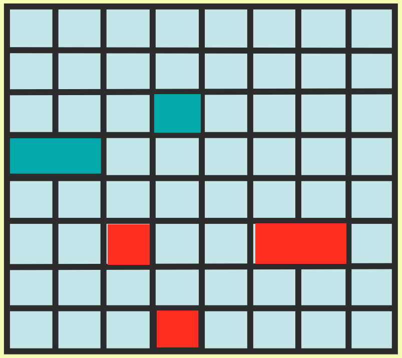
Consider seed size as object of selection, influencing dispersal and competitive ability

www.urbanext.uiuc.edu

Ezoe; Levin and Muller-Landau

u = resident seed size

v = invader seed size



Fitness of Invader

$$r(v \mid u) = \sum_{\vec{x}} \frac{P(v)\delta(v,\vec{x})}{P(v)\delta(v,\vec{x}) + P(u)\left(1 - \delta(u,\vec{x})\right)} - 1$$

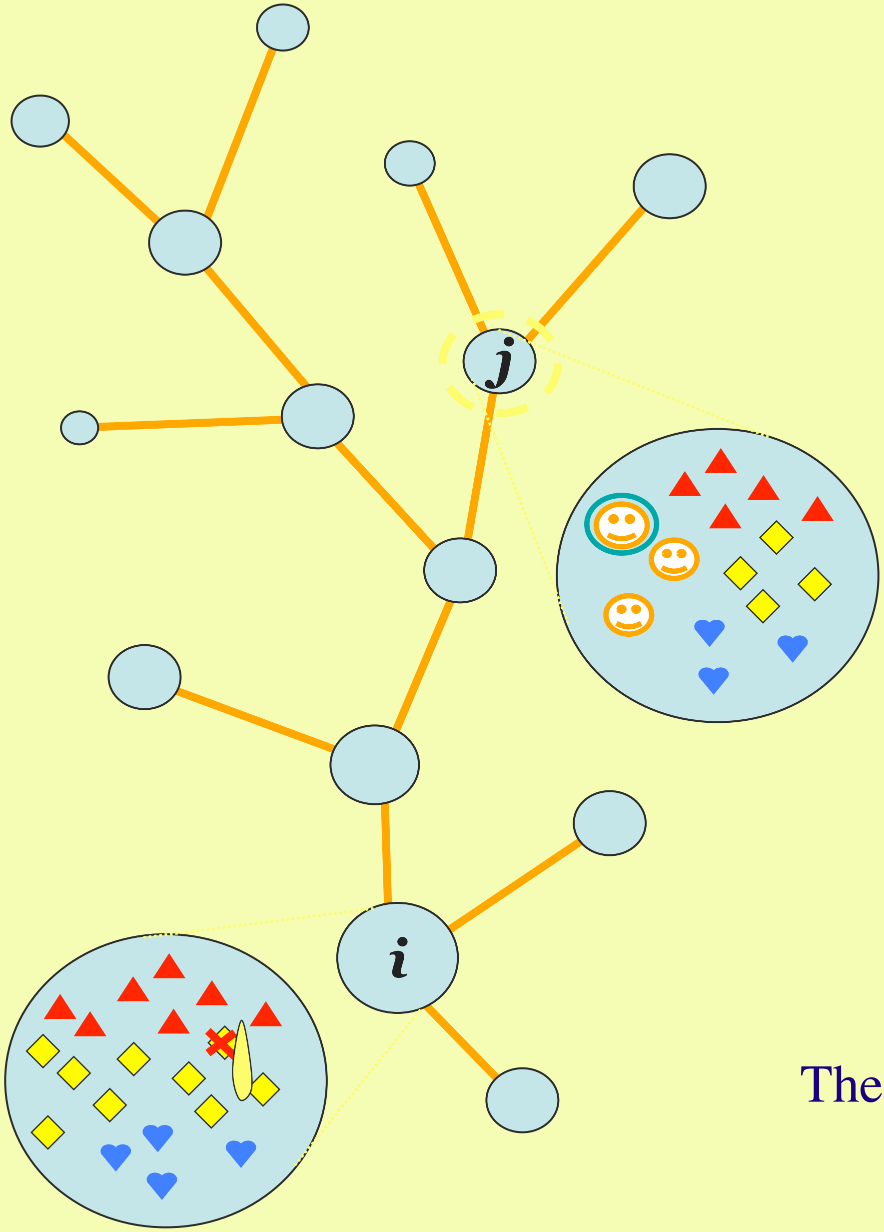
where $\vec{x}$ is displacement vector

Note that: $r\,(u|u)=0$ for all u

For this model

- Can characterize evolutionary stable strategies
- ESSes may not be convergence stable
- Multiple ESSes may exist

Muneepeerakul et al.



In each **time step**:

- Every unit in the system has an **equal probability of dying** .

- This may be replaced by a unit from some local community with a **success probability** determined by the dispersal kernels, abundance distribution, and dispersal cost. (Next slides.)

At the beginning of each **generation**:

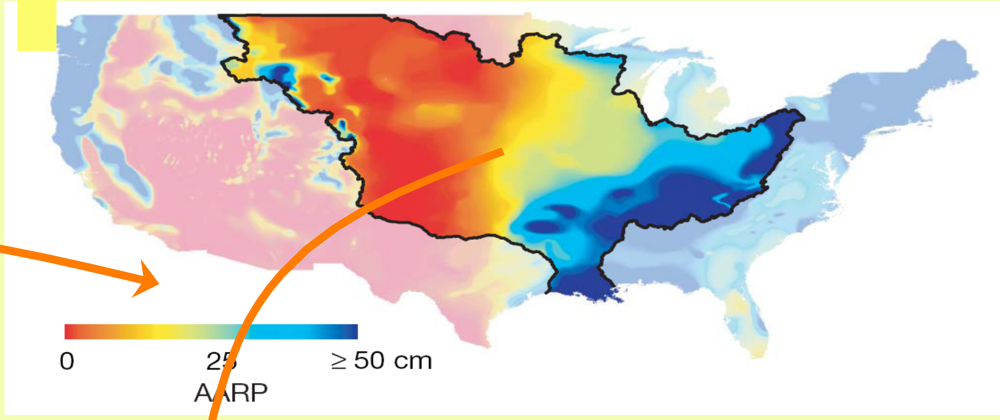
- A certain number of randomly selected units **slightly change their dispersal kernel** (mutation/ speciation/adaptation).

- Success probabilities are **updated**.

Then, the process is repeated until there is **no directional change in dispersal kernels**.

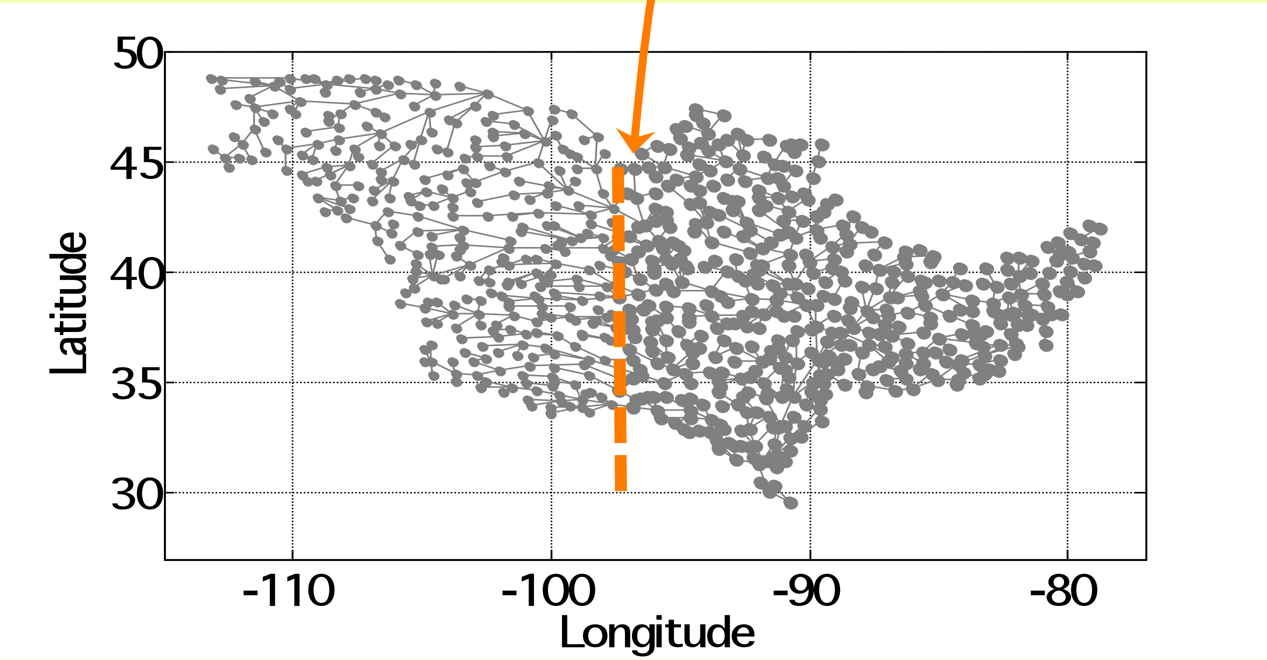
Landscape

Baseline case: idealized version of the Mississippi-Missouri basin



Muneepeerakul et al. (*Nature* 2008)

Photo sources: http://www.nationalatlas.gov/ printable/images/pdf/precip/ pageprecip_us3.pdf



Second Application: Stoichiometry

Redfield ratios

(in marine organic matter)

P : N : C: $-O_2$

(oxygen required to respire marine organic matter)

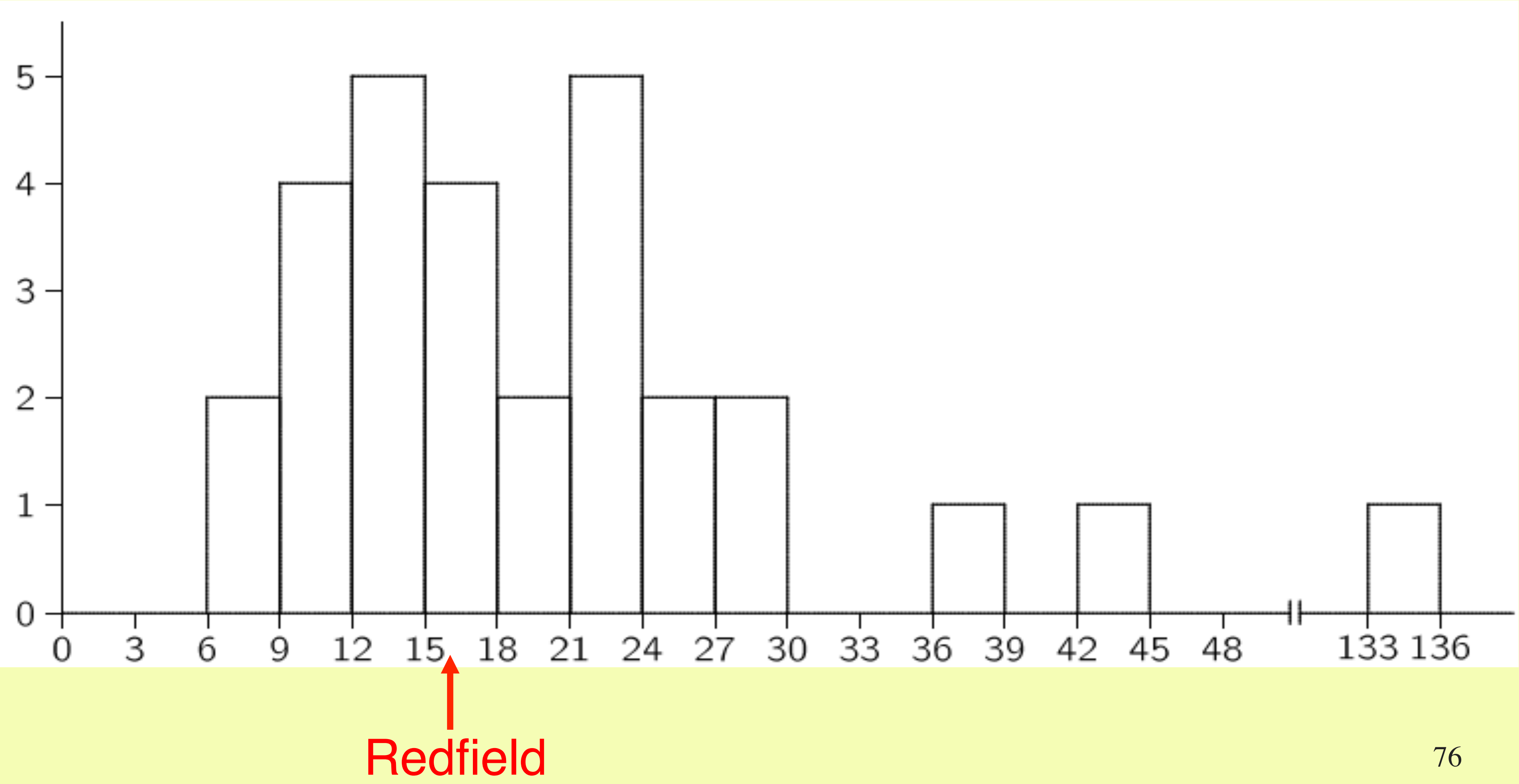
1 : 16 : 106 : 138

(subject to some debate)

Competition between N-fixers and other phytoplankton

Structural N:P Ratios, Phytoplankton

Klausmeier et al., Nature



- To what extent are ratios in the water column simply integrating what the biota do?

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- To what extent are evolutionary patterns in the biota simply reflective of environmental inputs?

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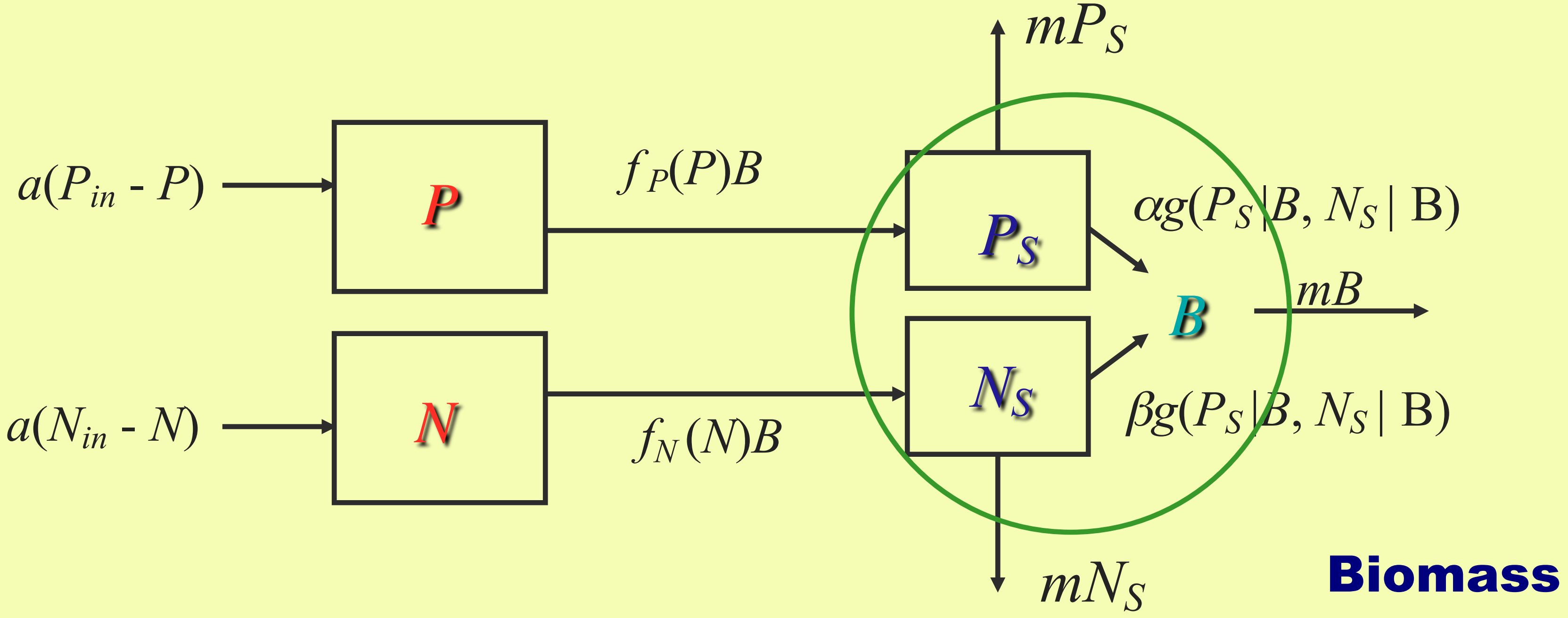
- To what extent are evolutionary patterns in the biota simply reflective of environmental inputs?
- What accounts for coexistence?

The evolutionary ecology of nutrient utilization

- Trait-dependent dynamics on ecological time scales
- Competition dynamics on evolutionary time scales

In a game-theoretic sense, what strategies are most successful at resource acquisition?

Klausmeier, Levin, Lichtman, Daufresne *(Nature; L&O)*



mP_S

$a(P_{in} - P)$

P

$f_P(P)B$

P_S

$\alpha g(P_S|B, N_S|\text{B})$

B

mB

$a(N_{in} - N)$

N

$f_N(N)B$

N_S

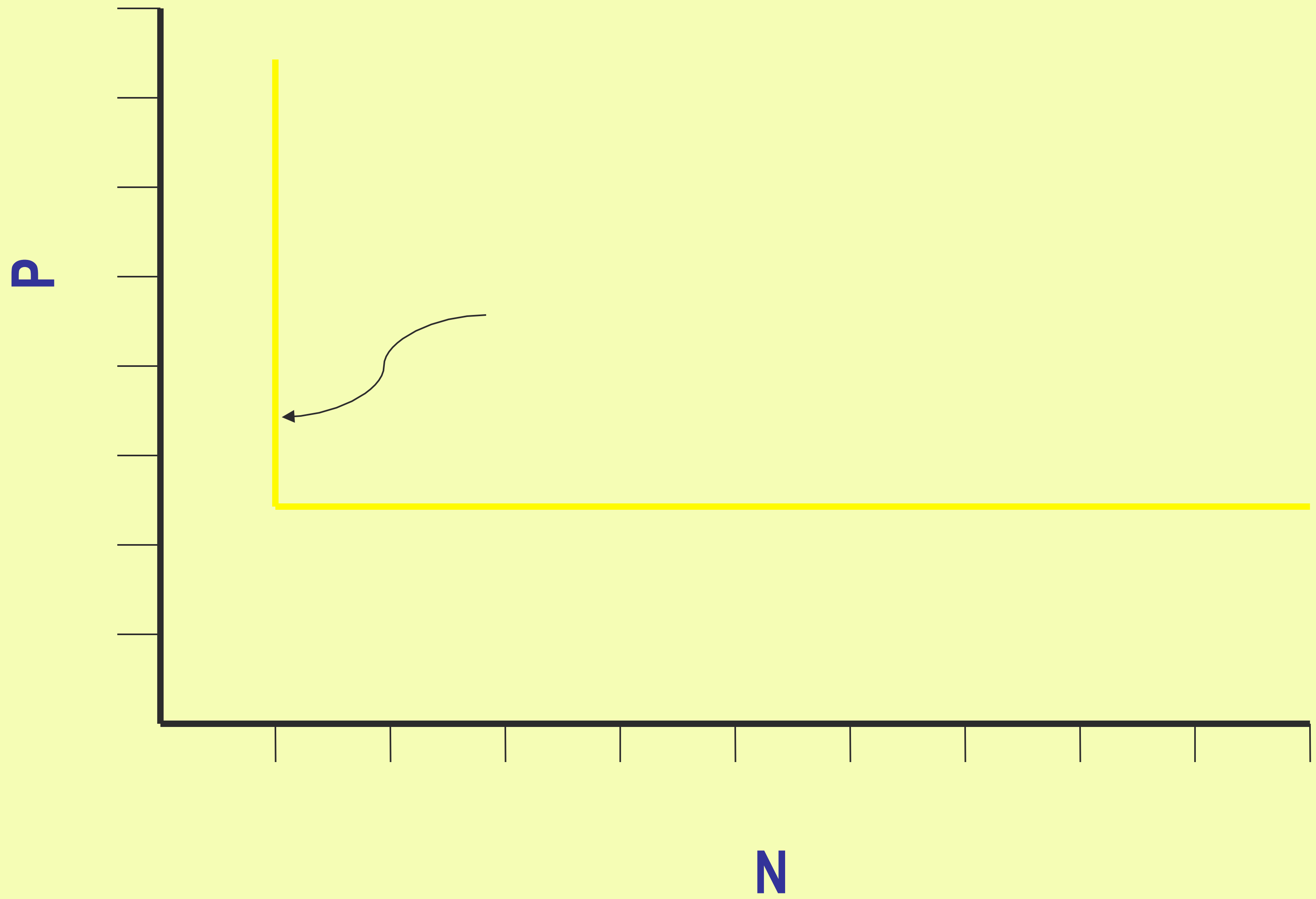
$\beta g(P_S|B, N_S|\text{B})$

mN_S

Biomass

Inorganic nutrients

Stored nutrients


P
N

Evolutionary time scale: Organisms must allocate carbon to

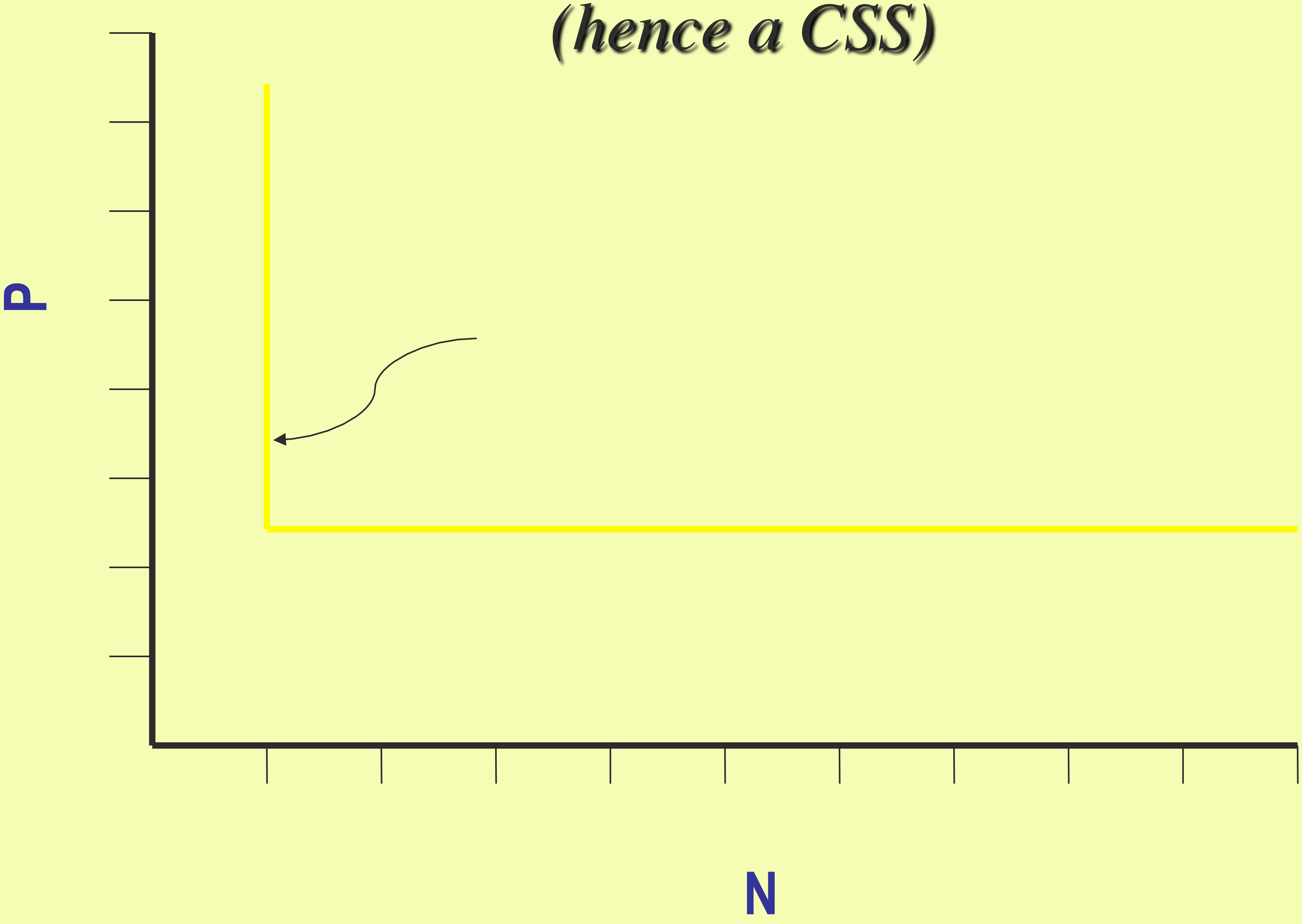
- *Proteins (uptake)*
- *Ribosomes (growth)*
- Each with characteristic stoichiometry

Allocation patterns determine overall stoichiometry, as well as allocation to uptake versus growth

To address evolution

- Expand dimension of the system from 5 to 8 by introducing an invader at a resident’s equilibrium
- Compute outcome of competition
- Look for continuously stable strategies, and other asymptotic outcomes
- Note that this process assumes separable time scales

There is a unique ESS, which is convergence stable *(hence a CSS)*



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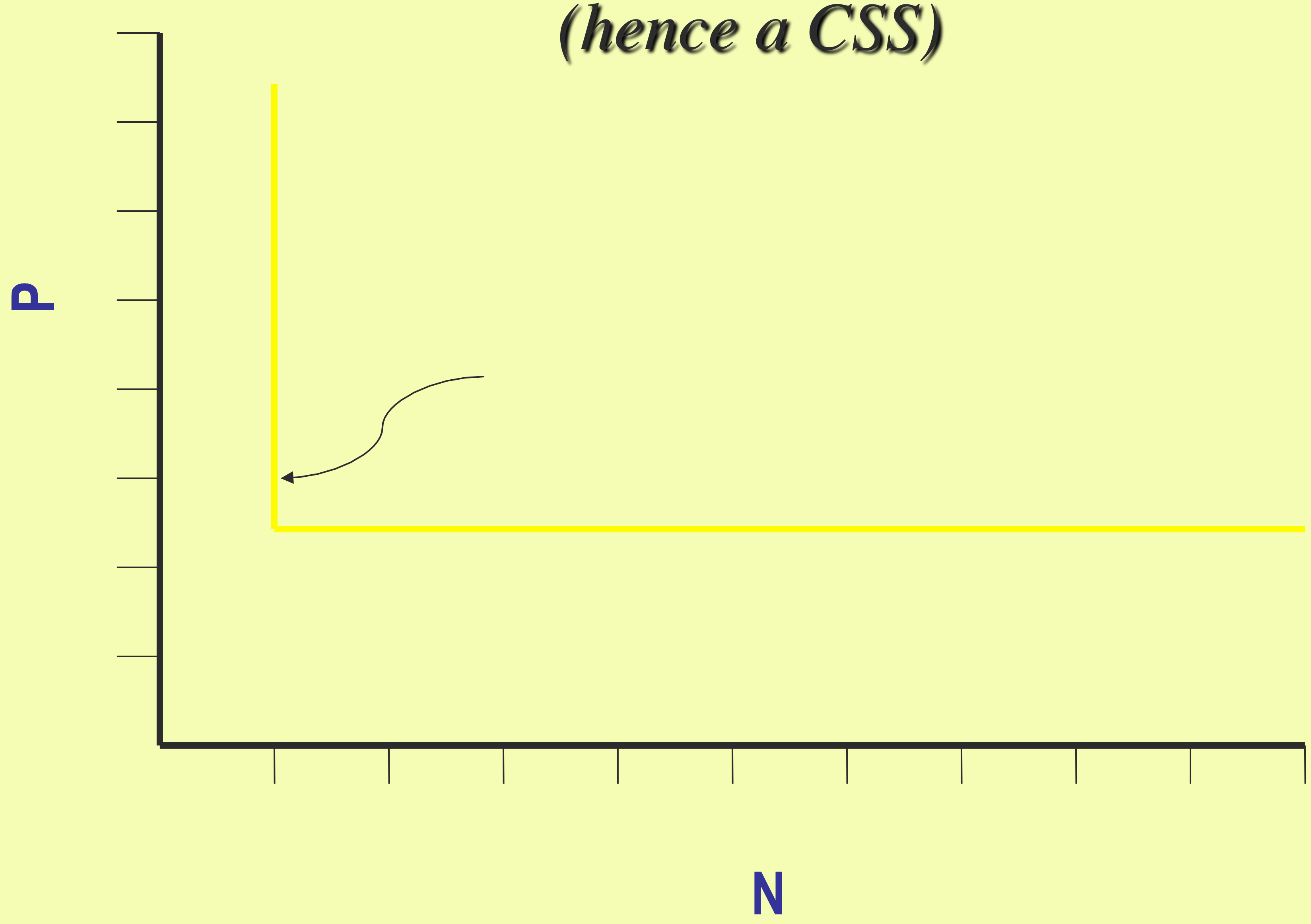
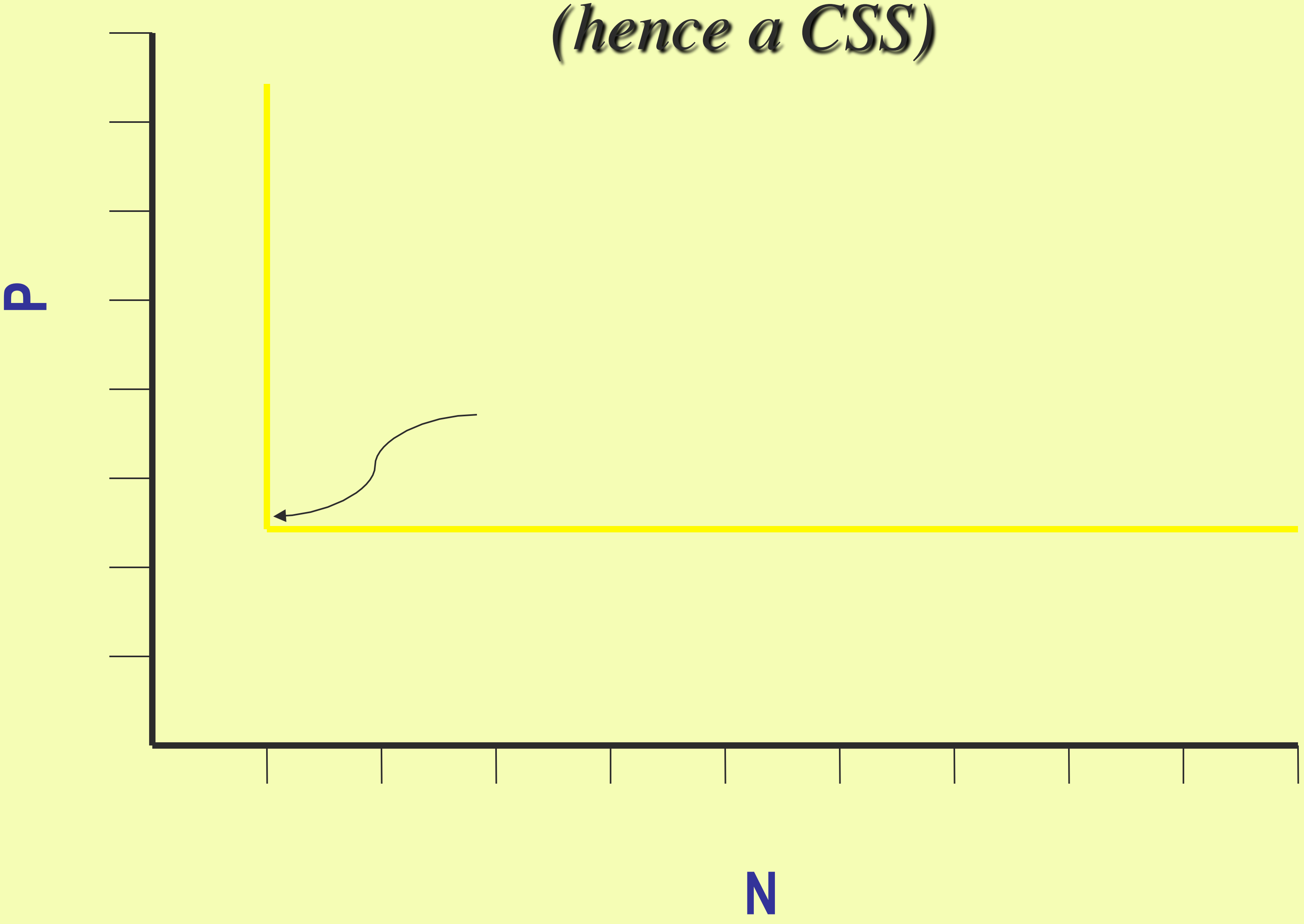


There is a unique ESS, which is convergence stable *(hence a CSS)*

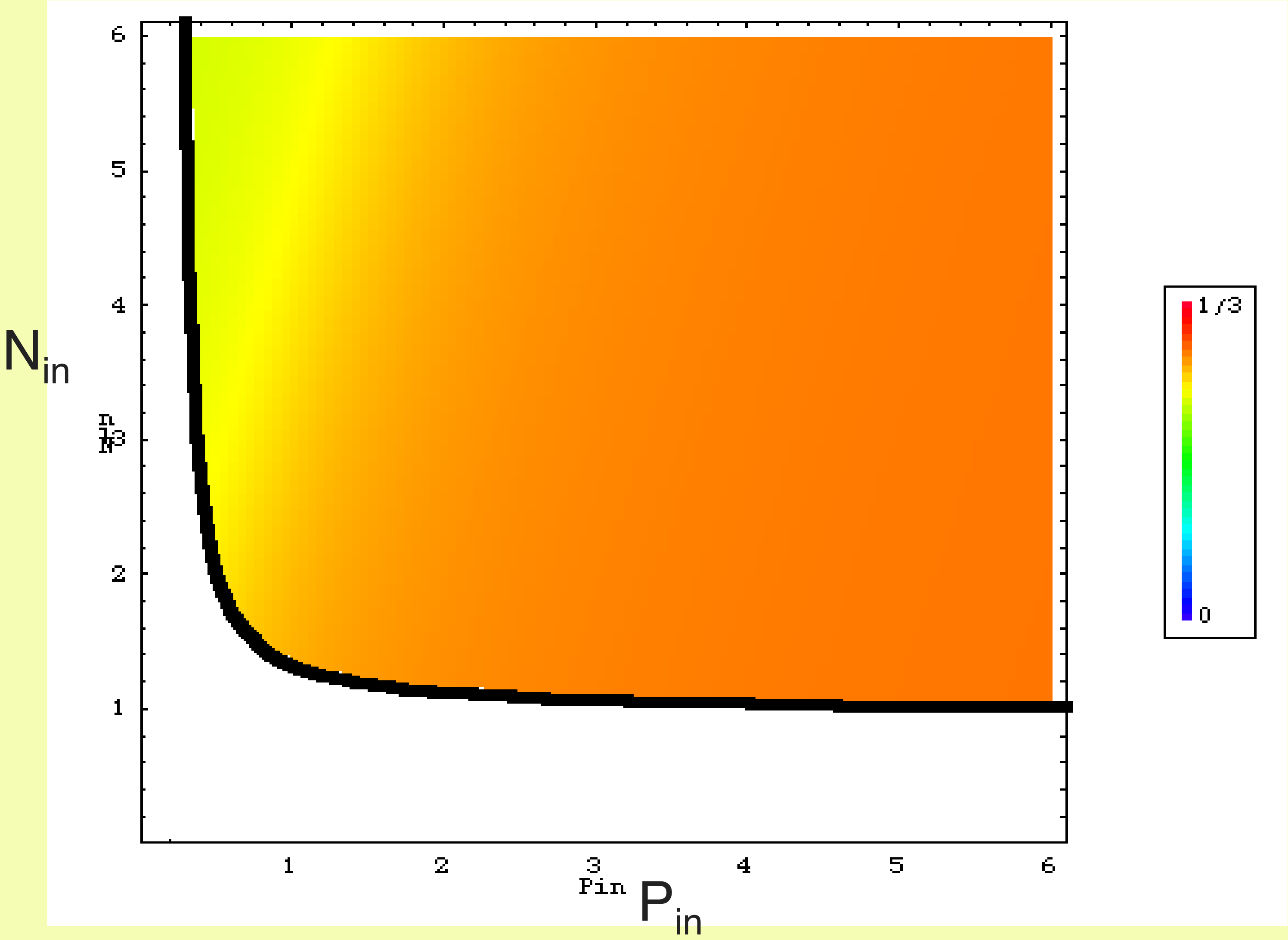


System evolves to co-limitation

$$(P_{in} - P) / \alpha = (N_{in} - N) / \beta$$

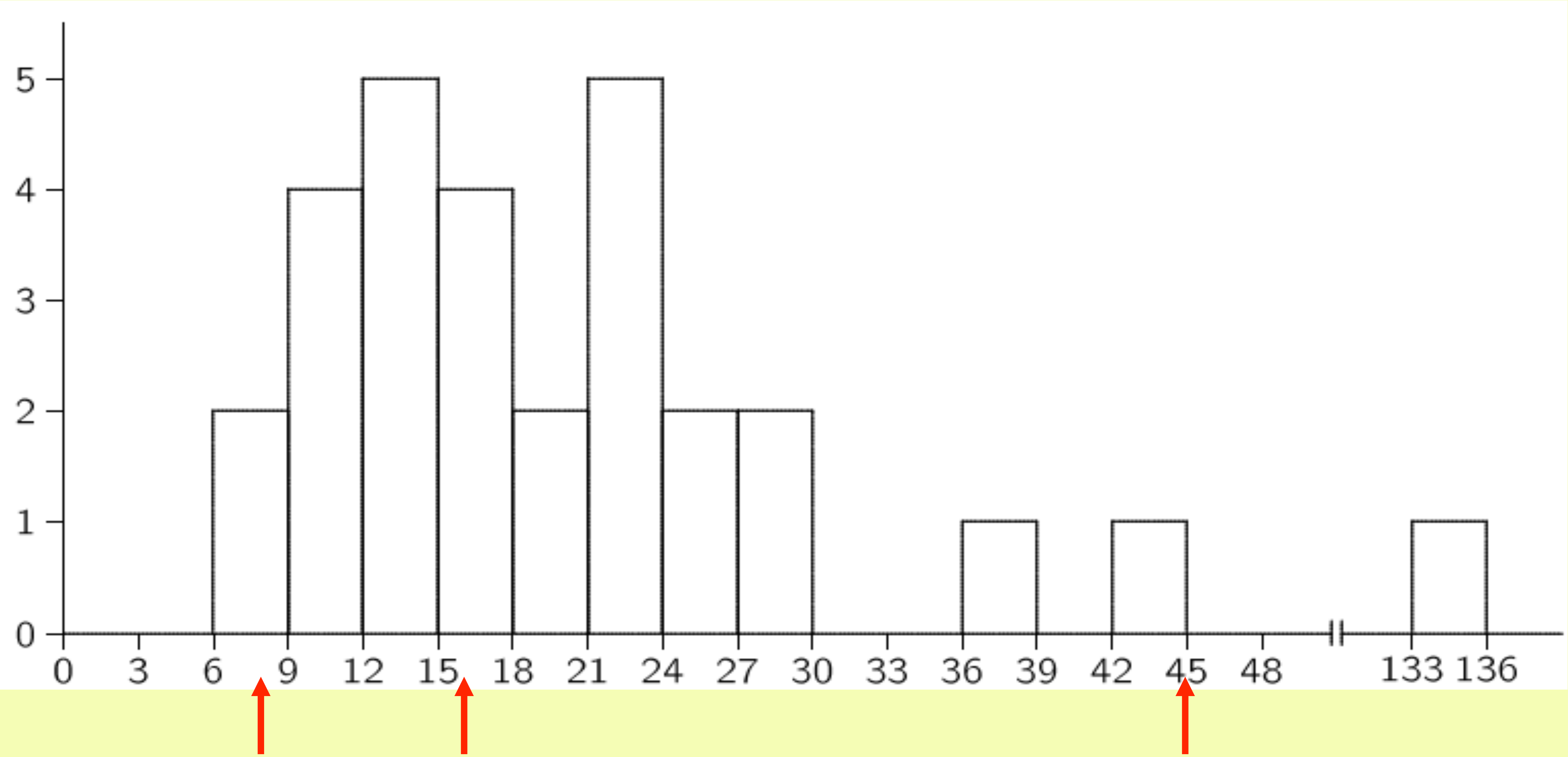
This accords well with intuition

CSS Allocation to Ribosomes



In the presence of environmental variation, there may be increased selection for rapid growth

Optimal N:P Ratios



μ_{max} Redfield *Eq.*

Conclusions

- By allowing for environmental fluctuations, we can approximate observed Redfield ratios well

Conclusions

- By allowing for environmental fluctuations, we can approximate observed Redfield ratios well
- Such fluctuations also facilitate coexistence

Extensions

- Light limitation (*Nature*)
- Spatial and temporal variation, and mixing
- Successional patterns
- Community assembly (Follows and Chisholm)

Spatial coexistence

with Mick Follows et al., MIT

- What explains distribution of phytoplankton globally?
- Embed ecological models of the oceans in a general circulation model
- Allow evolution to operate within this model, with the goal of
- Explaining distribution of ecological types

With Michael Raghib, others

Towards a Trait-Based Ecology, the MIT-DARWIN Model

$$\frac{\partial N_i}{\partial t} = -\overbrace{\nabla \cdot (\mathbf{u}\, N_i) + \nabla \cdot (K\, \nabla N_i)}^{\mathbf{u} \text{ and } \mathbf{K} \text{ from ECCO2 GCM}} - \overbrace{\sum_j \mu_j P_j\, R_{ij}}^{\text{Phyto growth}} + \overbrace{S_{N_i}}^{\text{Remineralization \& other sources}}$$

$$\frac{\partial P_j}{\partial t} = -\nabla \cdot (\mathbf{u} P_j) + \nabla \cdot (K \nabla P_j) \overbrace{+\mu_j P_j}^{\text{Growth}} \overbrace{- m_j^P P_j}^{\text{Mortality}} - \overbrace{\sum_k g_{jk} \frac{P_j Z_{k,i=1}}{P_j + k_j^P}}^{\text{Grazing}} - \overbrace{\frac{w_j^P \partial P_j}{\partial z}}^{\text{Sinking}}$$

$$\frac{\partial Z_{ki}}{\partial t} = -\nabla \cdot (\mathbf{u}\, Z_{ki}) + \nabla \cdot (K\, \nabla Z_{ki}) - m_k^Z Z_{ki} + \sum_k g_{jk} \frac{P_j R_{ij}}{P_j + k_j^P}$$

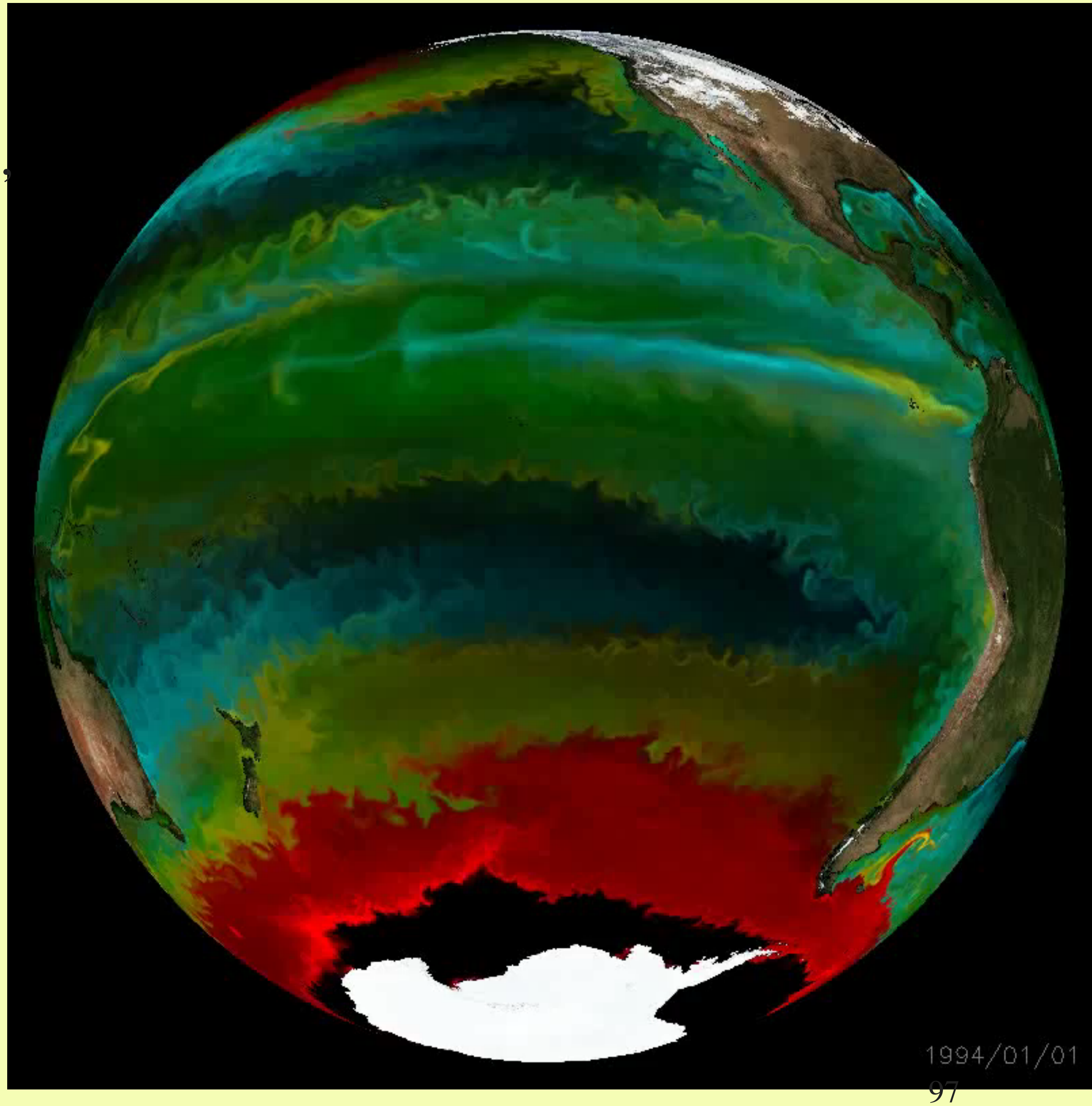
N/P/Z= nutrients/phytoplankton/zooplankton

C Wunsch & P Heimbach, *Physica D* **230**,197 (2007)   MJ Follows *et al*, *Science* **315**, 1843 (2007)

Follows, Dutkiewicz, Chisholm,

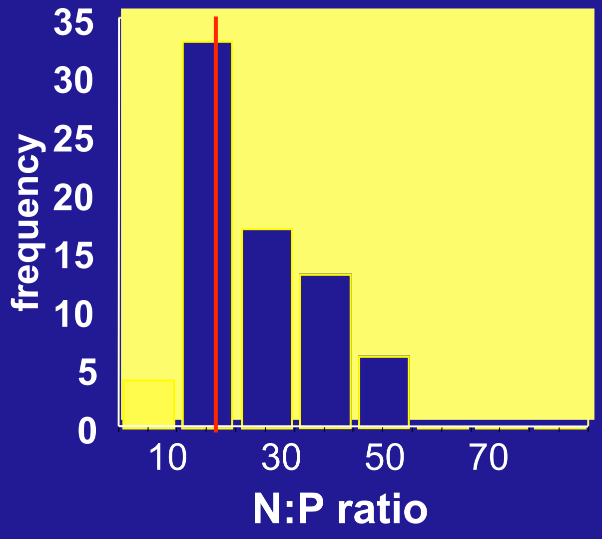
…

- Prochlorococcus
- Synechococcus
- Diatoms
- Large eukaryotes

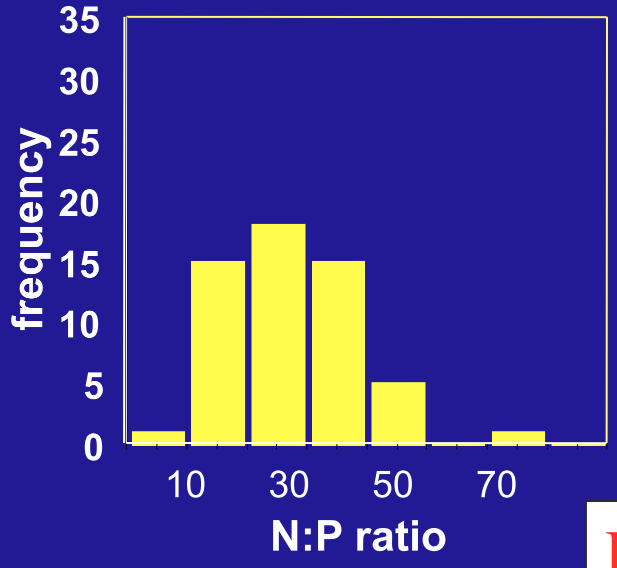


Terrestrial systems show different stoichiometric patterns

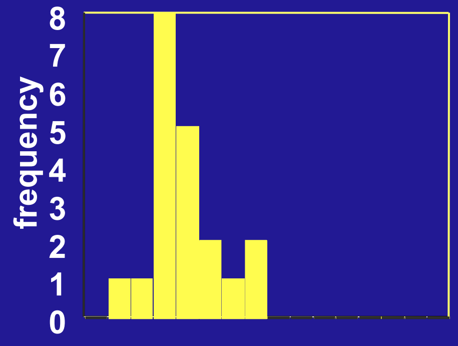
Nitrogen fixation, resource use, less than apparent potential



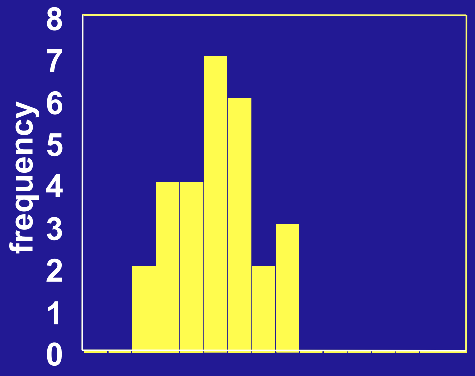
Marine particulate matter



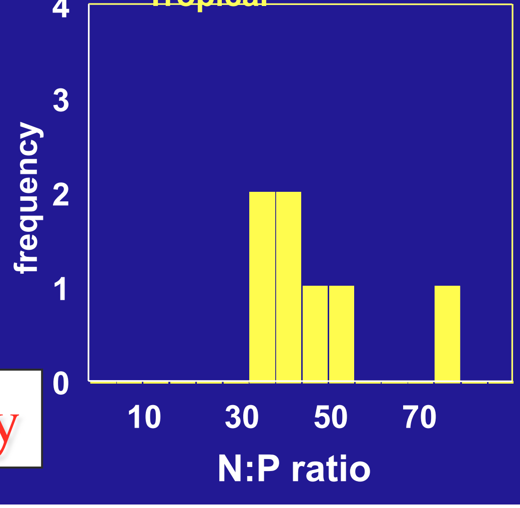
Global forest foliage



Coniferous Temperate



Broadleaf Temperate



Tropical

Hedin/McGroddy

Why don’t organisms fully exploit resources?

Terrestrial environments: Water-limited ecosystems

- Fundamentally limited by a single resource

Terrestrial environments: Water-limited ecosystems

- Fundamentally limited by a single resource
- Great diversity of morpho-physiological types

Terrestrial systems:
Evolution of water-use strategies

- Plants must balance assimilation and evapotranspiration through stomatal dynamics

(Zea, Rodriguez-Iturbe, Levin)

Terrestrial systems: Evolution of water-use strategies

- Plants must balance assimilation and evapotranspiration through stomatal dynamics
- Resource use is in a global commons

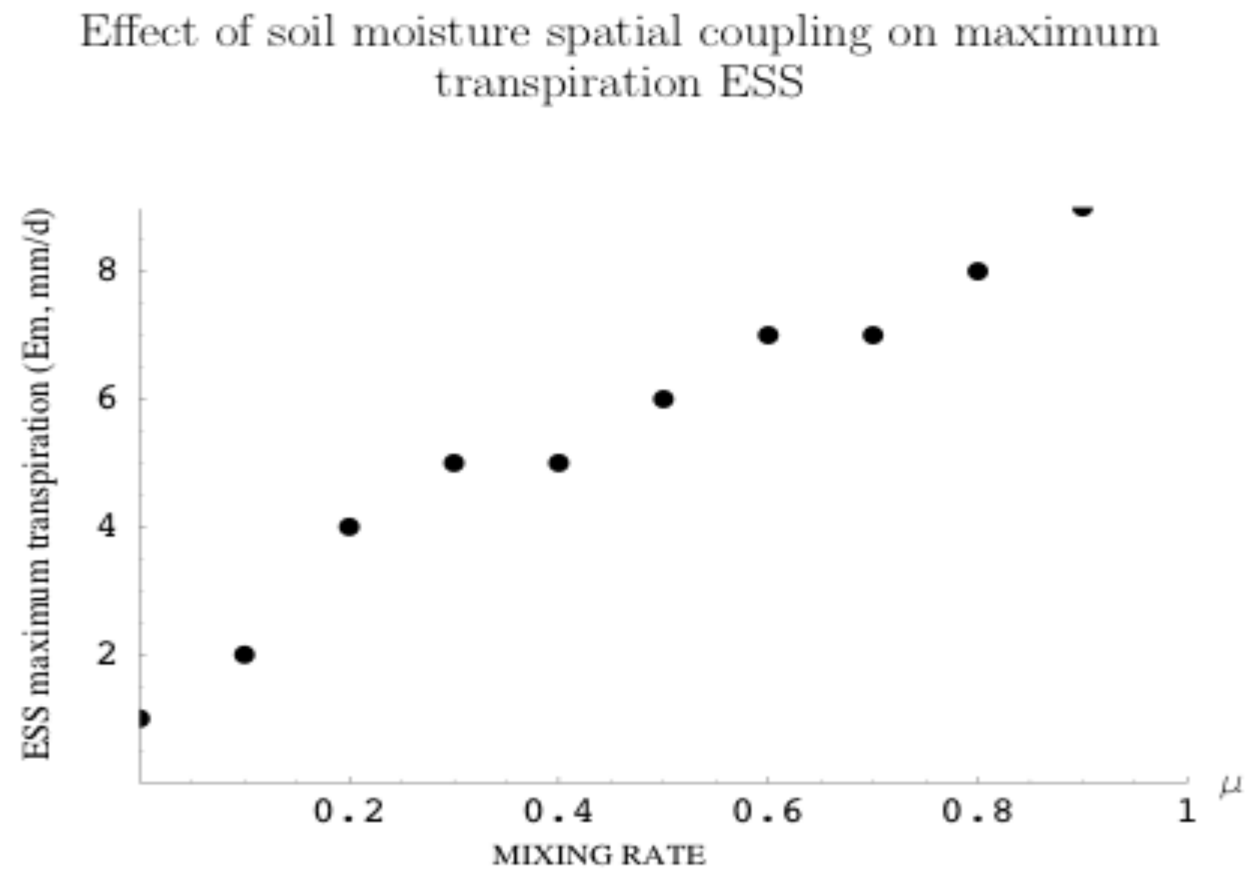
(Zea, Rodriguez-Iturbe, Levin)

Terrestrial systems:
Evolution of water-use strategies

- Plants must balance assimilation and evapotranspiration through stomatal dynamics
- Resource use is in a global commons
- Compute evolutionarily stable strategies

(Zea, Rodriguez-Iturbe, Levin)

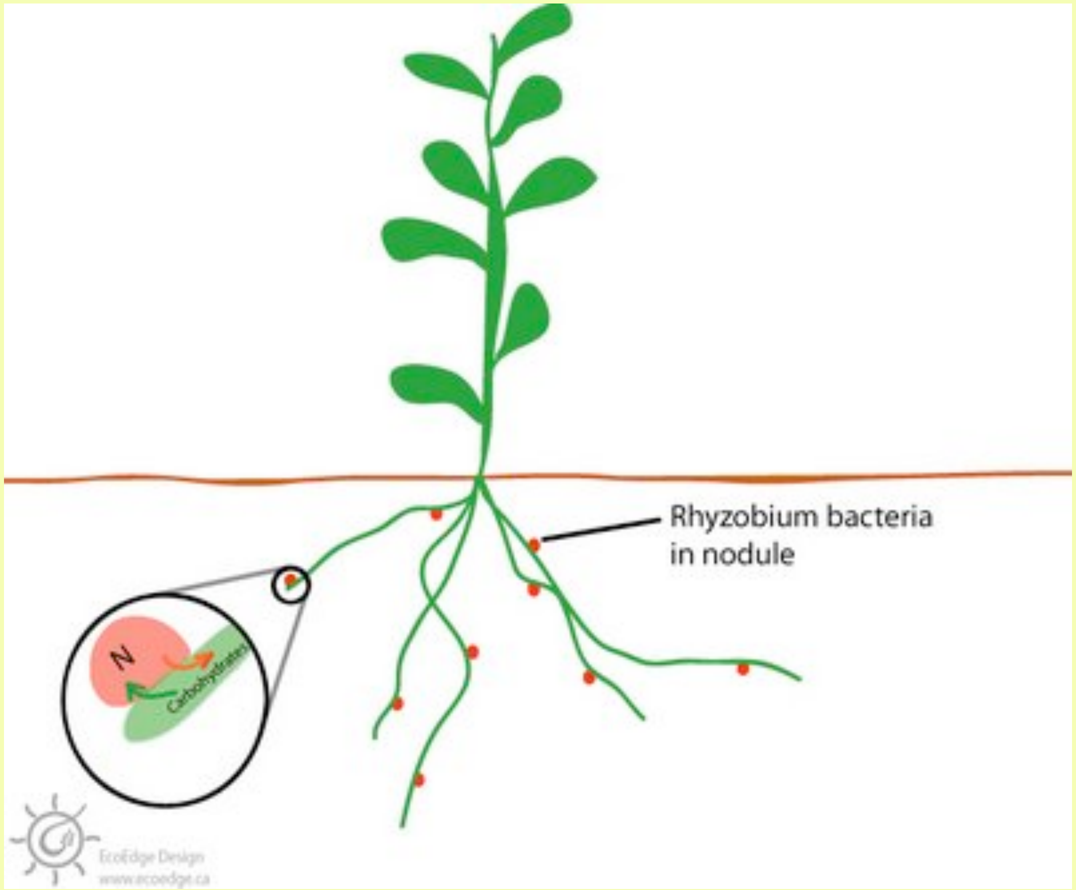
Prudent resource use disappears in a global commons



One also observes a lack of N-fixers even under apparent N limitation

Why?

Patterns of nitrogen fixation pose similar challenges in terrestrial and marine systems



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SabyMchrTsI

How should N-fixation depend on environmental conditions?

- Why isn’t there N-fixation where N is limiting?
- Why is there N-fixation where N is plentiful?
- Redfield invoked N-fixation

PNAS:2008

Evolutionary tradeoffs can select against nitrogen fixation and thereby maintain nitrogen limitation

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Contributed by Simon A. Levin, December 5, 2007 (sent for review July 3, 2007)

Symbiotic nitrogen (N) fixing trees are absent from old-growth temperate and boreal ecosystems, even though many of these are N-limited. To explore mechanisms that could select against N fixation in N-limited, old-growth ecosystems, we developed a simple resource-based evolutionary model of N fixation. When there are no costs of N fixation, increasing amounts of N fixation will be selected for until N no longer limits production. However, tradeoffs between N fixation and plant mortality or turnover, plant uptake of available soil N, or N use efficiency (NUE) can select against N fixation in N-limited ecosystems and can thereby maintain N limitation indefinitely (provided that there are losses of plant-unavailable N). Three key traits influence the threshold that determines how large these tradeoffs must be to select against N fixation. A low NUE, high mortality (or turnover) rate and low losses of plant-unavailable N all increase the likelihood that N fixation will be selected against, and a preliminary examination of published data on these parameters shows that these mechanisms, particularly the tradeoff with NUE, are quite feasible in some systems. Although these results are promising, a better characterization of these parameters in multiple ecosystems is necessary to determine whether these mechanisms explain the lack of symbiotic N fixers—and thus the maintenance of N limitation—in old-growth

There are two potential answers to this second question, neither of which exclude the other: (*i*) there are phylogenetic constraints to the evolution of late-successional N fixers (in the sense of ref. 11) and (*ii*) there are traits inherent to N fixation that lead to selection against N fixers when they appear in old-growth systems. Given that N-fixing bacteria are ubiquitous in natural ecosystems (1), phylogenetically diverse (12), and that they form symbioses with hundreds of plant species from nine plant families (6), many of which are temperate and boreal trees, phylogenetic constraints might not explain the absence of old-growth N fixers. In this article, we therefore explore the second hypothesis, using a simple evolutionary model to investigate factors that can select against N fixers in an old-growth N-limited environment.

Before focusing on the evolutionary question, we briefly review recent models that have investigated the ecological question of successional dynamics. Vitousek and Field (7) developed a simulation model of N fixer versus nonfixer competitive dynamics, assuming that fixation of atmospheric N is energetically more costly than soil N uptake when soil N is plentiful, and that N fixers take all N from fixation. In their model, N fixation cannot be suppressed unless there are addi-

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Facultative versus Obligate Nitrogen Fixation Strategies and Their Ecosystem Consequences

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Online enhancement: appendix.

ABSTRACT: Symbiotic nitrogen (N) fixers are critical components of many terrestrial ecosystems. There is evidence that some N fixers fix N at the same rate regardless of environmental conditions (a strategy we call obligate), while others adjust N fixation to meet their needs (a strategy we call facultative). Although these strategies are likely to have qualitatively different impacts on their environment, the relative effectiveness and ecosystem-level impacts of each strategy have not been explored. Using a simple mathematical model, we determine the best facultative strategy and show that it excludes any obligate strategy (fixer or nonfixer) in our basic model. To provide an explanation for the existence of nonfixers and obligate fixers, we show that both costs of being facultative and time lags inherent in the process of N fixation can select against facultative N fixers and also produce the seemingly paradoxical patterns of sustained N limitation

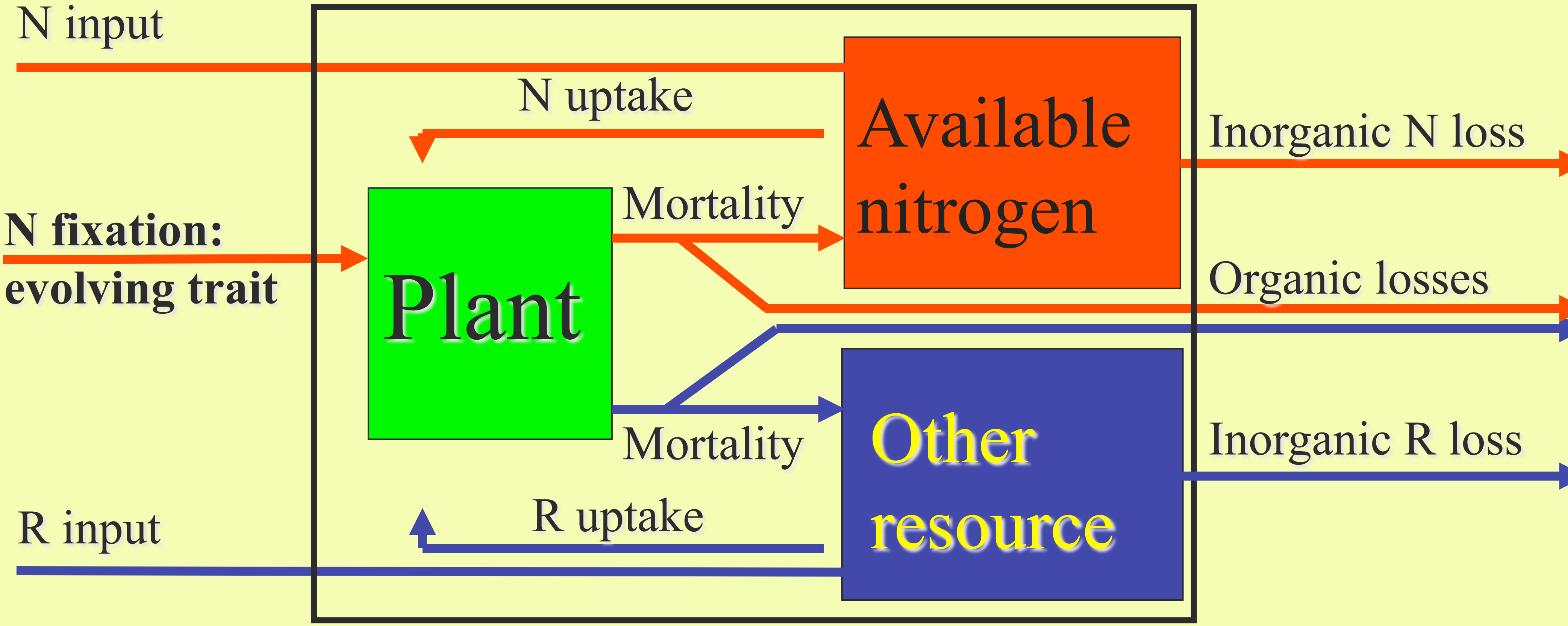
forests could easily be overcome by N fixers, who are conspicuous in these ecosystems in their absence only (Vitousek and Howarth 1991; Vitousek and Field 1999; Rastetter et al. 2001; Vitousek et al. 2002; Menge et al. 2008). In contrast, chronic N richness in many tropical forests may result from biological N fixation (BNF) by leguminous trees, which are ubiquitous in the tropics, but the potential reasons for fixing more than is necessary (overfixation) are at present unclear (Jenny 1950; Vitousek et al. 2002; Hedin et al. 2003; Barron 2007).

Nitrogen fixers are the only ecosystem components that have the capacity to regulate N inputs on the basis of soil N availability (an index of ecosystem-level N demand), and

Menge/Levin/Hedin
Evolutionary model of N fixation

- Analytical resource competition model
- Population limited by N or “R”
- Gets N from soil or fixation (with a cost)
- Determine evolutionarily/continuously stable N fixation strategies

Model


N input
N uptake
Available nitrogen
Inorganic N loss
Mortality
N fixation: evolving trait
Plant
Organic losses
Mortality
Other resource
Inorganic R loss
R uptake
R input

N=nitrogen
R=other resource

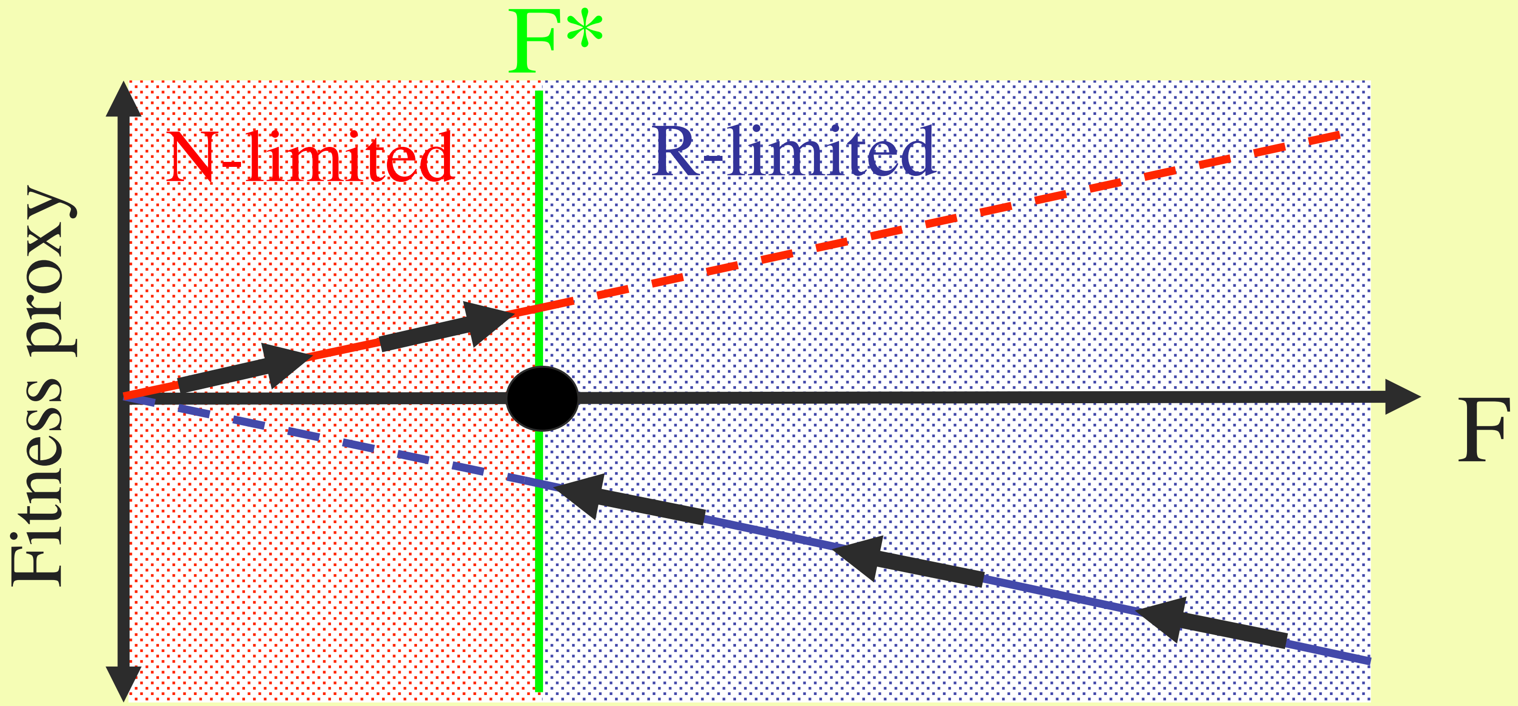
Model

Menge, Hedin, Levin

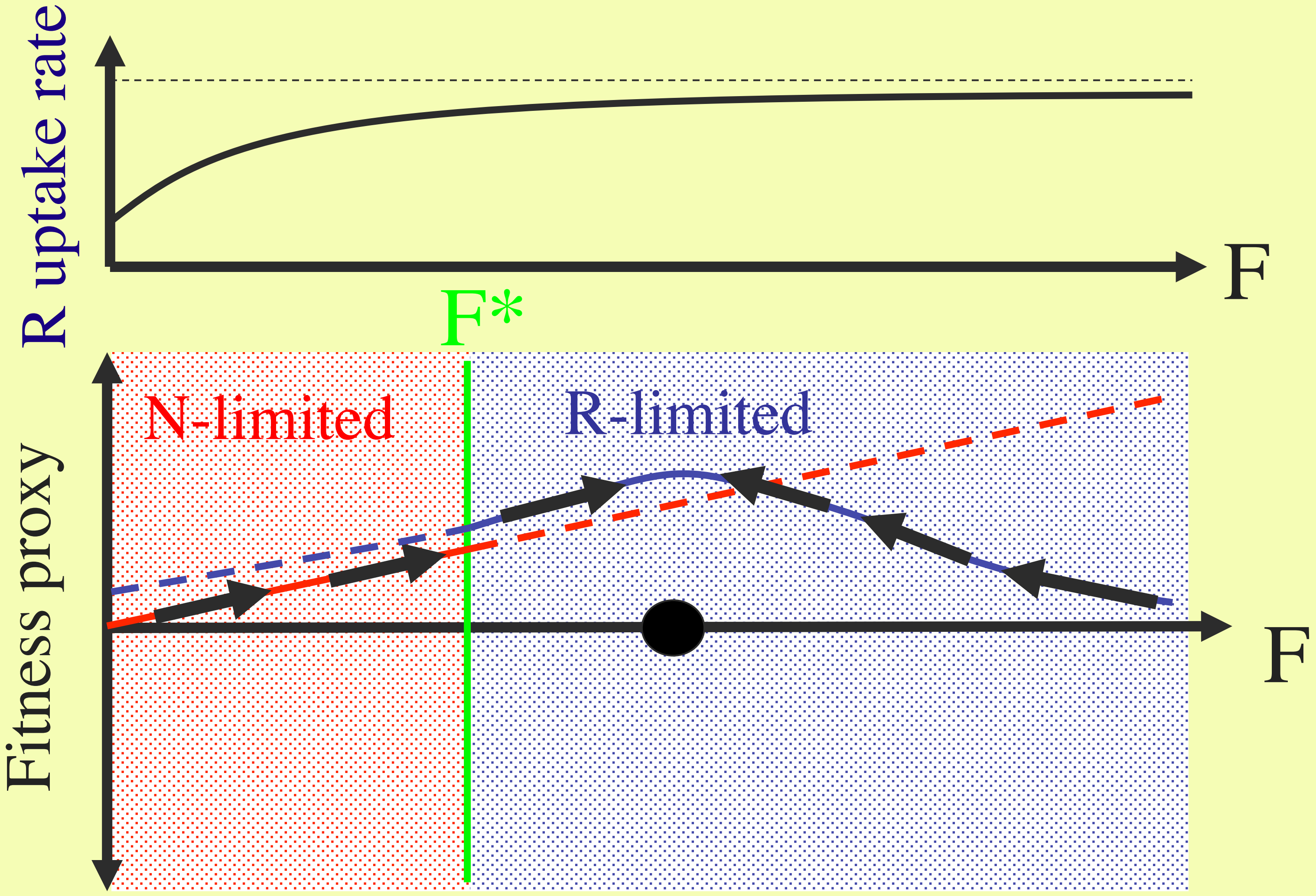
$$
\begin{aligned}
\frac{dX}{dt} &= X(\mathrm{MIN}[f(R), g(N)] - \mu) \\
\frac{dN}{dt} &= I_N - k_N N - \frac{1}{w_N} X(\mathrm{MIN}[f(R), g(N)] - w_N F - \mu(1 - \delta_N)) \\
\frac{dR}{dt} &= I_R - k_R R - \frac{1}{w_R} X(\mathrm{MIN}[f(R), g(N)] - \mu(1 - \delta_R)) \\
f(R) &= \nu_R R - \theta F \\
g(N) &= \nu_N N + w_N F
\end{aligned}
$$

Again, embed in an evolutionary model

Basic result:
Co-limited N fixer evolves if non-fixer would be N-limited



If R uptake rate ↑ with fixation: R-limited N fixer can evolve



CONCLUSIONS

A central problem in sustainability is to understand how to characterize the robustness of macroscopic properties of ecosystems and the biosphere

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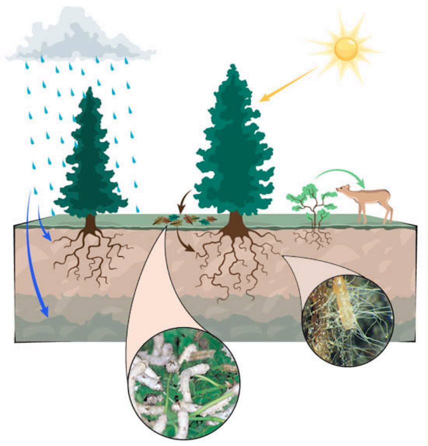
CONCLUSIONS,
AND FURTHER THOUGHTS

…in terms of microscopic ecological and evolutionary dynamics at the level of organisms and populations



askabiologist.asu.edu

Ecosystems and the biosphere are complex adaptive systems

- Properties emergent from interactions on ecological and evolutionary time scales
- At organizational levels far below those of whole systems

The unification of population biology and ecosystems science means

- Going beyond thinking about ecosystems and the biosphere as if they are evolutionary units, maximizing throughput
- Rather, they exhibit patterns emergent from processes at much lower levels of organization

We need to bridge the gap across scales, from the evolutionary to the ecological

Ultimately, only by providing such bridges between the *microscopic* and *macroscopic* can we develop a science of sustainability

Claudio Carere