Trait-Based Approaches to Plankton Ecology

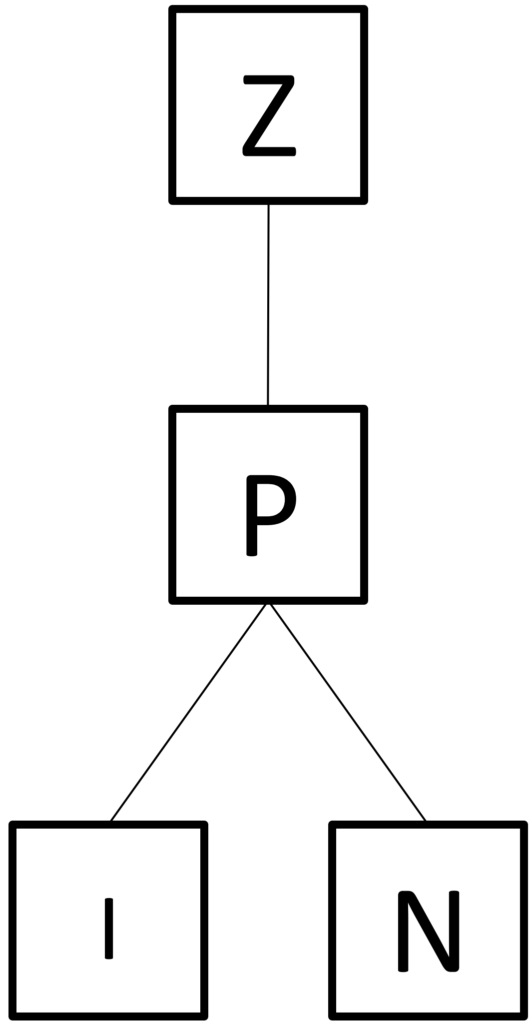
Christopher A Klausmeier

Elena Litchman

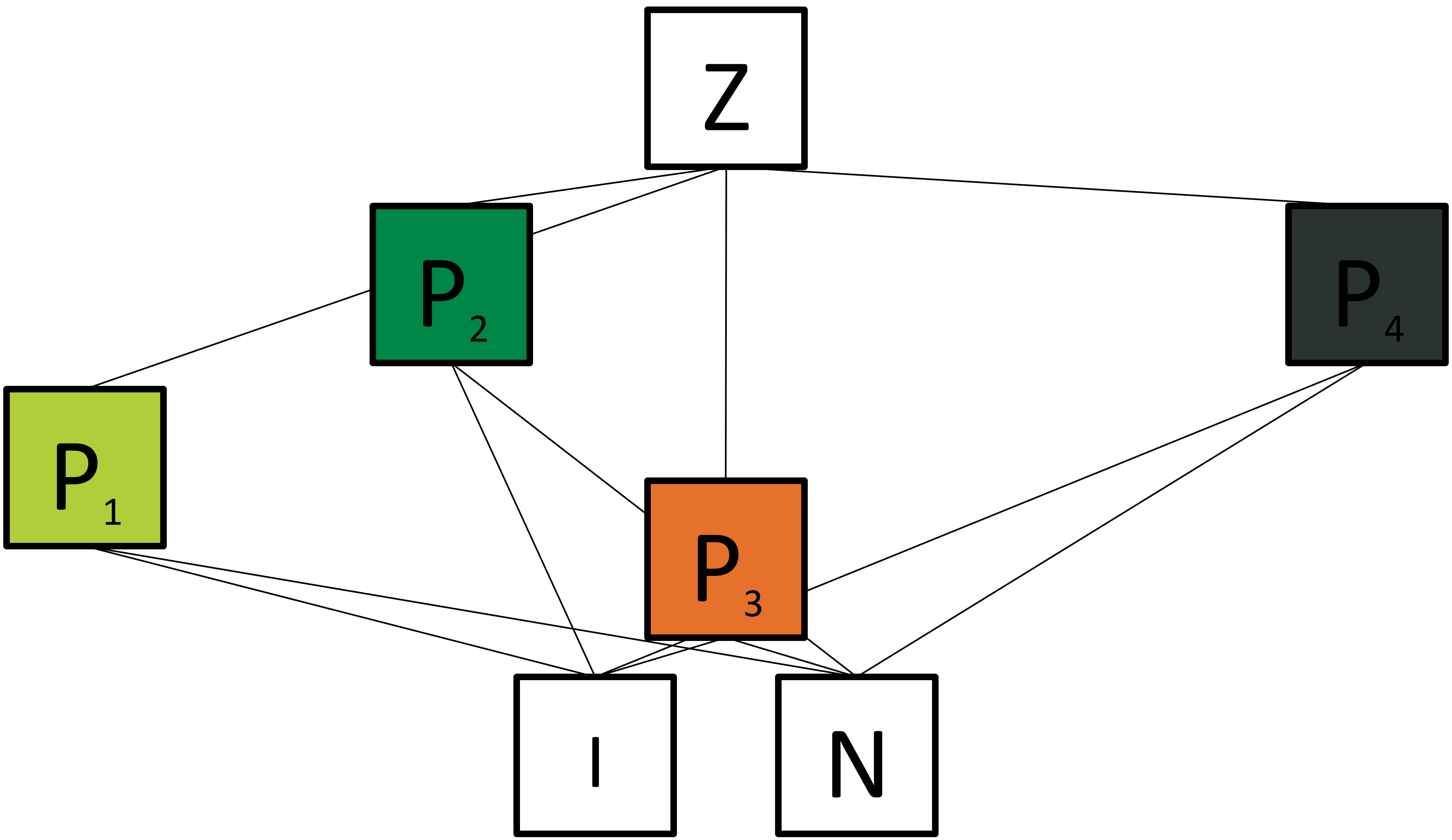
Kellogg Biological Station

Michigan State University

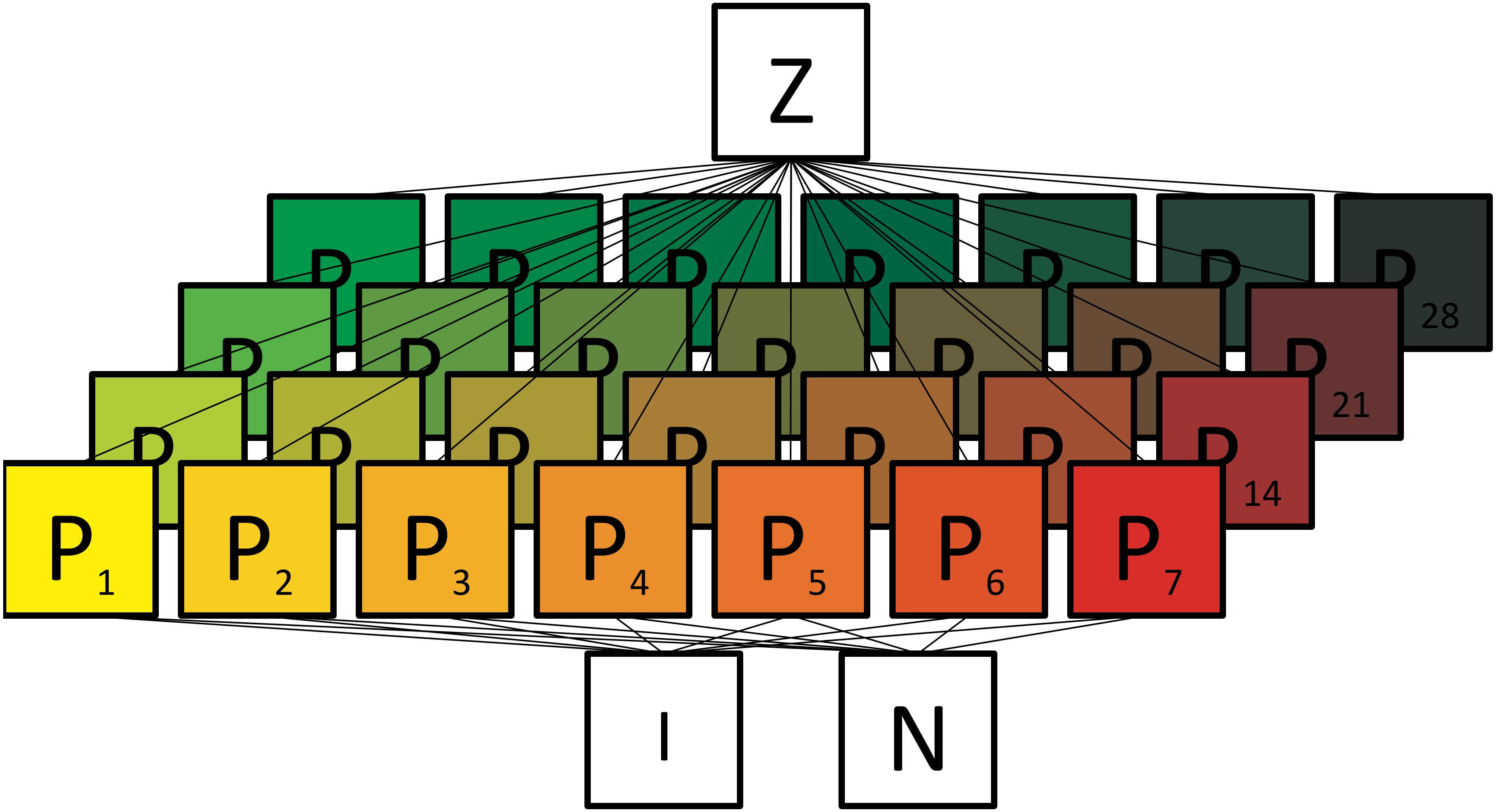
NPZ



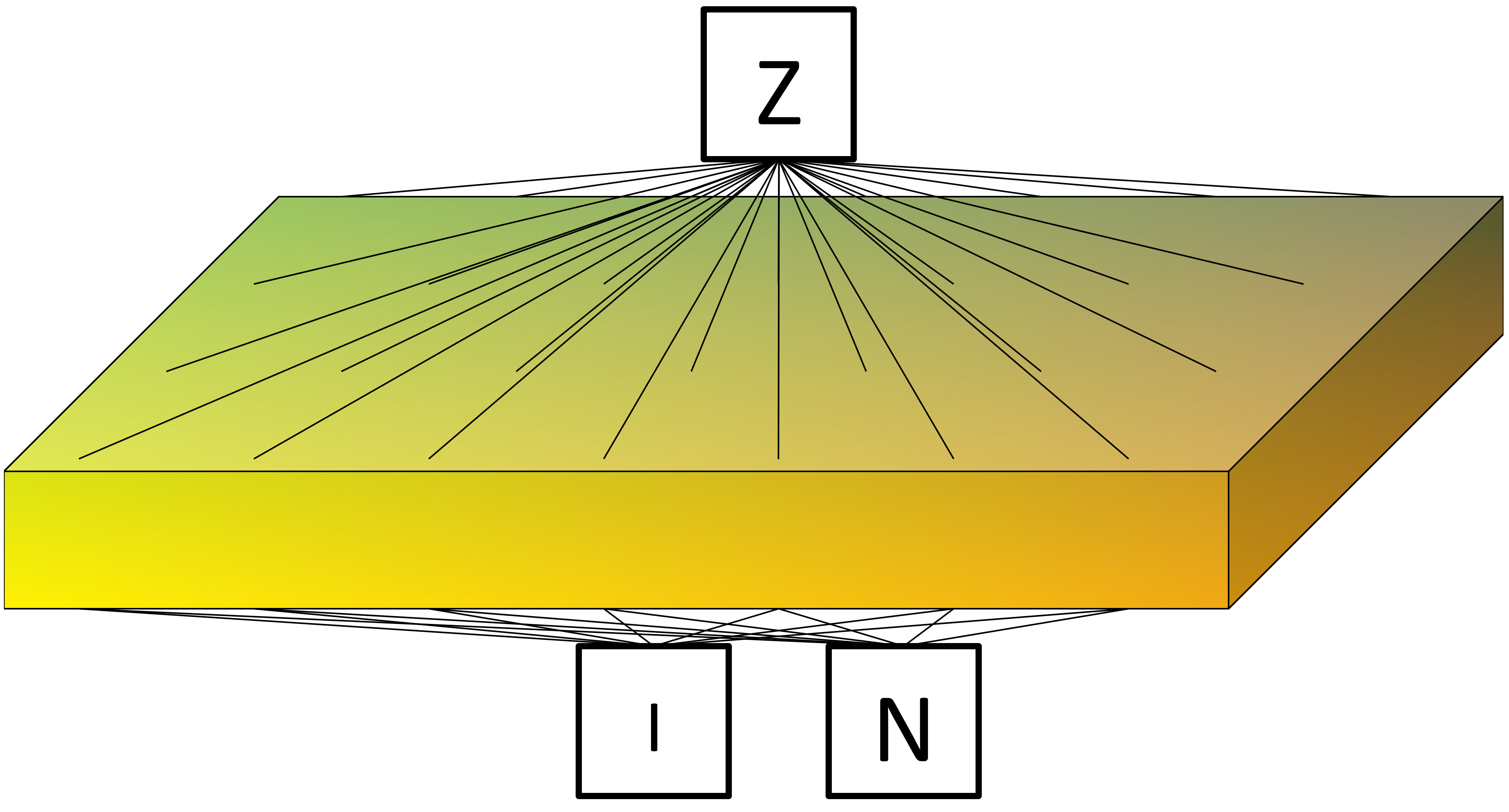
Plankton Functional Groups



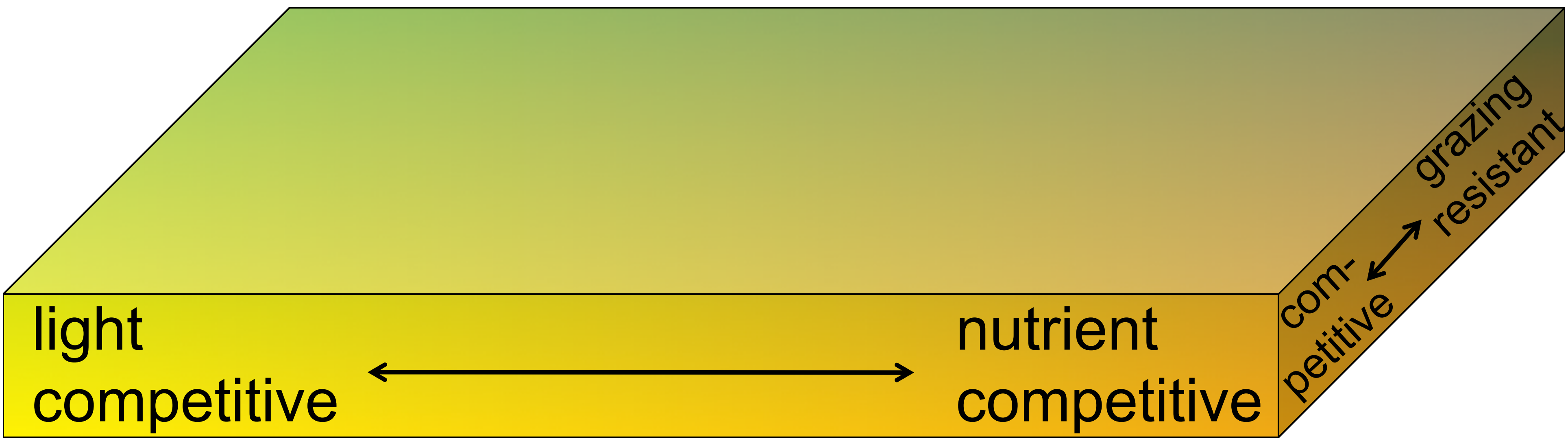
Many Species



Continuum of Strategies

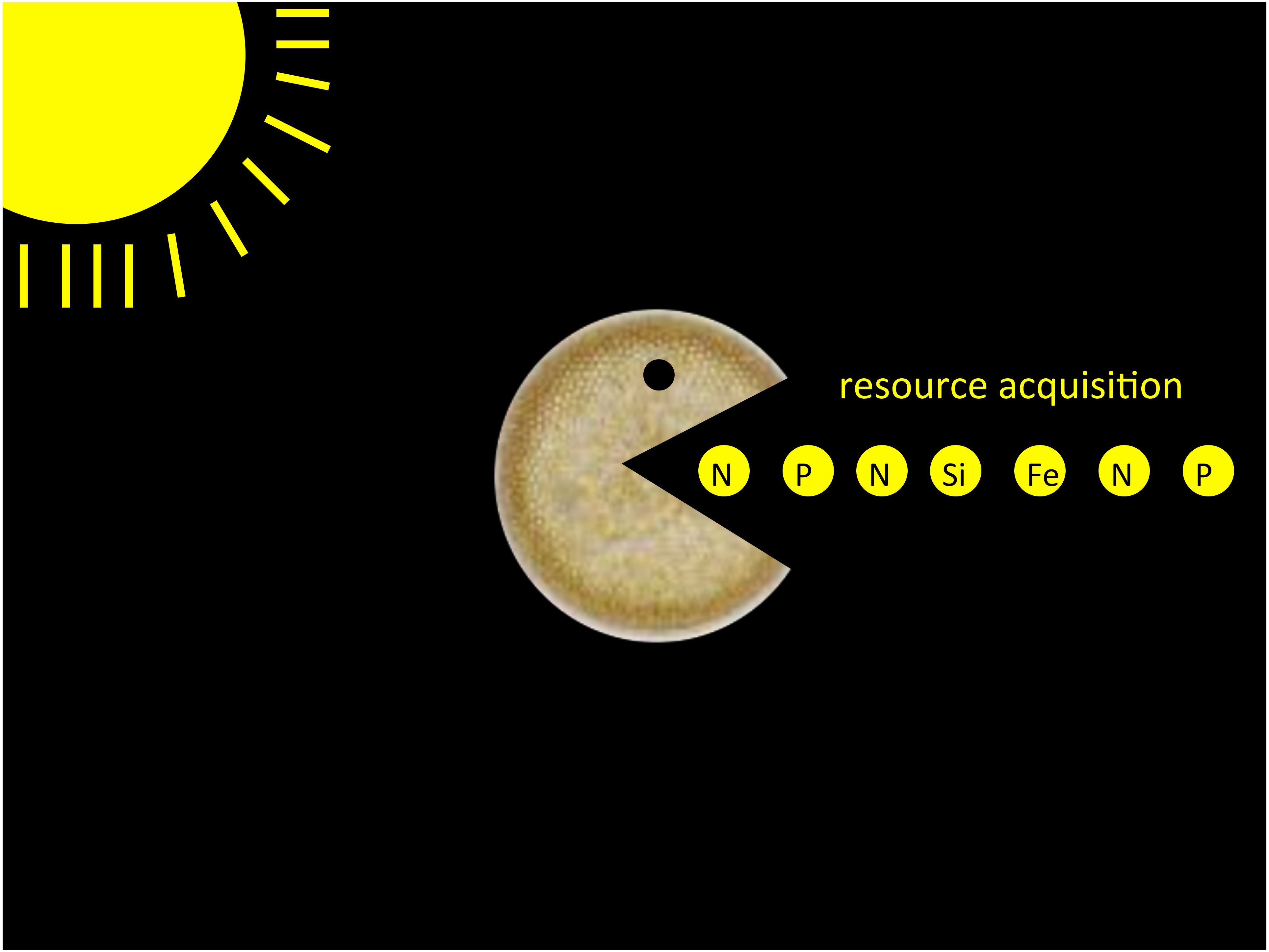


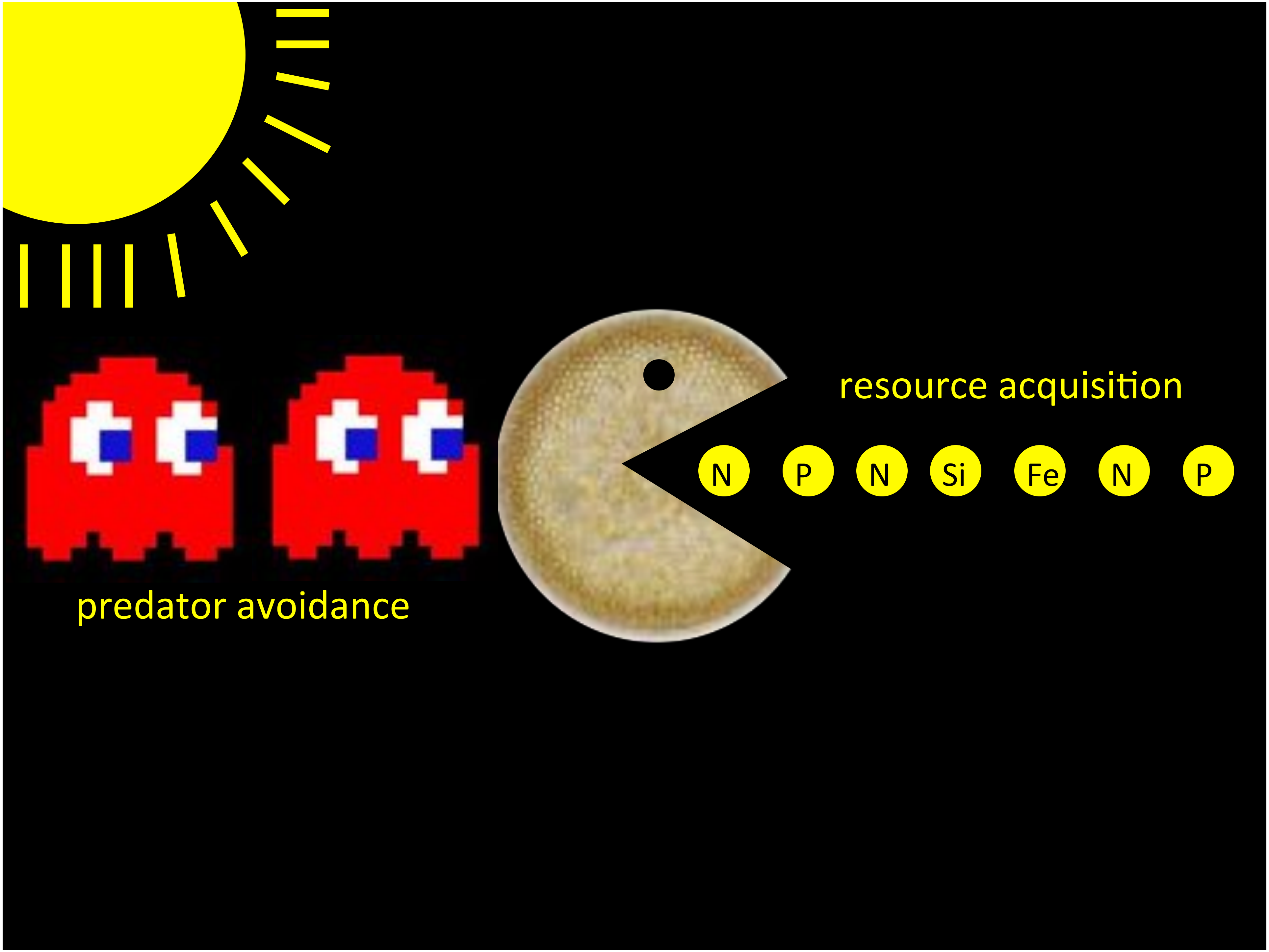
Continuum of Strategies

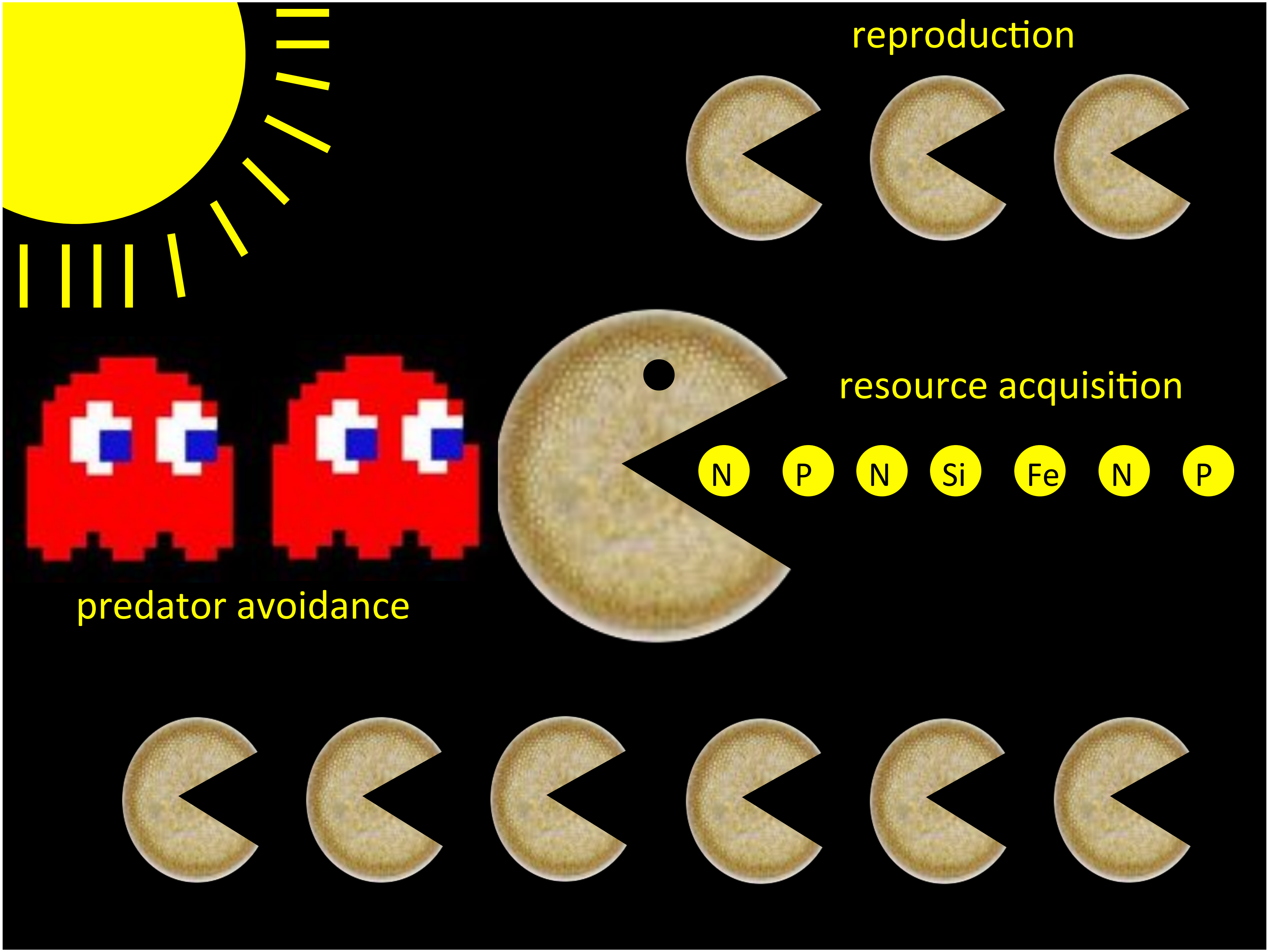


Trait-Based Approach

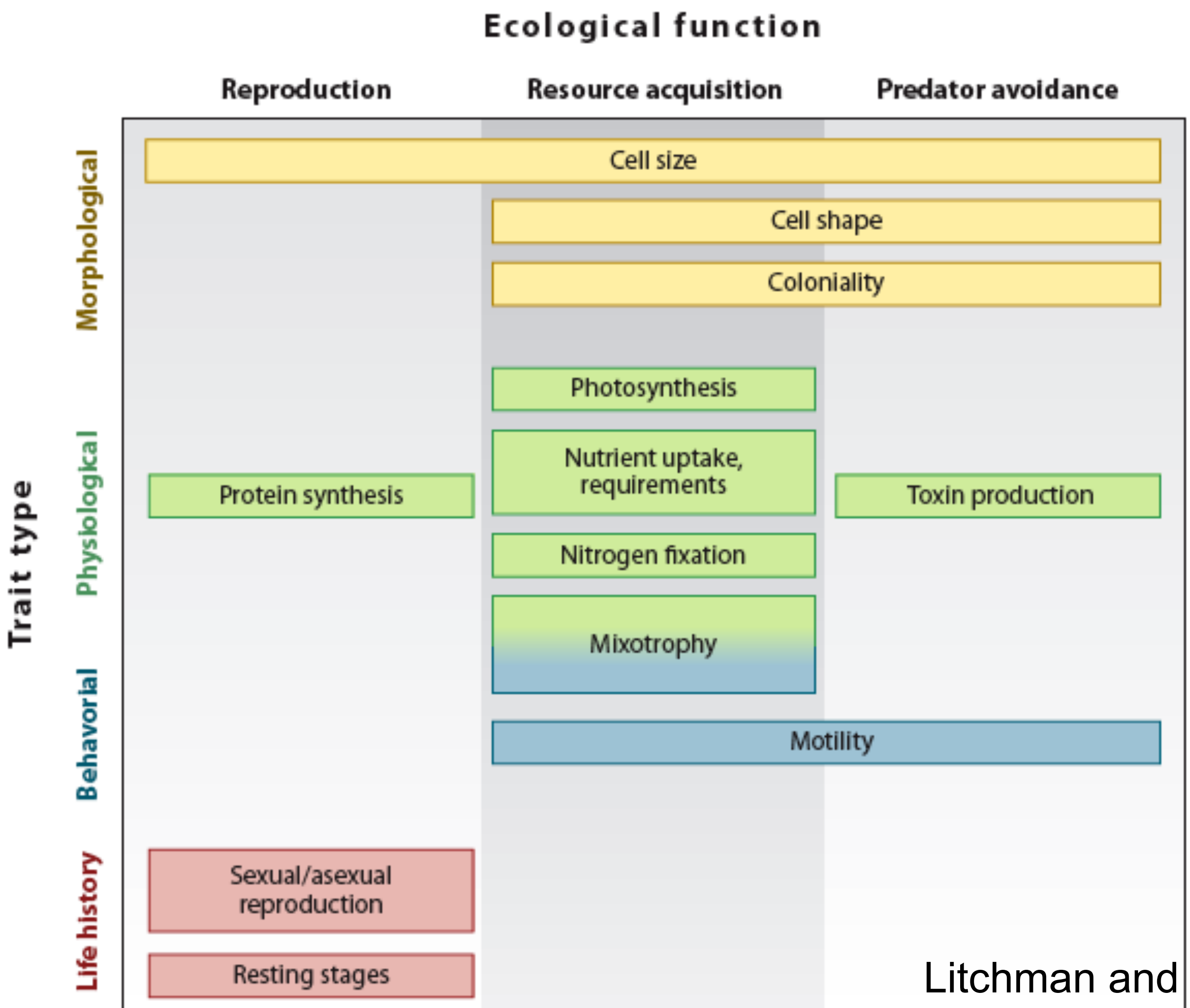
1. Ecologically relevant traits
2. Trade-offs between these traits
3. Mechanistic models of population interactions
4. Fitness
5. Source of novel phenotypes


resource acquisition
N
P
N
Si
Fe
N
P


resource acquisition
N
P
N
Si
Fe
N
P
predator avoidance


reproduction
resource acquisition
N
P
N
Si
Fe
N
P
predator avoidance

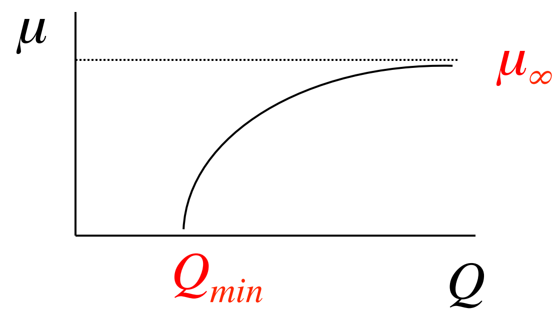
1) Ecologically relevant traits



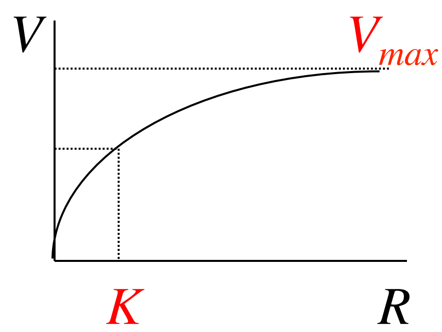
Litchman and Klausmeier 2008
Annual Rev. Ecol. Evol. Syst.

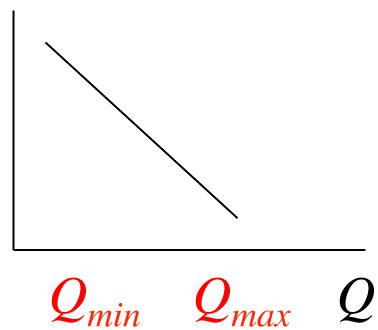
Nutrient Utilization Traits

growth $$\mu = \mu_\infty \left(1 - \frac{Q_{\min}}{Q}\right)$$



nutrient uptake $$V = V_{\max} \frac{R}{K + R} \frac{Q_{\max} - Q}{Q_{\max} - Q_{\min}}$$





Traits:

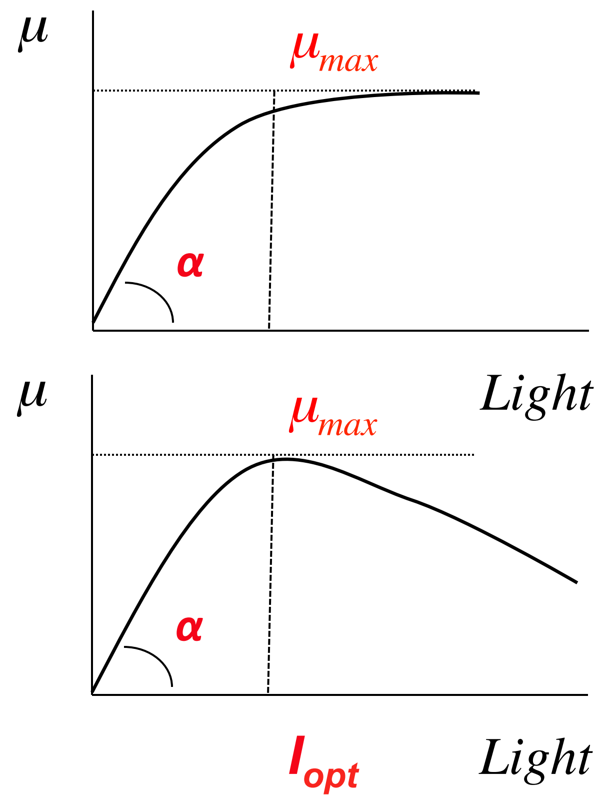
- $\boldsymbol{\mu_\infty}$, growth rate at infinite quota
- $\boldsymbol{Q_{min}}$, minimum internal nutrient content
- $\boldsymbol{Q_{max}}$, maximum internal nutrient content
- $\boldsymbol{V_{max}}$, maximum uptake rate of nutrient
- ***K*,** half-saturation constant for nutrient uptake

Light Utilization Traits

$$\mu = \mu_{\max} \frac{\mu_{\max} I}{I + \dfrac{\mu_{\max}}{\alpha}}$$

Eilers & Peeters (1988):

$$\mu(I) = \frac{\mu_{\max} I}{\dfrac{\mu_{\max}}{\alpha} l^2 I^2 + \left(1 - 2\dfrac{\mu_{\max}}{\alpha} l\right) I + \dfrac{\mu_{\max}}{\alpha}}$$



Traits:

- μ_{max}, maximum growth rate
- α , initial slope of the growth-irradiance curve
- I_{opt} , growth saturation irradiance

2) Trade-offs between traits

- Allocation of finite resources / time
- Physical / genetic constraints

3) Mechanistic models of population interactions

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - f(P)Z$$

$$\frac{dZ}{dt} = ef(P)Z - mZ$$

$$\frac{\partial b}{\partial t} = \min\left(f_R(R), f_I(I)\right)b - mb + D\frac{\partial^2 b}{\partial z^2} + \frac{\partial}{\partial z}\left(v\left(\frac{\partial g}{\partial z}\right)b\right)$$

$$\frac{\partial R}{\partial t} = -\frac{b}{Y}\min\left(f_R(R), f_I(I)\right) + D\frac{\partial^2 R}{\partial z^2}$$

$$I(z) = I_{\mathrm{in}} e^{-\int_0^z \left(a_{\mathrm{bg}} + ab(Z)\right)\,dZ}$$

- Spatial / temporal heterogeneity
- Age / size structure

4) Fitness

Growth rate of a rare species trying to invade a resident community (dominant eigenvalue, Floquet exponent, Lyapunov exponent)

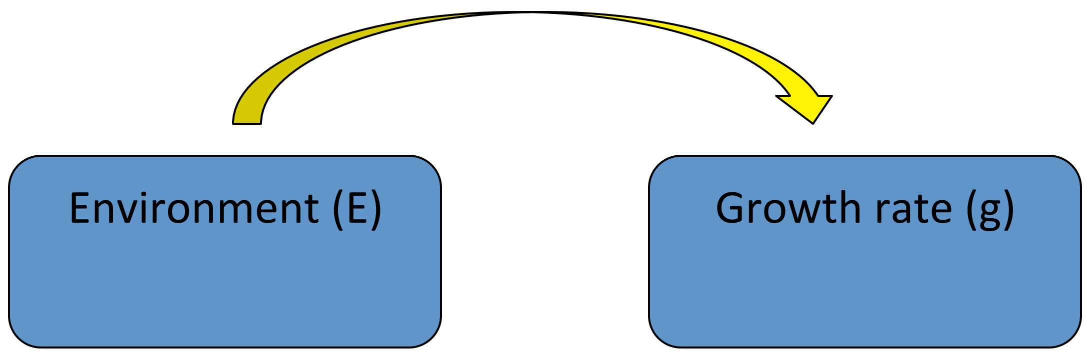
(Metz, Nisbet & Geritz 1992)

5) Source of novel phenotypes

- Standing genetic variation
- Rare mutation
- Immigration
- Everything is everywhere

Linking traits and community structure

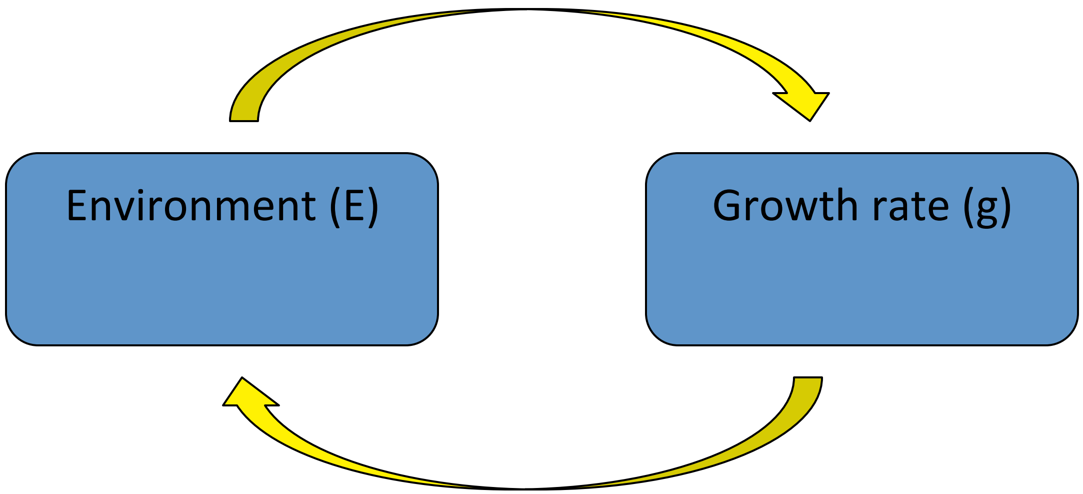
- Fitness = growth rate = g(E,traits)



- Frequency-independent: maximize growth rate

Linking traits and community structure

- Interspecific interactions: species affect environment too: E(traits, abundances)



- Frequency-dependent

Simplest case: resource competition

Minimize break-even nutrient concentration, *R** (Tilman 1982)

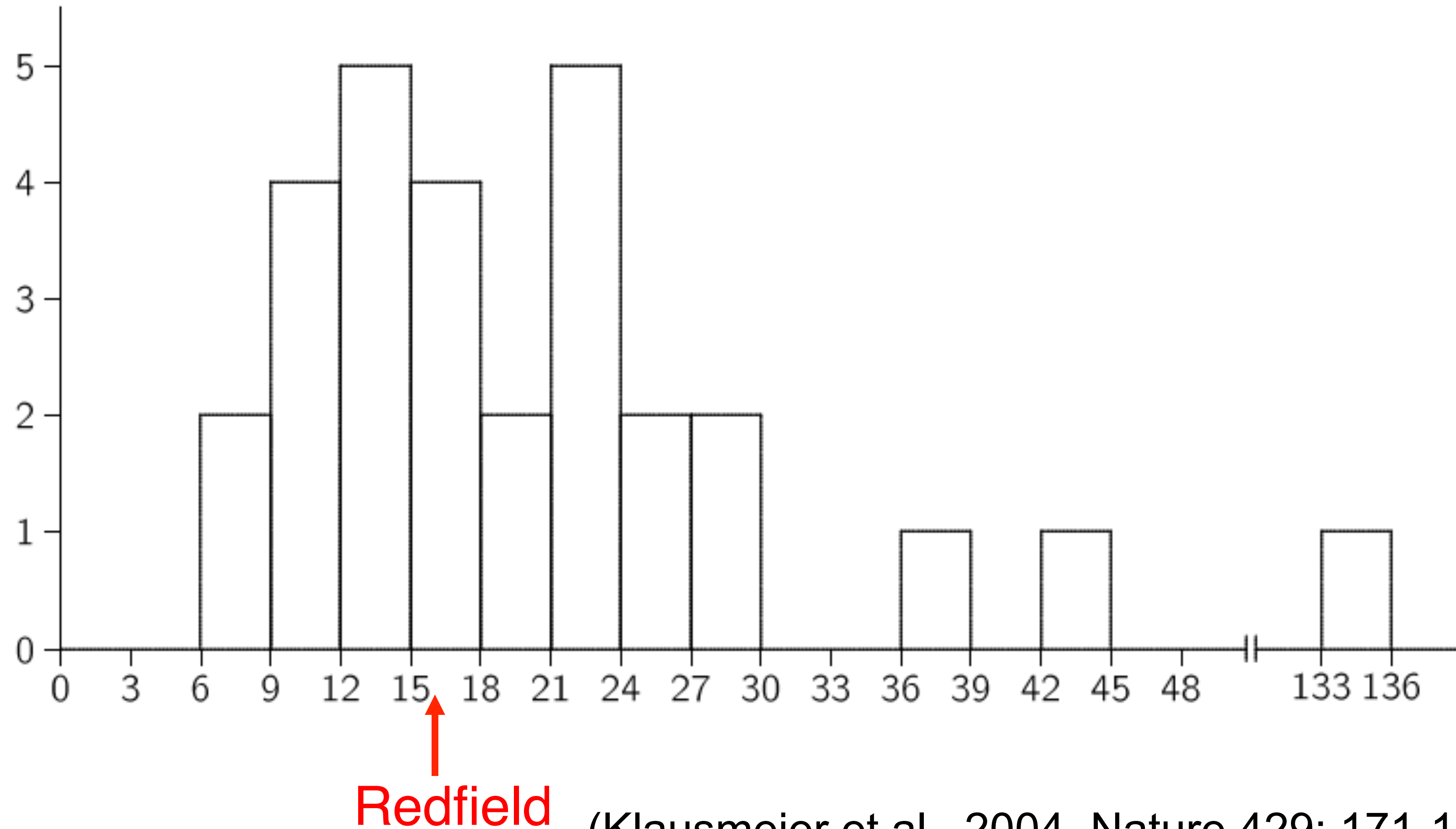
$$R^* = \frac{K \mu_\infty Q_{\min} m}{V_{\max}(\mu_\infty - m) - \mu_\infty Q_{\min} m}$$

*R** decreases (competitive ability increases) when

↑ μ_∞ (growth at max Q)
V_{max} (max uptake rate)

↓
- K (half-saturation constant)
- Q_{min} (min quota)
- m (mortality)

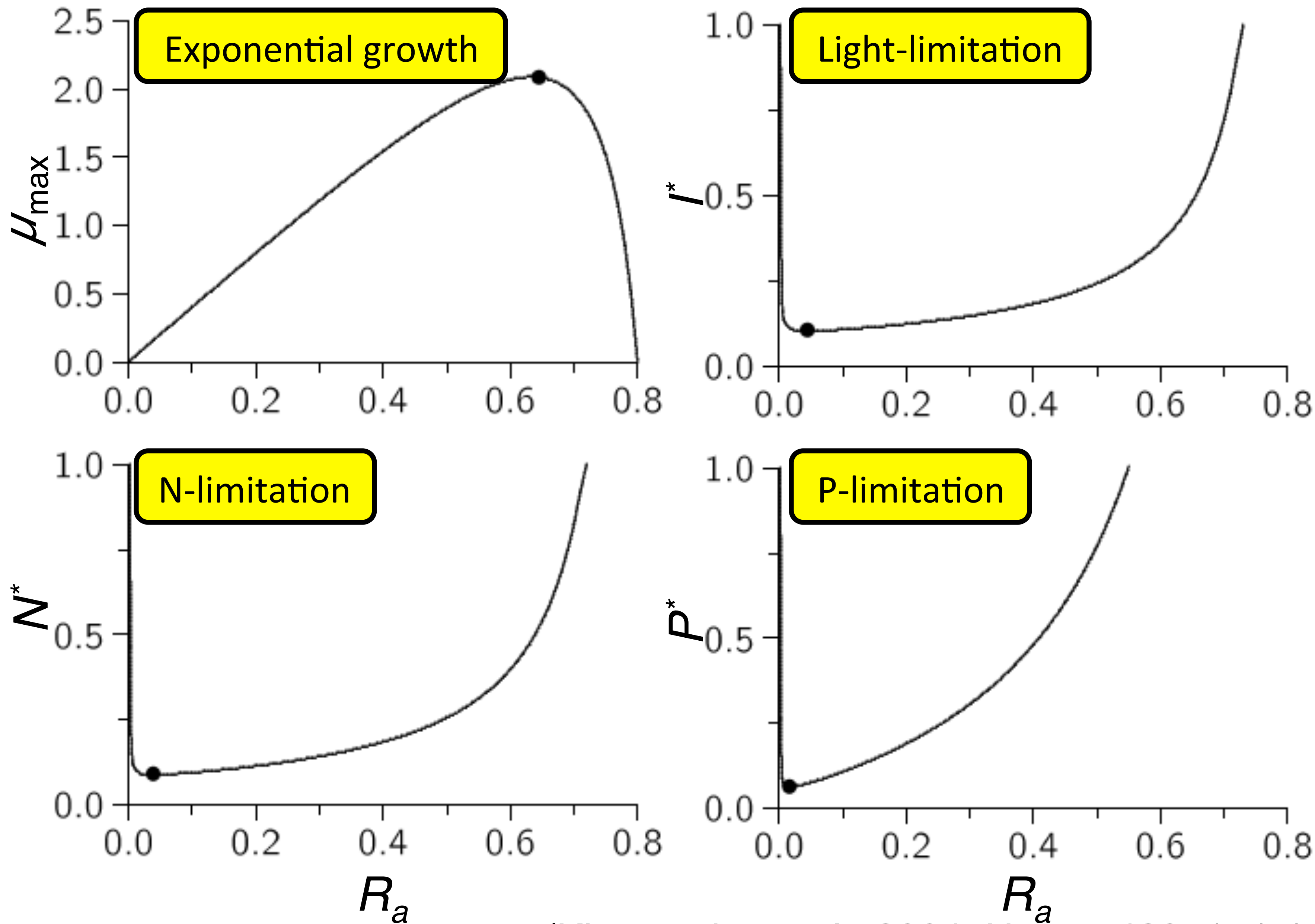
Ex 1: Optimal N:P Ratios



(Klausmeier et al., 2004, Nature 429: 171-174)

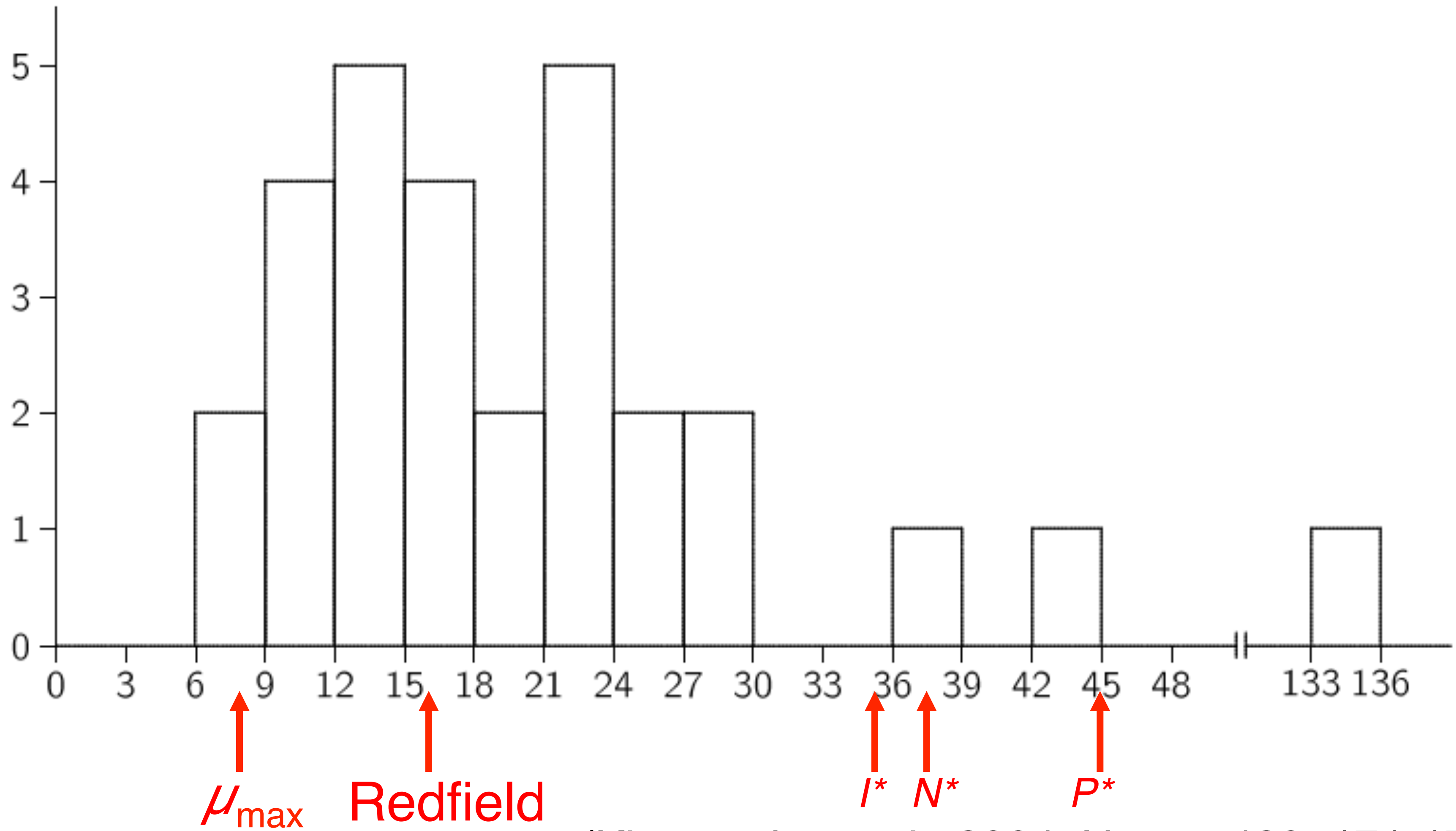
Ex 1: Optimal N:P Ratios

- Cell is made up of different types of machinery and factory walls
  - Uptake machinery, R_u per carbon
  - Assembly machinery, R_a per carbon
- Each component has its own N:P stoichiometry (N_x, P_x)
- Uptake machinery should be N-rich (proteins/ chloroplasts)
- Assembly machinery should be N- and P-rich (ribosomes)[Growth Rate Hypothesis]
- Trade-off between uptake and assembly machinery



(Klausmeier et al., 2004, Nature 429: 171-174)

Ex 1: Optimal N:P Ratios



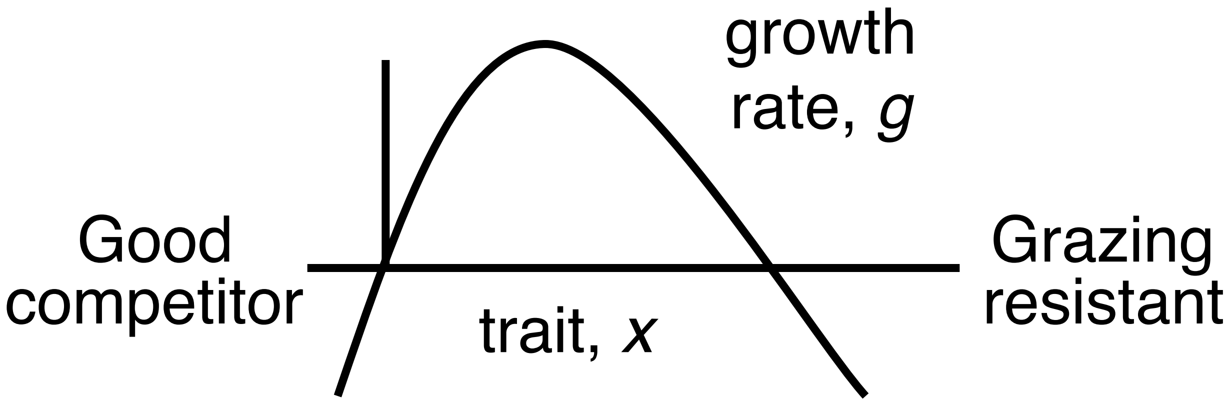
(Klausmeier et al., 2004, Nature 429: 171-174)

General case

$$\frac{dN_i}{dt} = g(x_i; \vec{N}, \vec{x}) N_i$$

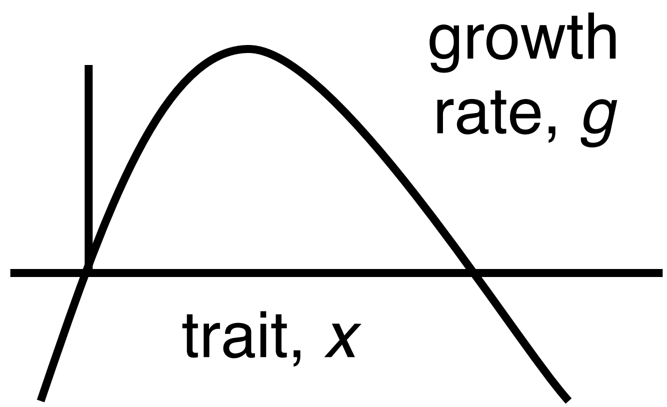
(Geritz et al. 1998 *Evol Ecol*)

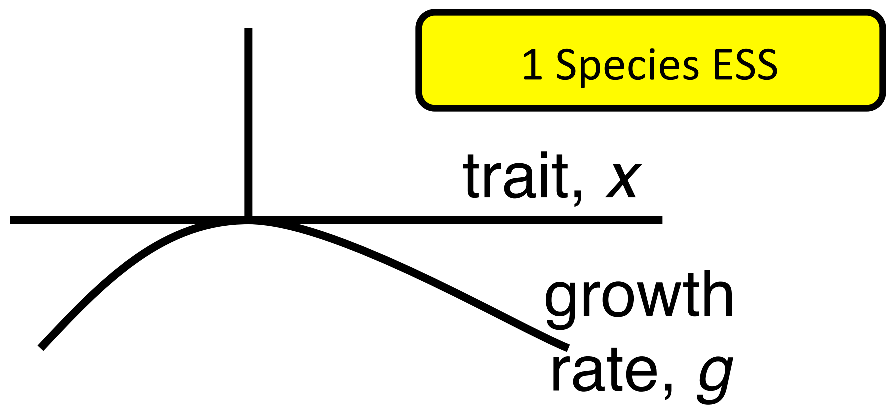
General case



(Geritz et al. 1998, Evol. Ecol)

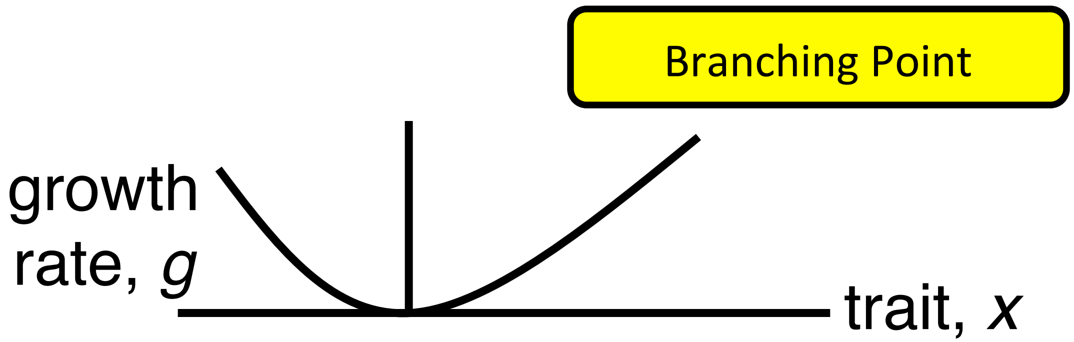
General case





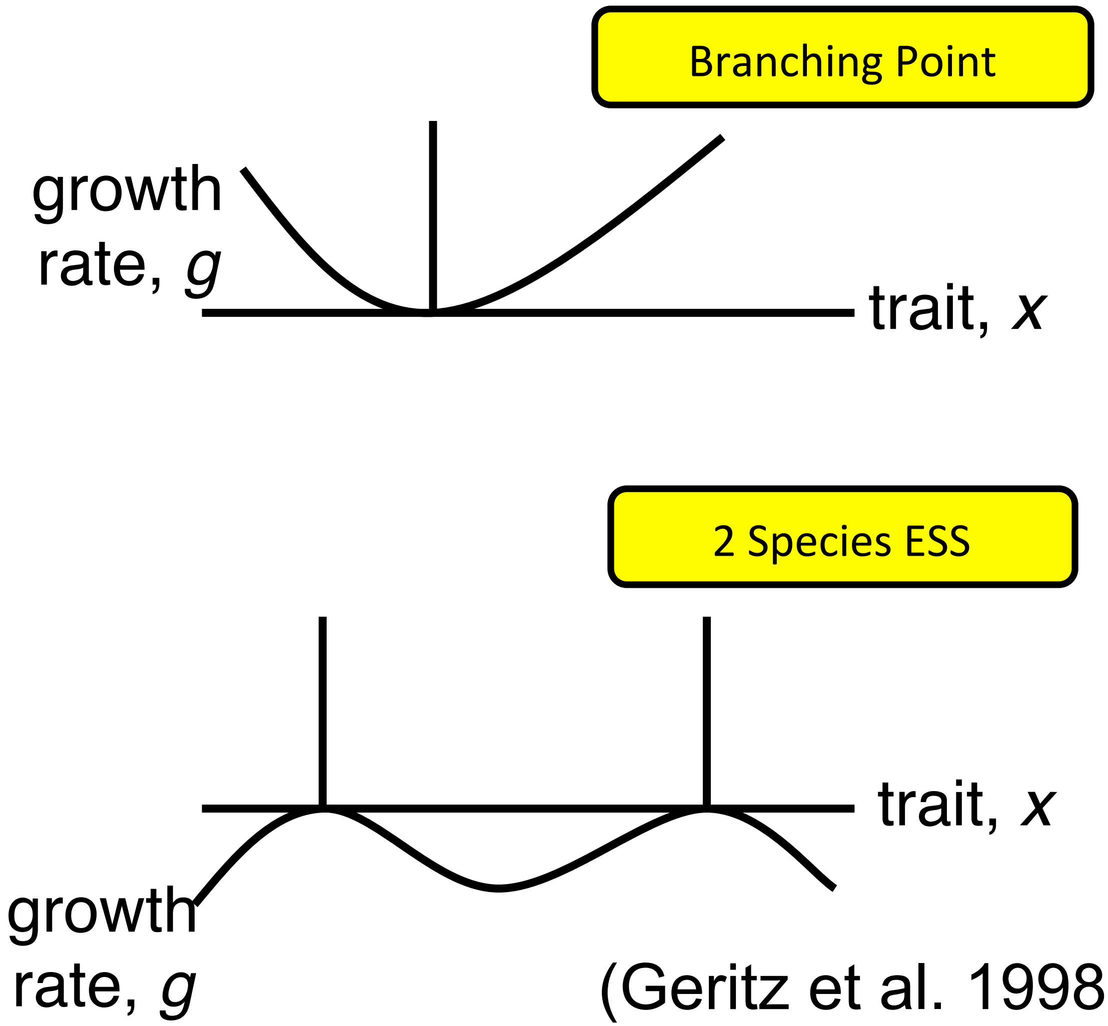
(Geritz et al. 1998, Evol. Ecol)

General case



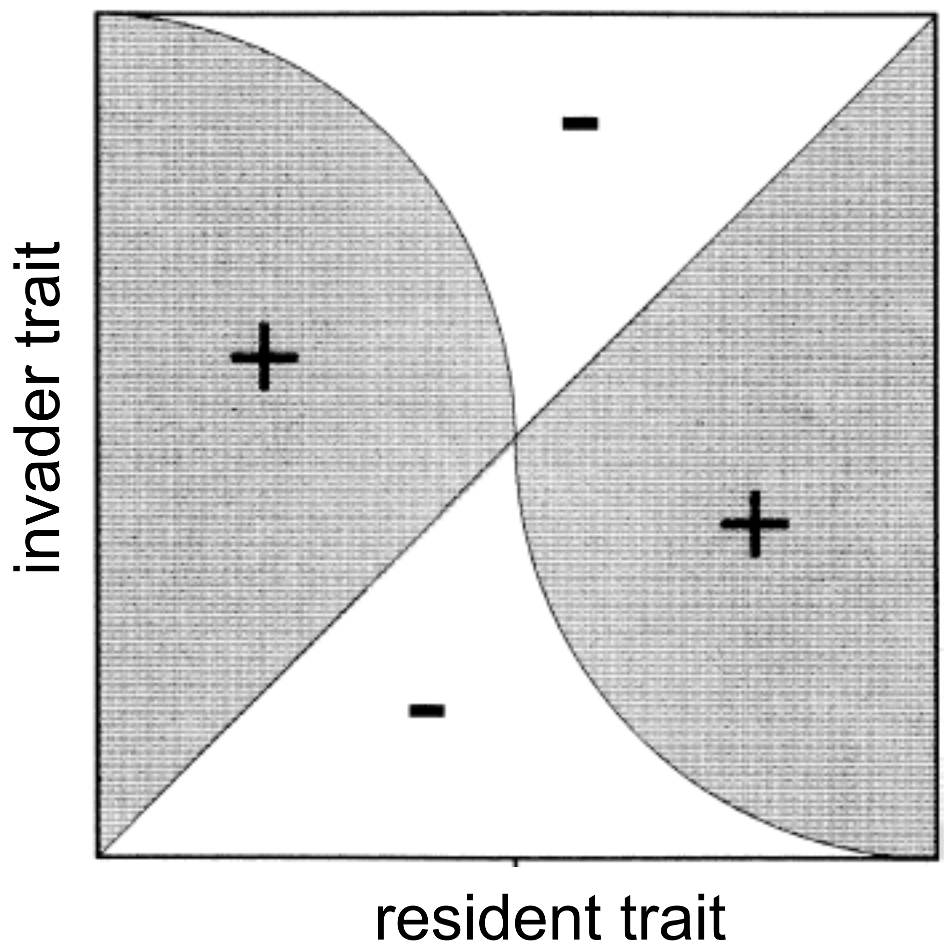
(Geritz et al. 1998, Evol. Ecol)

General case



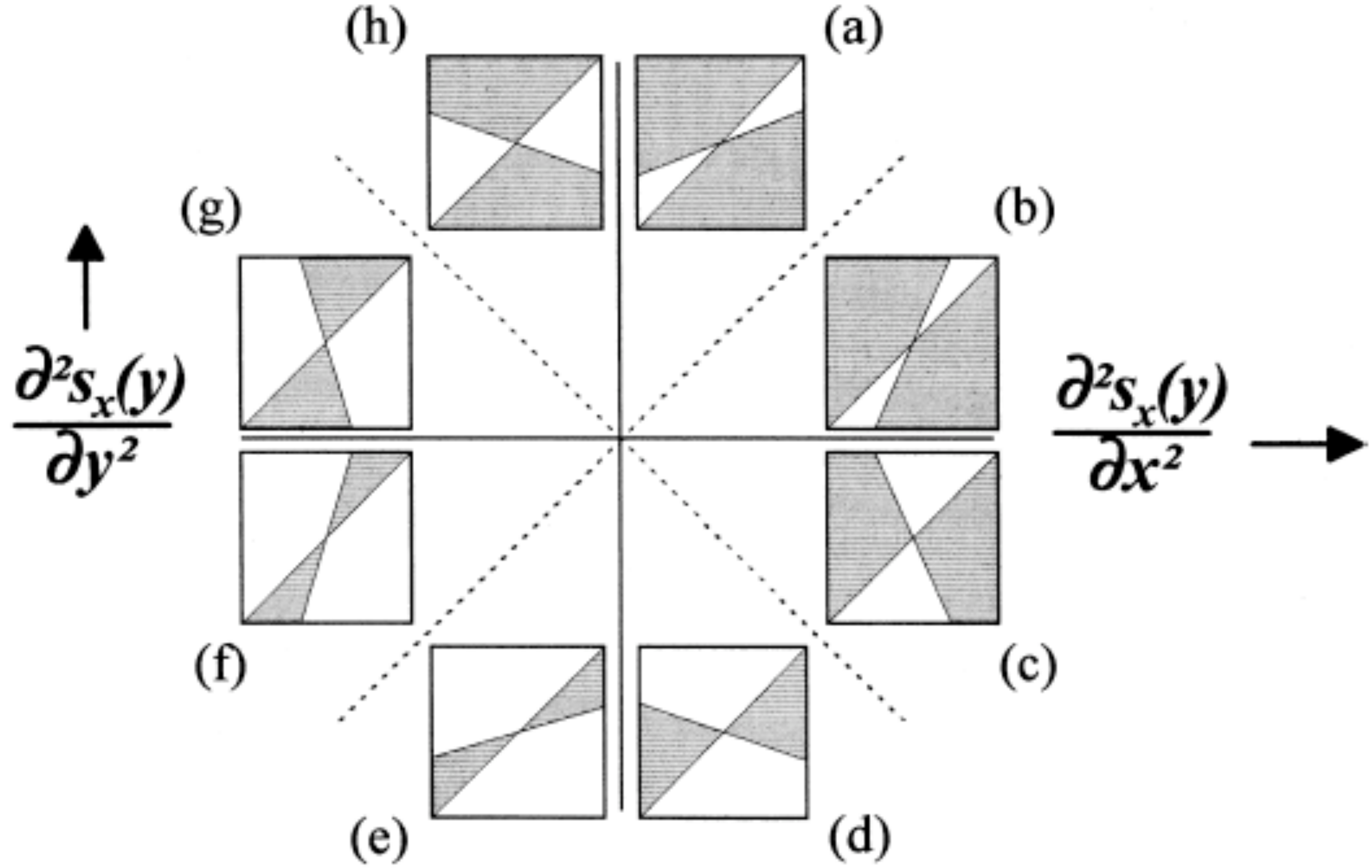
(Geritz et al. 1998, Evol. Ecol)

Pairwise invasibility plots (PIPs)



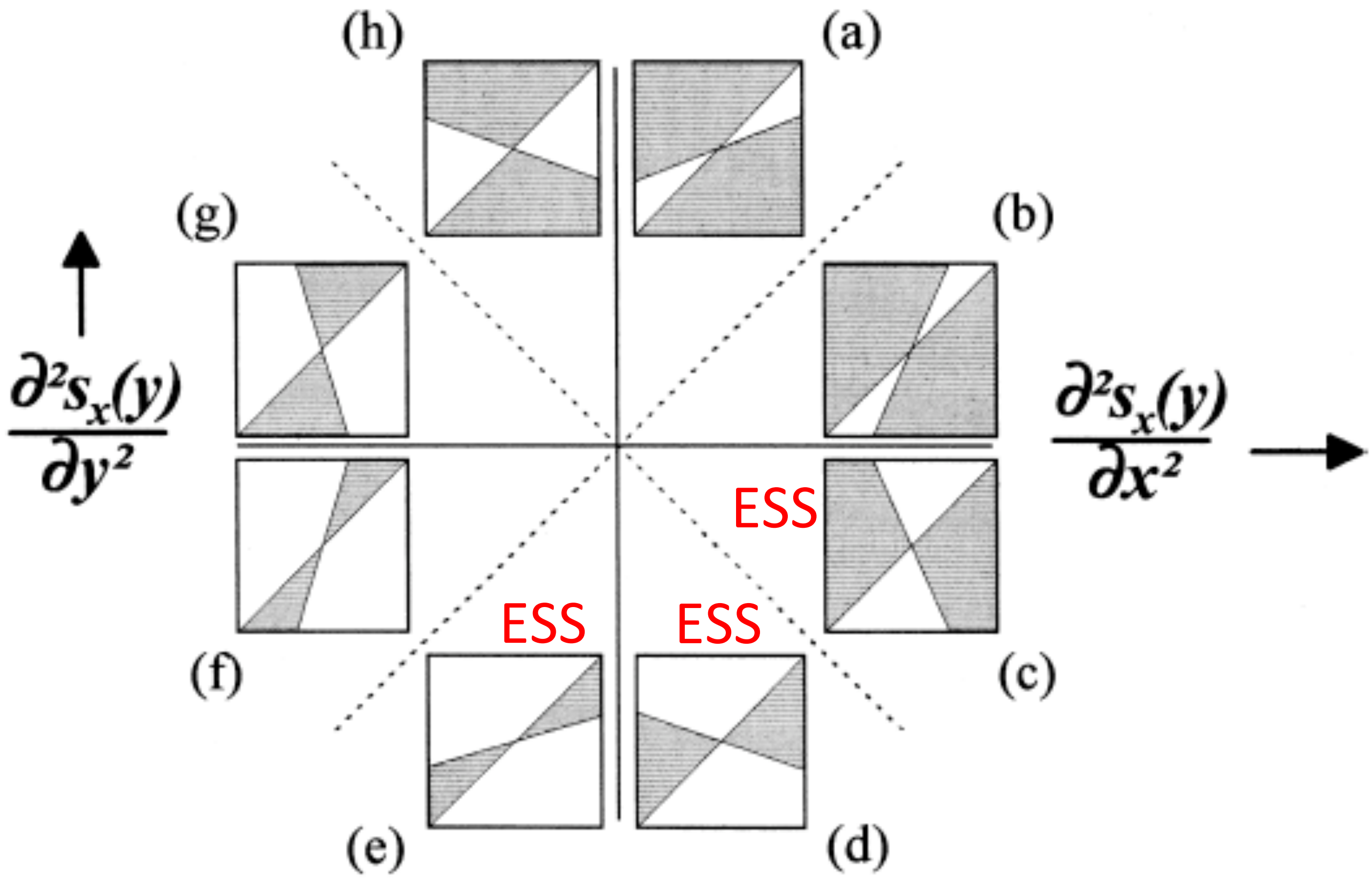
(Geritz et al. 1998, Evol. Ecol)

Eightfold classification



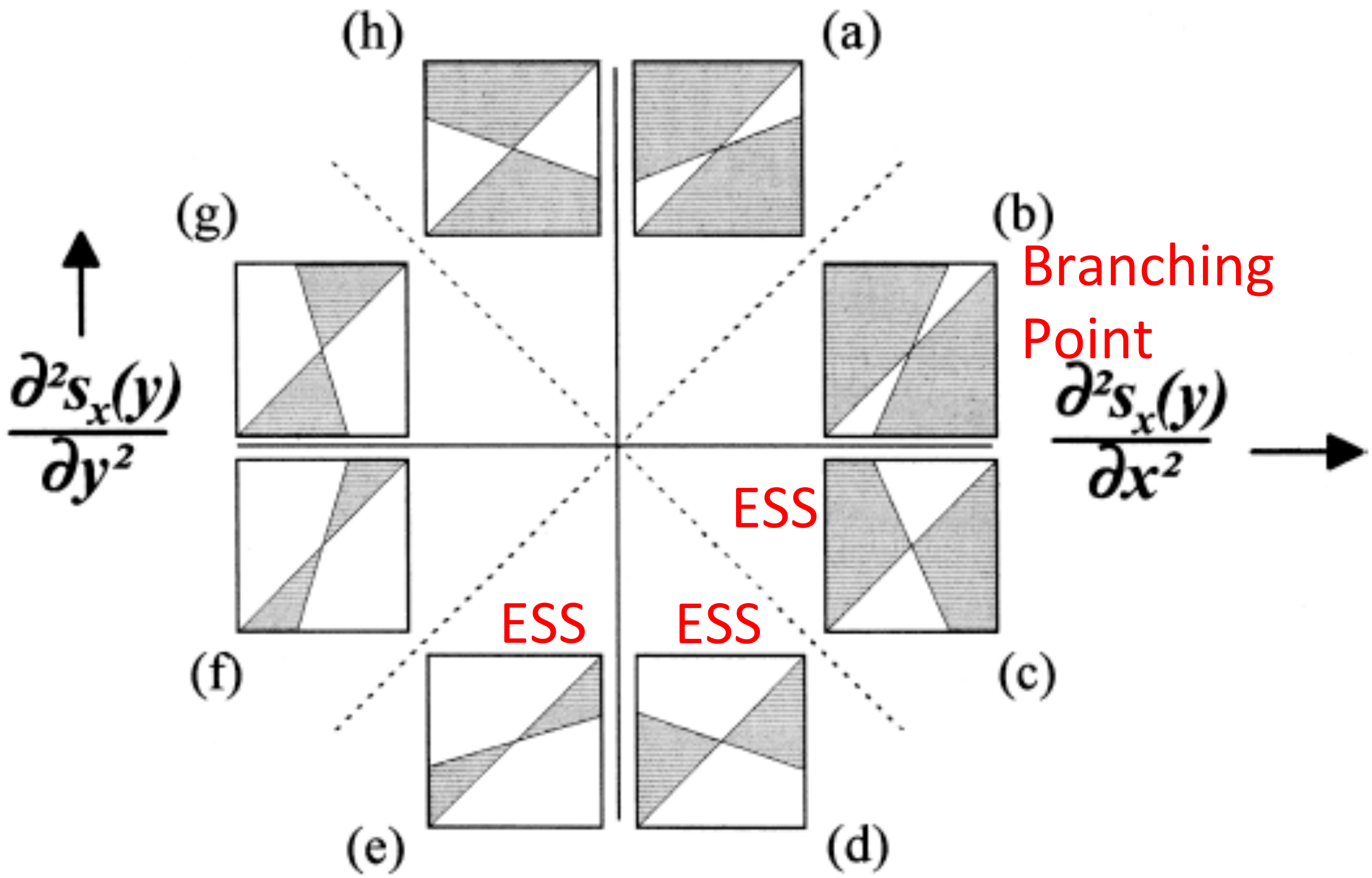
(Geritz et al. 1998, Evol. Ecol)

Eightfold classification



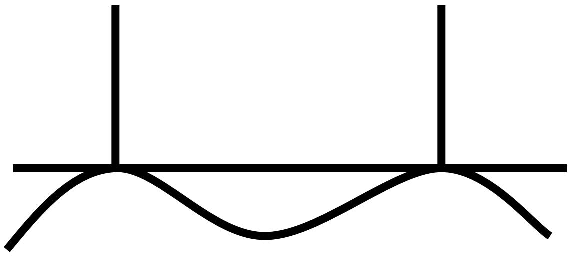
(Geritz et al. 1998, Evol. Ecol)

Eightfold classification

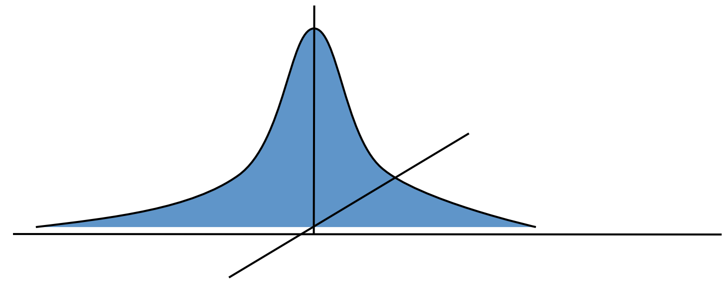


(Geritz et al. 1998, Evol. Ecol)

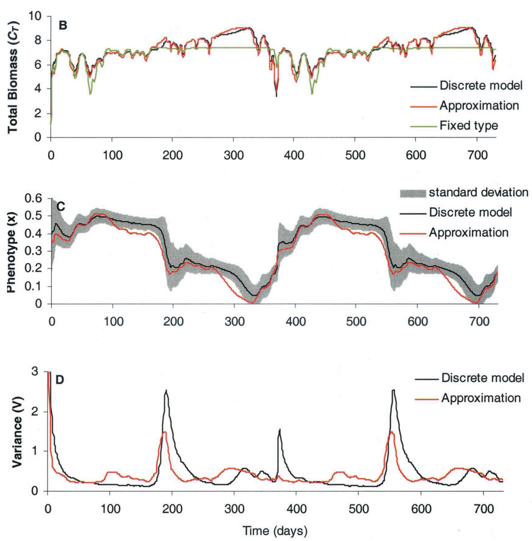
Related approaches



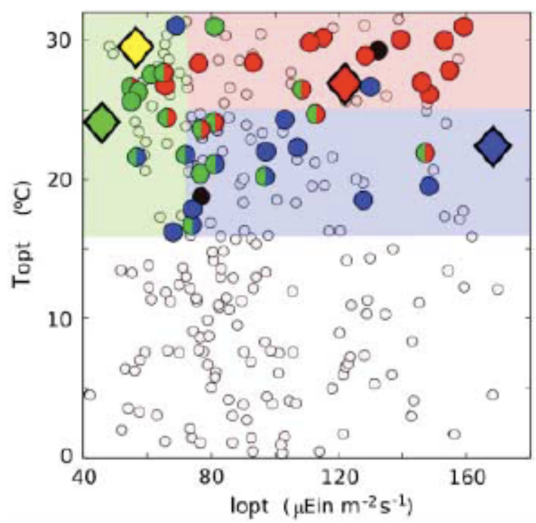
ESS Maximum Approach
(Brown, Vincent)



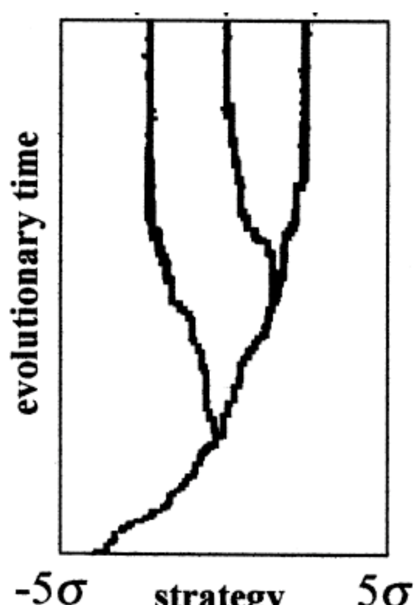
Quantitative Genetics
(Lande, Abrams)



Complex Adaptive Systems
(Wirtz, Norberg et al., Bruggeman)



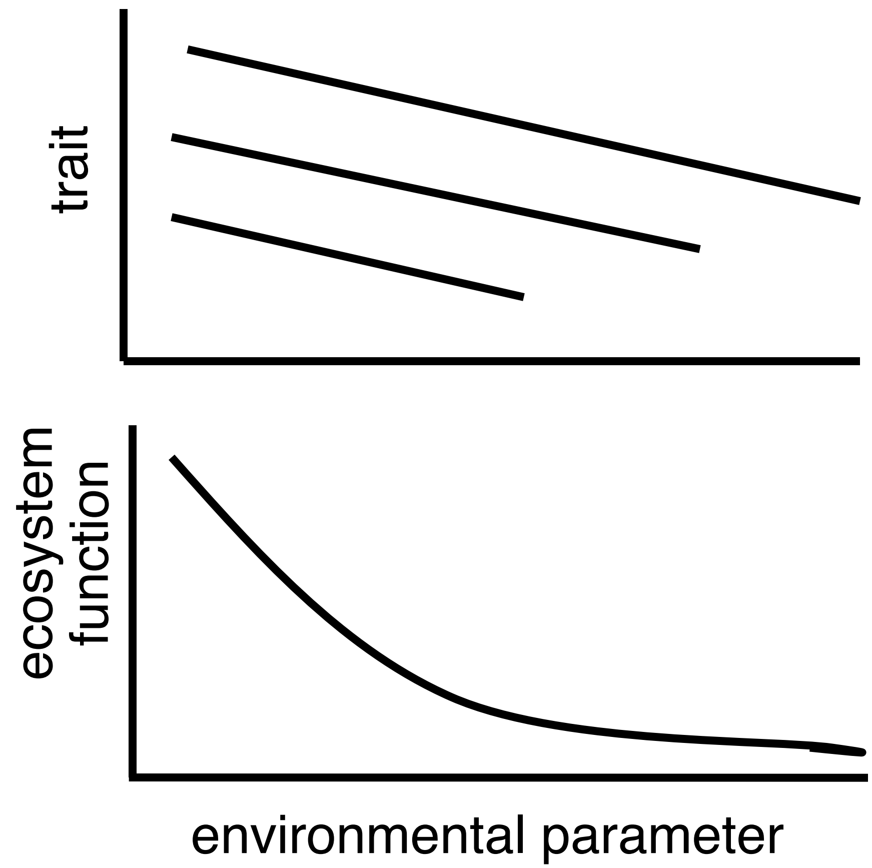
Monte Carlo Sampling
(Follows et al.)



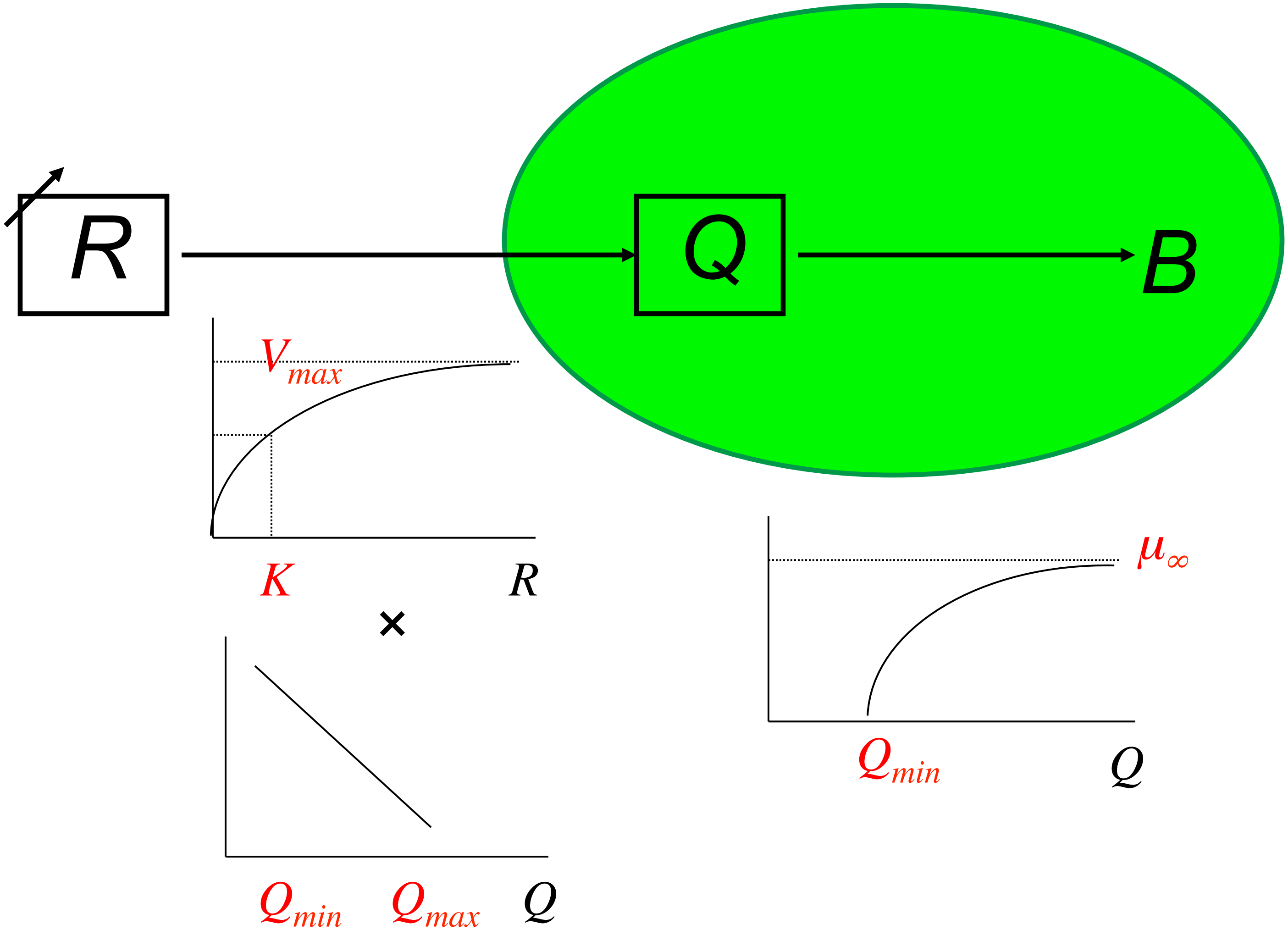
Adaptive Dynamics
(Geritz, Metz, Dieckmann, Law)

The Big Questions

- How do community structure (diversity, species traits) and ecosystem functions depend on abiotic environmental parameters?
- How will ecosystems reorganize in the face of human impacts?

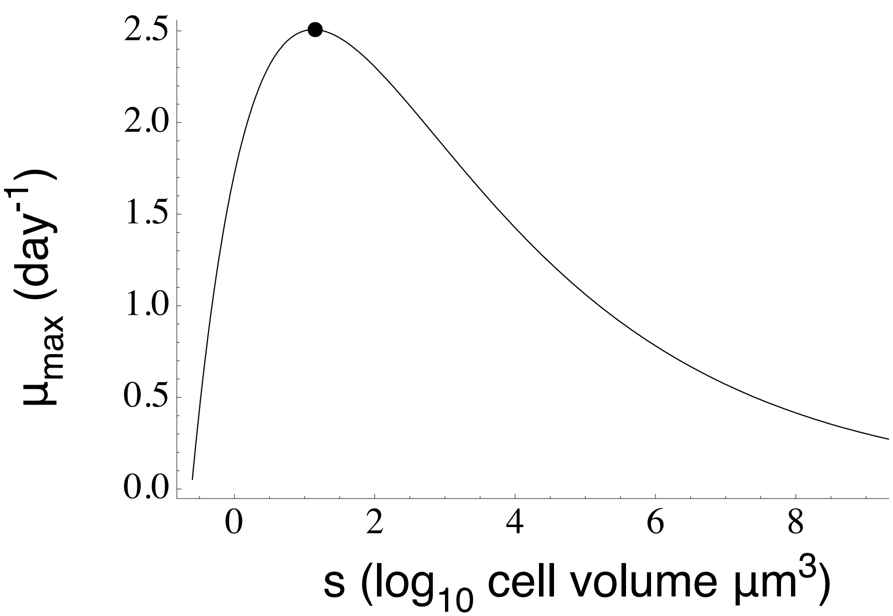


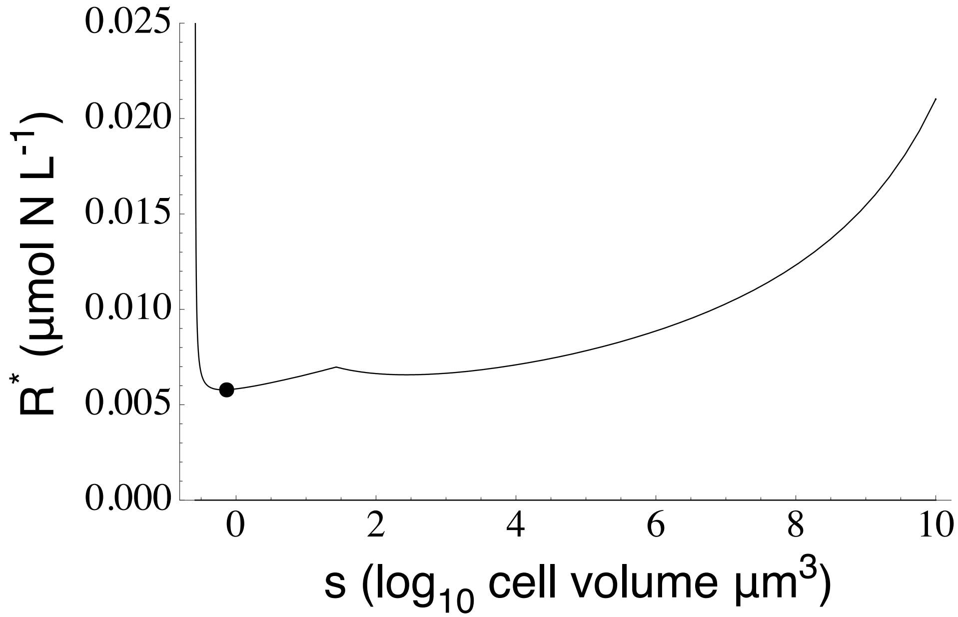
Ex 2: Diatom Size Evolution



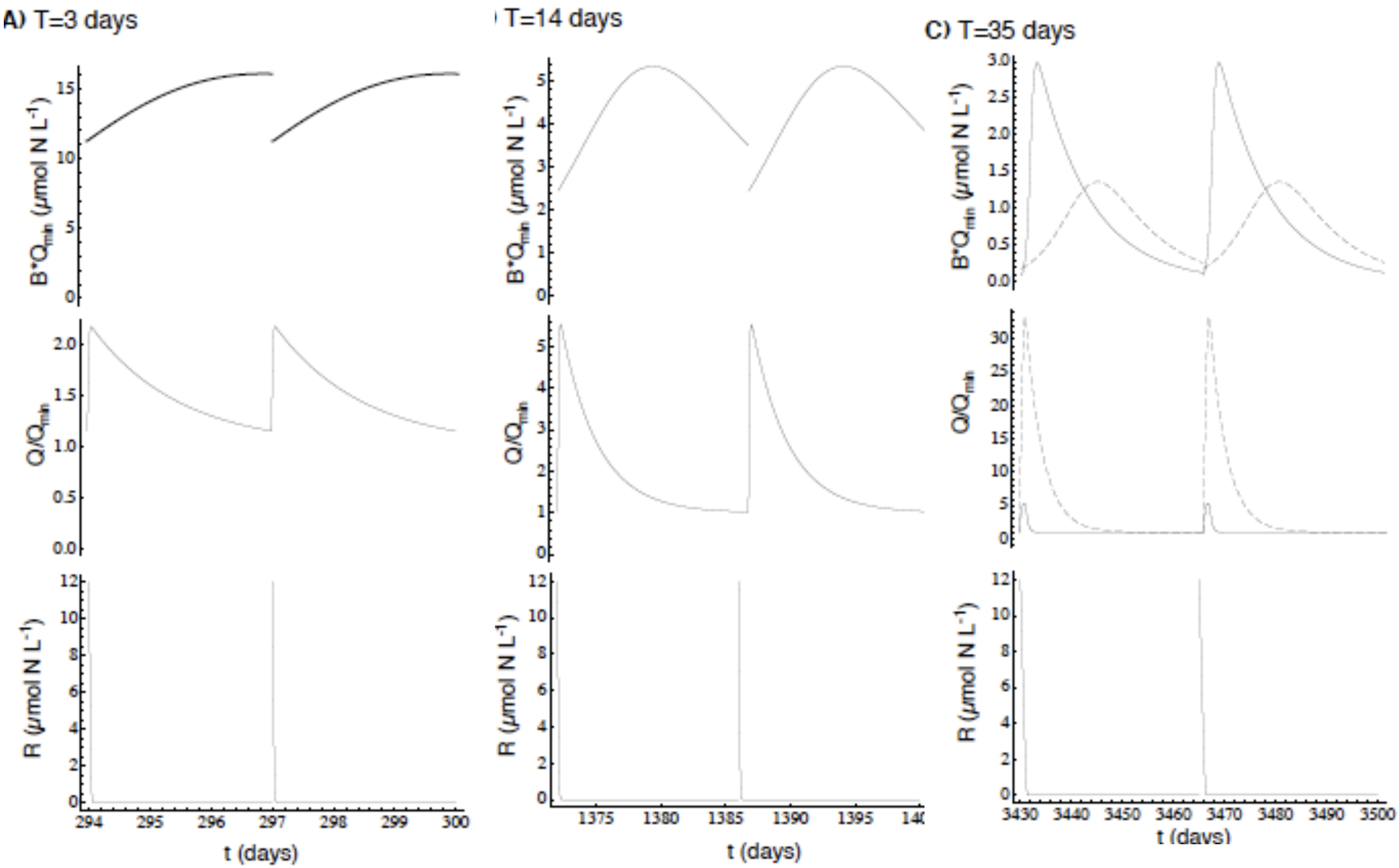
(Litchman et al, 2009 PNAS)

Exponential growth and equilibrium



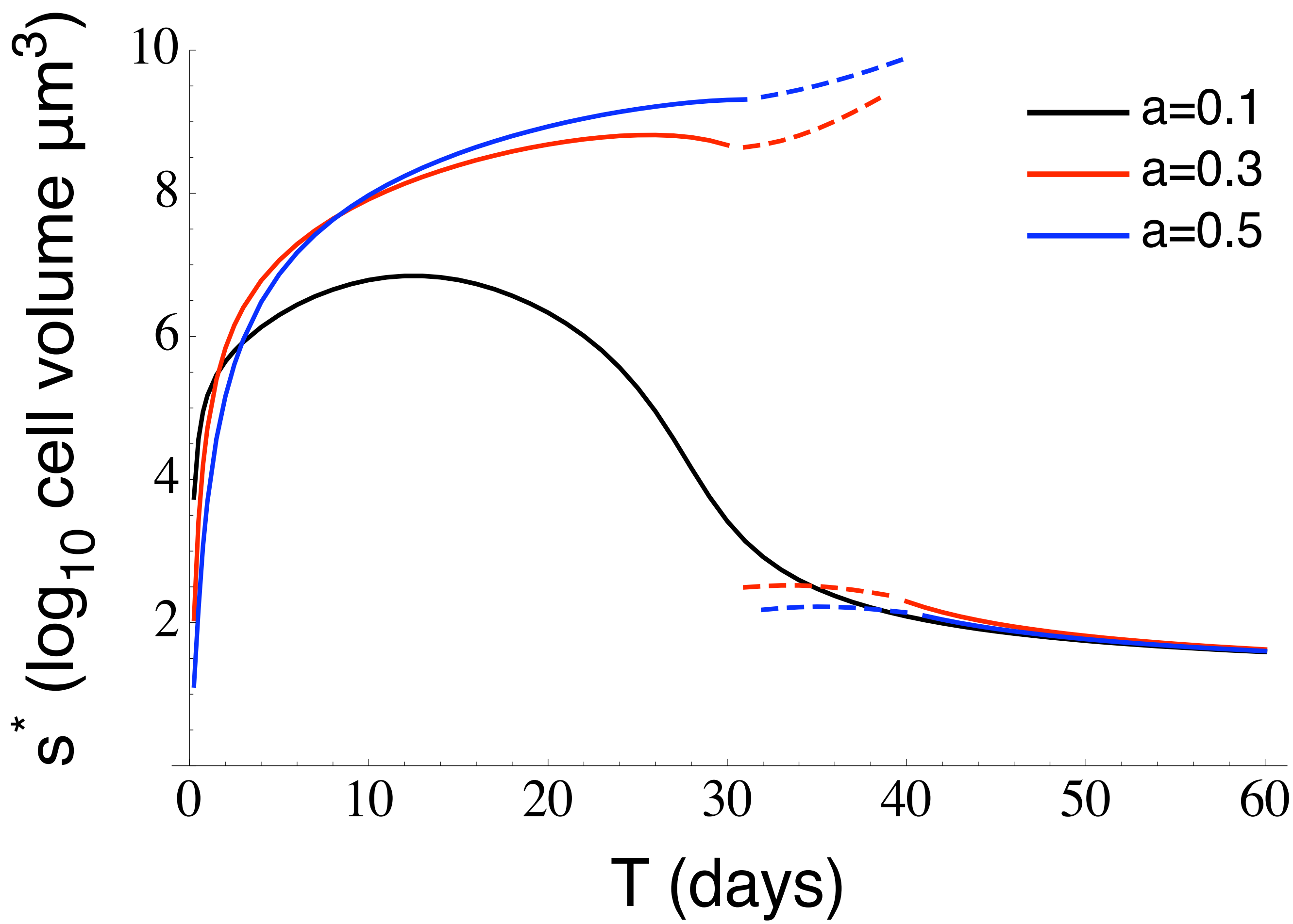


(Litchman et al, 2009 PNAS)



A) T=3 days
T=14 days
C) T=35 days
B*Q_min (μmol N L^-1)
Q/Q_min
R (μmol N L^-1)
t (days)

ESS cell size in pulsed environment



(Litchman et al, 2009 PNAS)

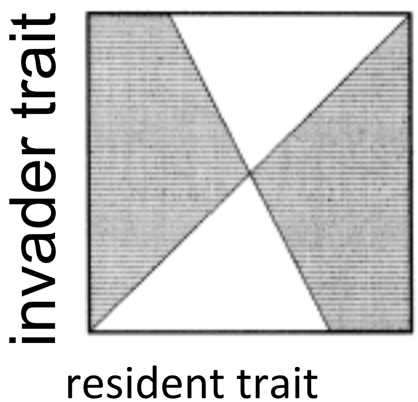
Other aquatic examples

- **Follows et al. 2007 Science** – optimum temperature and irradiance in a global ocean model
- **Bruggeman and Kooijman 2007 L&O** – light vs nutrient competitive ability in a seasonal 1D water column
- **Clark et al. 2013 L&O –** cell size in a global ocean model

Trait-Based Approaches…

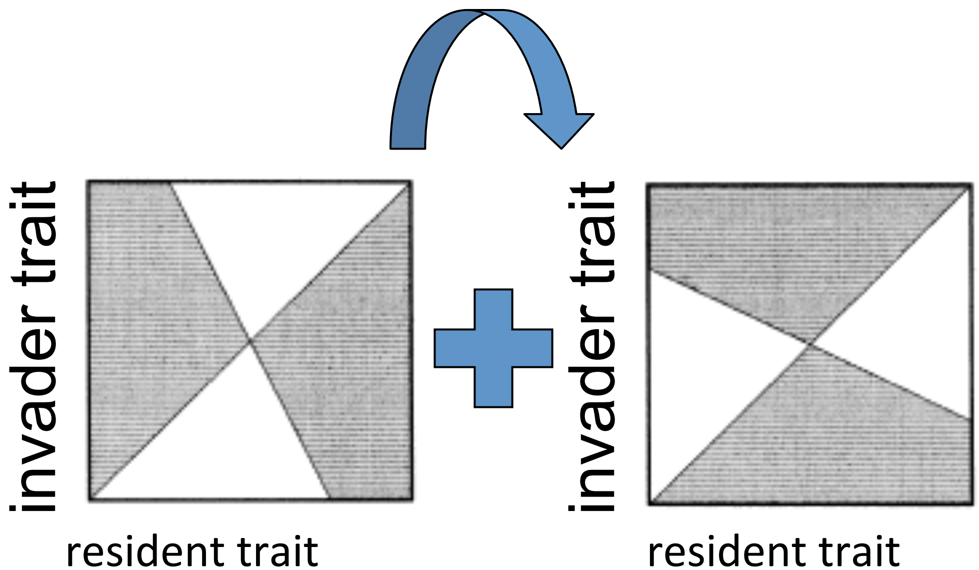
- Are agnostic on level of adaptation
  - Species sorting (community assembly)
  - Microevolution
  - Physiological / behavioral
- Offer new perspectives on
  - Neutral vs. niche
  - Species coexistence

Robustness of Coexistence Mechanisms



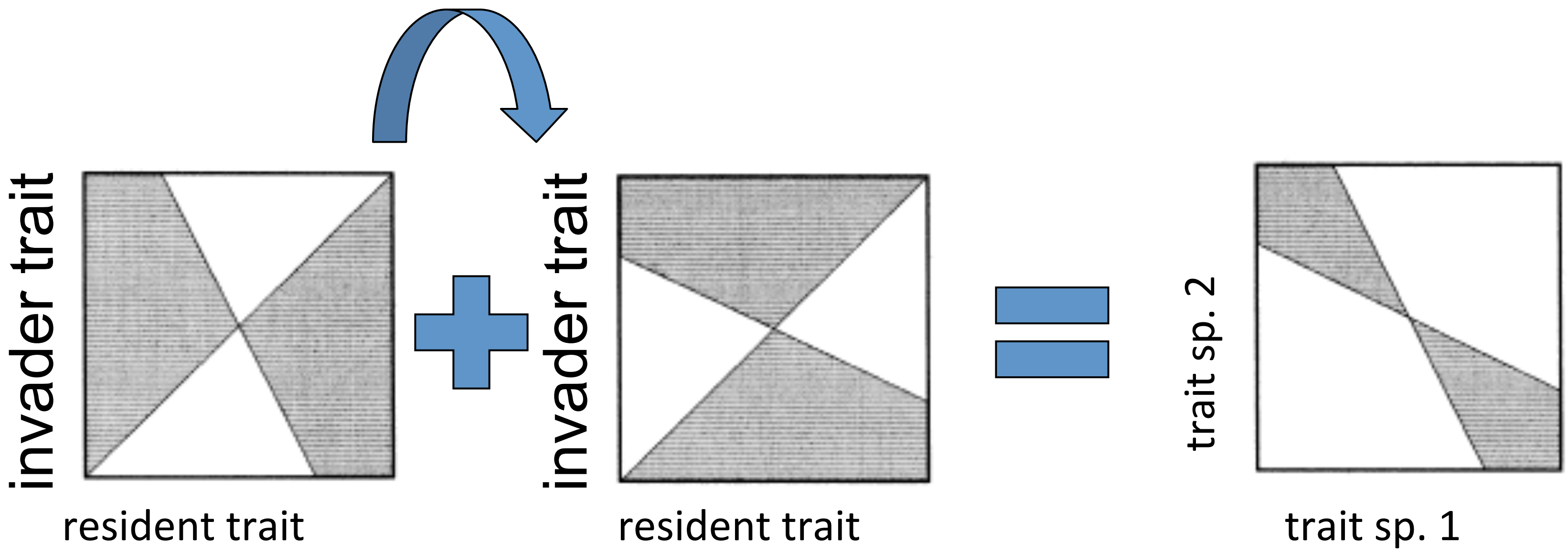
(Geritz et al. 1998, Evol. Ecol)

Robustness of Coexistence Mechanisms



(Geritz et al. 1998, Evol. Ecol)

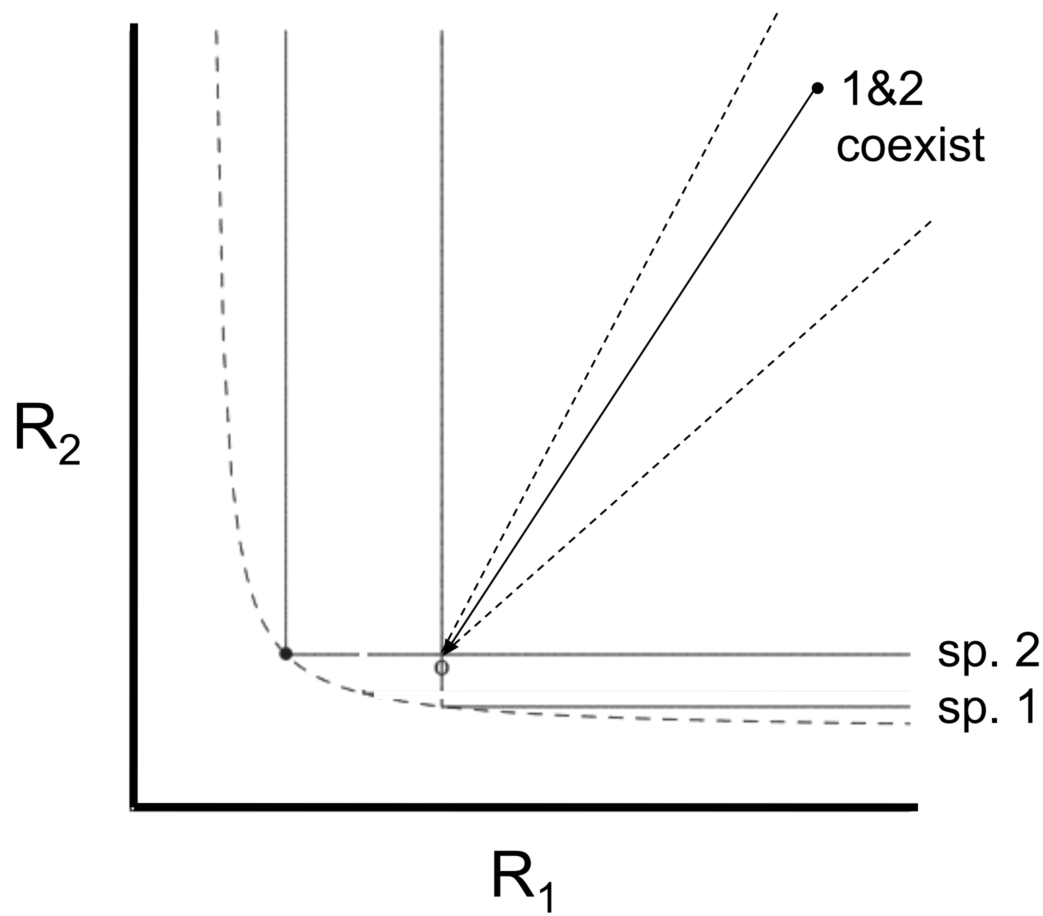
Robustness of Coexistence Mechanisms



⇒ Ecological coexistence does not imply evolutionary coexistence!

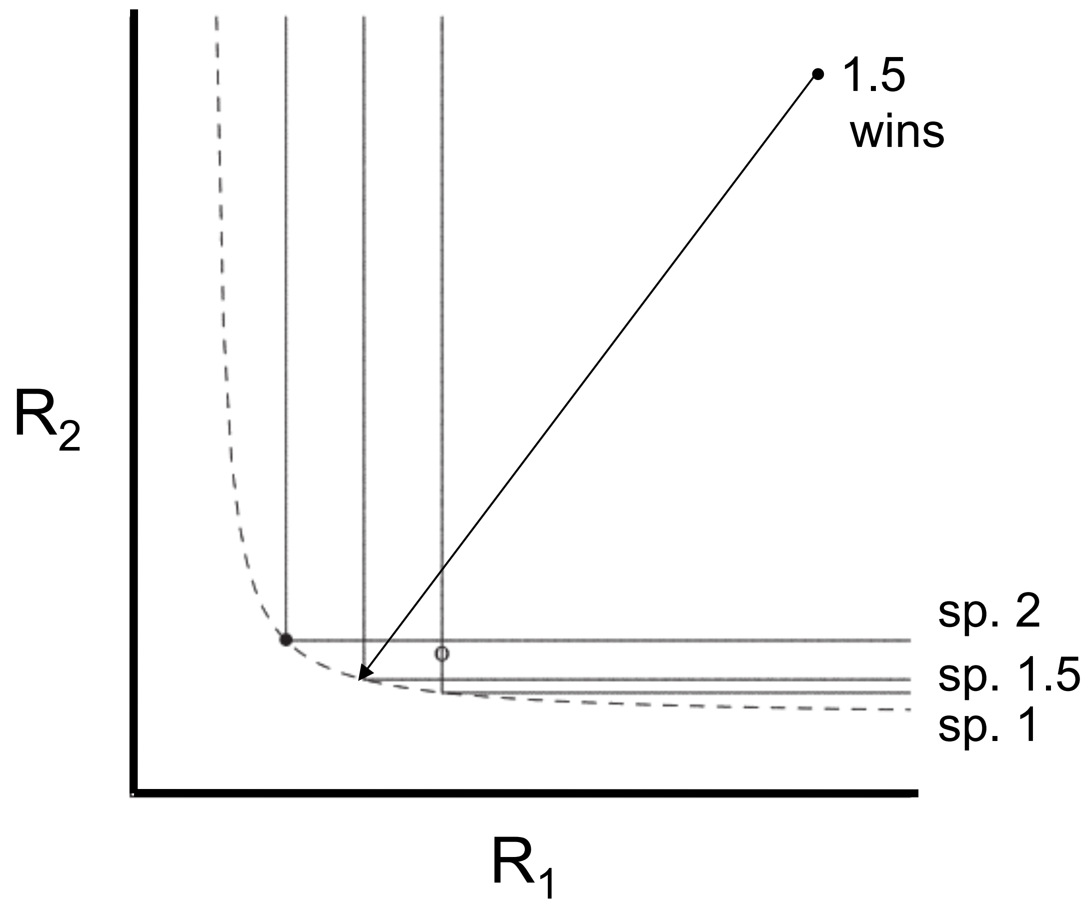
(Geritz et al. 1998, Evol. Ecol)

Resource acquisition trade-off



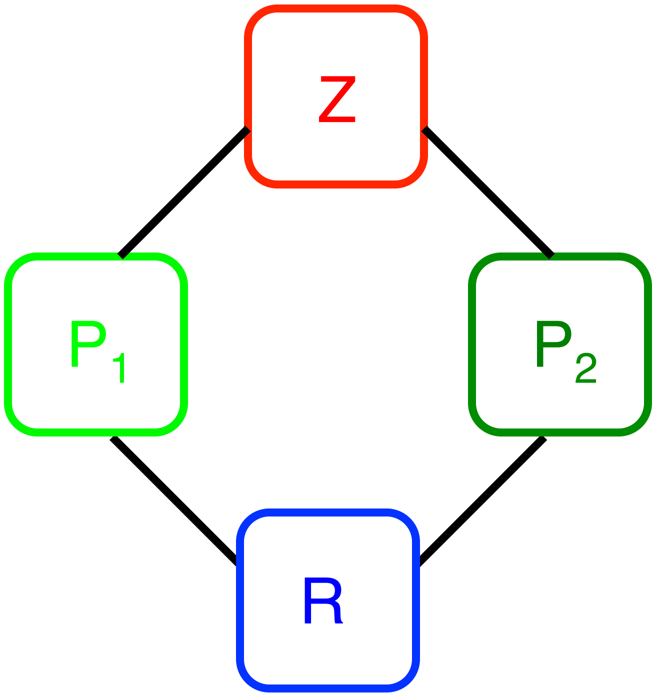
(after Tilman 1982; Klausmeier et al. 2007)

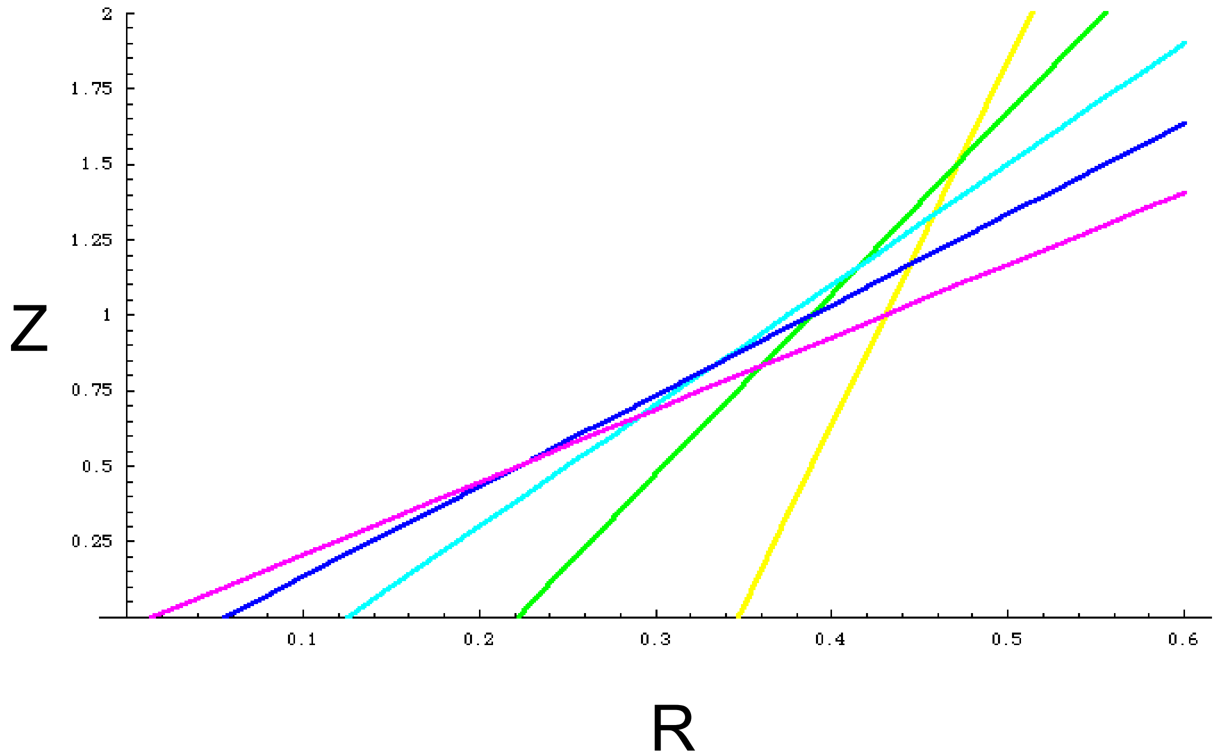
Resource acquisition trade-off



(after Tilman 1982; Klausmeier et al. 2007)

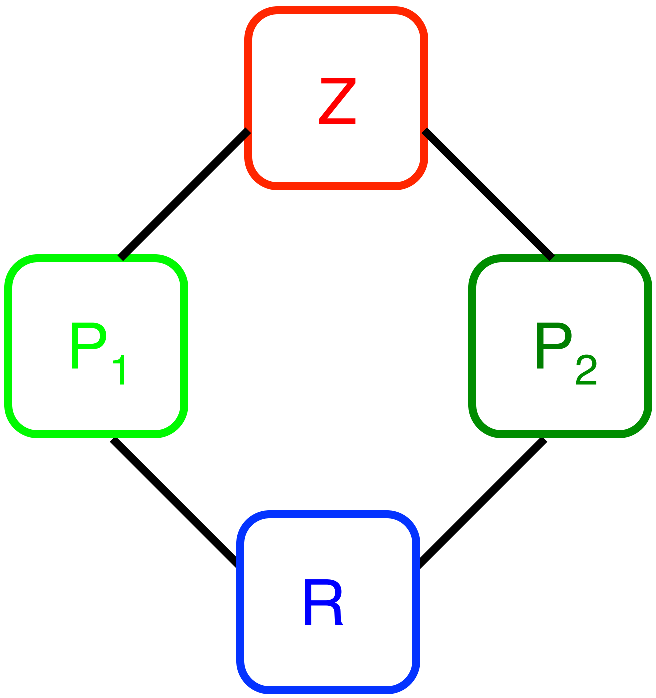
Competition–predator resistance trade-off

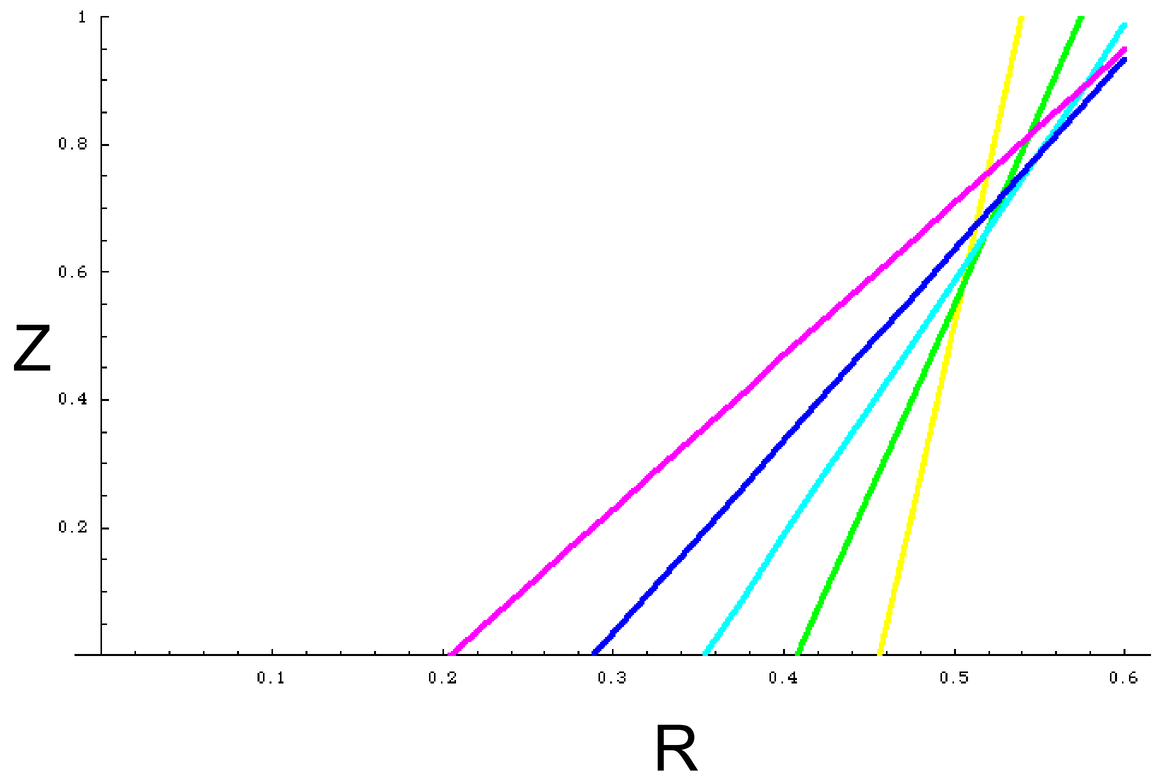




(after Leibold 1996)

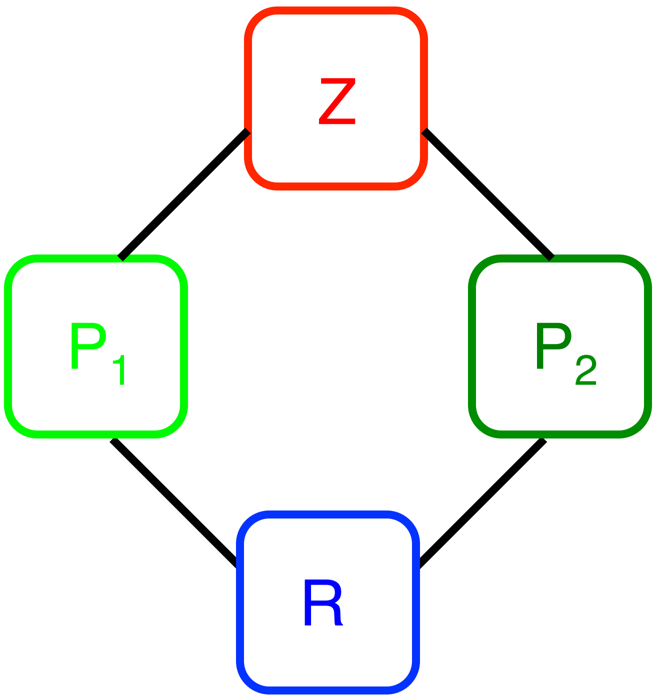
Competition–predator resistance trade-off

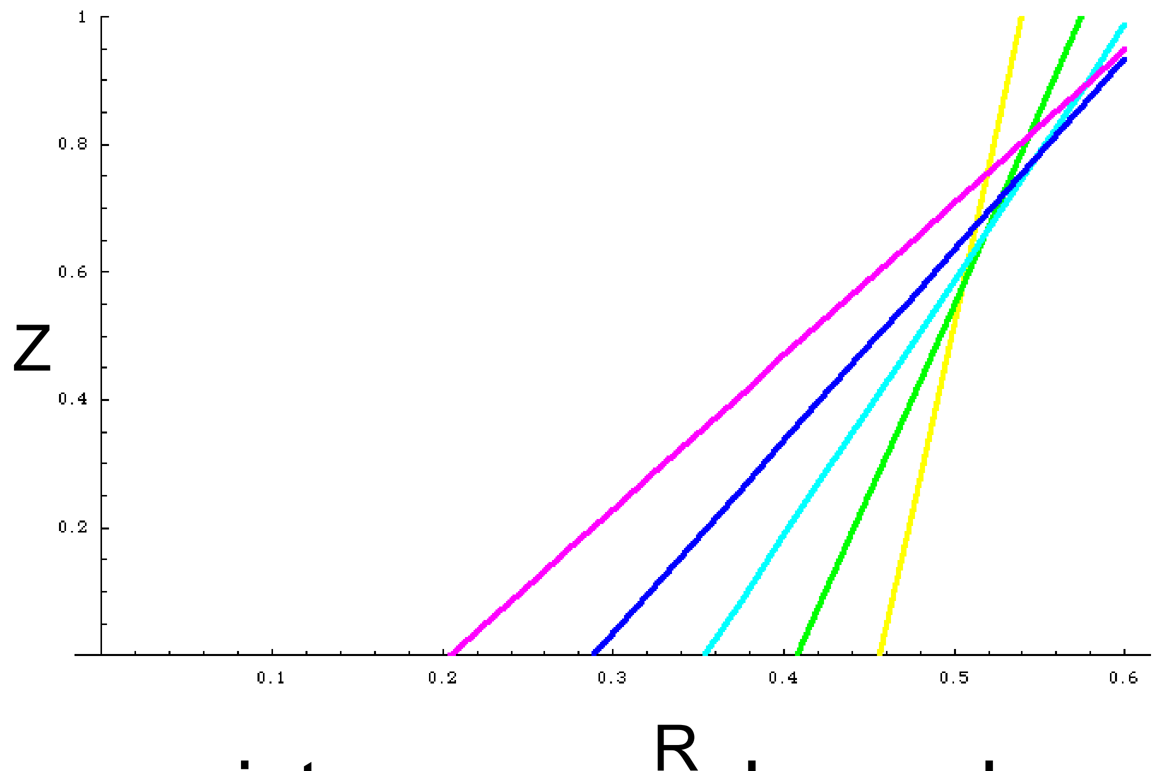




(after Leibold 1996)

Competition–predator resistance trade-off

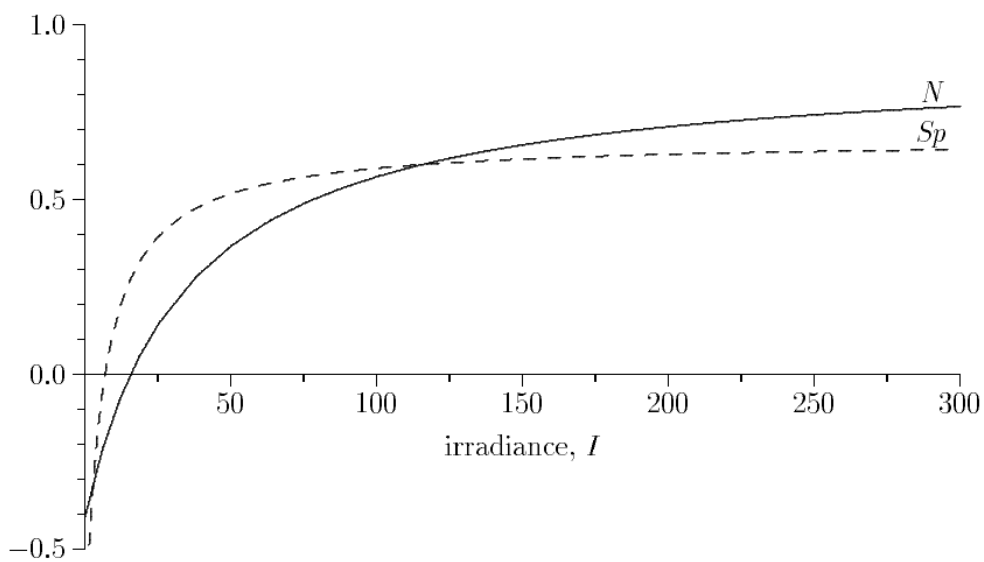


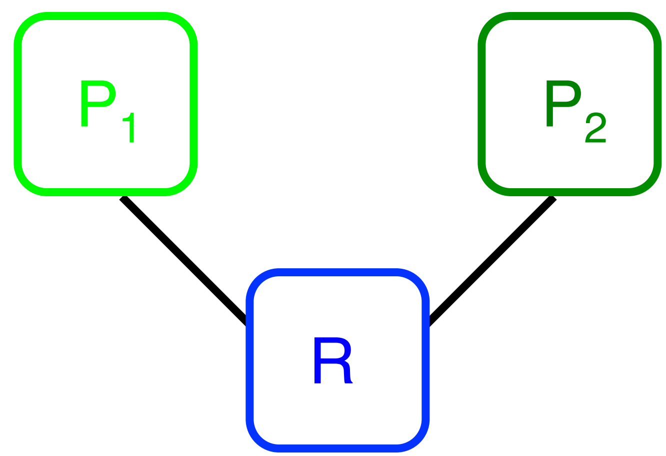


⇒ Evolutionary coexistence may depend on trade-off <u>shape</u>

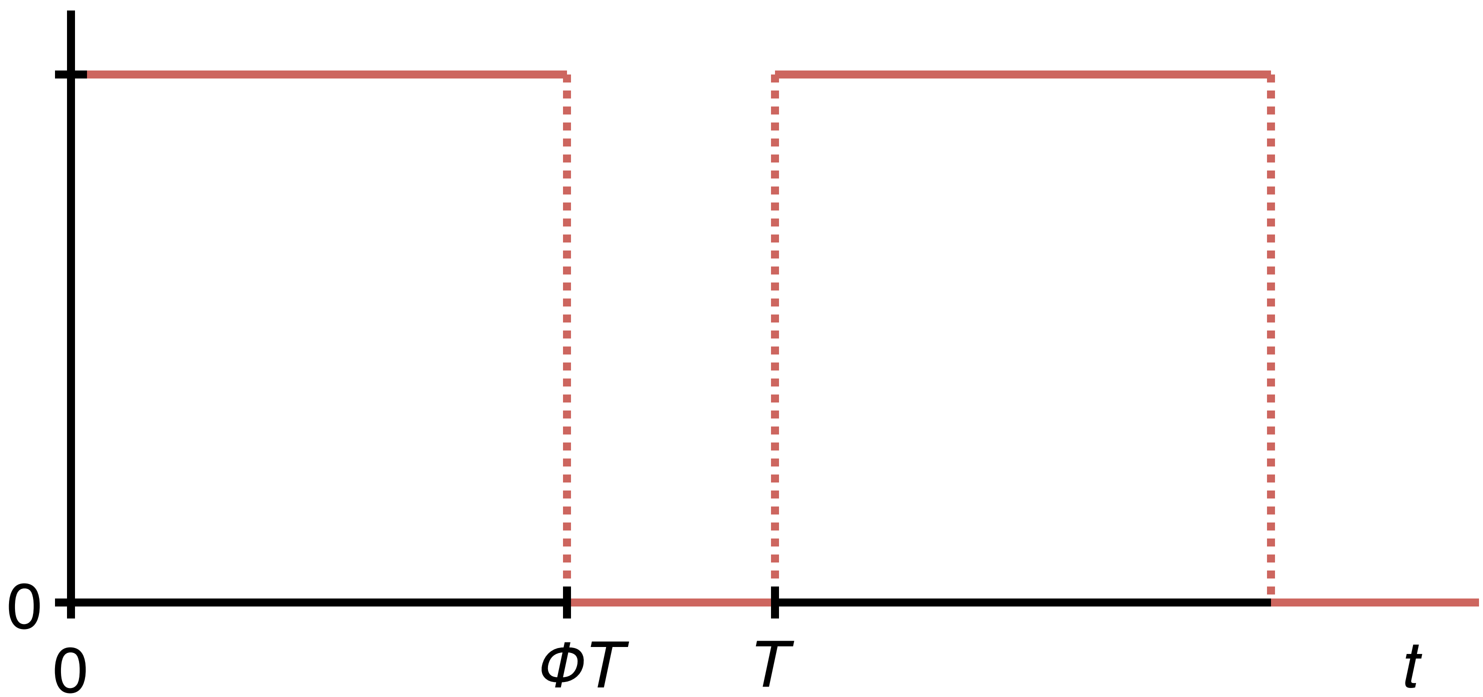
Growth rate–competition trade-off

- At equilibrium, only one species survives
- Trade-off: growth rate vs. equilibrium competitive ability



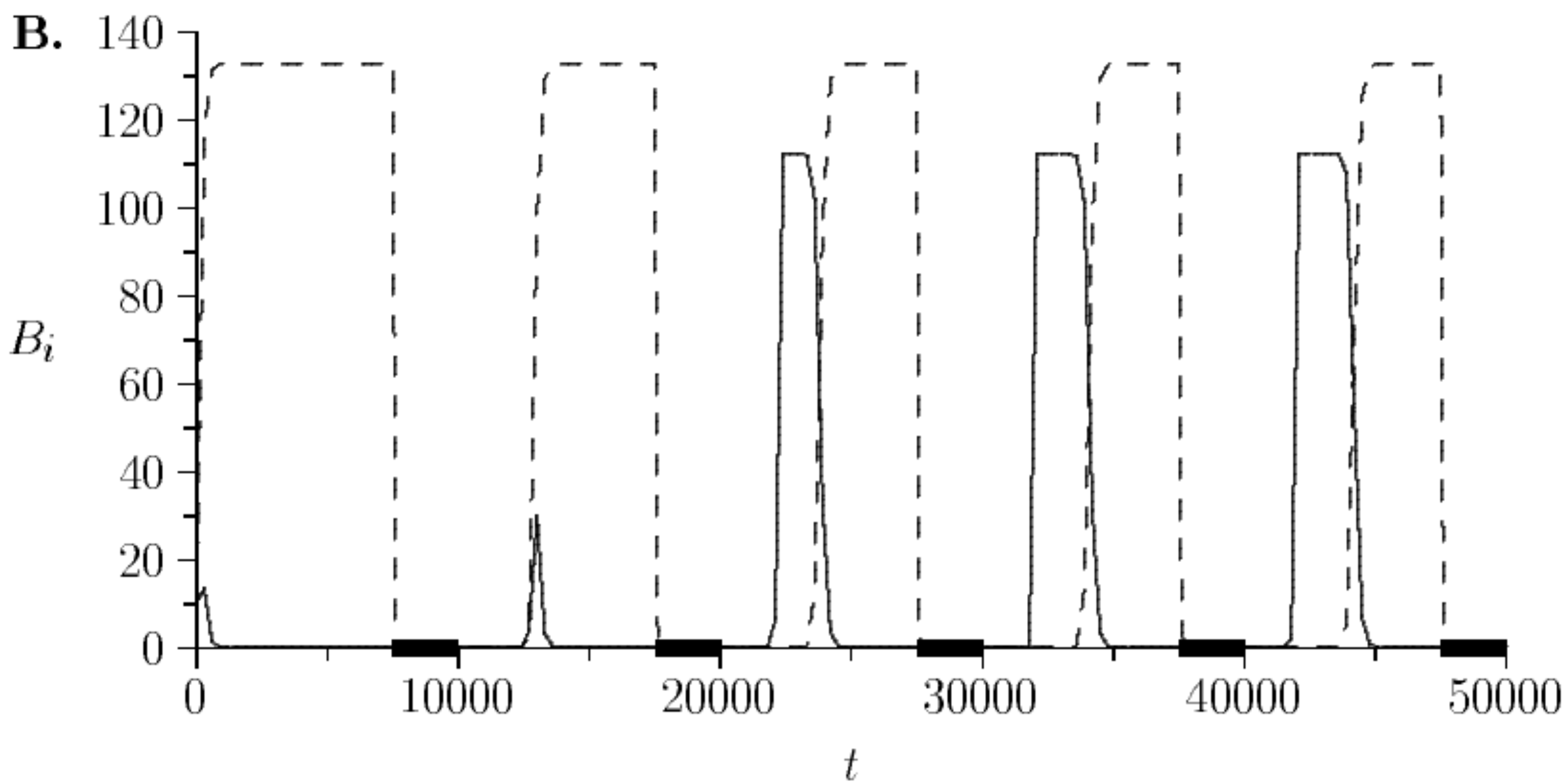


Seasonal Forcing



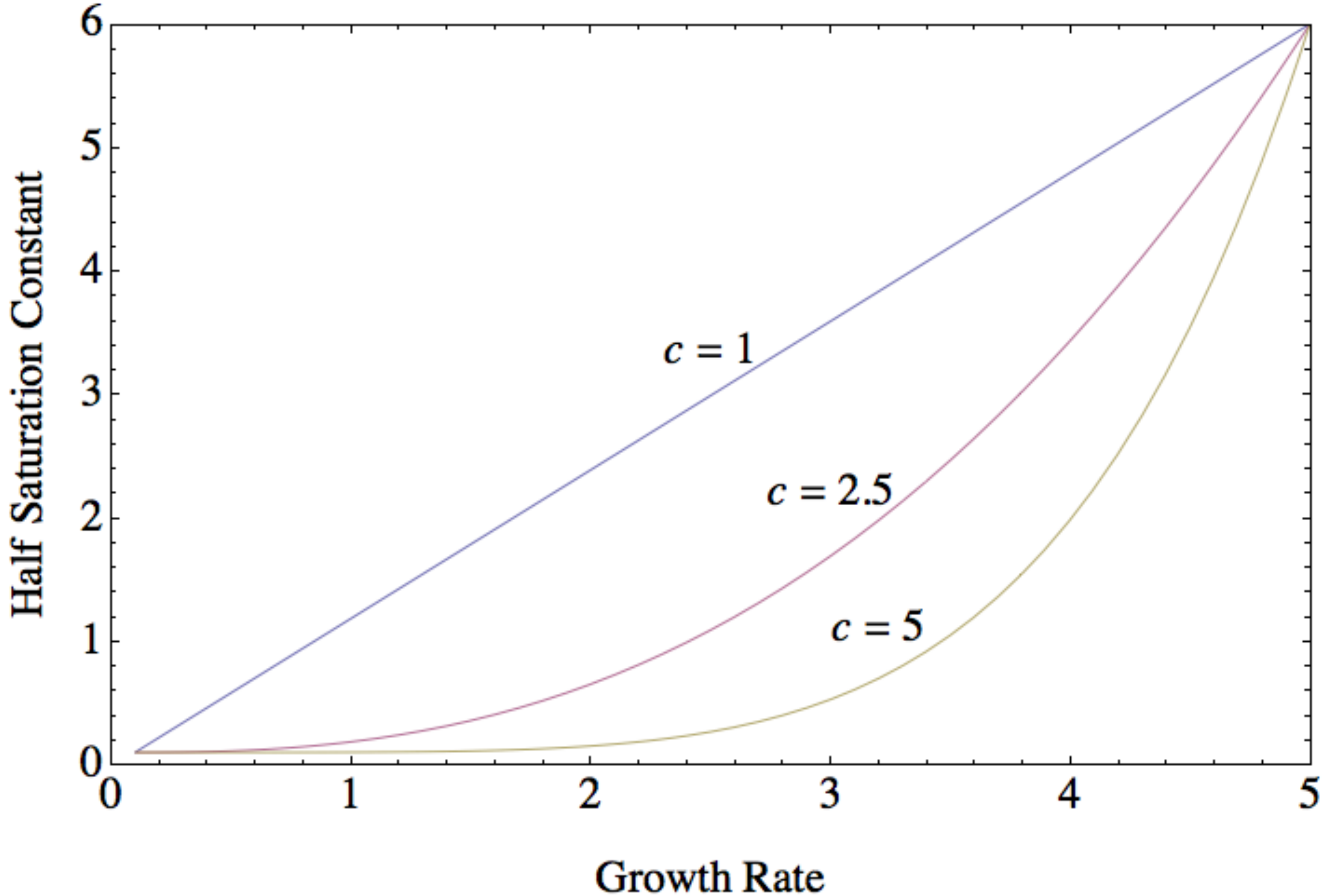
T – period
Φ – growing proportion

Growth rate–competition trade-off



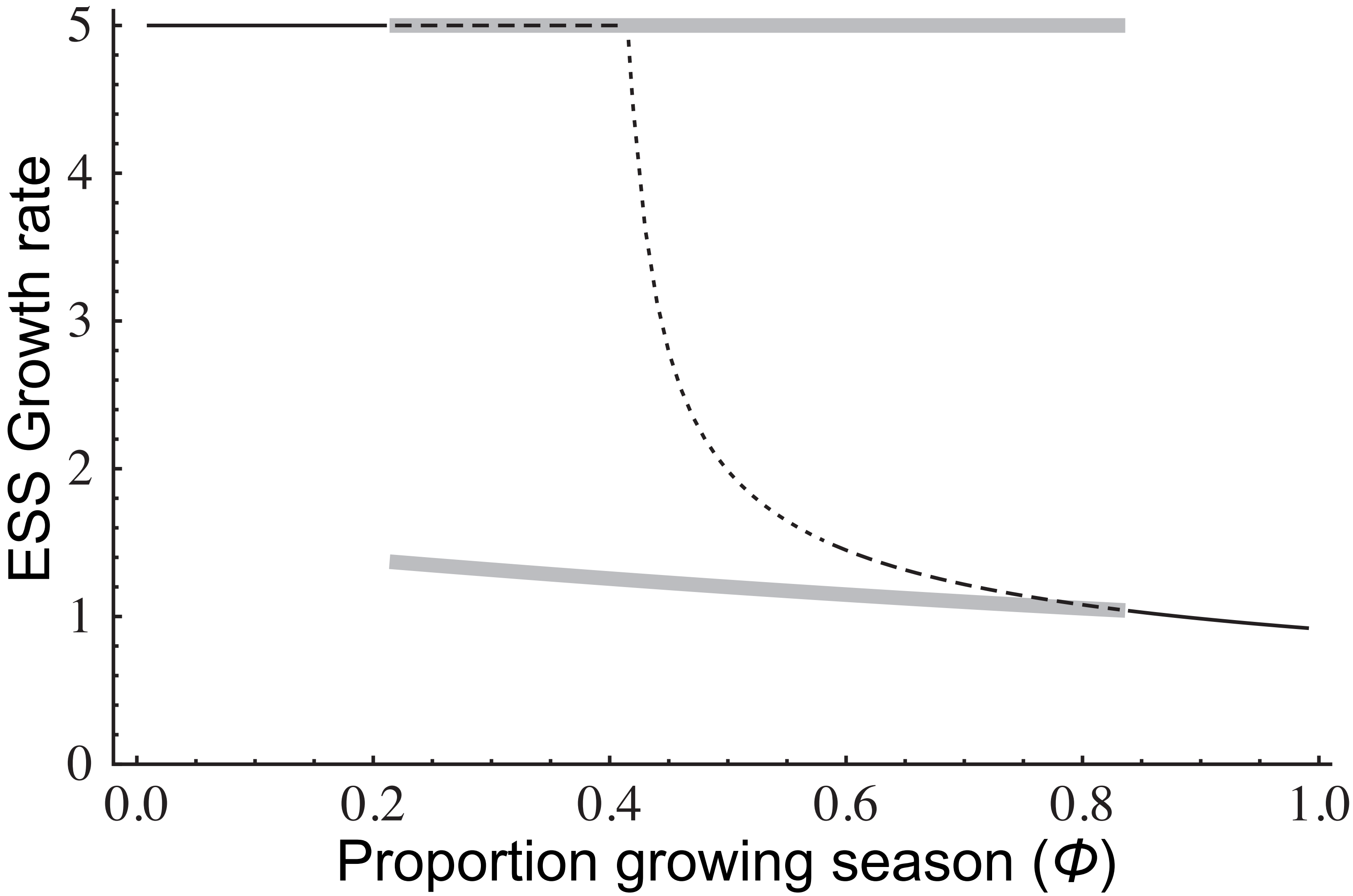
(Litchman & Klausmeier 2001 *Am Nat*)

Growth rate–competition trade-off



(Kremer & Klausmeier *in press* J Theor Bio)

Growth rate–competition trade-off



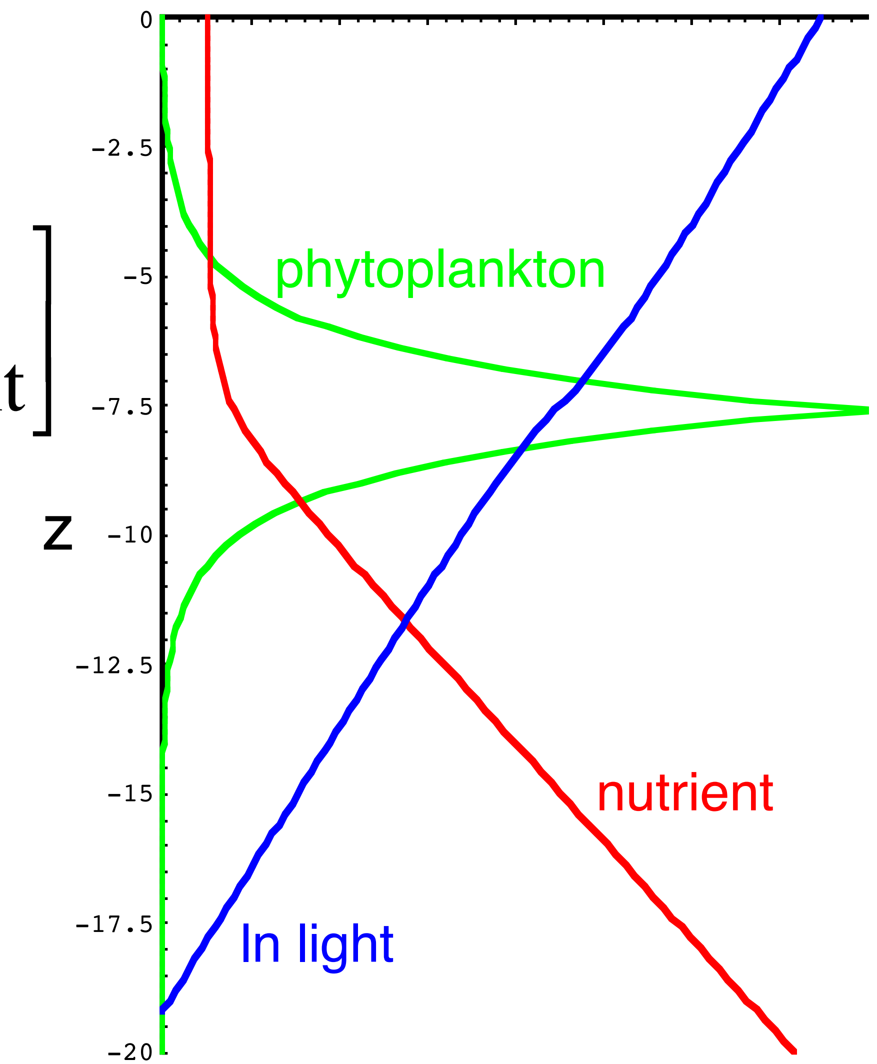
(Kremer & Klausmeier *in press* J Theor Bio)

Mechanism 4) Light–nutrient trade-off in poorly-mixed water column

$$\frac{\partial n}{\partial t} = gn + D\frac{\partial^2 n}{\partial z^2}$$

$$= \left[\text{growth-loss}\right] + \left[\begin{matrix}\text{passive} \\ \text{movement}\end{matrix}\right]$$

$$g = \min\left(f_R\left(R\right), f_I\left(I\right)\right) - m$$

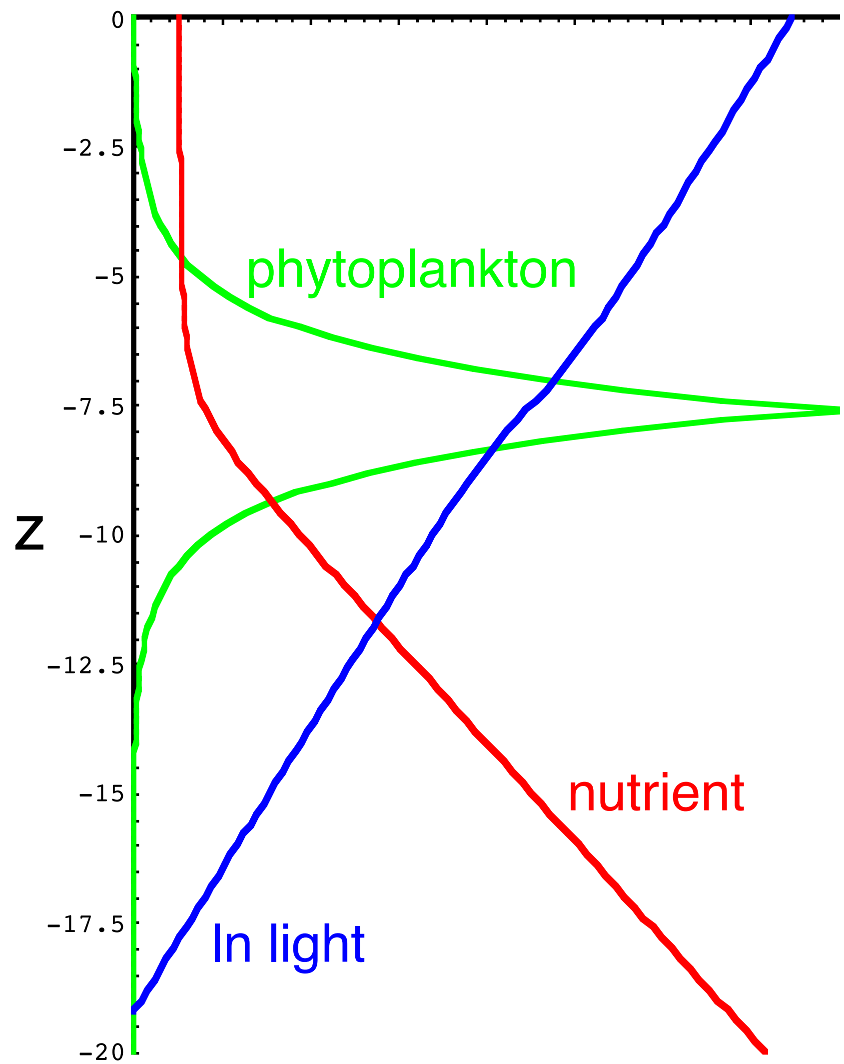


Fitness in a Spatially Variable Environment

$$\frac{1}{n}\frac{\partial n}{\partial t} = g(x) + D\frac{\partial^2}{\partial z^2}$$

$$\lambda(x) = \text{dominant eigenvalue}$$

$$\text{of } \frac{1}{n}\frac{\partial n}{\partial t}$$



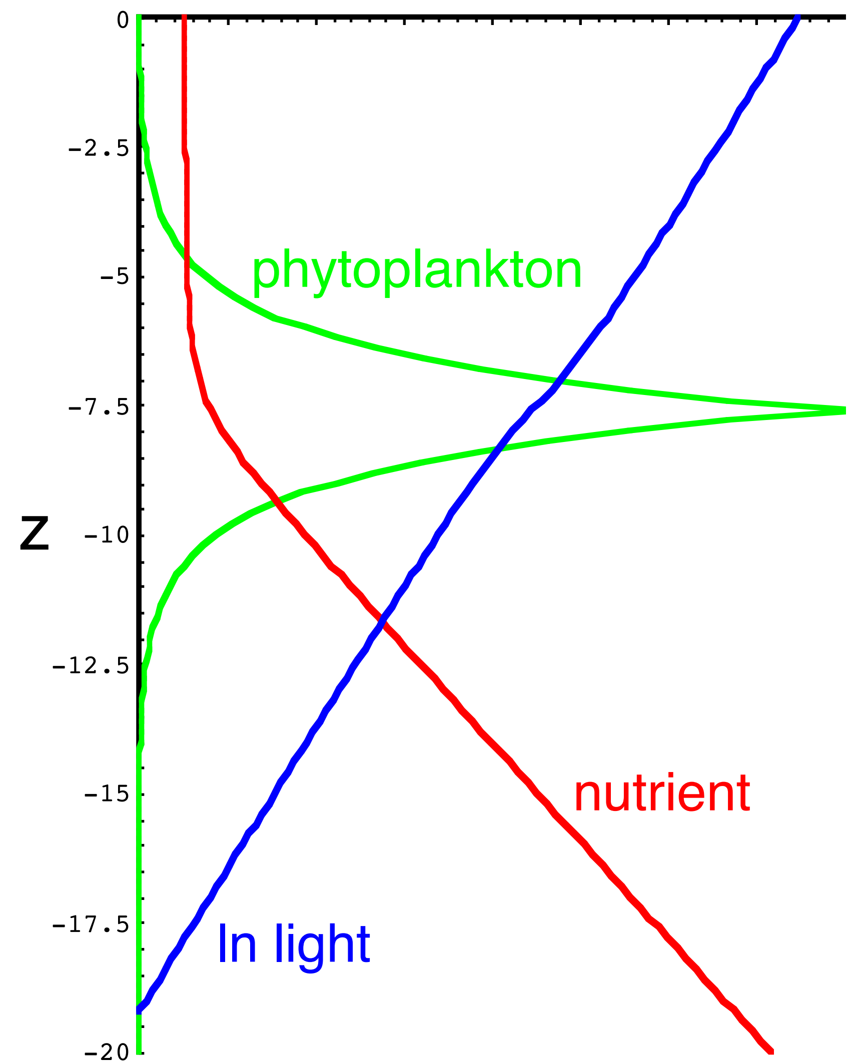
Fitness in a Spatially Variable Environment

$$\frac{1}{n}\frac{\partial n}{\partial t} = g(x) + D\frac{\partial^2}{\partial z^2}$$

$$\lambda(x) = \text{dominant eigenvalue}$$

$$\text{of } \frac{1}{n}\frac{\partial n}{\partial t}$$

$$\frac{d\lambda}{dx} = 0 \Rightarrow \text{singular strategy}$$



Fitness in a Spatially Variable Environment

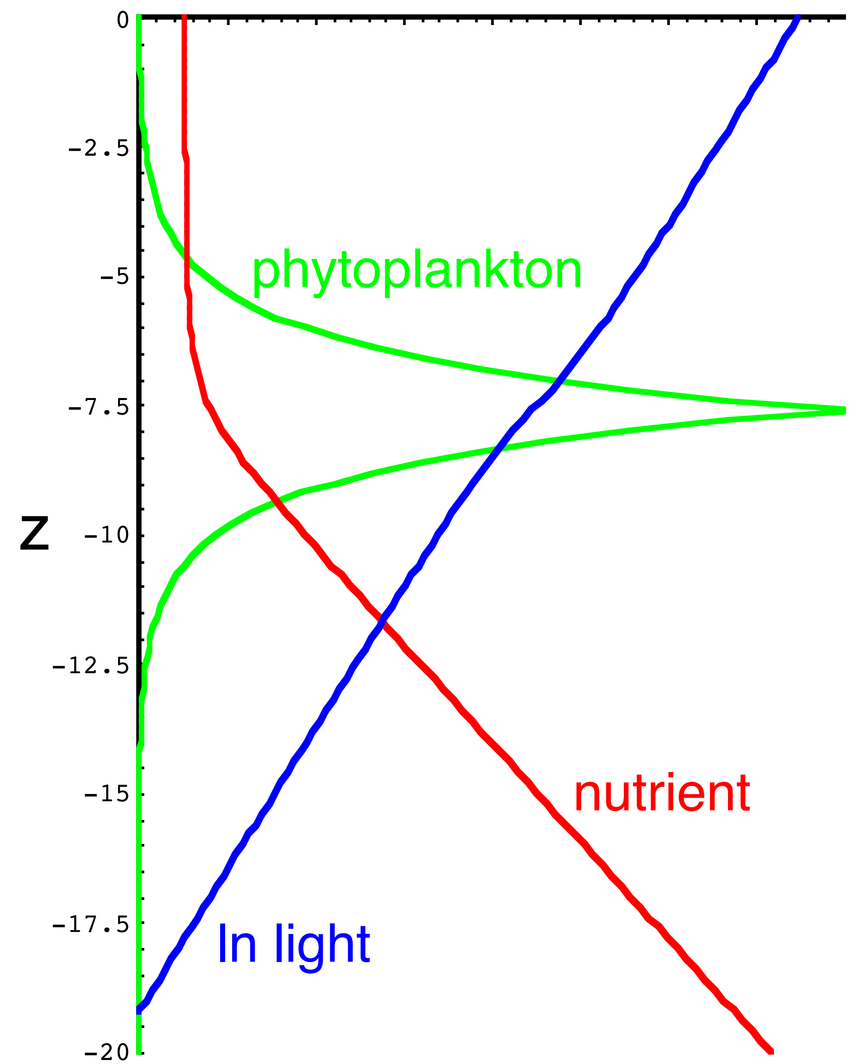
$$\frac{1}{n}\frac{\partial n}{\partial t} = g(x) + D\frac{\partial^2}{\partial z^2}$$

$$\lambda(x) = \text{dominant eigenvalue}$$

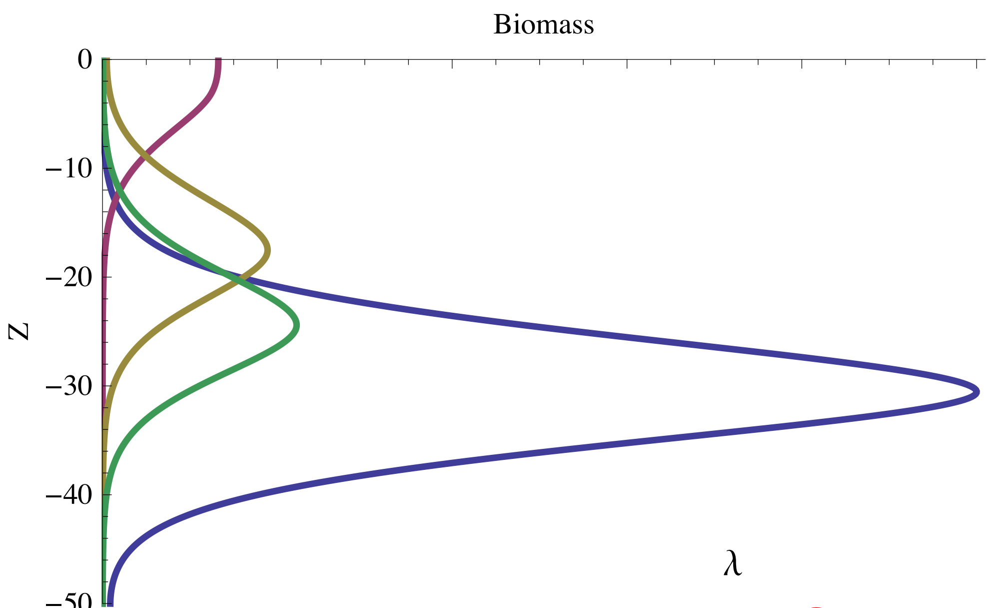
$$\text{of } \frac{1}{n}\frac{\partial n}{\partial t}$$

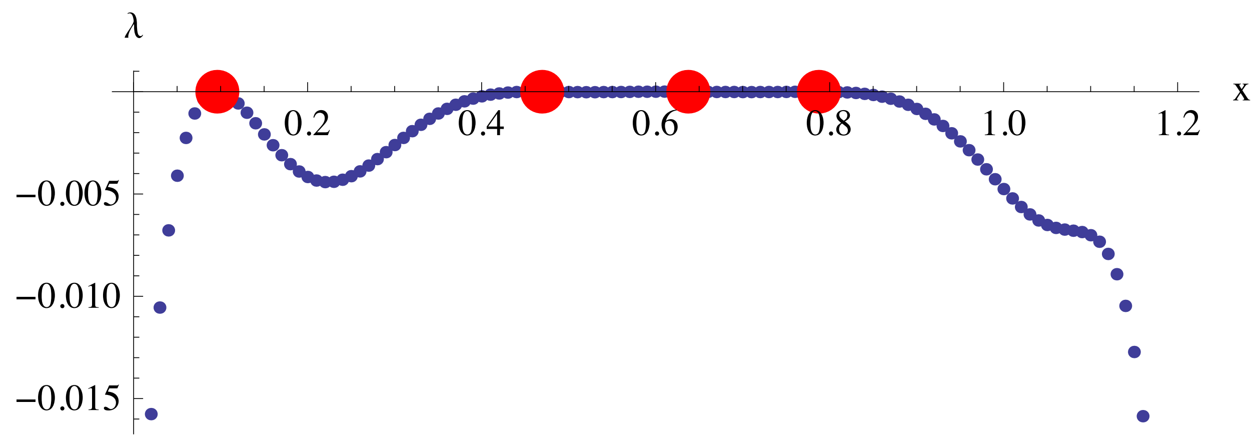
$$\frac{d\lambda}{dx} = 0 \Rightarrow \text{singular strategy}$$

$$\frac{d\lambda}{dx} = \frac{\int \frac{\partial g}{\partial x} n^2}{\int n^2}$$

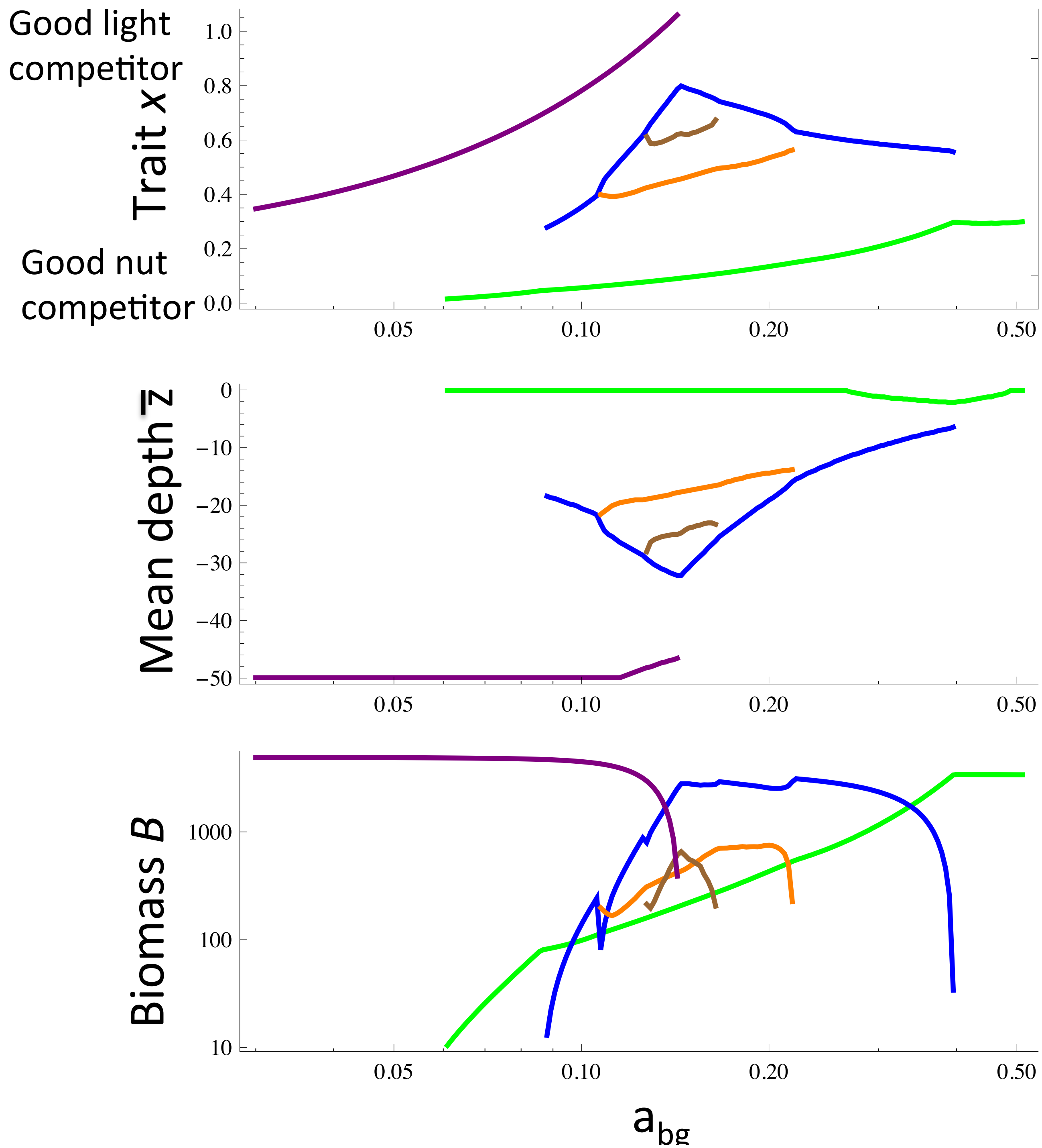


ESS

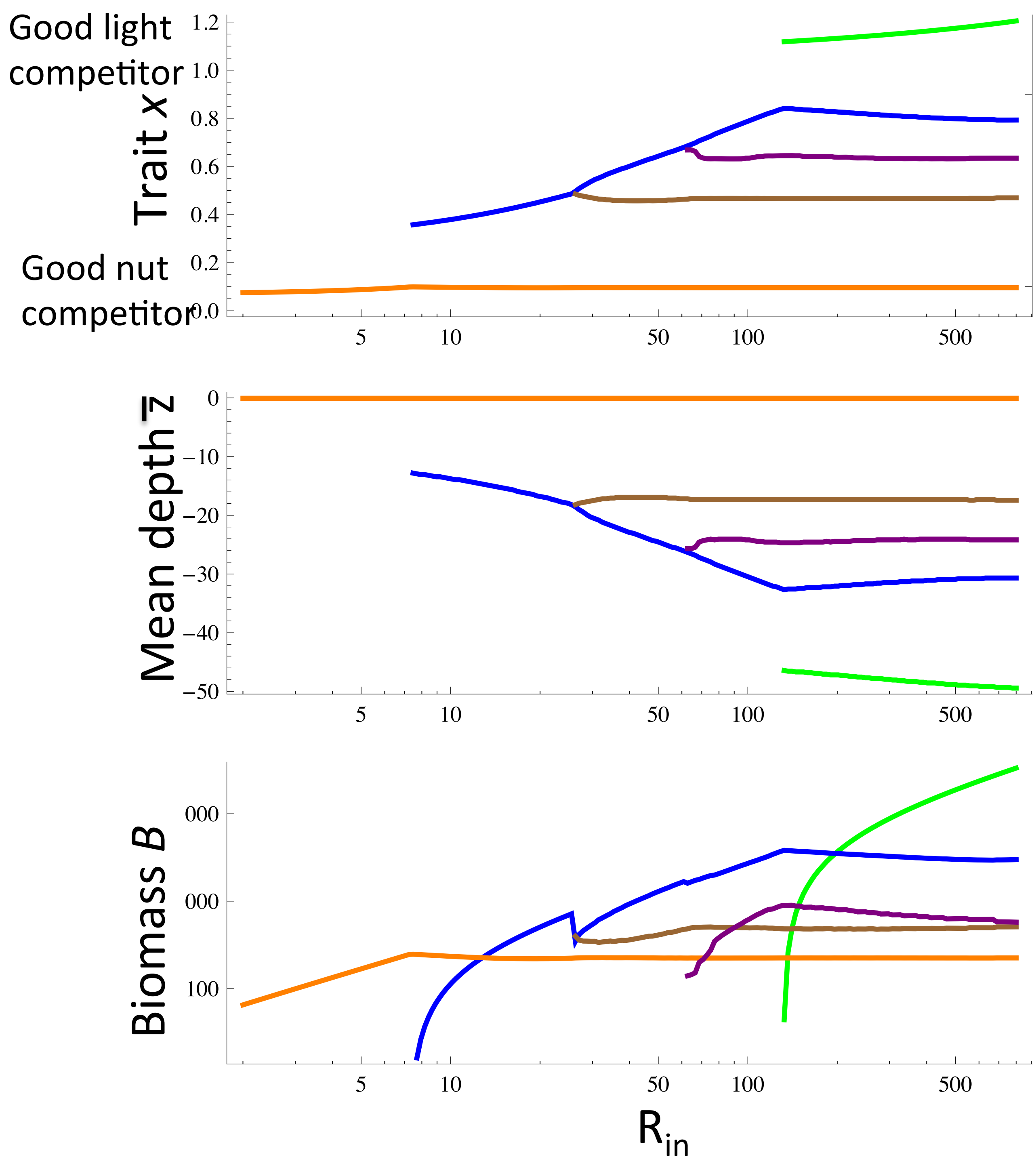




Light attenuation



Nutrient supply



Interplay between evolution and species sorting

$$g_i = \frac{1}{N_i}\frac{dN_i}{dt}$$

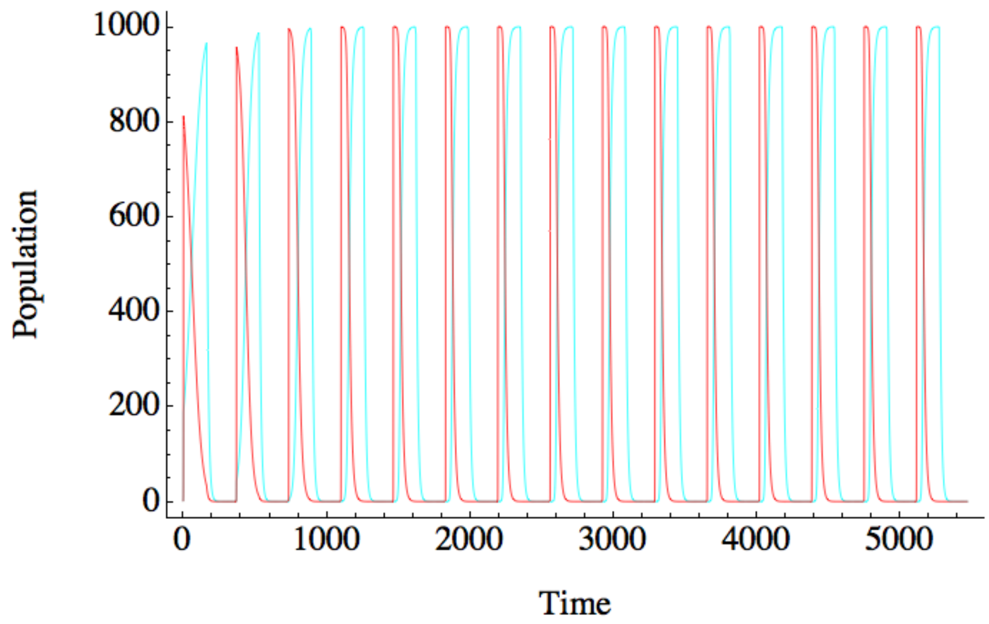
Per capita growth rate, or fitness

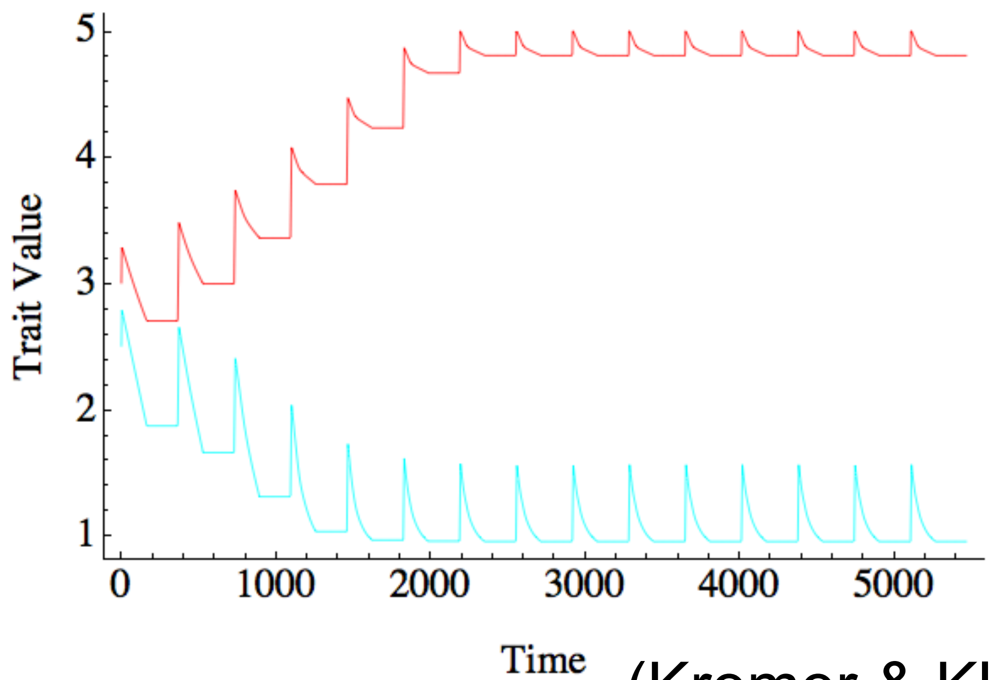
$$\frac{d\mu_i}{dt} = \sigma \cdot \frac{dg_i}{d\mu_i}$$

Change in trait value

Where σ is the "evolution rate"

(Kremer & Klausmeier *in press* J Theor Bio)

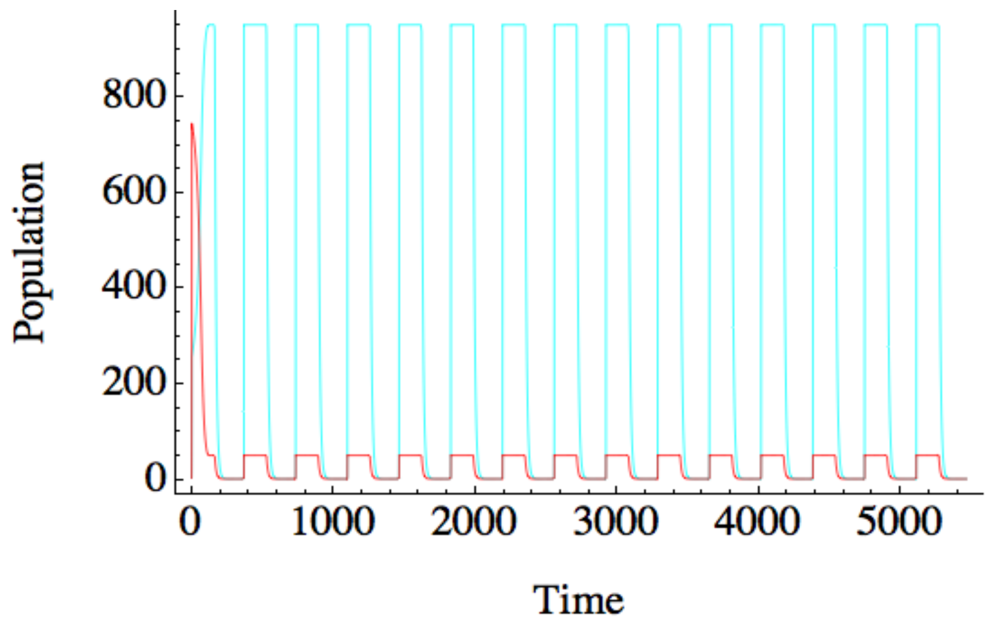


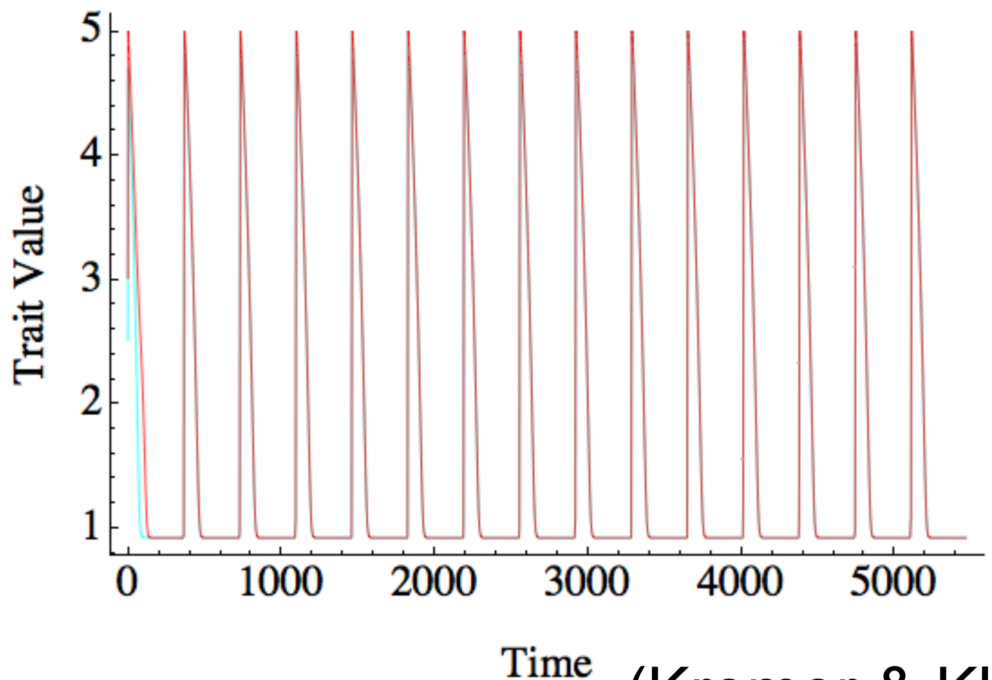


Time Series Examples: Branching Point

Evolution rate small (0.1)

(Kremer & Klausmeier *in press* J Theor Bio)



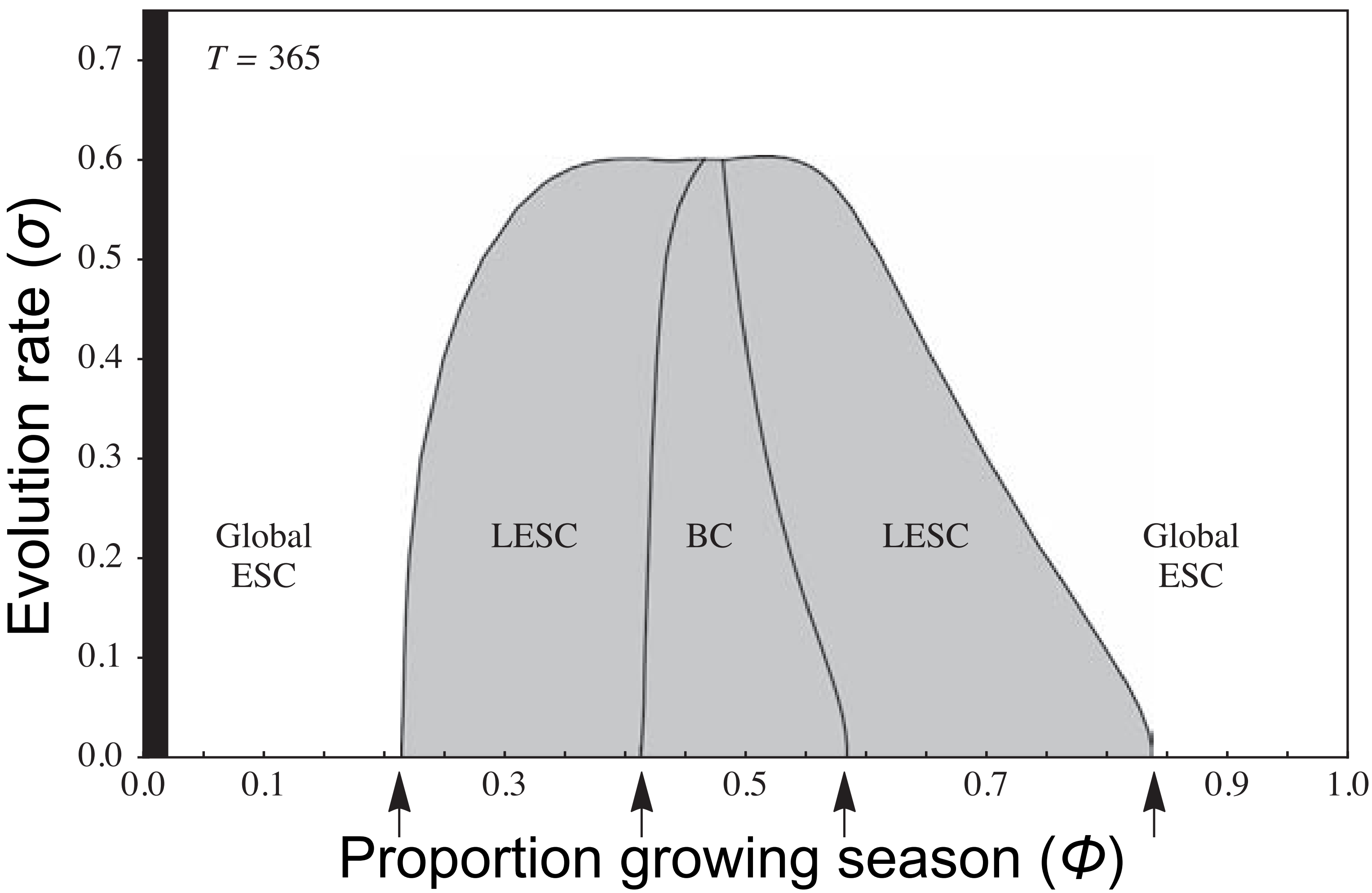


Time Series Examples: Single Species ESS

Evolution rate large (1.0)

(Kremer & Klausmeier *in press* J Theor Bio)

Increased evolution rate prevents species coexistence



(Kremer & Klausmeier *in press* J Theor Bio)

Evolutionary ecology in space

$$\frac{\partial N_i}{\partial t} = g_i N_i + \frac{1}{2} V_i \frac{\partial^2 g_i}{\partial z^2}\Big|_{z=\bar{z}_i} N_i + D \frac{\partial^2 N_i}{\partial x^2}$$

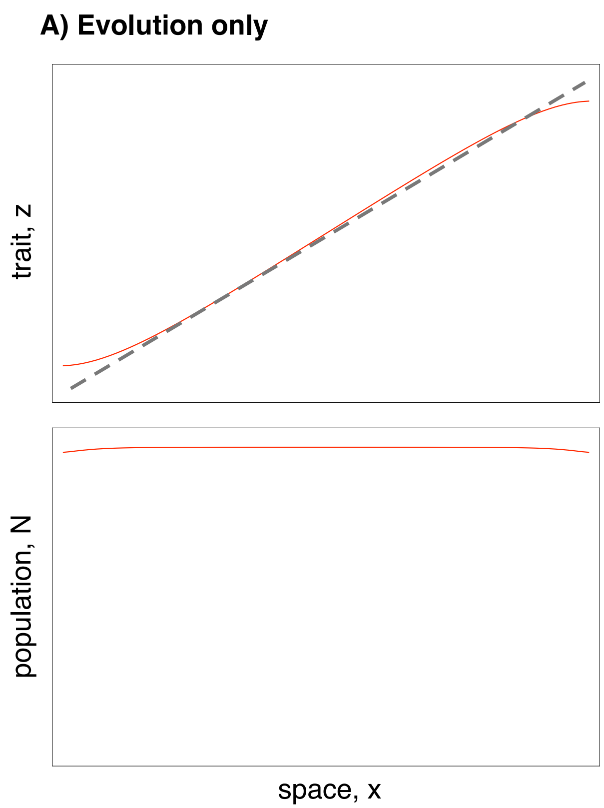
$$= \begin{bmatrix}\text{population} \\ \text{dynamics}\end{bmatrix} + \begin{bmatrix}\text{genetic} \\ \text{load}\end{bmatrix} + [\text{dispersal}]$$

$$\frac{\partial \bar{z}_i}{\partial t} = V_i \frac{\partial g_i}{\partial z}\Big|_{z=\bar{z}_i} + D \left(\frac{\partial^2 \bar{z}_i}{\partial x^2} + 2 \frac{\partial \log N_i}{\partial x} \frac{\partial \bar{z}_i}{\partial x} \right)$$

$$= \begin{bmatrix}\text{directional} \\ \text{selection}\end{bmatrix} + \begin{bmatrix}\text{gene} \\ \text{flow}\end{bmatrix}$$

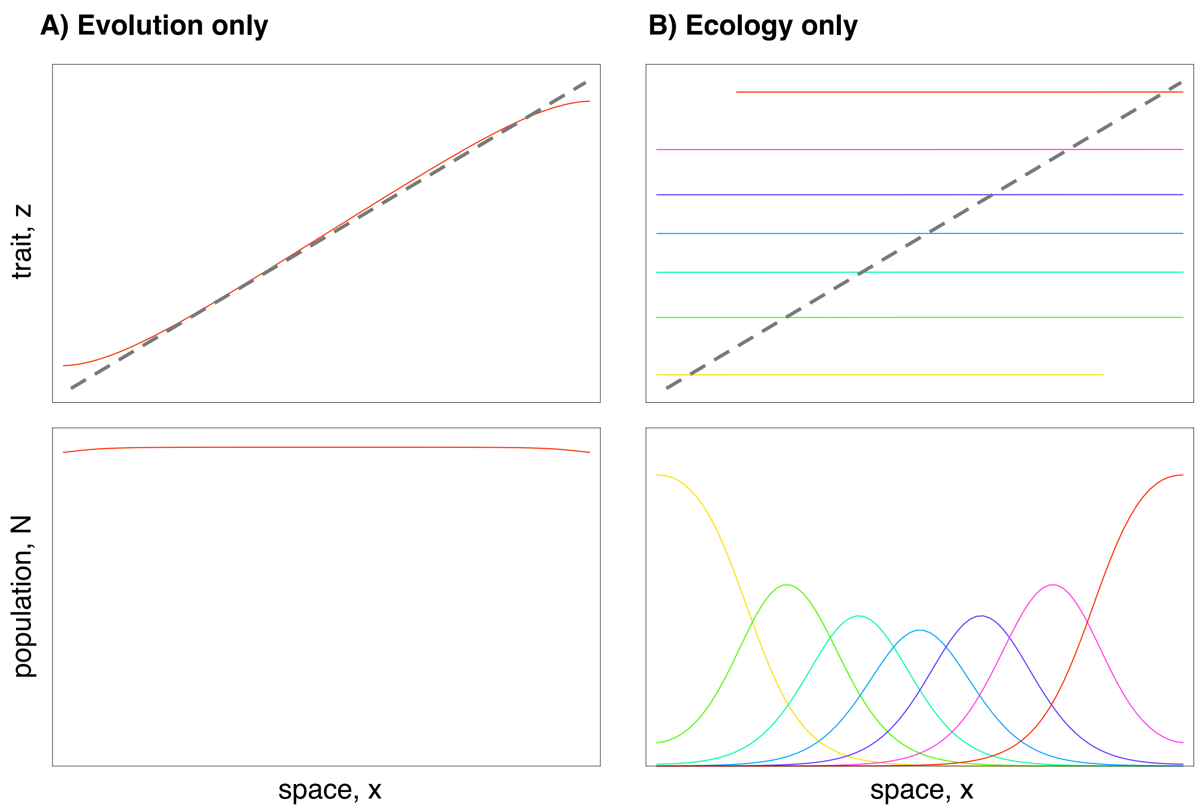
(Case and Taper 2000)

Evolutionary ecology in space



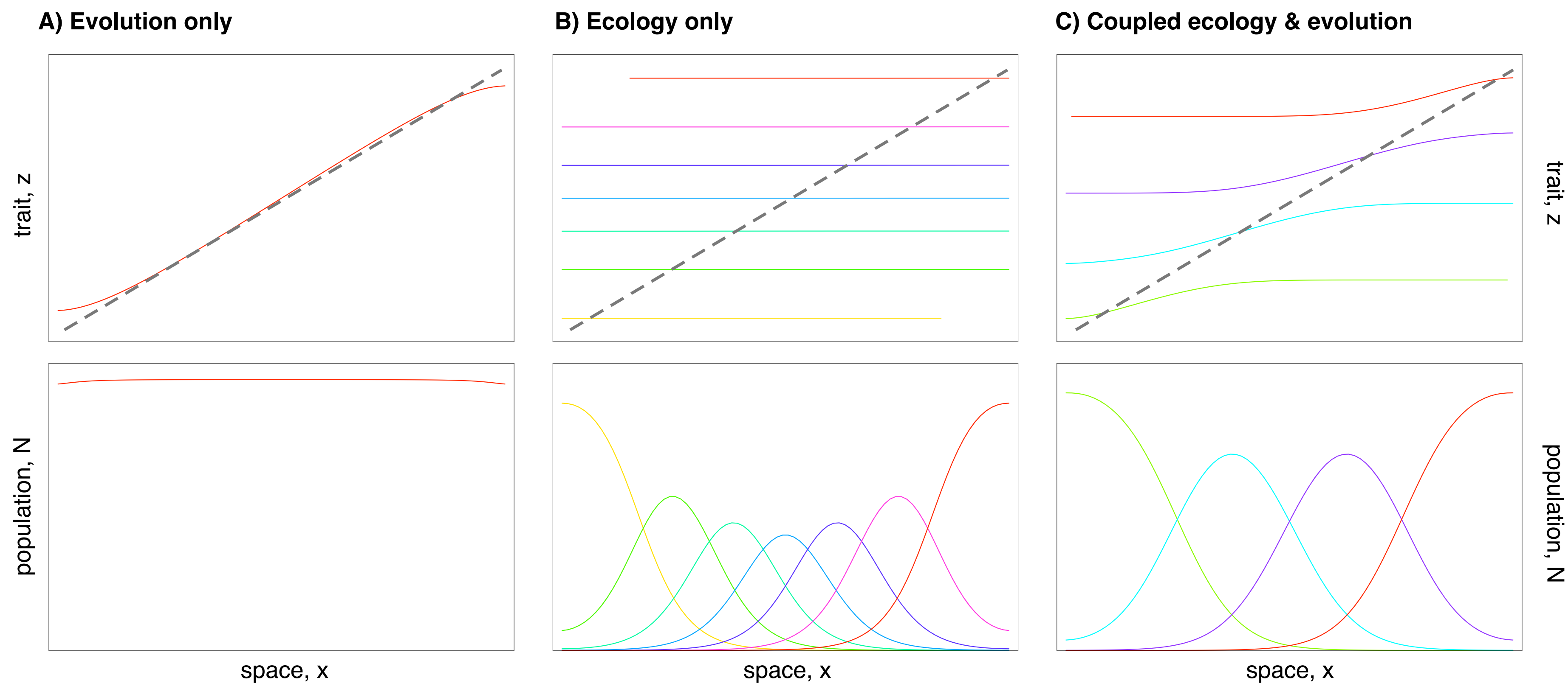
(Norberg, Klausmeier, Urban, Vellend unpublished)

Evolutionary ecology in space



(Norberg, Klausmeier, Urban, Vellend unpublished)

Evolutionary ecology in space

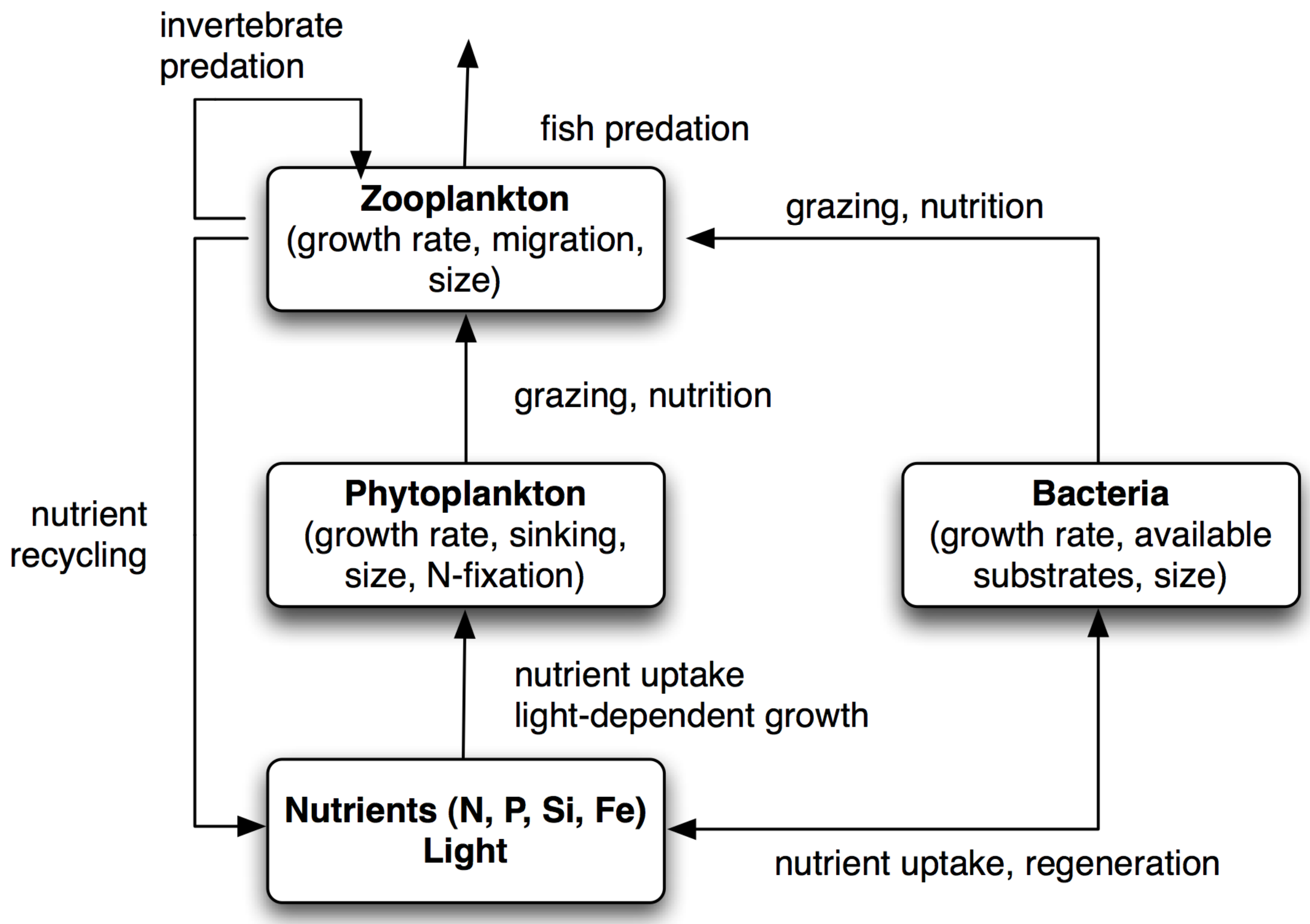


(Norberg, Klausmeier, Urban, Vellend unpublished)

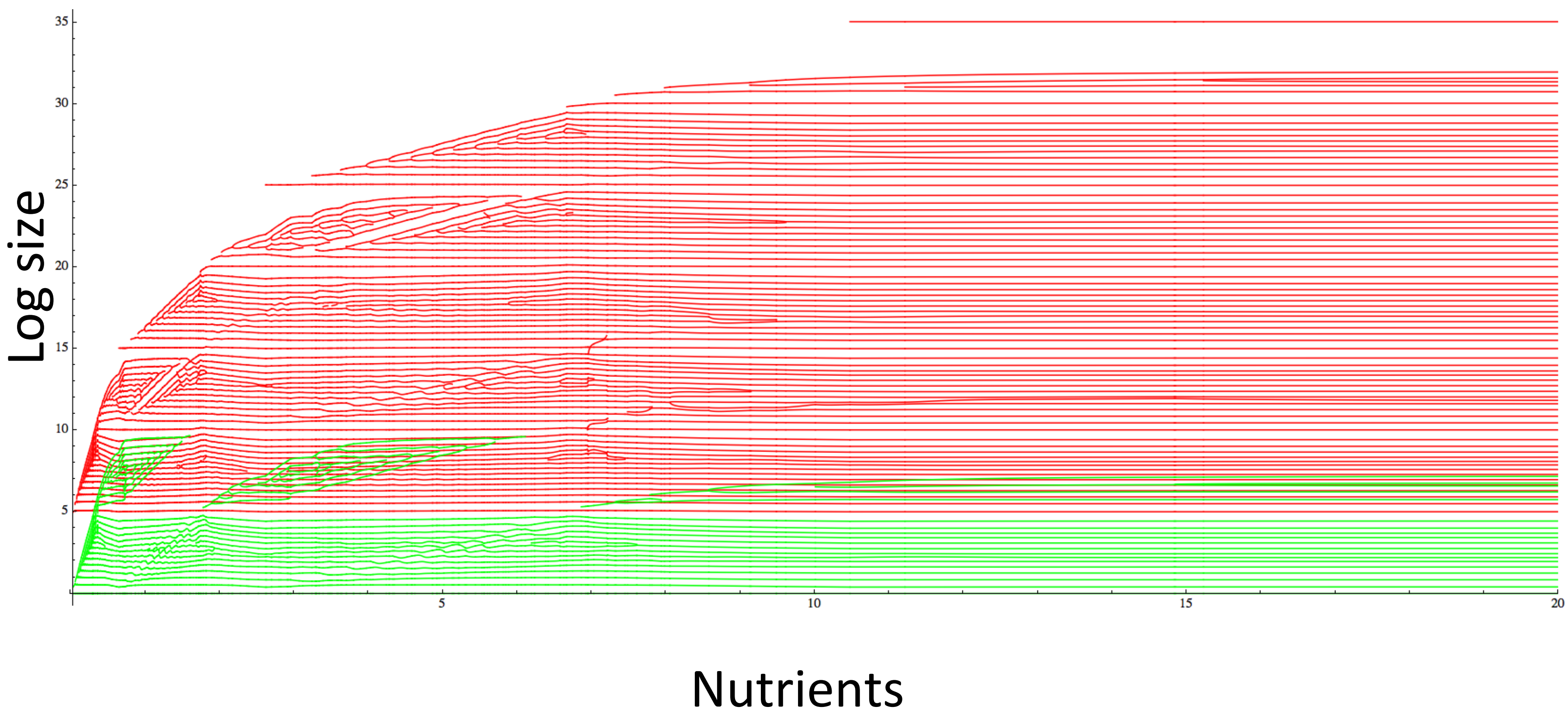
Scaling Up to Complex Communities

1. Food webs
2. Species abundance distributions

Traits in a Food Web Perspective



Traits in a Food Web Perspective



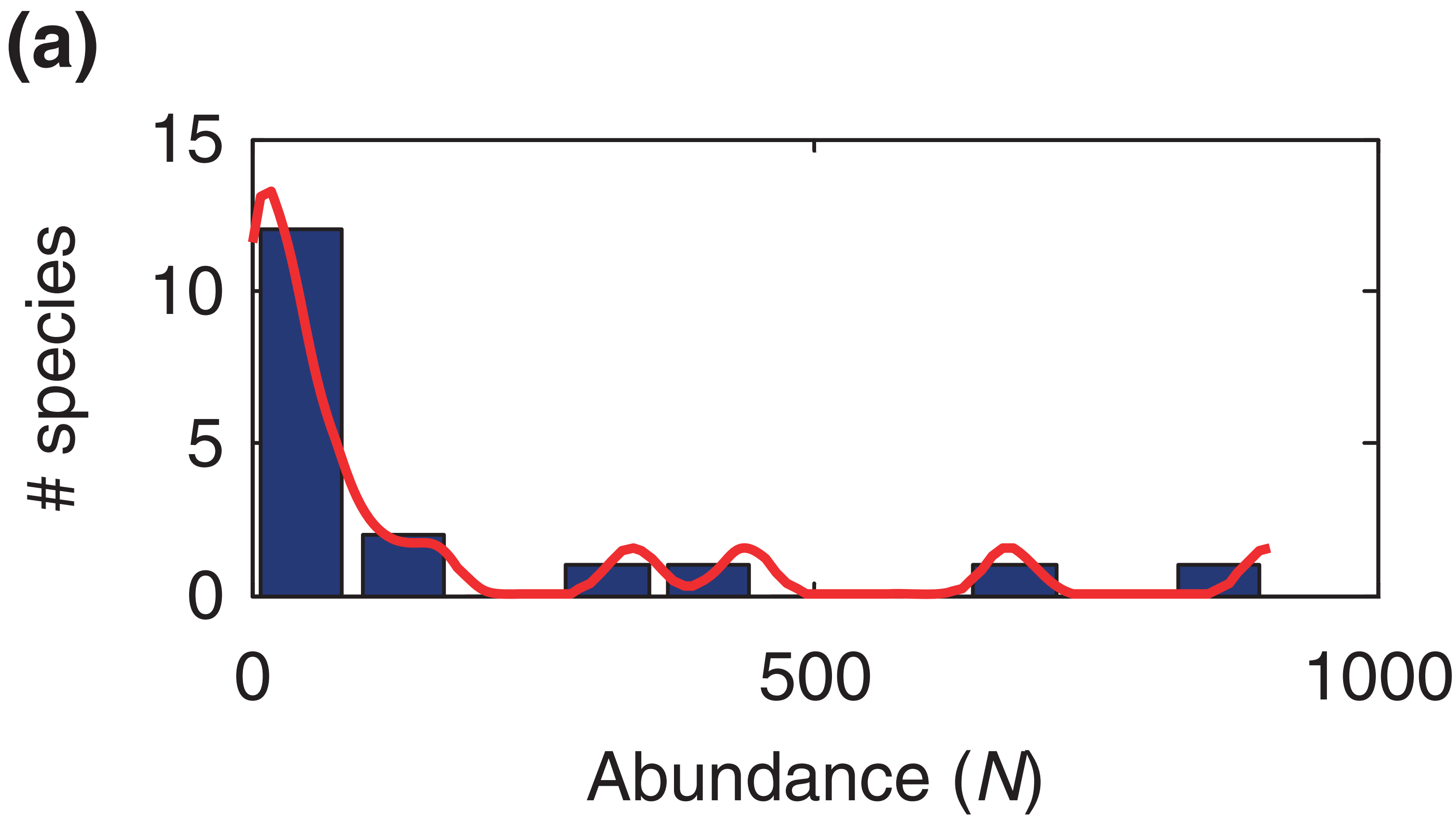
(With Helene Weigang & Ken Andersen)

Species Abundance Distributions (SADs)

- "Vector of the abundances of all species present in a community" (unlabeled)
- Intermediate-complexity description of diversity

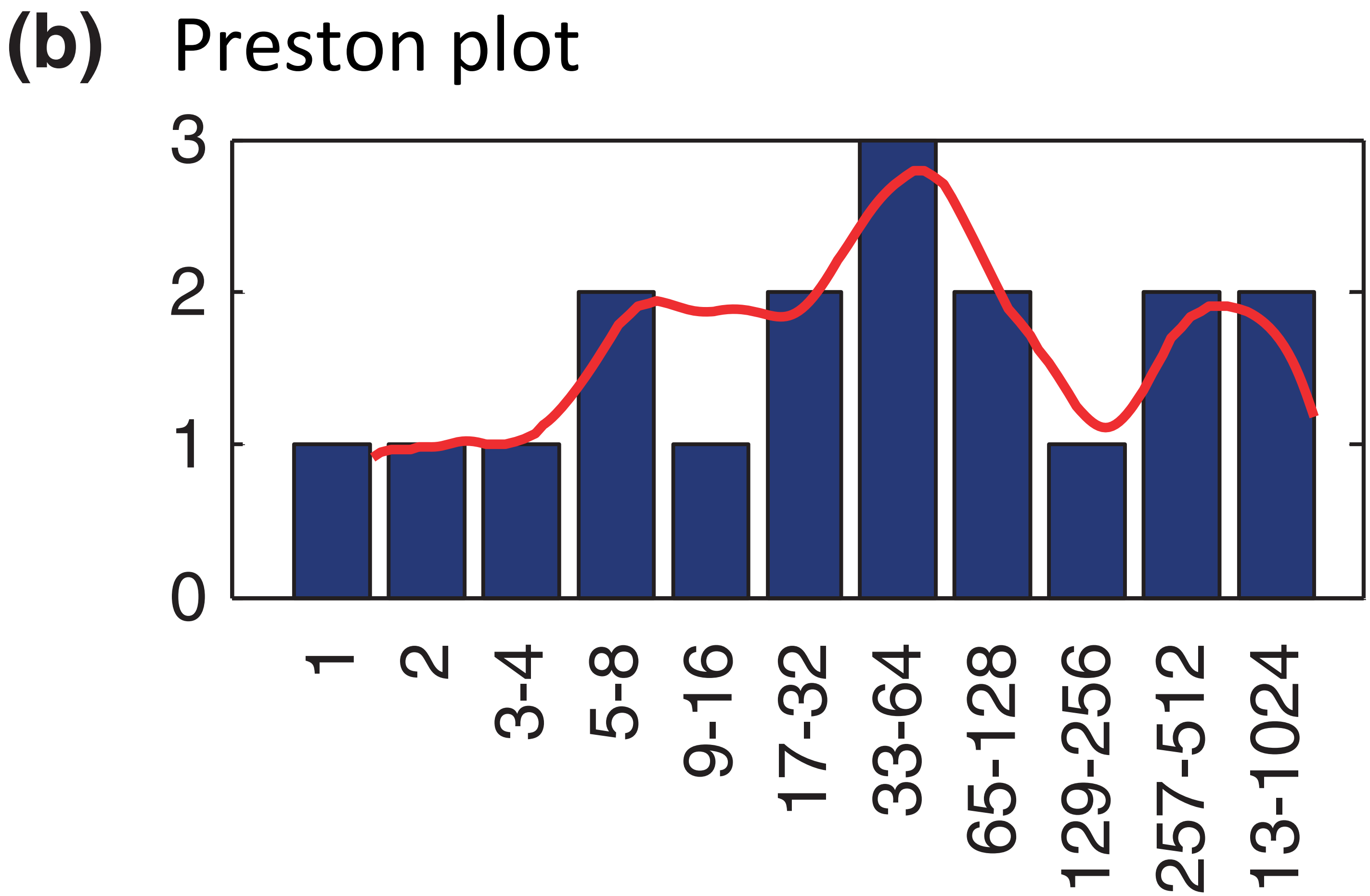
(McGill et al. 2007 *Eco Let*)

Three Ways to Look at SADs



(McGill et al. 2007 *Eco Let*)

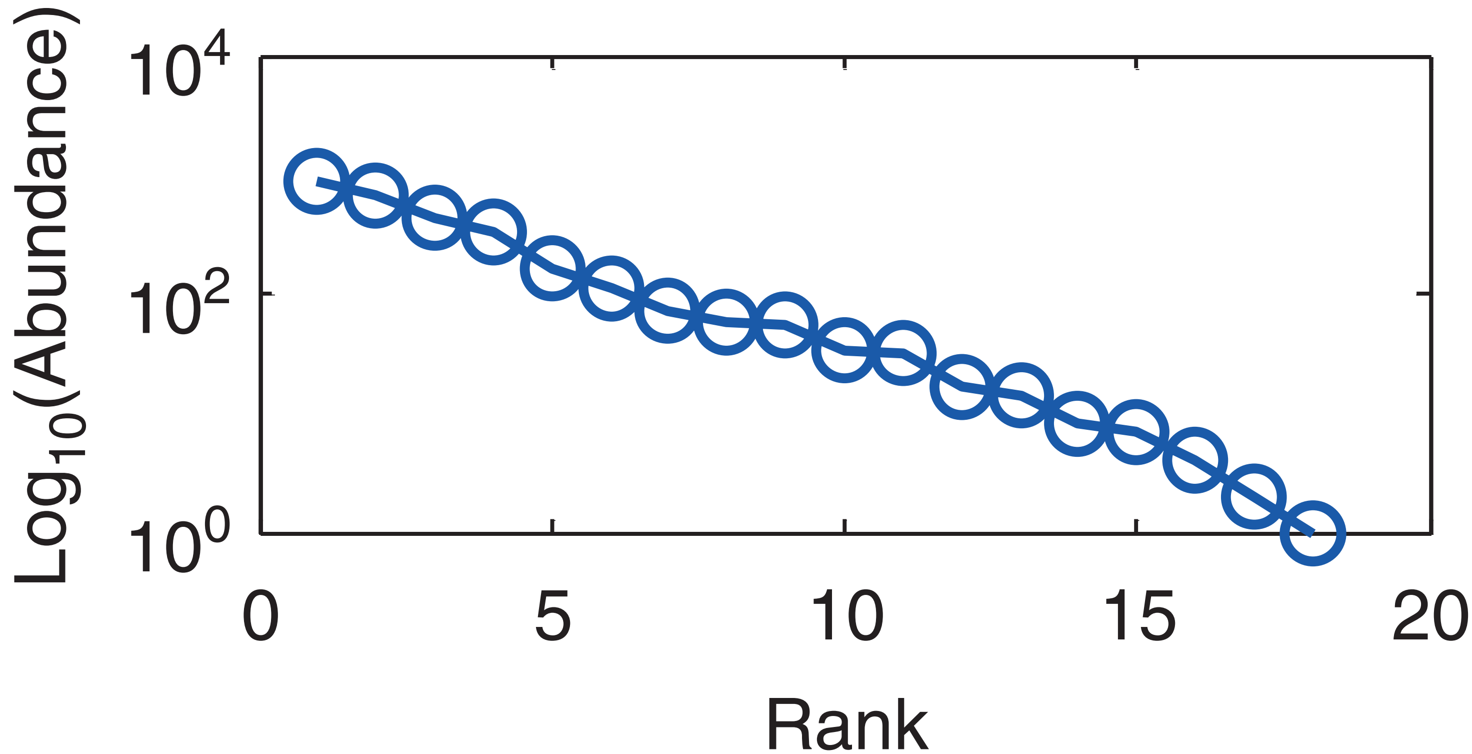
Three Ways to Look at SADs



(McGill et al. 2007 *Eco Let*)

Three Ways to Look at SADs

(c) Whittaker plot or rank-abundance curve



(McGill et al. 2007 *Eco Let*)

Table 2 Dozens of theories attempting to explain (and in most cases provide a mechanism to) the hollow curve SAD exist. This table briefly summarizes them and organizes them into related families. For a similar analysis performed a few years earlier see Marquet *et al.* (2003)

Family	SAD	Comments
Purely statistical	1. Logseries	Fisher *et al.* (1943) used a gamma distribution to describe the underlying 'true' abundance for purely empirical reasons, and then using the gamma random variable as the parameter of a Poisson distribution to describe the discrete samples that occur in finite real world samples gives a negative binomial distribution (which he then truncates the 0-abundance category and takes a limit). Boswell & Patil (1971) later showed that many other arguments can also produce the logseries.
	2. Negative binomial	Brian (1953) is one of the few people to use the seemingly obvious negative binomial (usually 0-truncated)
	3. Gamma	A variety of population dynamic models lead to a gamma distribution (Dennis & Patil 1984; Engen & Lande 1996a; Diserud & Engen 2000), which seems to fit some data well (Plotkin & Muller-Landau 2002)
	4. Gamma-binomial or Gambin	Compounding the gamma with a binomial sampling process (cf. the Poisson compounded with the gamma to produce the logseries) gives a one parameter distribution where the single parameter seems to be a good measure of the environmental complexity (Ugland *et al.* 2007)
Purely statistical (lognormal subfamily)	5. Lognormal I – Preston's discrete, binned approximation	A discretized version of the lognormal (Preston 1948; Hubbell 2001) is probably no longer justified given modern computing power
	6. Lognormal II – true continuos lognormal	The original lognormal (Galton 1879; McAlister 1879; Evans *et al.* 1993) which has received extensive application to ecology (Gray 1979; Dennis & Patil 1984, 1988; McGill 2003c)
	7. Lognormal III – left truncated (veiled) lognormal	As in number 6, but with left truncation (Cohen 1949) to match Preston's idea of unveiling. Has rarely been used in practice (and which in fact usually does not fit the data as well as the untruncated version McGill 2003a)
	8. Lognormal IV – Poisson lognormal	Mixes the lognormal with the Poisson (cf. the logseries which mixes the gamma and the Poisson; Bulmer 1974; Kempton & Taylor 1974). Requires an iterative likelihood method on a computer to fit which is often not available in standard statistical packages (Yin *et al.* 2005), and is sometimes confusingly called a truncated lognormal (Kempton & Taylor 1974; Connolly *et al.* 2005).
	9. Lognormal V – Delta lognormal	A mixture of the continuous lognormal and a Bernoulli variable to allow zeros to occur with a probability *P* (Dennis & Patil 1984, 1988)
Branching process	10. Generalized Yule	Yule (1924) applied what is now known as the Galton-Watson branching process to model the number of species within a genus (which has a distribution similar to individuals within species). Kendall (1948b) and Simon (1955) generalized this work and used it as a model of population dynamics and abundance. Chu & Adami (1999) analysed this again in an ecological context, and Nee (2003) showed that this distribution provides extremely good fits to SADs.
	11. Zipf-Mandelbrot	Using a different type of branching process known as a scaling (or fractal) tree, Mandelbrot (1965) generalized Zipf's (1949) Law in linguistics to produce the Zipf-Mandelbrot distribution. This has been applied to SADs by several authors (Frontier 1985; Wilson 1991; Frontier 1994, 1985; Wilson *et al.* 1996).
	12. Fractal branching model	Mouillot *et al.* (2000) introduce a fractal branching (tree-like) extension to the niche pre-emption model (#19)
Population dynamics	13. Lotka-Volterra	The generalized Lotka-Voltera models with random parameters can produce a hollow curve (Lewontin *et al.* 1978; Wilson *et al.* 2003).
	14. Hughes	A detailed single species population dynamic model with random parameters (Hughes 1986) can produce hollow curves

Table 2 (*continued*)

Family	SAD	Comments
	15. Stochastic single species	Population dynamic models with stochastic noise can produce hollow curve SADs (Tuljapurkar 1990; Engen & Lande 1996a; Diserud & Engen 2000; Engen *et al.* 2002). Most of these models produce either a lognormal or a gamma distribution under quite general conditions on the population dynamics (Dennis & Patil 1984, 1988)
	16. Logistic-J	Dewdney (2000) has developed a simulation of random encounters and random transfer of resources that produces what he calls the logistic-J SAD.
Population dynamics (Neutral model subfamily)	17. Neutral	The ability of neutral models (with populations performing a coupled version of a random walk or drift) to produce SADs has excited much attention (Chave 2004; Alonso *et al.* 2006; McGill *et al.* 2006b). Bell (2000, 2001, 2003) and Hubbell (1979, 2001) have pushed this idea extensively recently, but it was shown much earlier by Caswell (1976) and Watterson (Watterson 1974) that with or without zero-sum dynamics neutral drift produces realistic SADs (Etienne *et al.* 2007a).
	18. Coalescent neutral theory	A coalescent version of neutral theory (Etienne & Olff 2004b; Etienne 2005) has shown that neutral population dynamics have some similarities to the branching processes described above.
Niche partitioning	19. Geometric or niche preemption	Motomura (1932) used a model where each species takes a constant fraction of the remaining resources.
	20. Broken stick	MacArthur (1957, 1960) developed the opposite model where the niche space is broken up simultaneously and with random fractions and is known as the broken stick model. This model has the distinction of being one of the very few SAD models ever developed to have been strongly rejected by its inventor (MacArthur 1966; 'Let us hope these comments do not draw additional attention to what is now an obsolete approach to community ecology, which should be allowed to die a natural death.'). Cohen (1968) showed that the same math of the broken stick could be produced by an exactly opposite set of biological assumptions from those of MacArthur.
	21. Sugihara	Sugihara (1980) crossed Motomura's (1932) and MacArthur's (1957) models by breaking the stick randomly but in sequential fashion. Nee *et al.* (1991) showed this produced realistic left skew.
	22. Random fraction	Tokeshi (1993, 1996) has since developed a variety of niche apportionment models with various combinations of models 19–21.
	23. Spatial stick breaking	Marquet *et al.* (2003) explored the consequences of adding spatial structure to niche breakage models.
Spatial distribution of individuals	24. Continuum	Several authors (Gauch & Whittaker 1972; Hengeveld *et al.* 1979) showed that the roughly Gaussian bell-curved shape of abundance across a gradient or species range produces hollow curve SADs in local communities since at any one point most species are found in the tail of their bell-curve across species while a few species are found in the peak of their bell-curve (thereby flipping the emphasis from local interactions between species to regional spatial processes of individual species). McGill & Collins (2003) expanded this theory and provided empirical evidence that this mechanism is in fact explaining as much as 87% of the variation in local abundances.
	25. Fractal distribution	Harte *et al.* (1999) showed that starting only with an assumption that the distributions of individuals within a species were self-similar across spatial scale could lead to a realistic SAD. Although the initial formulation was found to not have a good fit to the data (Green *et al.* 2003)
	26. Multifractal	Borda-de-Agua *et al.* (2002) extend the fractal distribution model to cover multifractals (fractal dimension changes with scale)
	27. HEAP	A newer model, also based on a different description of the distribution of individuals across space has been developed (Harte *et al.* 2005).

(McGill et al. 2007 *Eco Let*)

Some SAD Theories

- Purely statistical
  - Log series (Fisher)
  - Lognormal (Preston)
- Niche partitioning
  - Broken stick (MacArthur, Sugihara)
- Population dynamics
  - Neutral theory (Hubbell)

(McGill et al. 2007 *Eco Let*)

Four Fundamental Processes in Community Ecology

- Selection
- Drift
- Speciation
- Dispersal

(Vellend 2010 *Q Rev Bio*)

Four Fundamental Processes in Community Ecology

- Selection
- Drift
- Speciation
- Dispersal

(Vellend 2010 *Q Rev Bio*)

Four Fundamental Processes in Community Ecology

- Selection
- Drift
- Speciation
- Dispersal

(Vellend 2010 *Q Rev Bio*)

Four Fundamental Processes in Community Ecology

- Selection
- Drift
- Speciation
- Dispersal

(Vellend 2010 *Q Rev Bio*)

Trait-Based Community Ecology in a Metacommunity Context

$$\frac{dN_i}{dt} = g(x_i; \vec{N}, \vec{x})N_i + i(x_i)$$

$$= \begin{bmatrix} \text{population} \\ \text{dynamics} \end{bmatrix} + \begin{bmatrix} \text{immigration} \end{bmatrix}$$

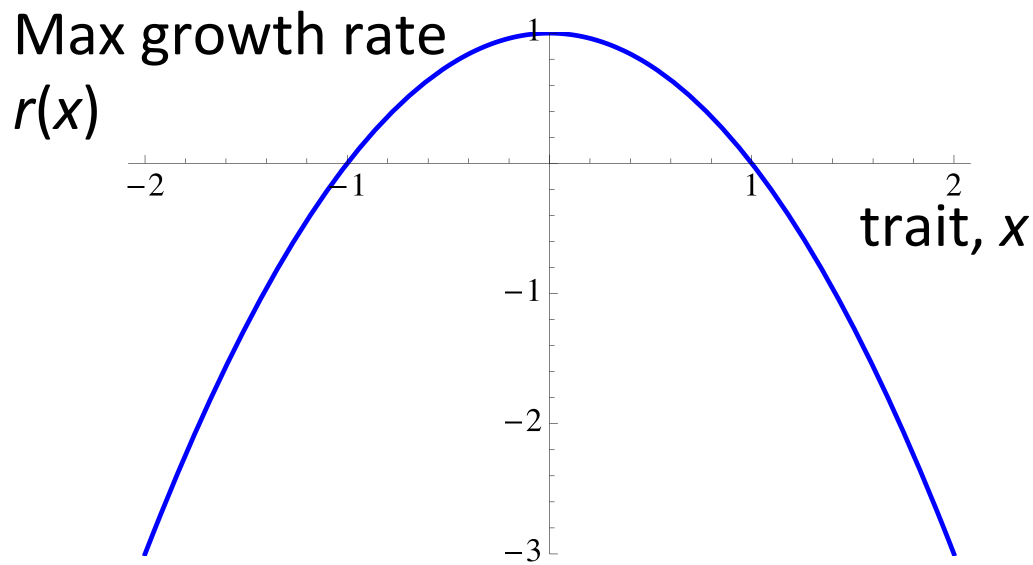
At Equilibrium

$$\widehat{N}(x) = \frac{i(x)}{-g(x)} = \frac{i(x)}{e(x)} = \frac{[\text{immigration}]}{[\text{exclusion}]}$$

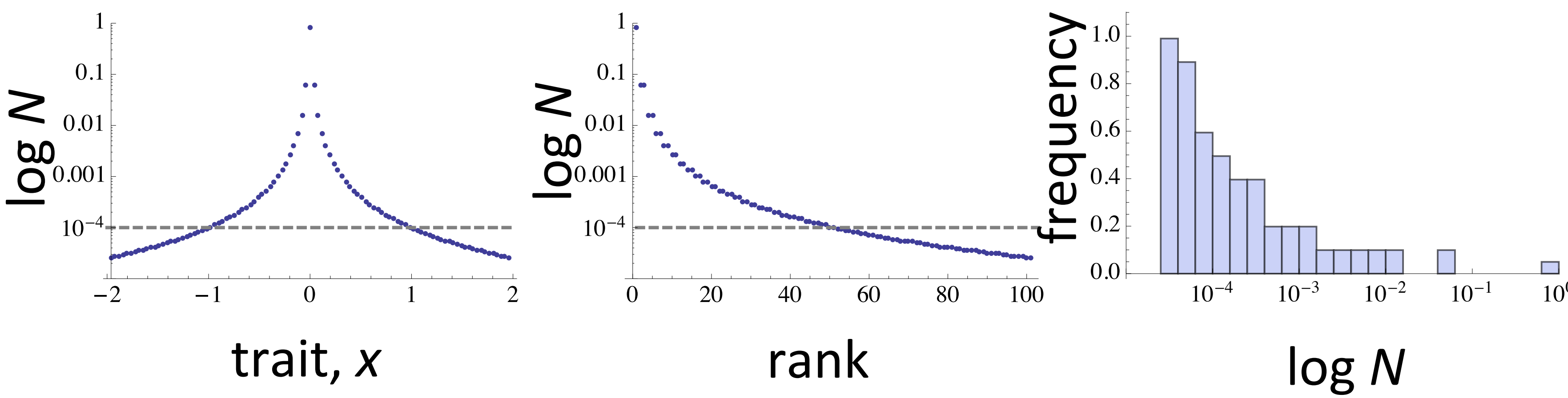
$$\log \widehat{N}(x) = \log i(x) - \log e(x)$$

Model 1: Lotka-Volterra Competition (1 Niche)

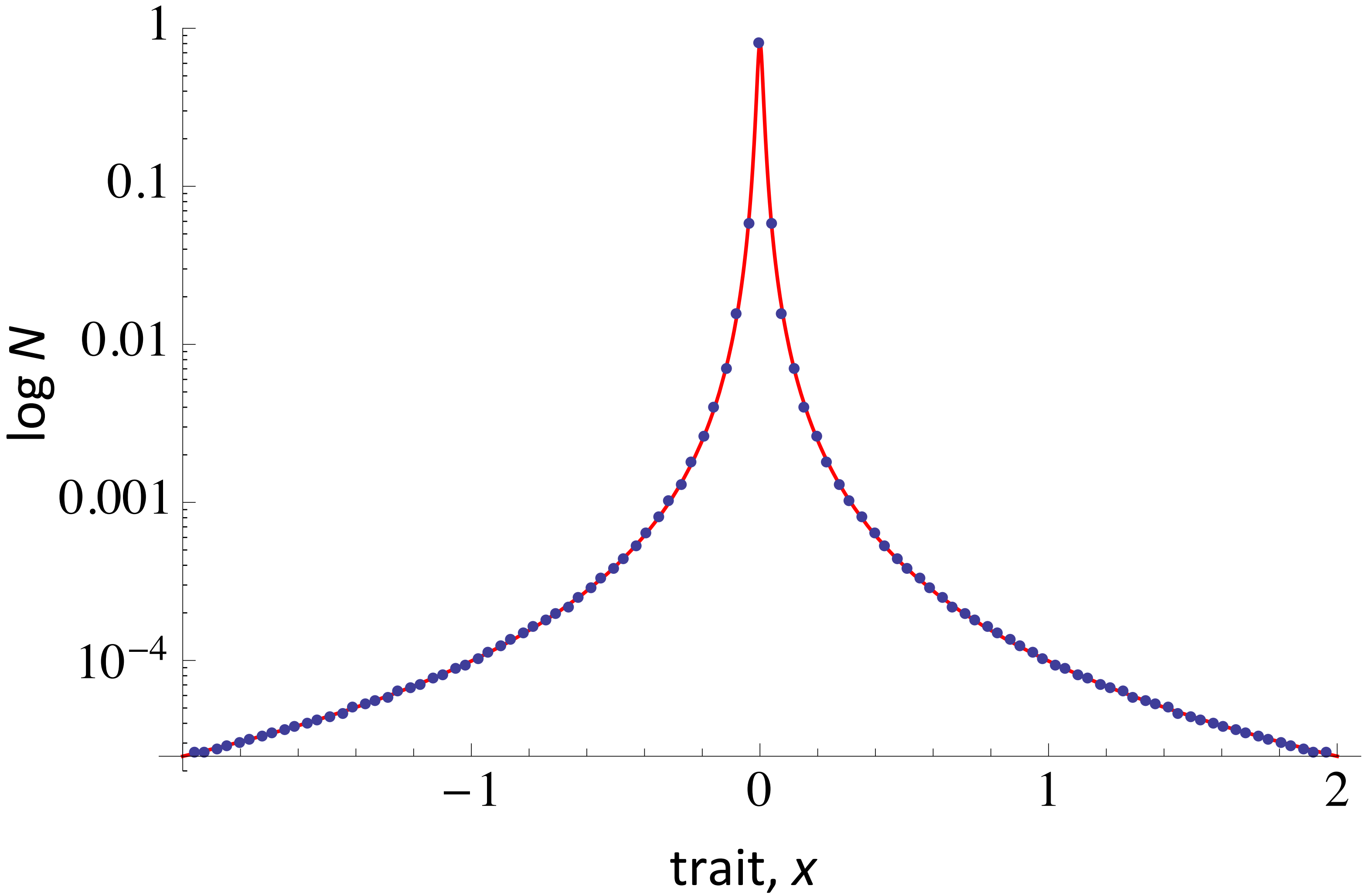
$$g(x_i) = r(x_i) - \sum_j r(x_j) N_j$$



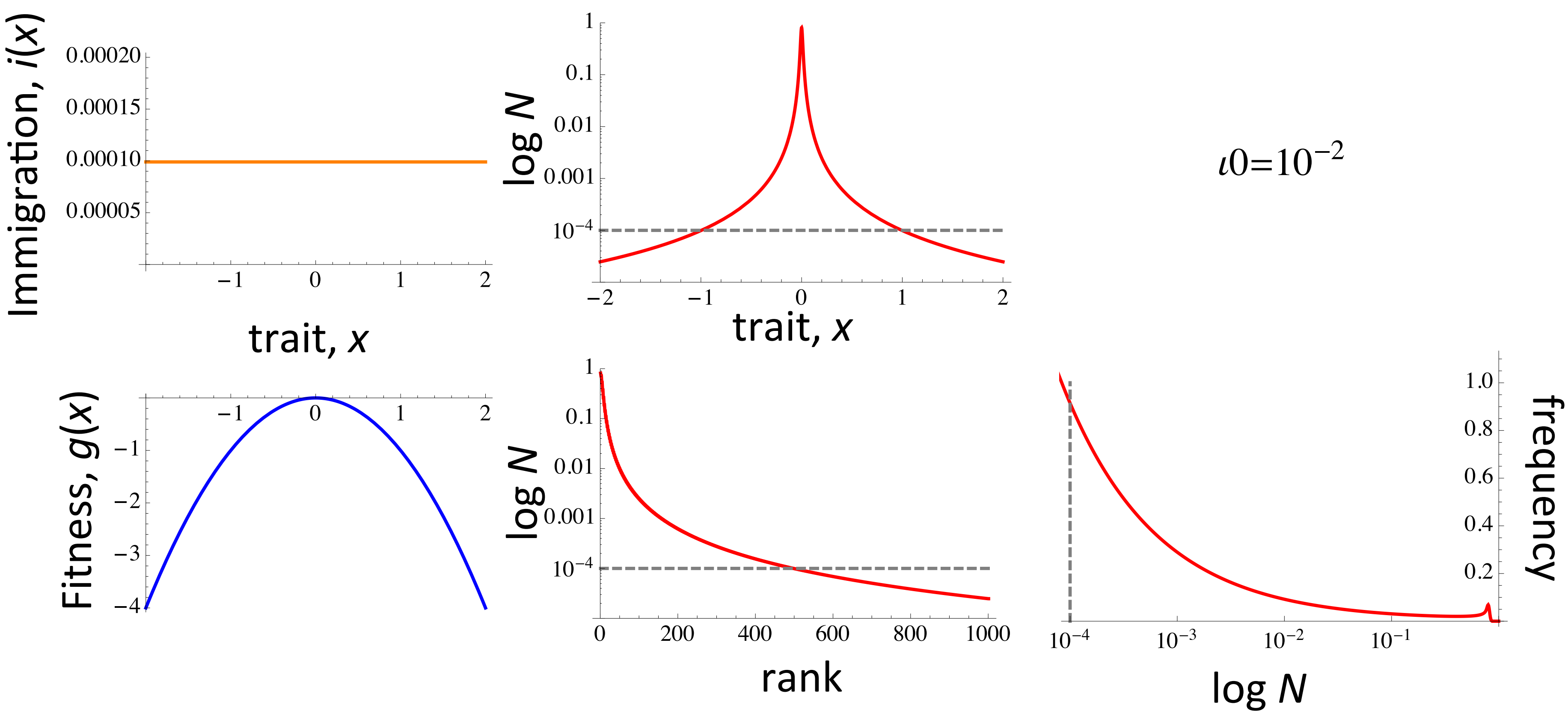
Model 1: Lotka-Volterra Competition (1 Niche)



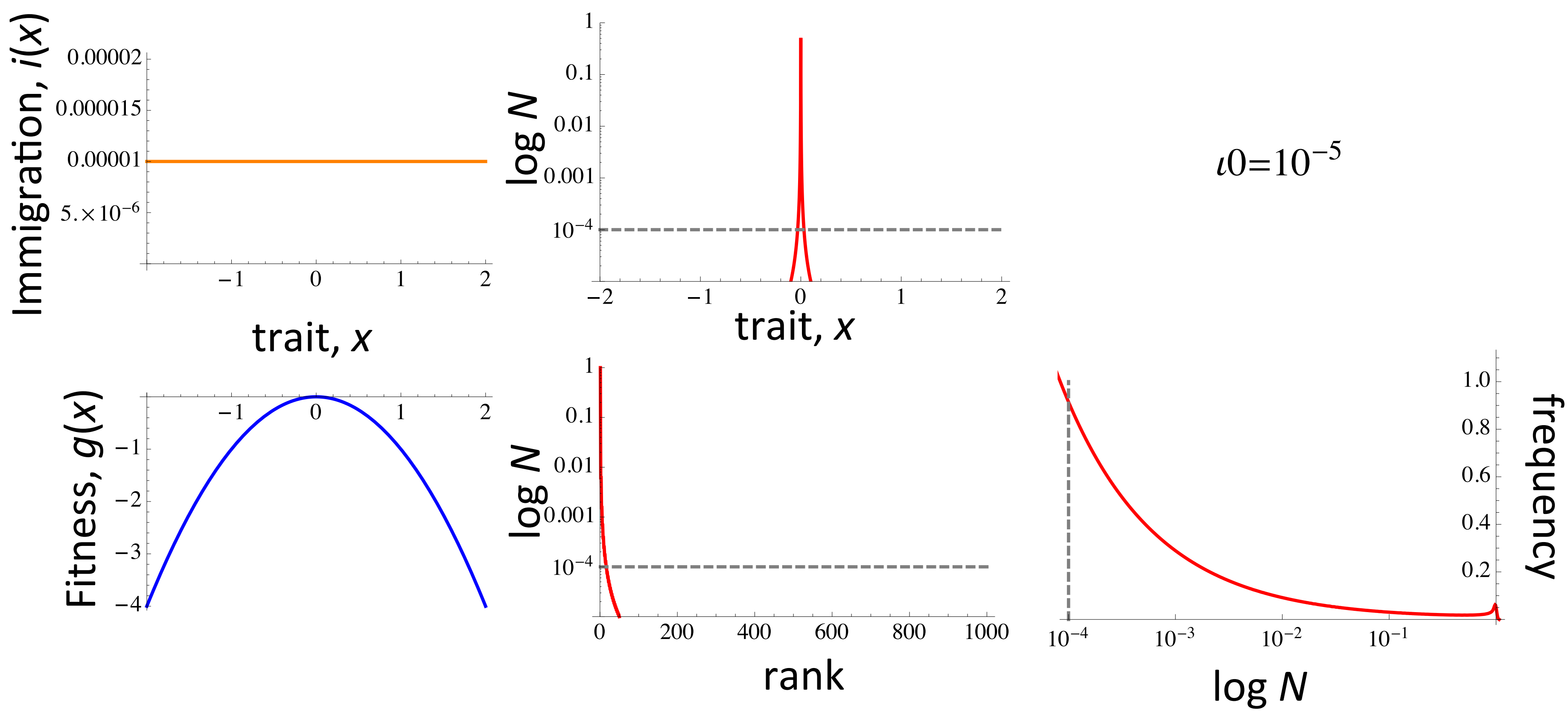
Continuous Approximation



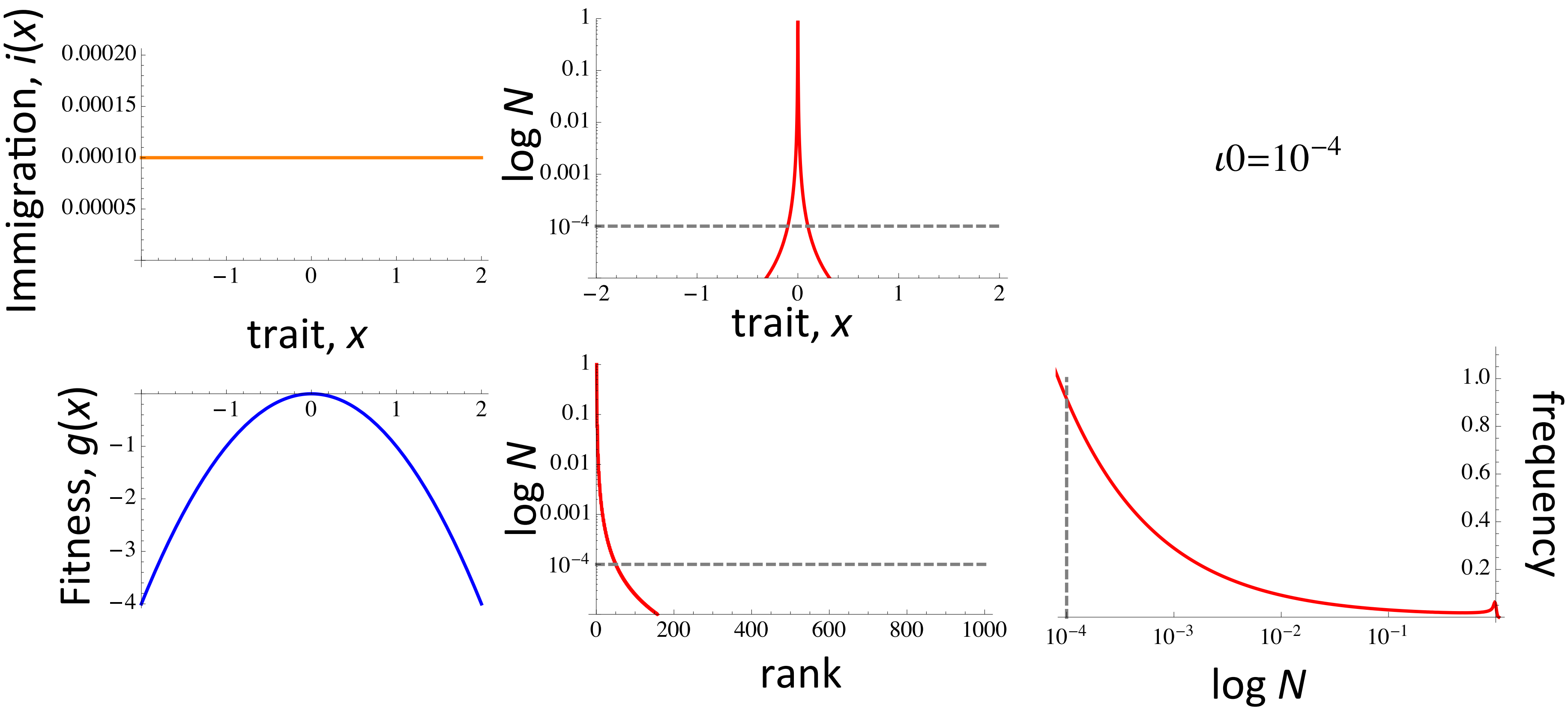
Continuous Approximation



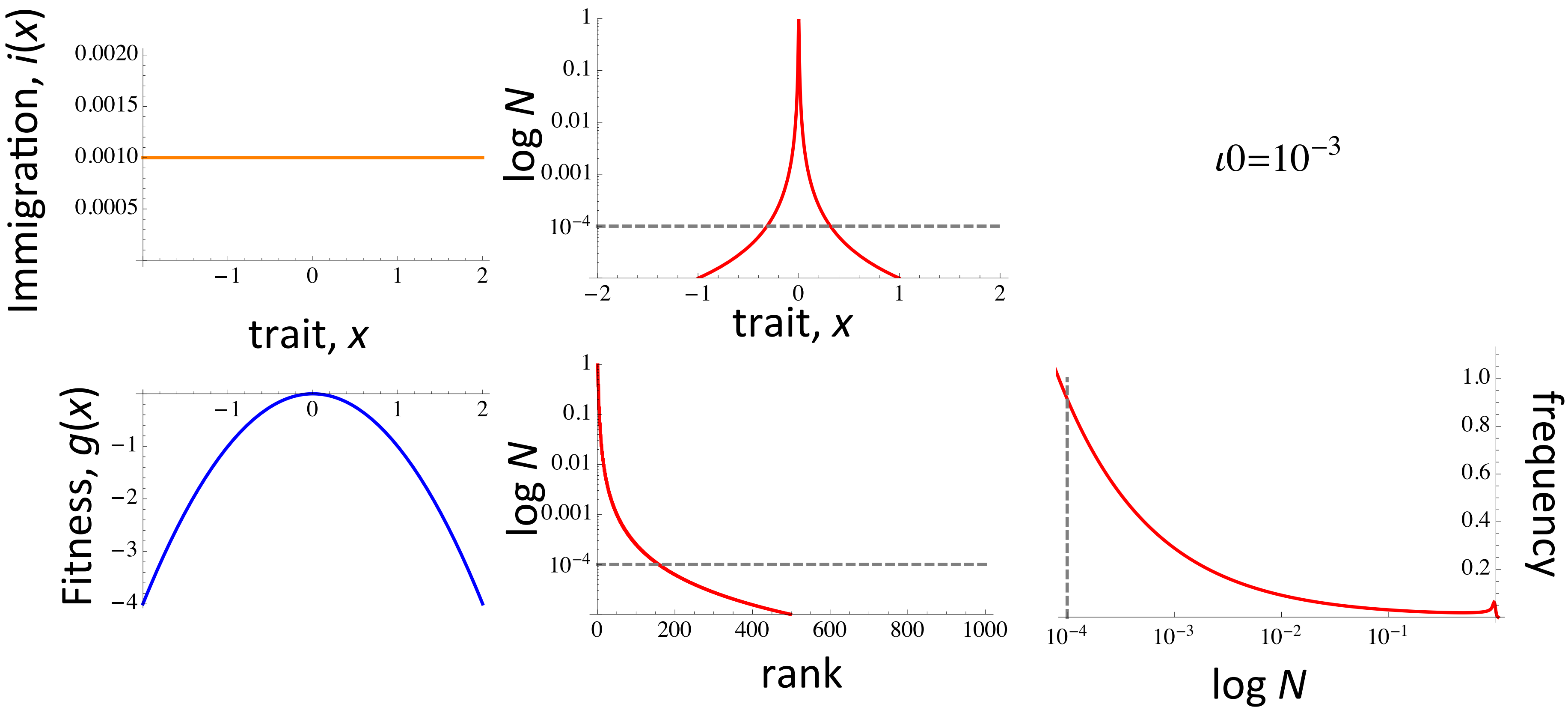
Effect of immigration rate



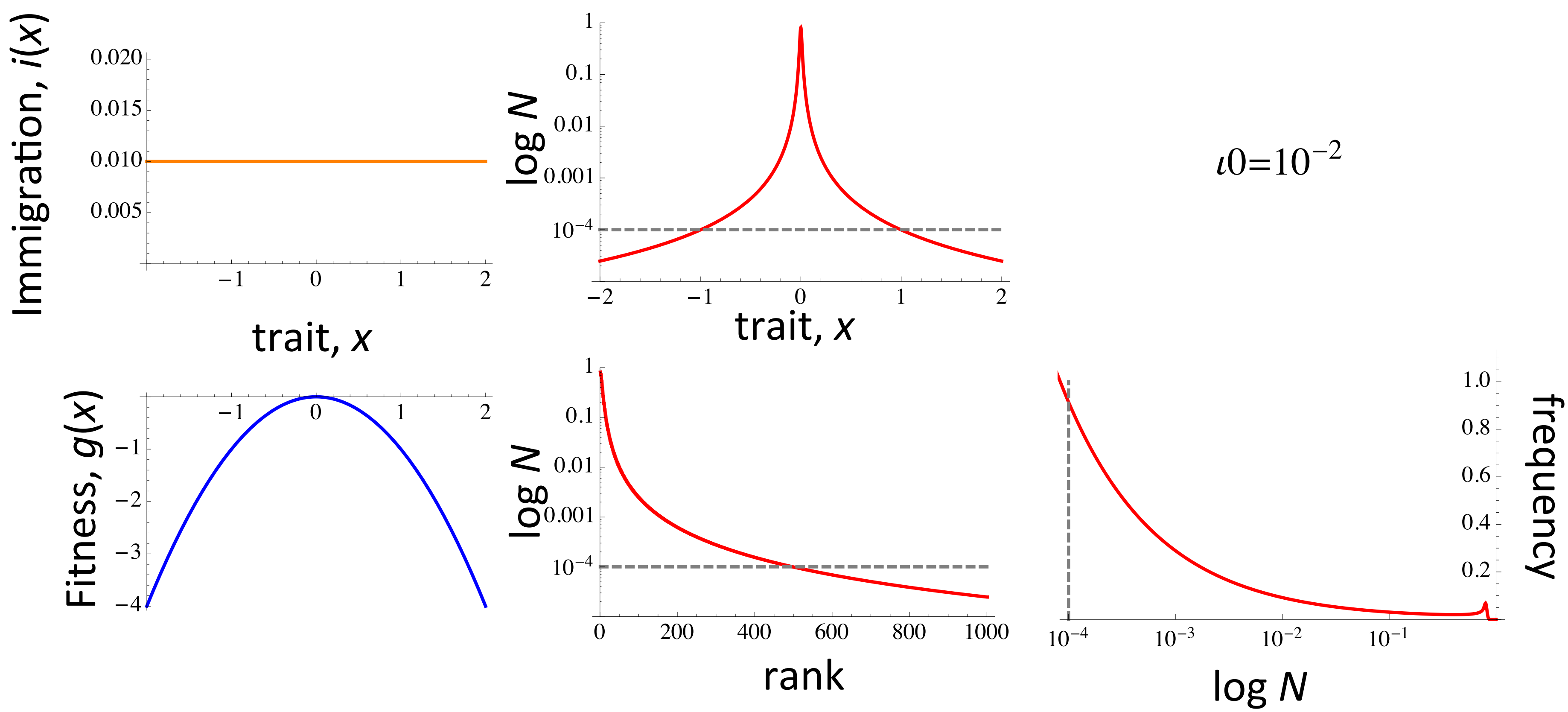
Effect of immigration rate



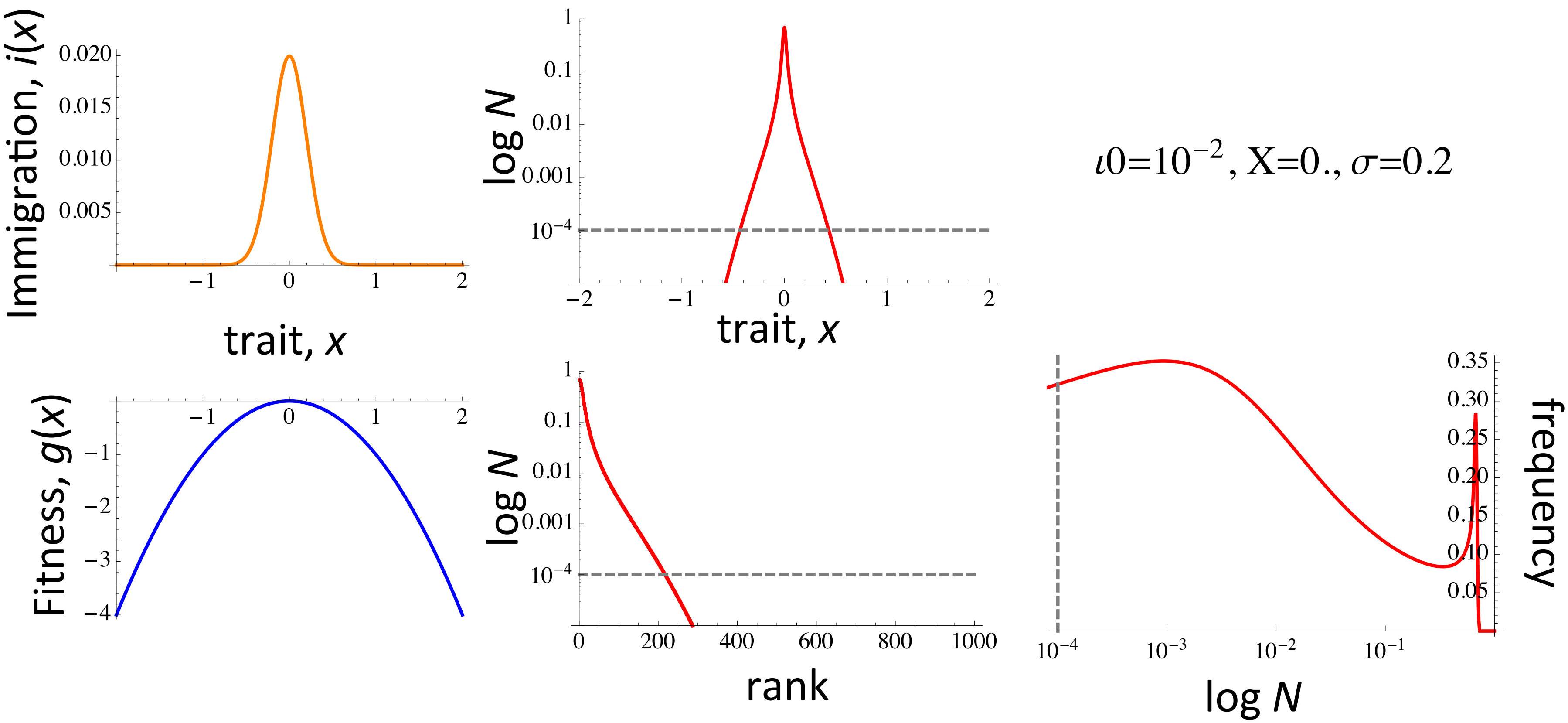
Effect of immigration rate



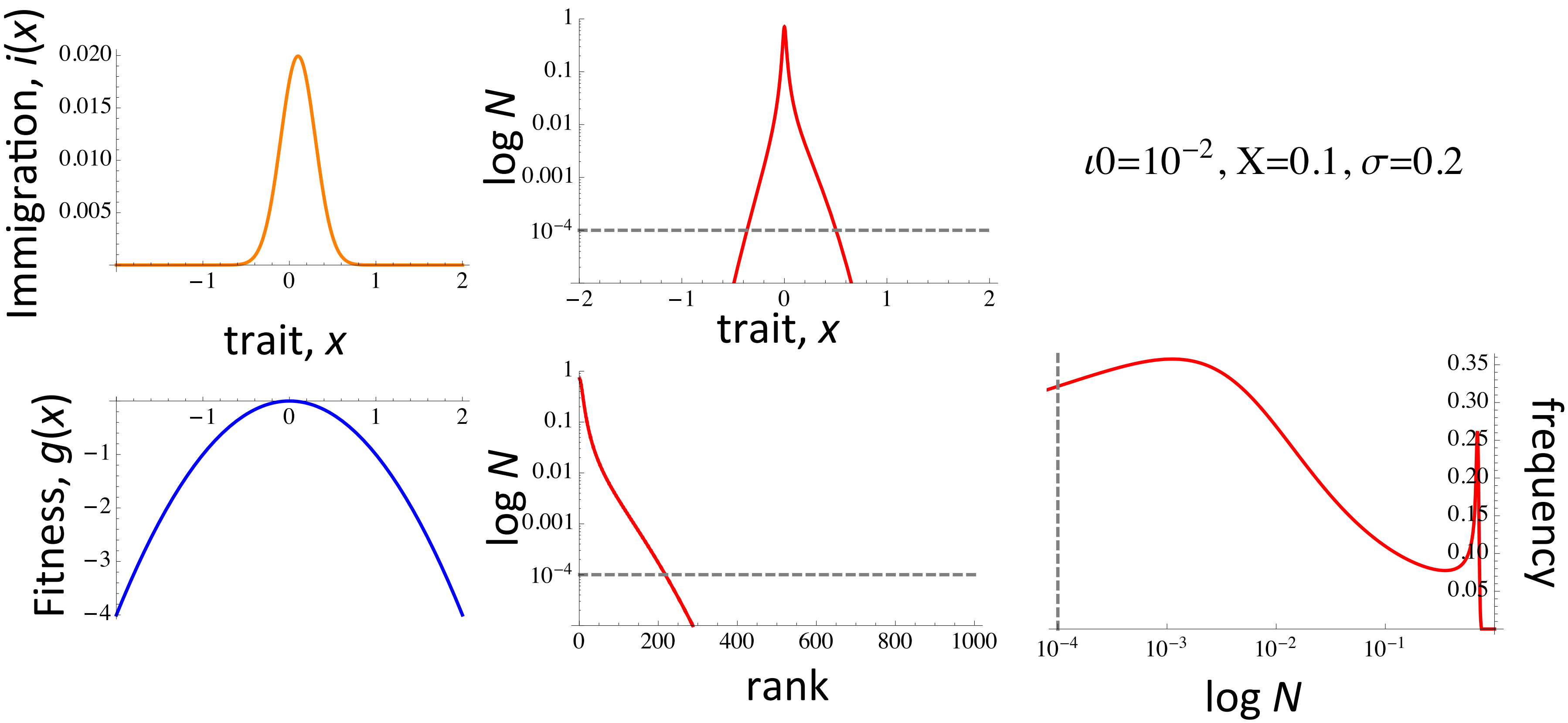
Effect of immigration rate



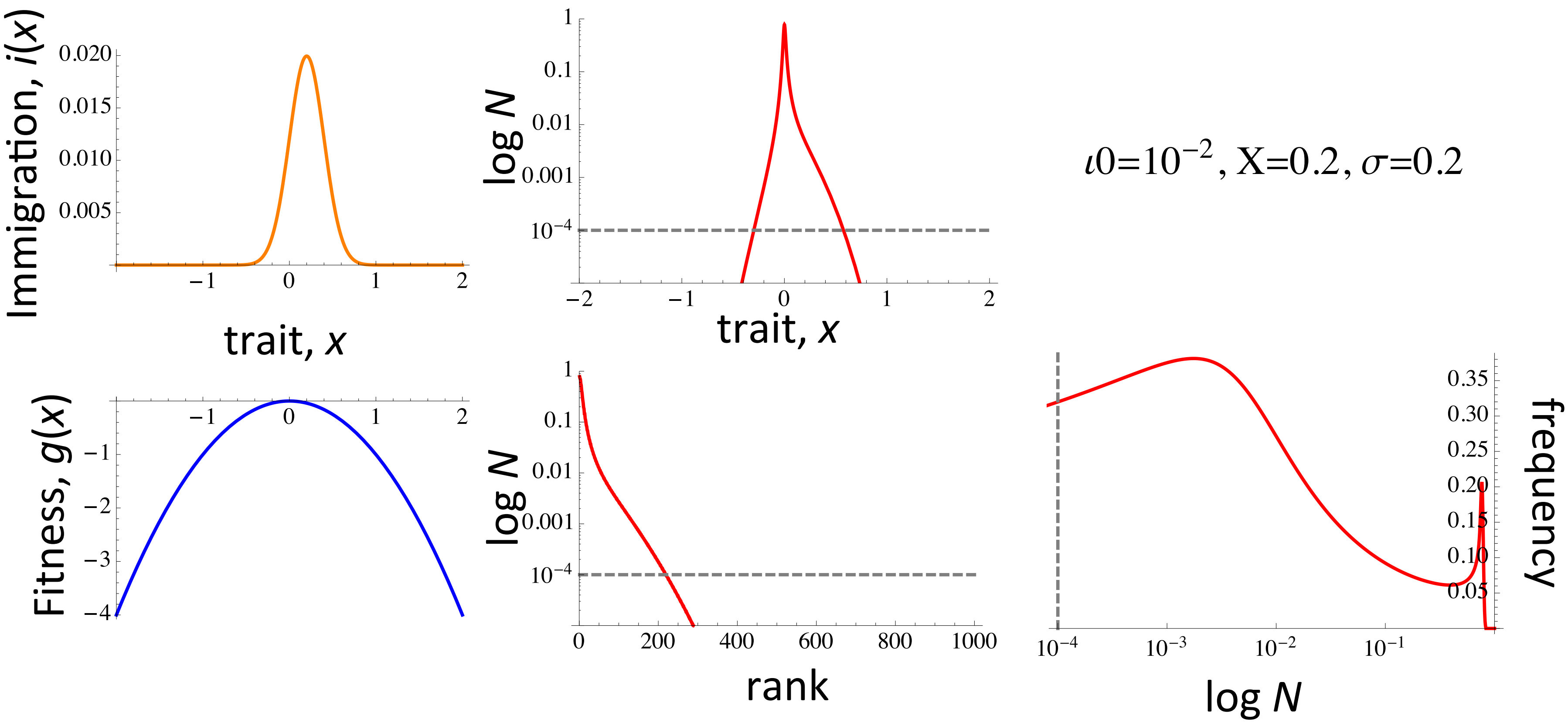
Normal immigration



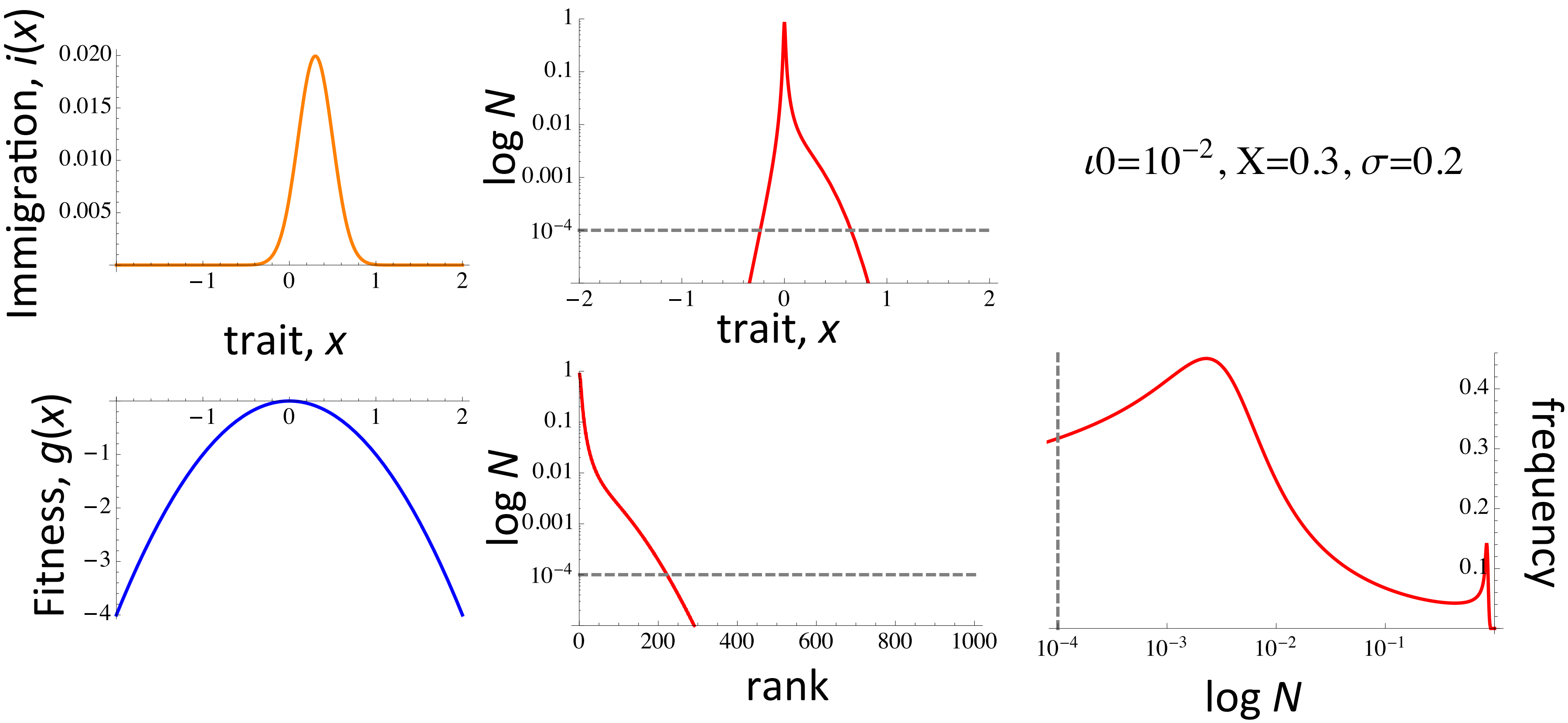
Normal immigration



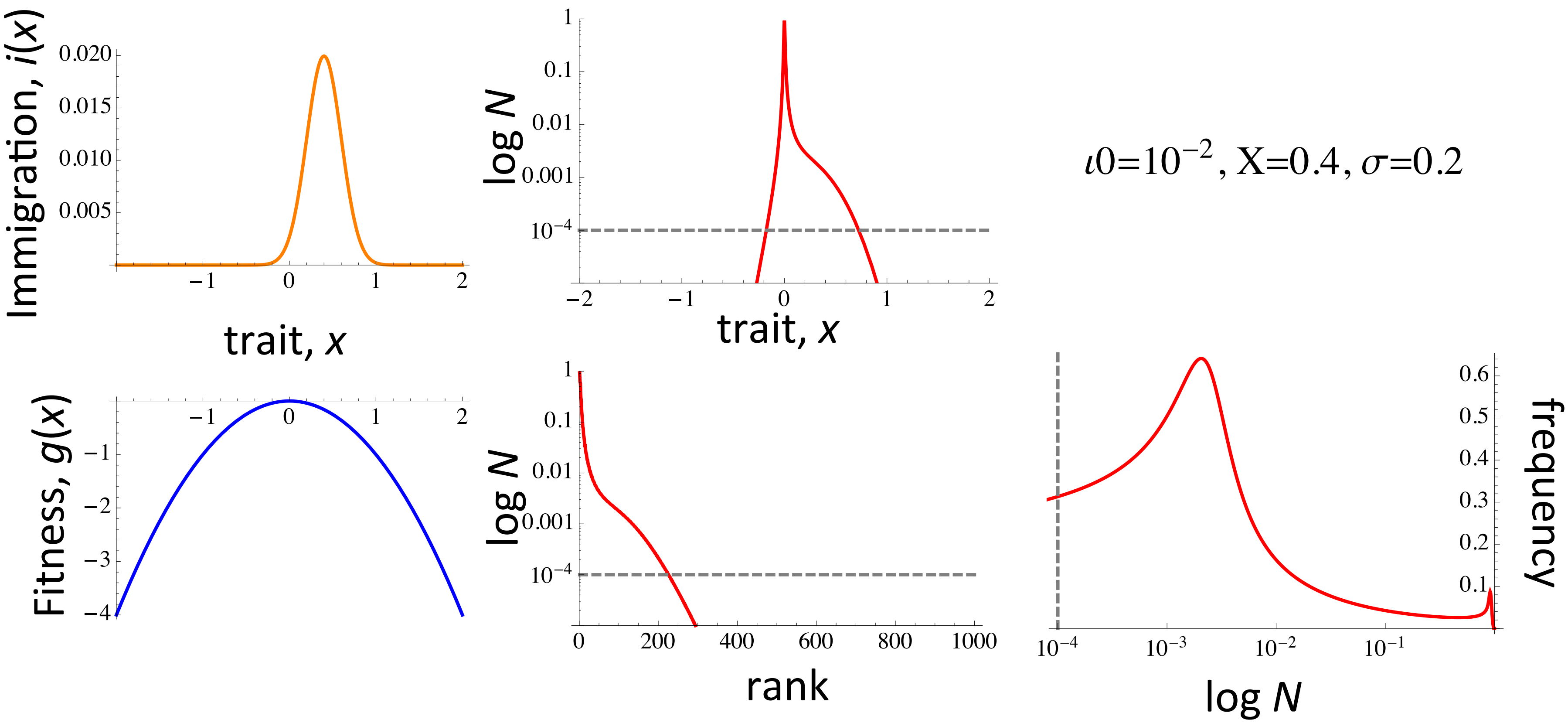
Normal immigration



Normal immigration

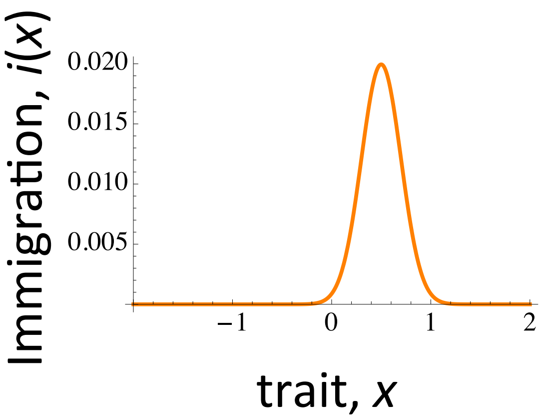


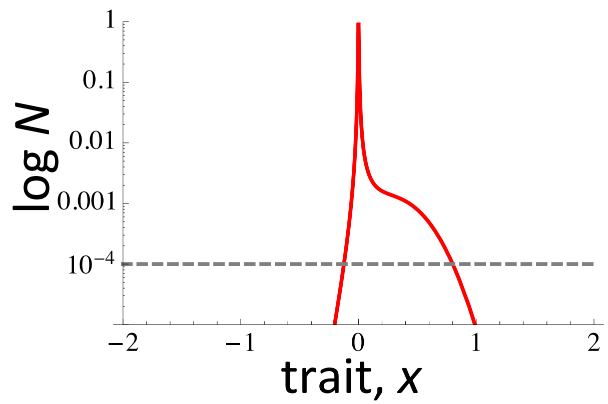
Normal immigration



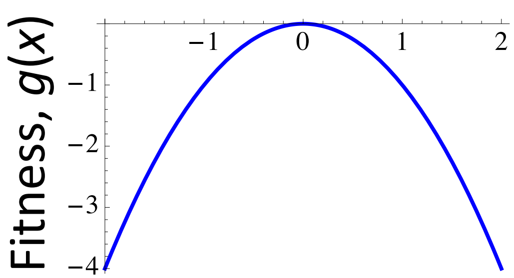
$\iota 0 = 10^{-2}$, $X = 0.4$, $\sigma = 0.2$

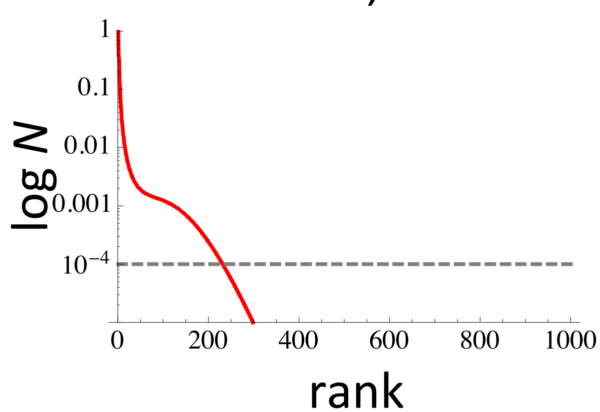
Normal immigration

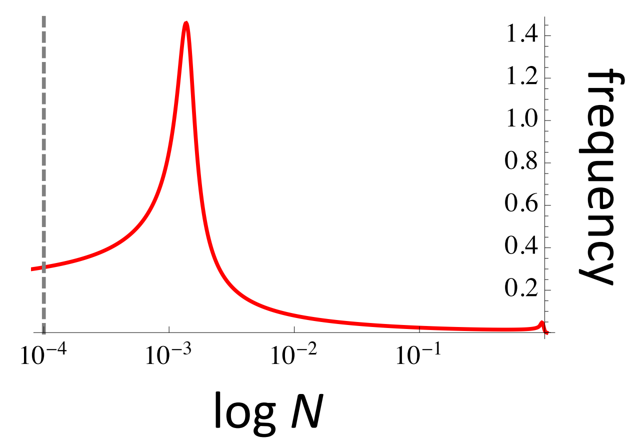




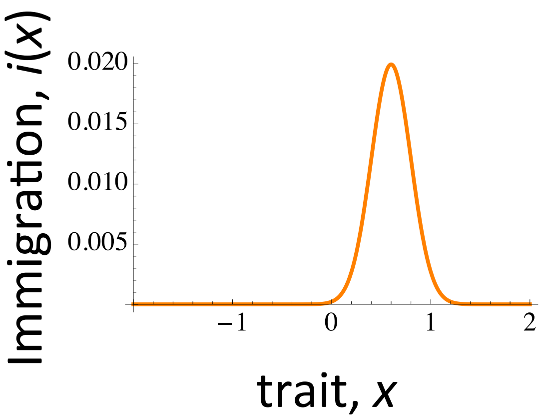
$\iota 0=10^{-2}, \mathrm{X}=0.5, \sigma=0.2$

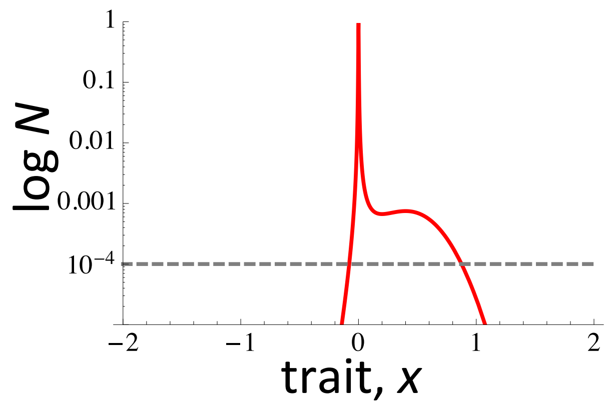




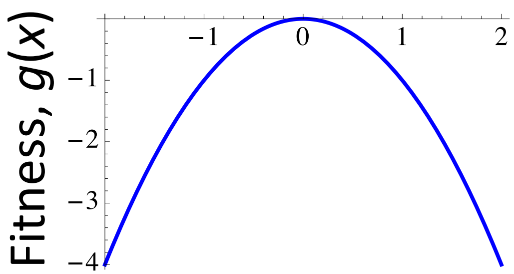


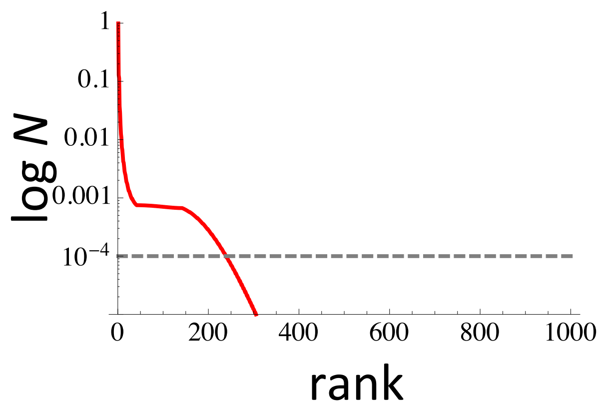
Normal immigration

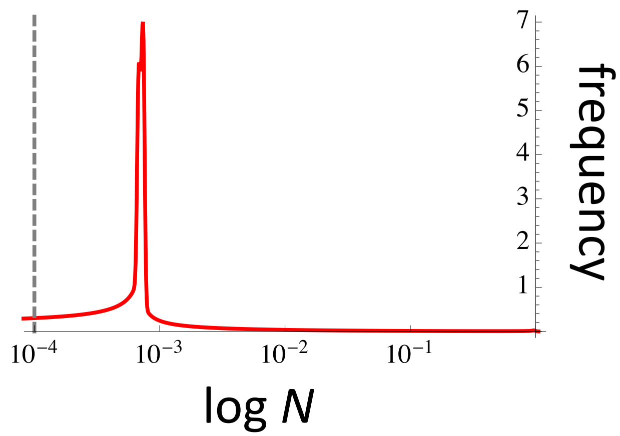




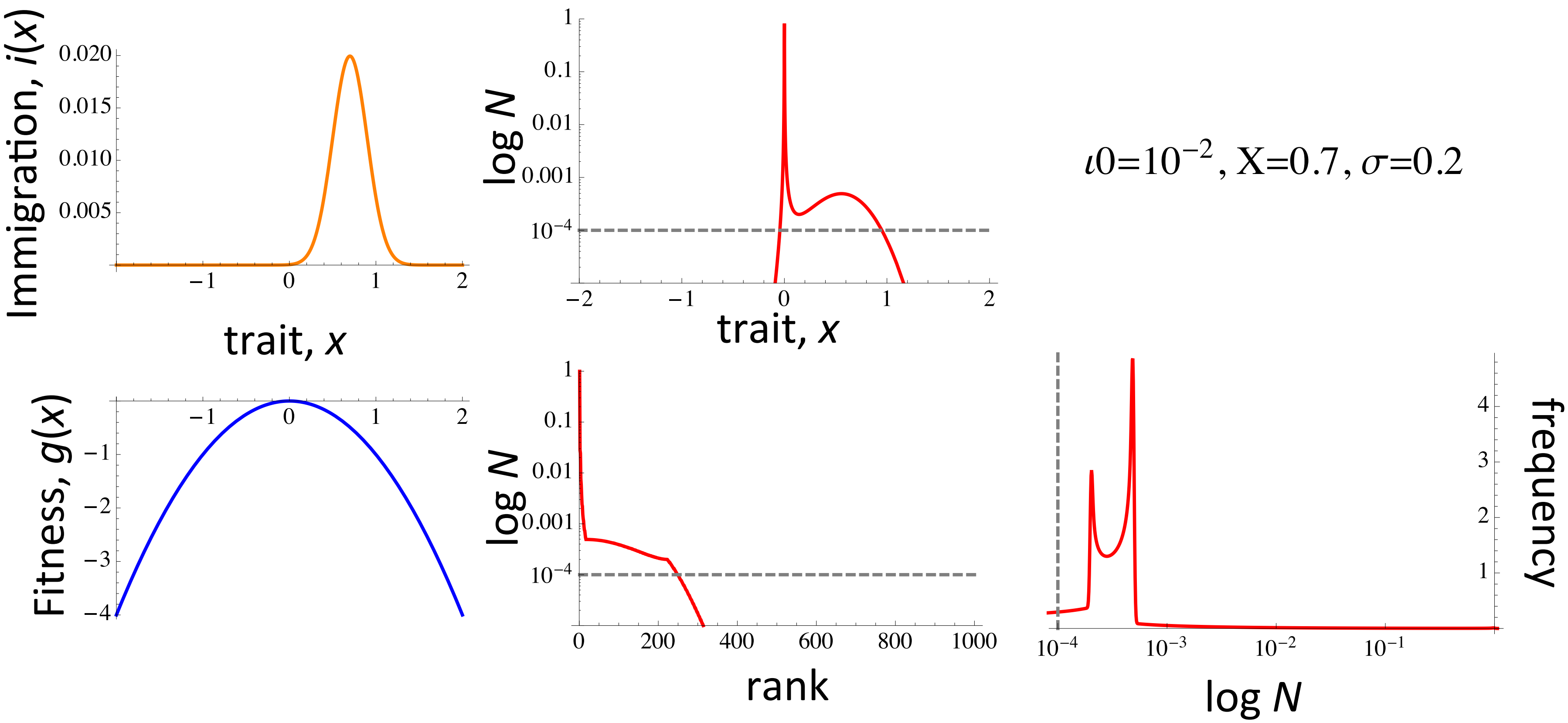
$\iota0=10^{-2}$, X=0.6, $\sigma=0.2$





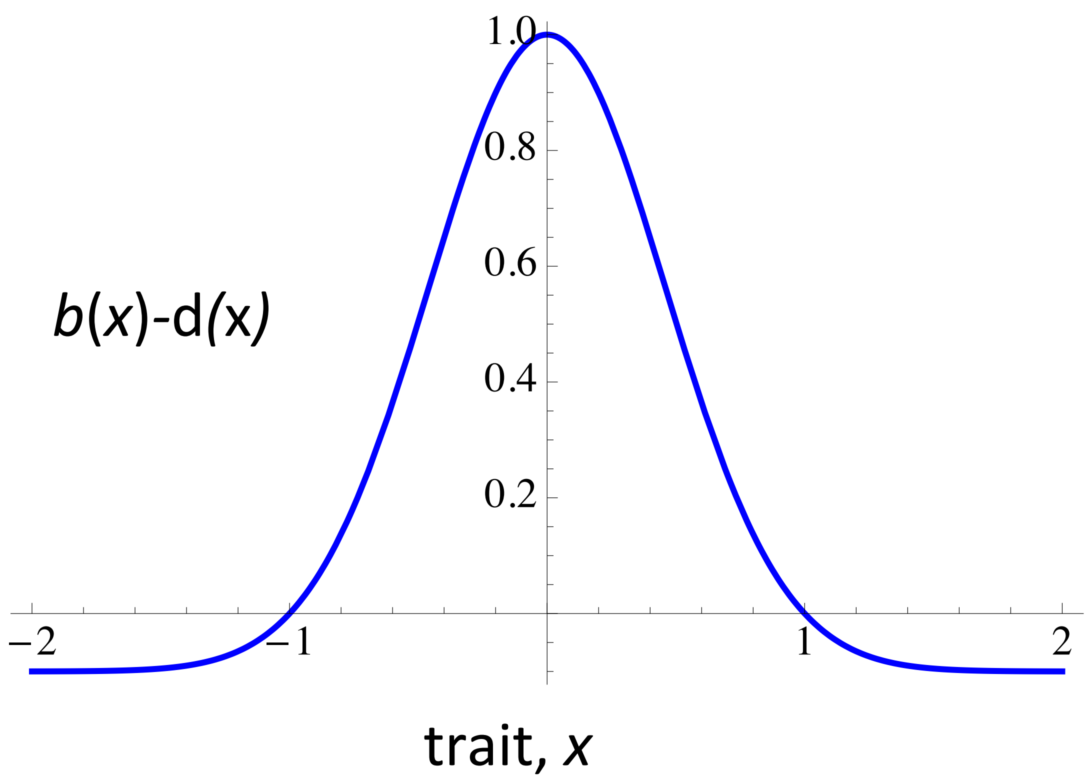


Normal immigration

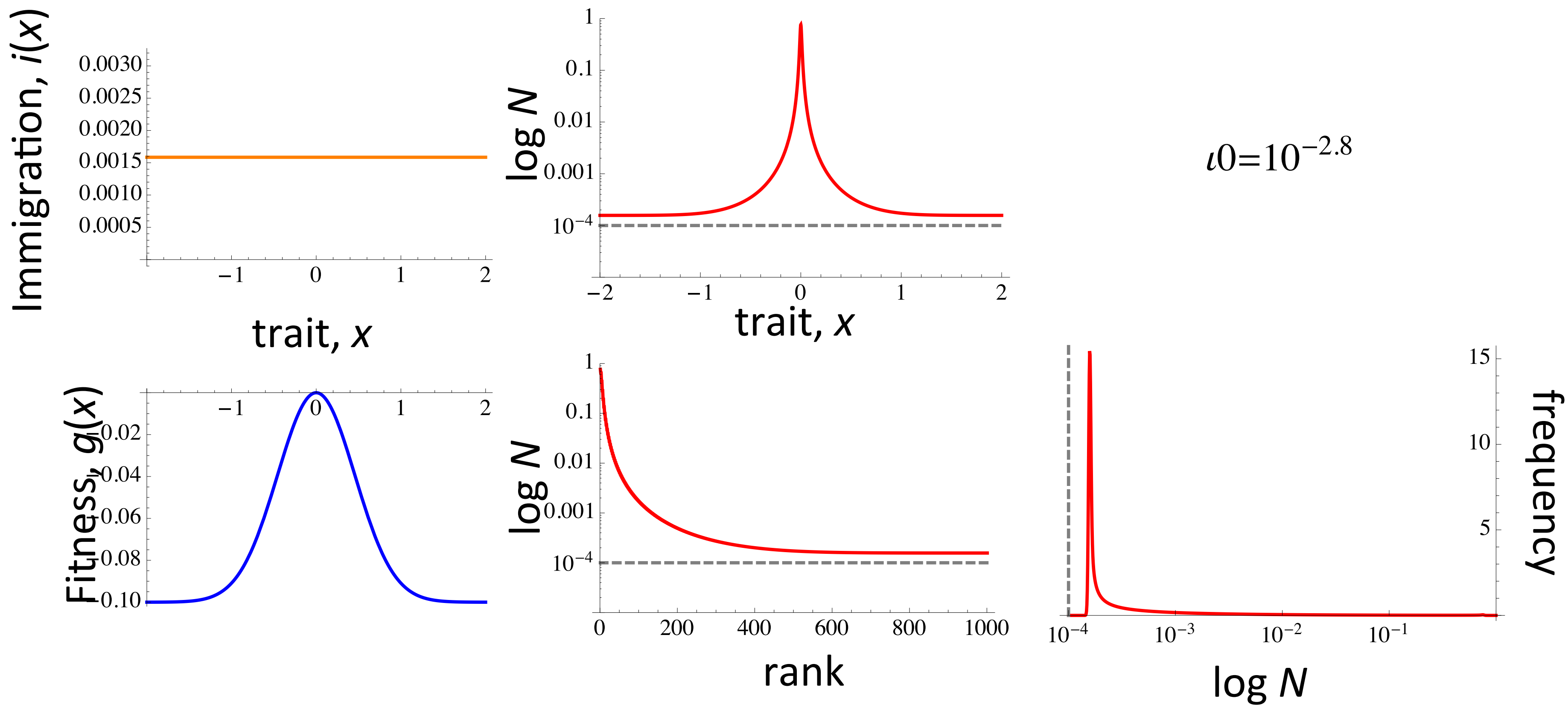


Model 2: Resource Competition (1 Niche)

$$g(x_i) = b(x_i)R - d$$

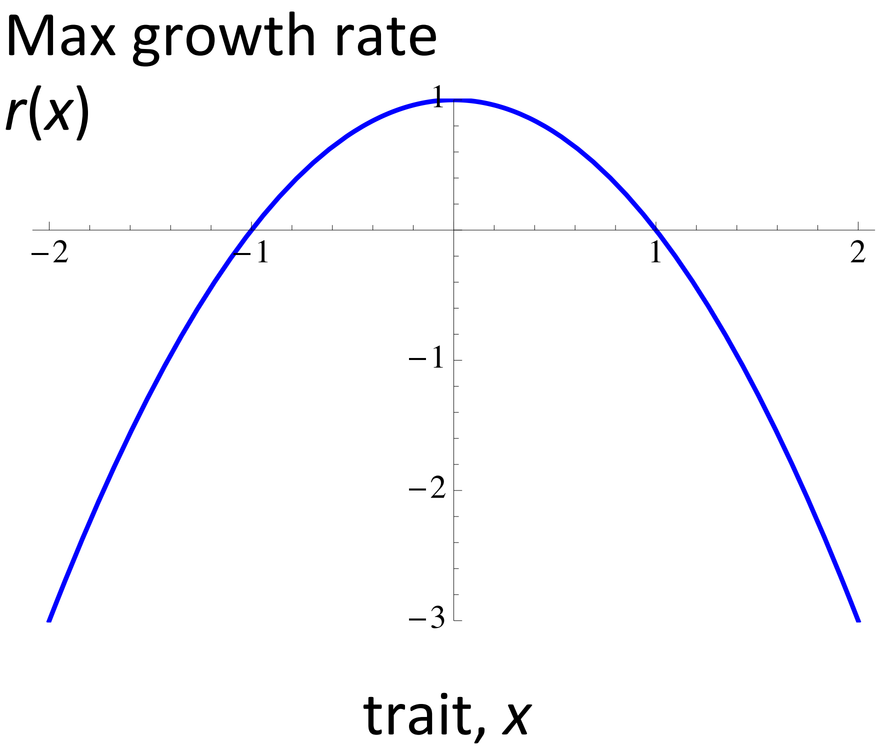


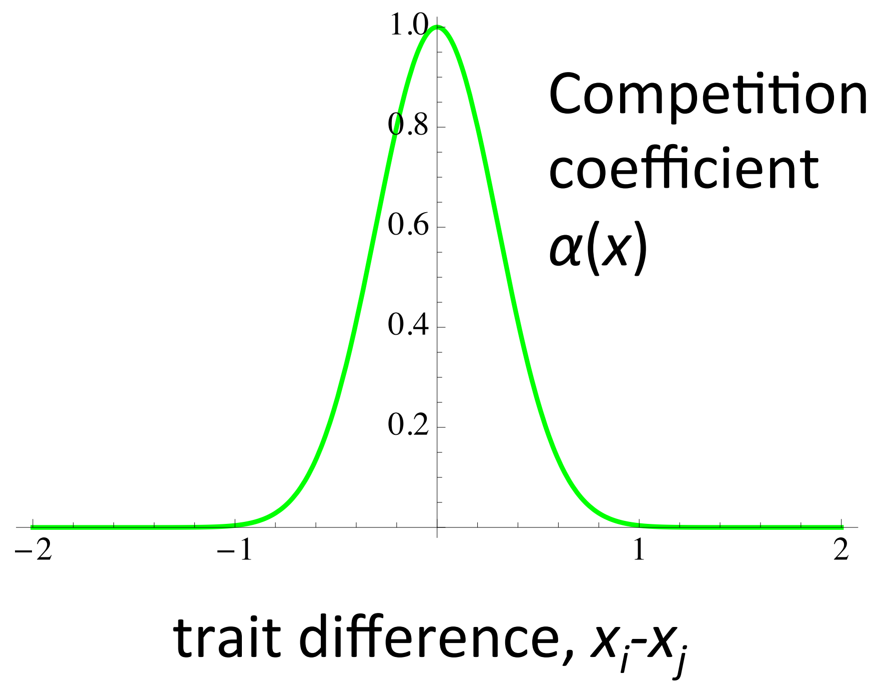
Model 2: Resource Competition (1 Niche)



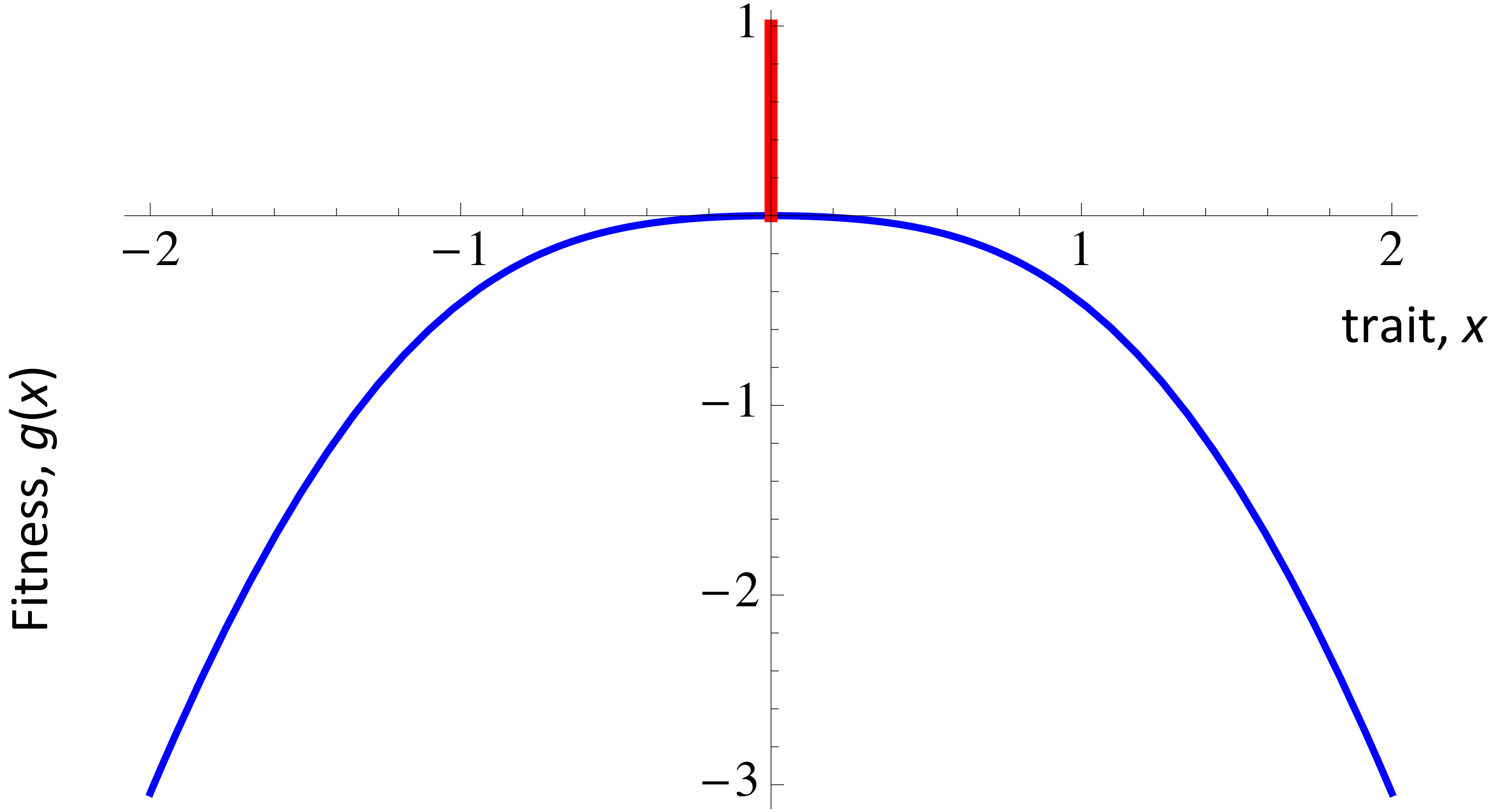
Model 3: Lotka-Volterra Competition (1+ Niches)

$$g(x_i) = r(x_i) - \sum_j \alpha(x_i - x_j) N_j$$

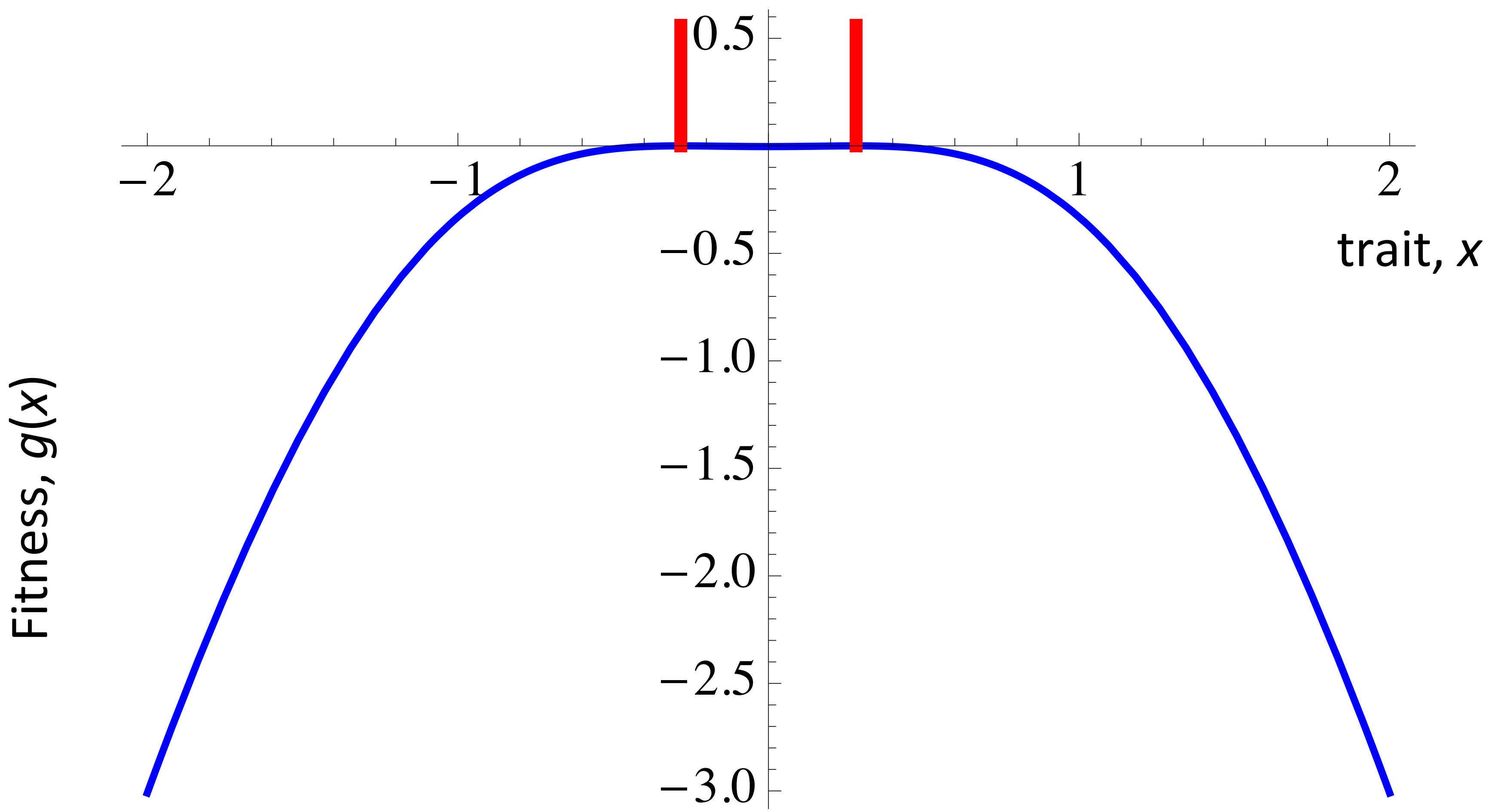




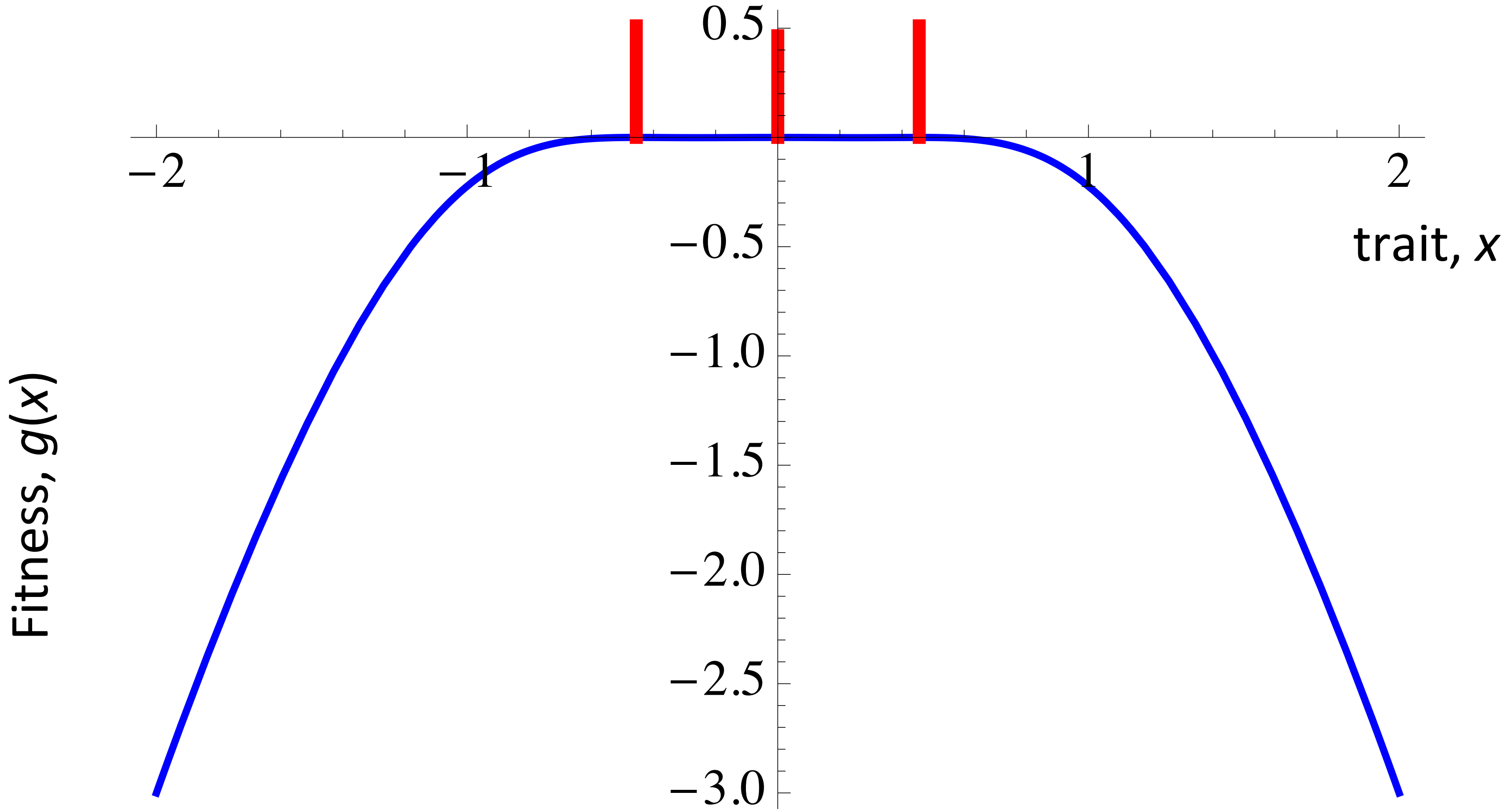
Diversity Depends on Niche Width



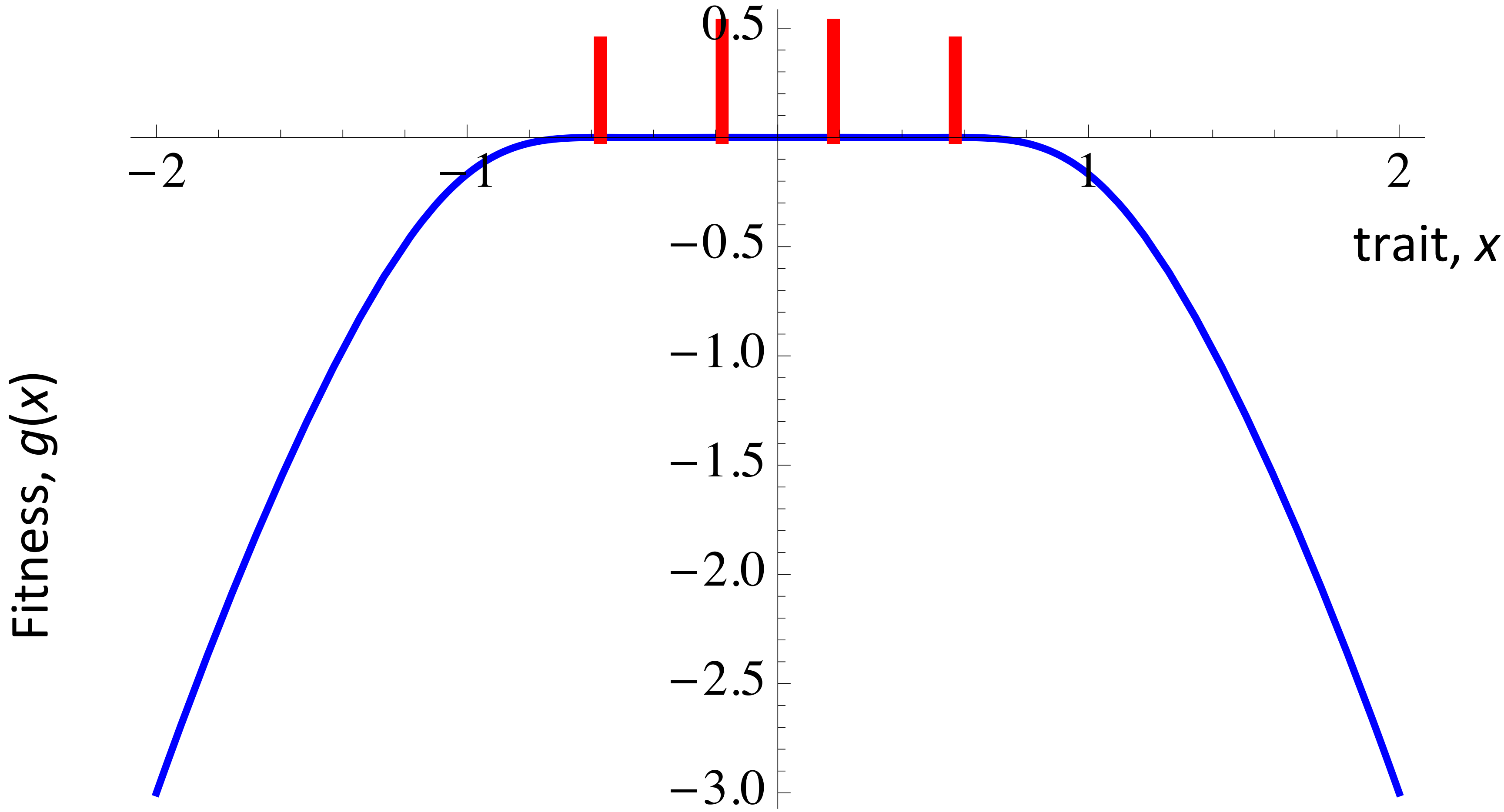
Diversity Depends on Niche Width



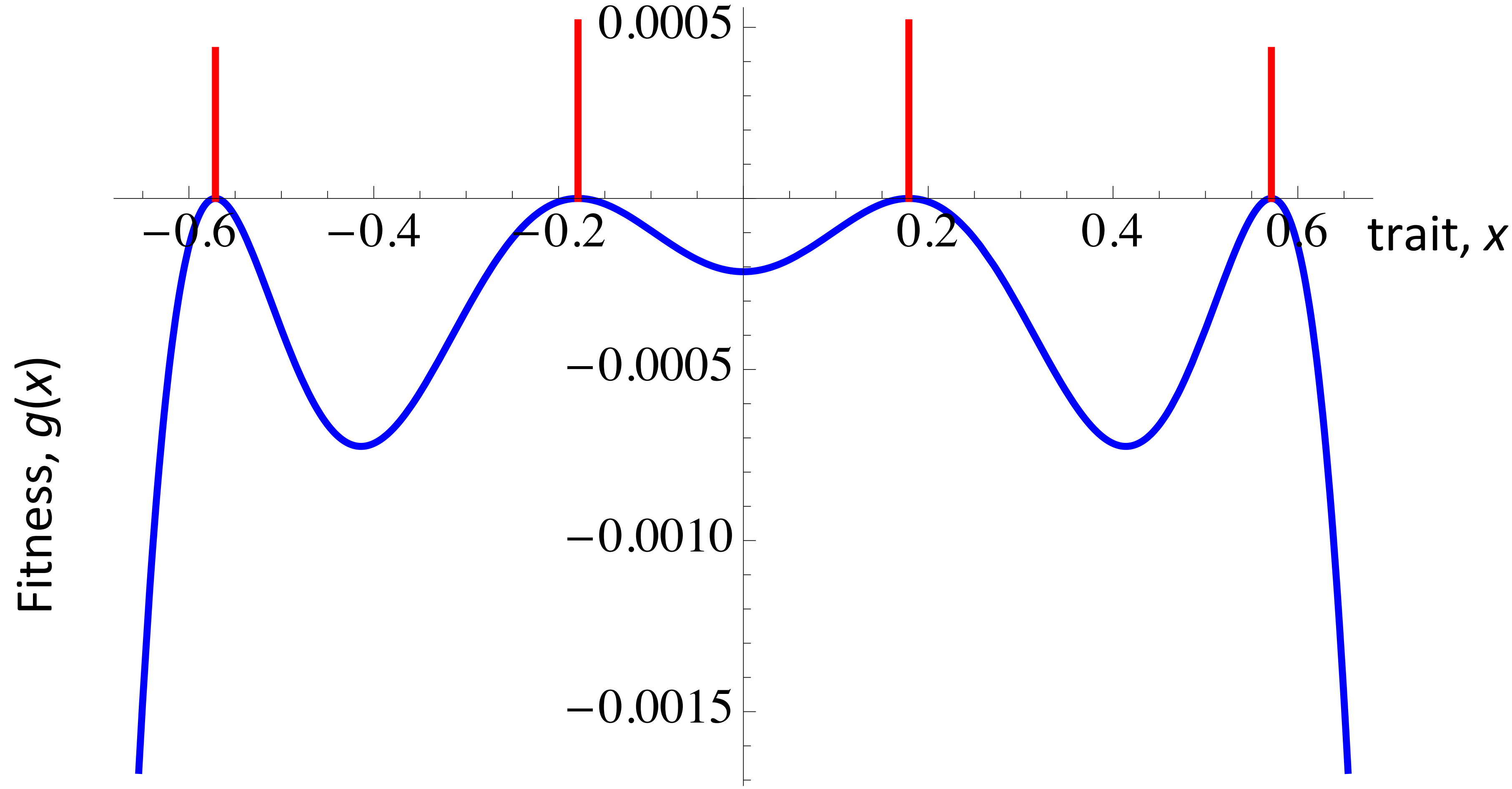
Diversity Depends on Niche Width



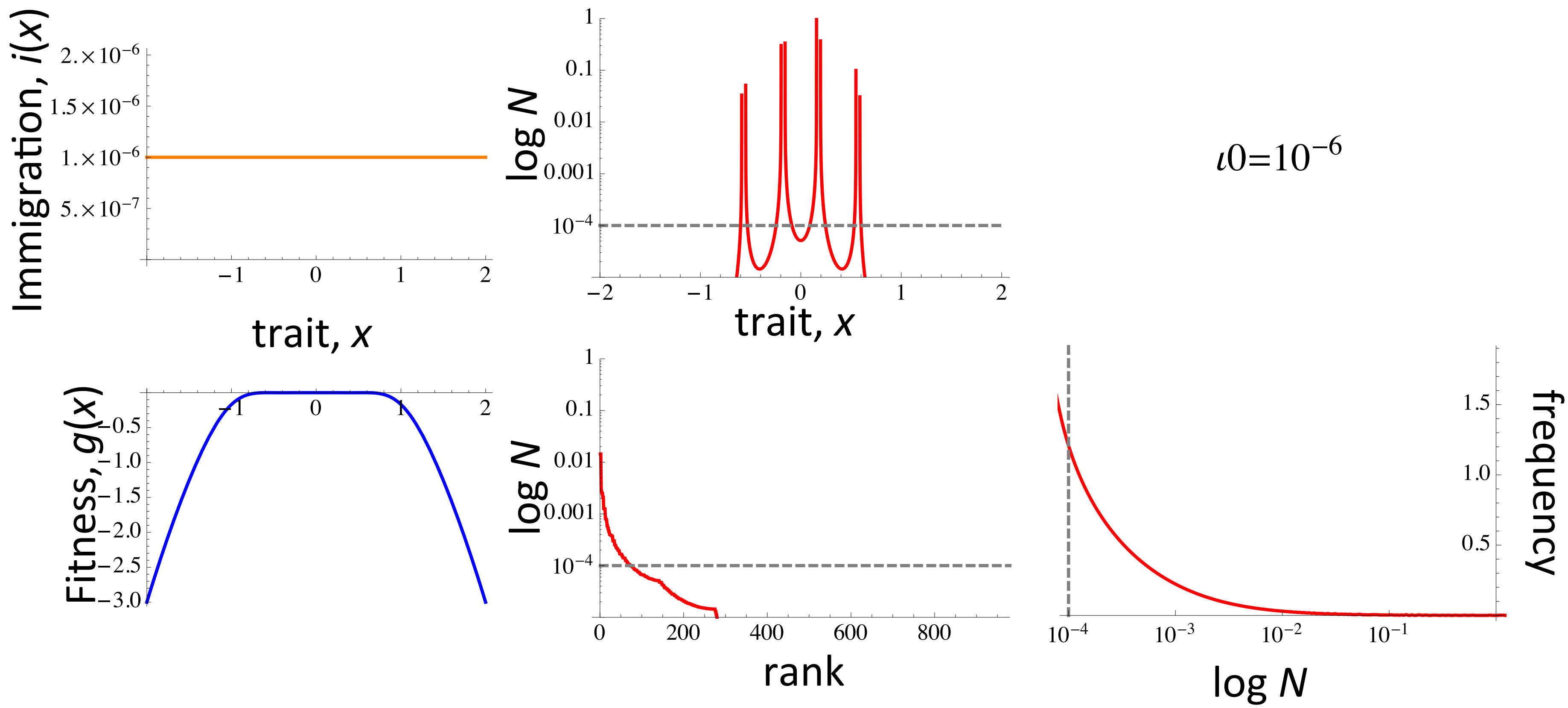
Diversity Depends on Niche Width



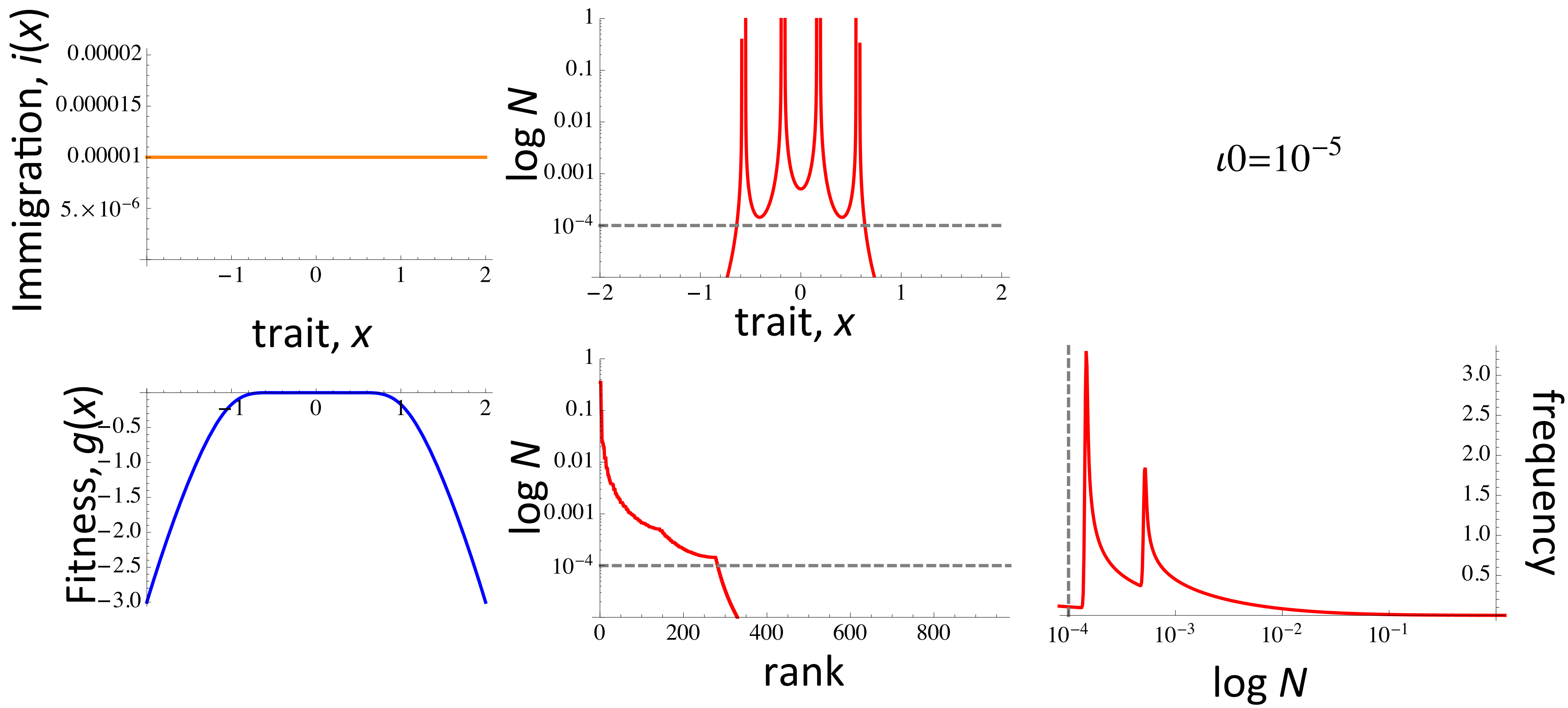
Flat Fitness Landscape Between Species



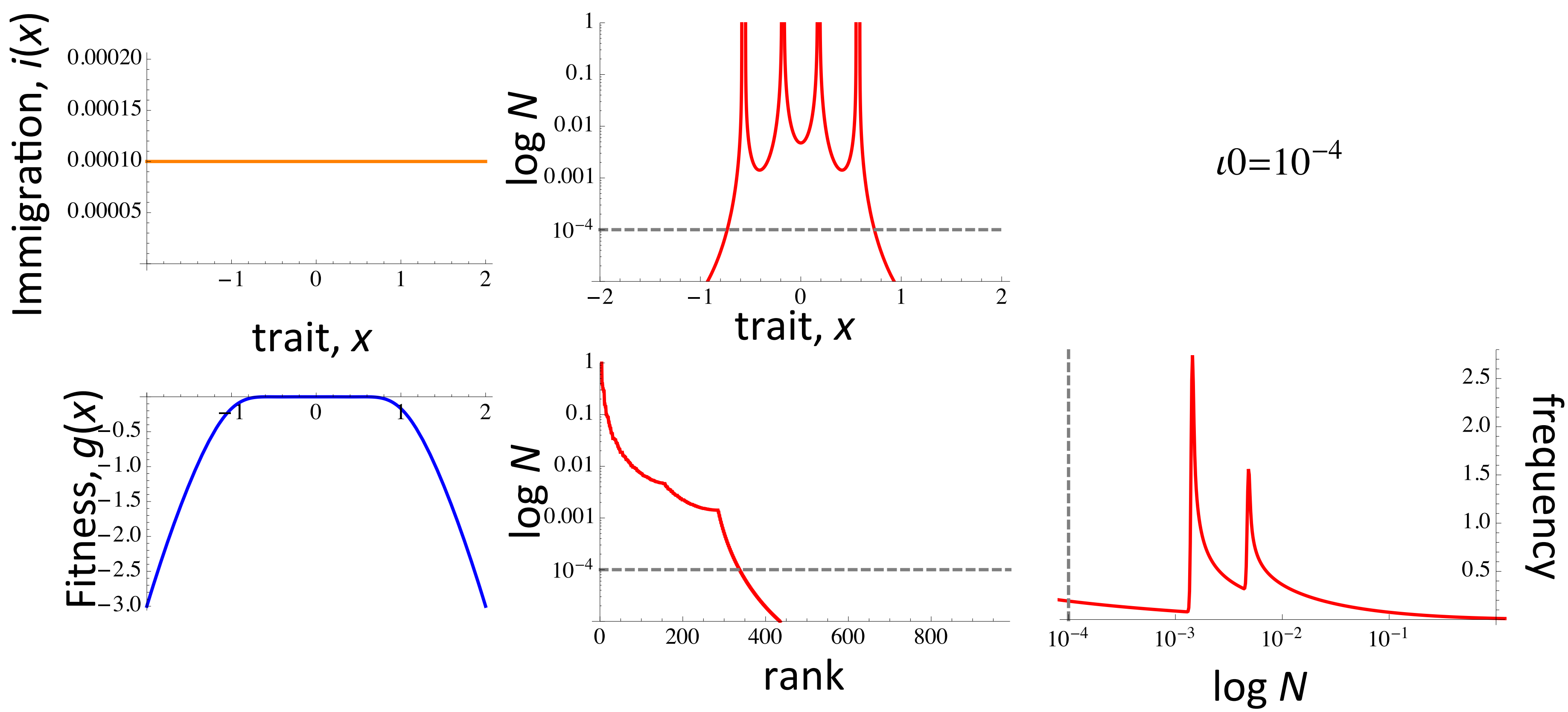
Model 3: 4 Niches



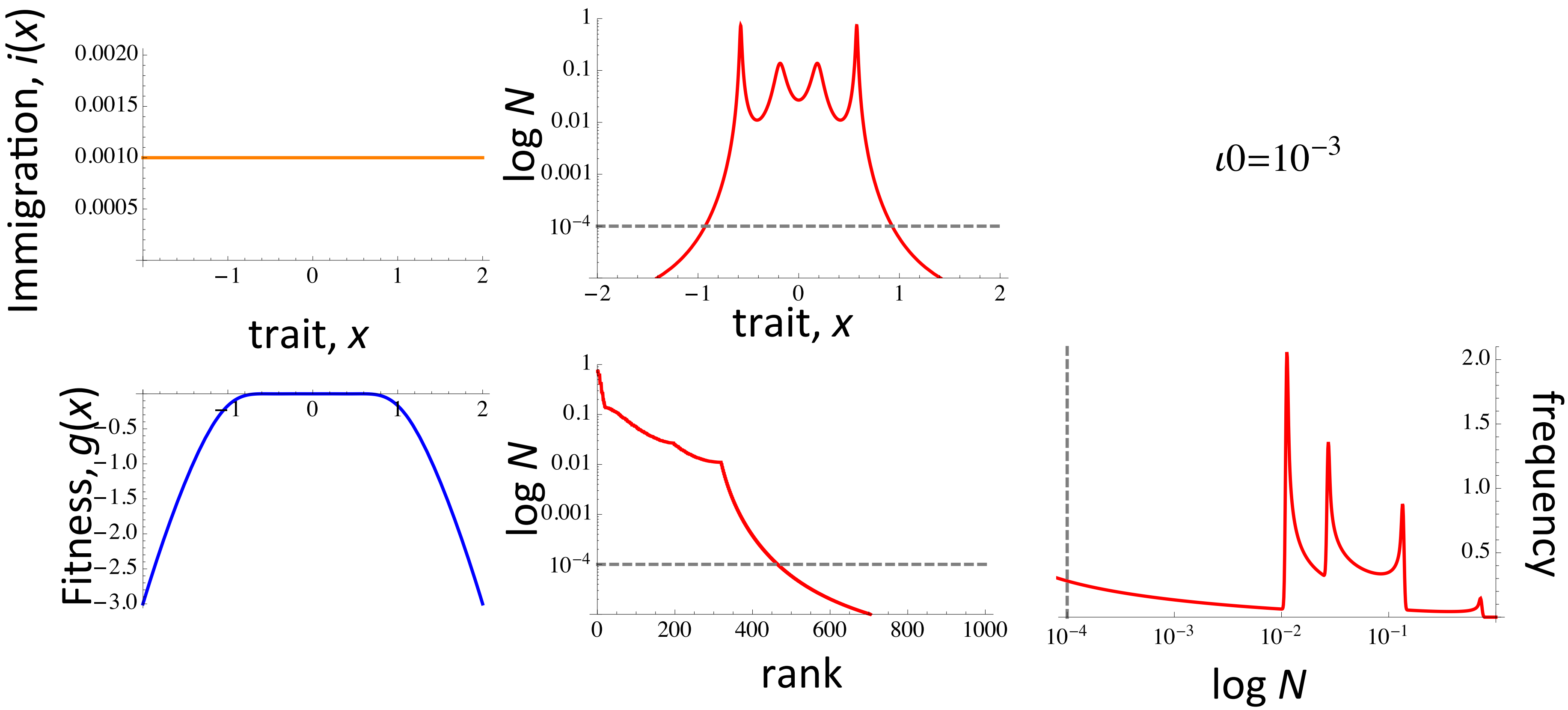
Model 3: 4 Niches



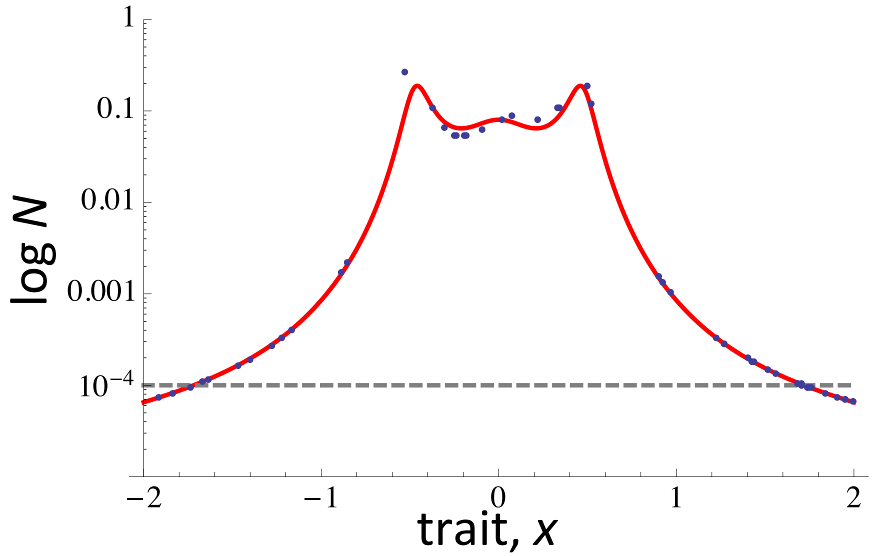
Model 3: 4 Niches

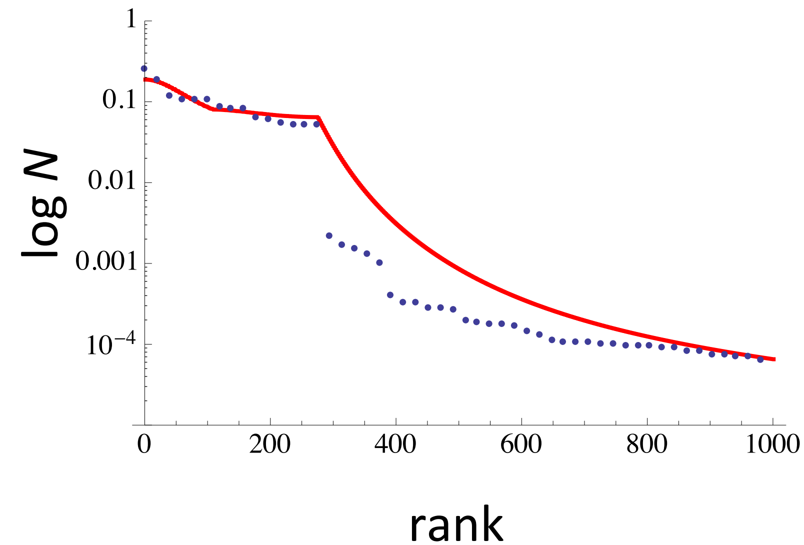


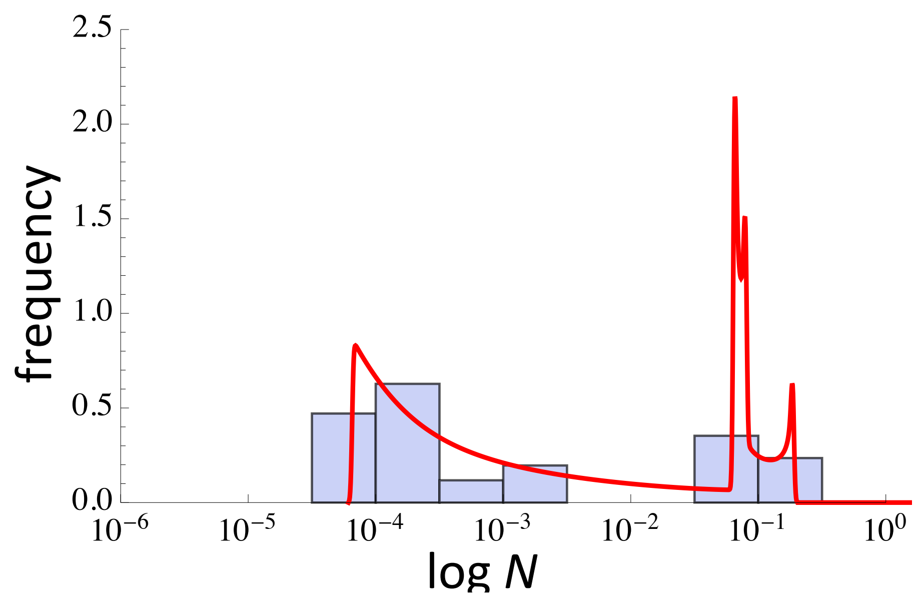
Model 3: 4 Niches



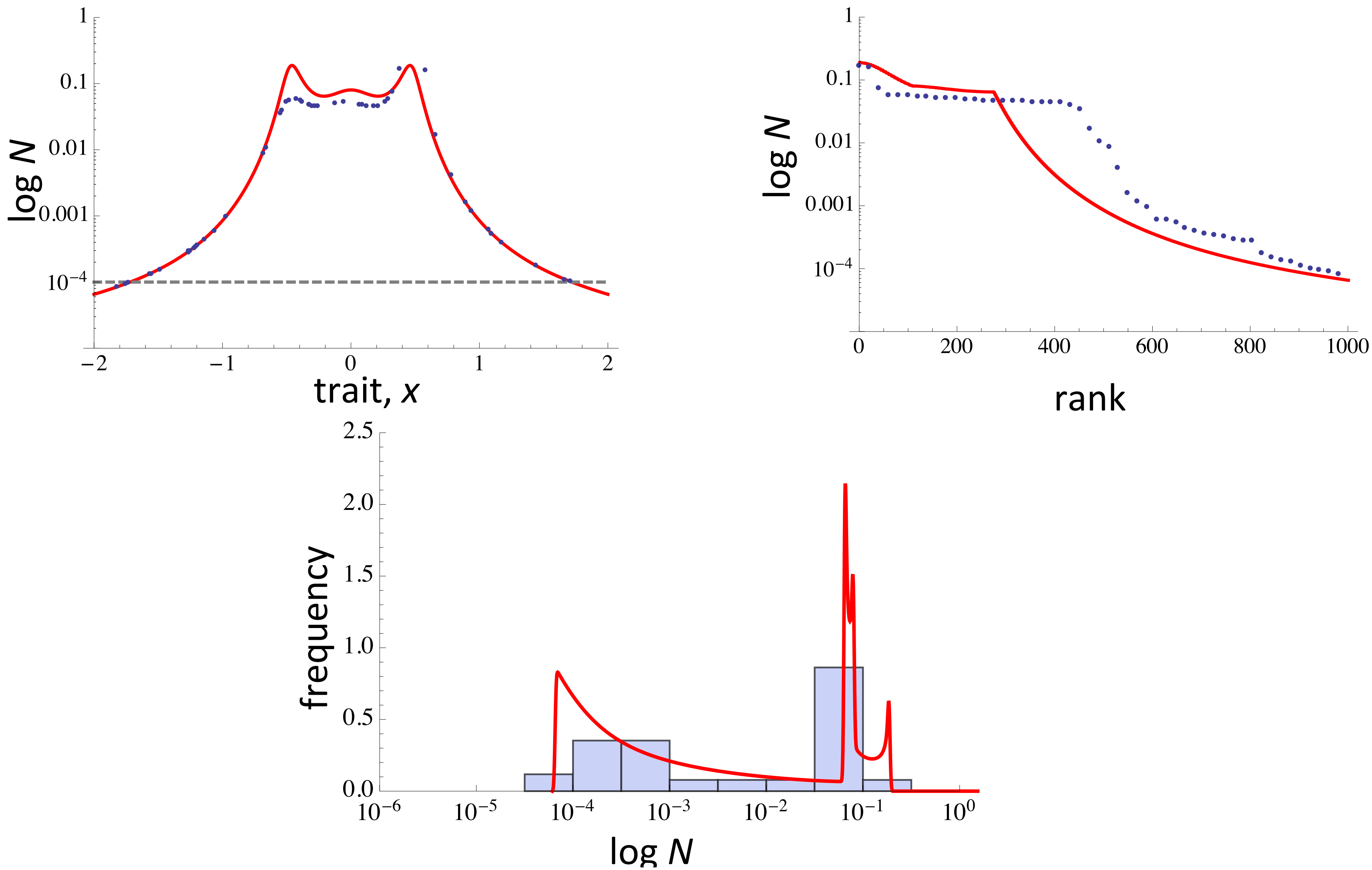
Back to Finite Species







Back to Finite Species



Conclusions

- Selection + immigration yields many realistic and complex SADs
- Increased immigration supports more rare species
- "Classic SADs" are not the only possibilities
- Multiple factors (local and regional) determine a species' abundance
- Complex patterns may be hard to detect in real communities
- Often bimodal: core / satellite species

"Because the ecosystem structure and function are, by design, emergent and not tightly prescribed, this modeling approach is ideally suited for studies of the relations between marine ecosystems, evolution, biogeochemical cycles, and past and future climate change."

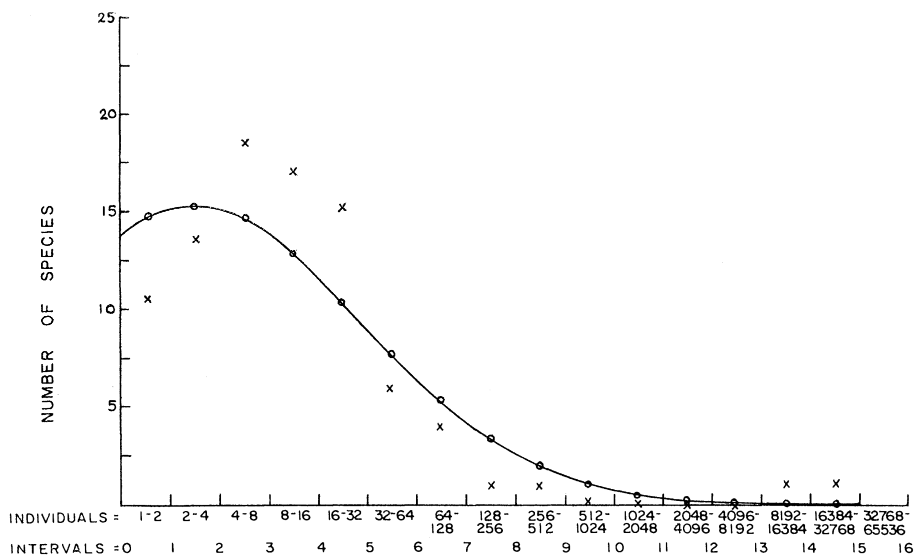
– Follows et al. 2007

Acknowledgments

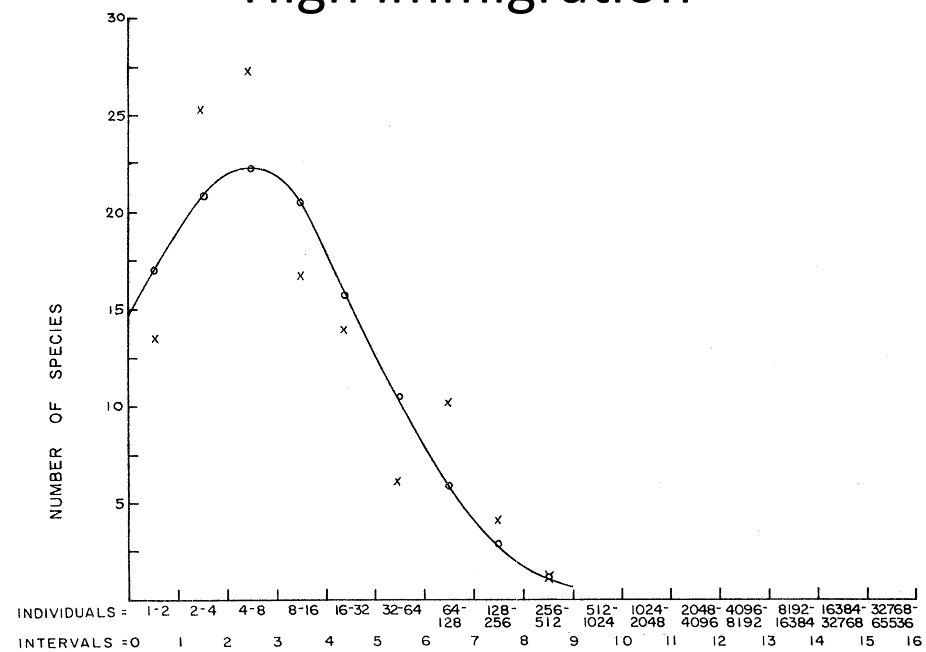
- NSF DEB & BioOc
- NCEAS
- James S McDonnell Foundation

Immigration Experiment

Low immigration



High immigration



(Patrick 1967 *PNAS*)