Resource Competition and Community Structure

OCEA0096-1 Modélisation des écosystèmes et des cycles biogéochimiques : Partim Ressources

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Resource Competition & Community Structure

Nutrient, light, food, ... Something that is required and consumed for growth.

Resource **Competition** & Community Structure

Different populations depends on the same resource

Resource Competition & **Community** Structure

Is cohabitation possible ? Under which conditions ?

Resource Competition & Community **Structure**

Abstract mathematical framework: Simple case, assumption, generalities.

Basics

What are Resource ?

A factor that

- has a given availability
- leads to higher growth as availability increases
- is consumed by the population(s)

Multiple factors can be considered as resources if they meet the above criteria for some range of other factors availability.

Consumption for Growth model

For n species competing for k resources :

$$\frac{d\,N_i}{N_i\,dt} = f_i(R_1, ..., R_k) - m_i \tag{1}$$

$$\frac{d\,R_j}{dt} = g_j(R_j) - \sum_{i=1}^{n} N_i f_i(R_1, ..., R_k) h_{i,j}(R_1, ..., R_k) \tag{2}$$

N_i population density of species i
R_j availability of resource j
f_i functional relationship between R_j and rate of population changes for N_i
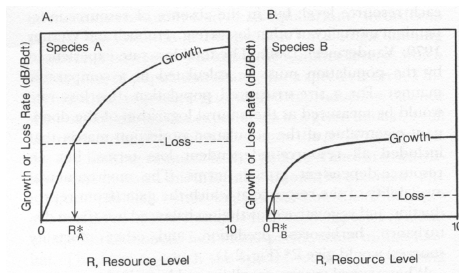g_j resource supply
m_i mortality rate for species i
$h_{i,j}$ amount of resource j required to create a new individual i

Assumptions

- pure competition : $\frac{\partial f_i}{\partial N_j} = 0$
- resources are not interactives : $\frac{\partial g_i}{\partial R_j} = 0$ for $i \neq j$
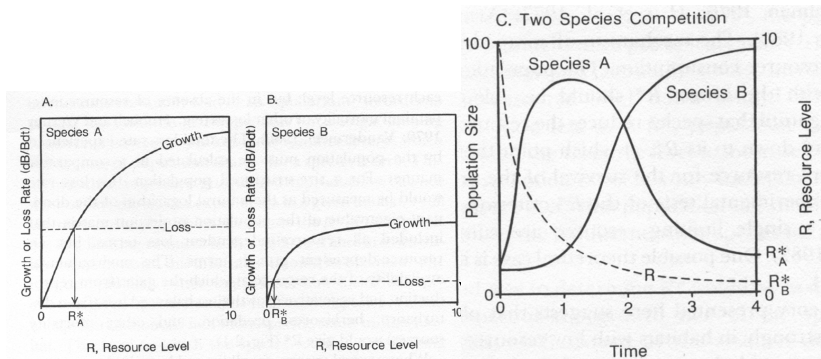
One resource

One resource

$$\frac{1}{N}\frac{\partial N}{\partial t} = f(R) - m \tag{3}$$

$$f(R*) = m \Rightarrow \frac{\partial N}{N \partial t} = 0 \tag{4}$$

R^*

The resource level for which growth $=$ mortality.

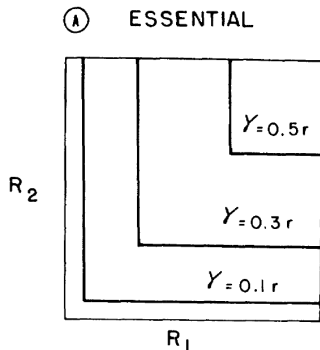# One resource

R^*

The resource level for which growth $=$ mortality.

The R^* Theory

If only one resource, the species with the lower R* overcompetes the others.

Two resource

Growth Isoclines

In the "resource-space", the γ-growth isoline is the locus $f_i(R_1, R_2) = \gamma$

(A) ESSENTIAL

R_2

$Y_{=0.5r}$

$Y_{=0.3r}$

$Y_{=0.1r}$

R_1

Different shape for different type of resources
Note that γ is the reproduction rate without mortality.

Type of resources

Essential Resources I
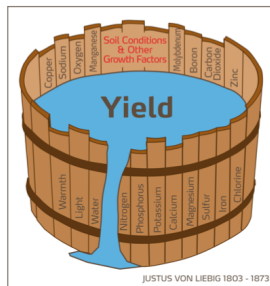
Justus von Liebig's law of the minimum, 1873 : *If one growth factor/nutrient is deficient, plant growth is limited, even if all other vital factor/nutrient are adequate .. plant growth is improved by increasing the supply of the deficient factor/nutrient.*

$$f(R_1, ..., R_k) = \min_{j=1,k}(f_j(R_j)) \qquad (3)$$

Essential Resources II

- No growth possible if one resource is lacking
- $f_i(R_1 = 0, R_2) \leq 0$ for all R_2 and $f_i(R_1, R_2 = 0) \leq 0$ for all R_1
- iso-growth lines never intersect the axis
- Examples
  - Nitrate, Phosphate, Light
- Counter-Example : $[NO_3^-]$ and $[NO_2^{2-}]$

(A) ESSENTIAL

R_2

$Y = 0.5 r$

$Y = 0.3 r$

$Y = 0.1 r$

R_1
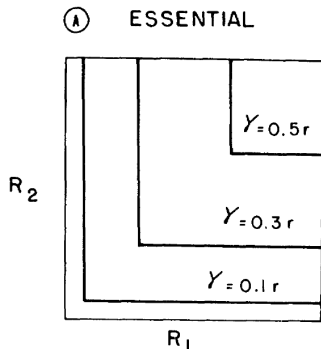
Essential Resources III
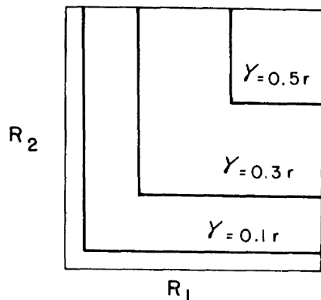
Figure 1: Noninteractive Essential
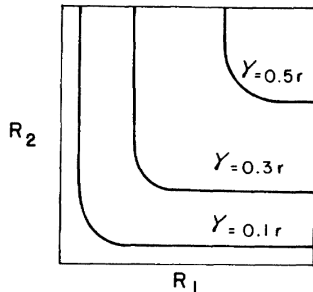
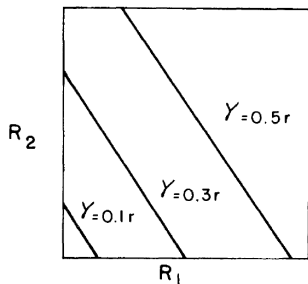**Figure 2:** Interactive Essential

Substitutable Resources

- Any resources can support growth on its own
- $f_i(R_1 = 0, R_2) > 0$ for some R_2 and $f_i(R_1, R_2 = 0) > 0$ for some R_1
- iso-growth lines intersect the axis
- Examples
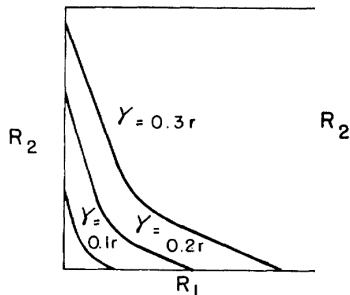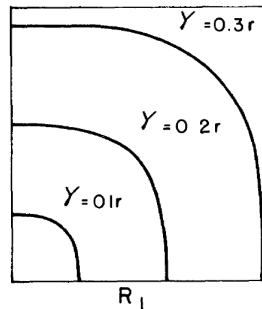 - Herbivorous and carnivorous diet
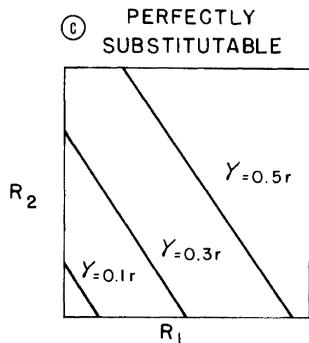
(c) PERFECTLY SUBSTITUTABLE

R_2

R_1

$Y_{=0.5r}$

$Y_{=0.3r}$

$Y_{=0.1r}$

Substitutable Resources
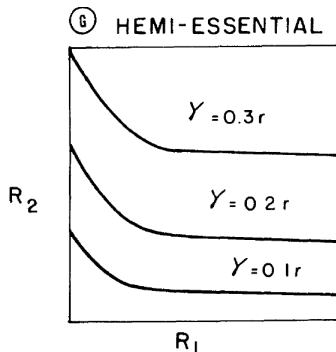
Hemi-essential Resources

- One is essential and can support growth on its own , the other can only partly substitute
- $f_i(R_1 = 0, R_2) > 0$ for some R_2 and $f_i(R_1, R_2 = 0) \leq 0$ for all R_1
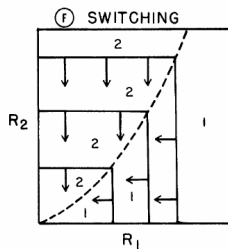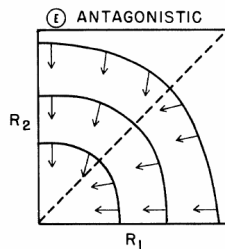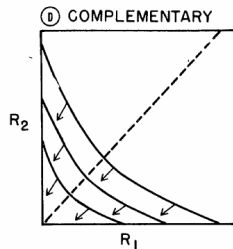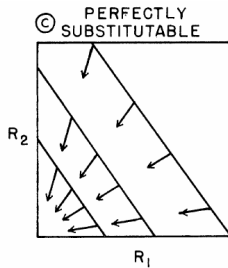- iso-growth lines intersect one axis

Ⓖ HEMI-ESSENTIAL

R_2

$Y = 0.3 r$

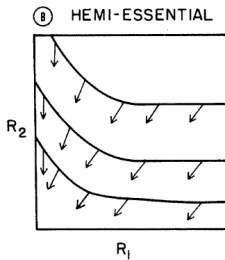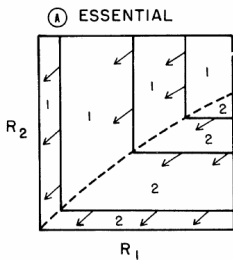$Y = 0.2 r$

$Y = 0.1 r$

R_1

Dynamics

Consumption vectors

- Represents changes in ressources following consumption for growth
- Depends on
  - Consumption(s) per individuals ($\rightarrow$ Characterisitc to species)
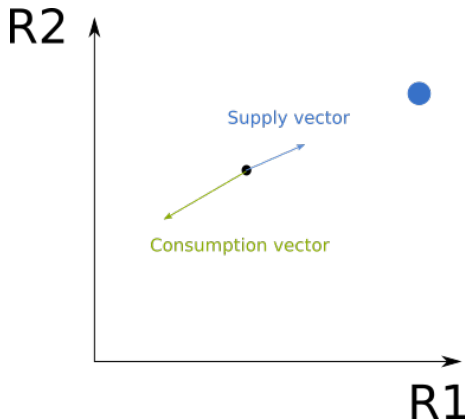 - Number of individuals
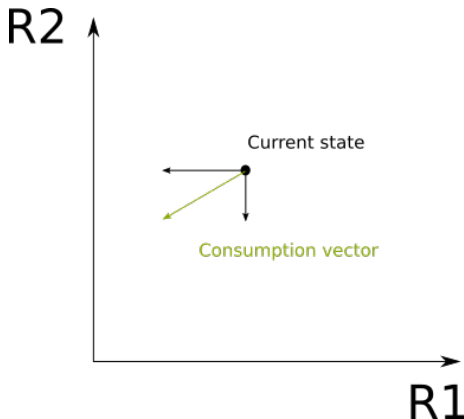
Consumption vectors

Supply vectors

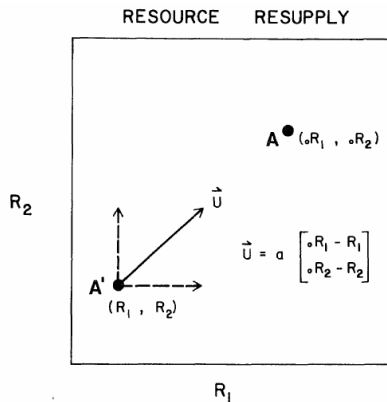- Represents the environmental supply of ressources
- Depends on
  - The environment (Supply point)
  - The actual state of resources

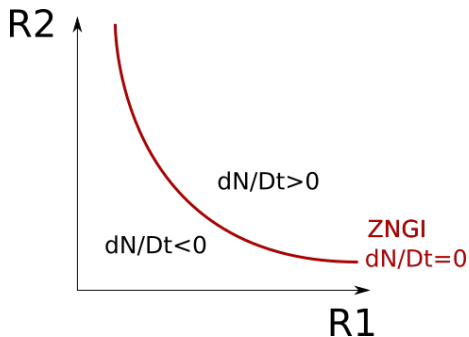# Supply vectors

- Constant "string" toward supply point
- $\frac{dR_1}{dt}|_{supply} = a(R_{1,0} - R_1)$ & $\frac{dR_2}{dt}|_{supply} = a(R_{2,0} - R_2)$

One species, two resources

ZNGI

Zero Net Growth Isoline: where $\gamma=$ mortality

One species, two resources
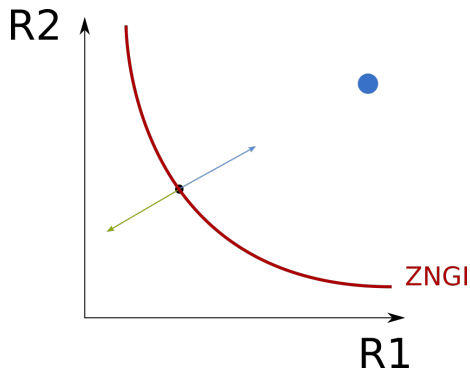
Equilibrium point: One species, two resources
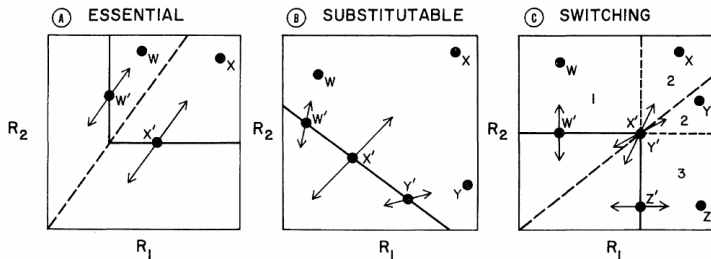
Equilibrium points set by

- Consumption vectors
- Supply point
- ZNGI

Equilibrium Points

Examples in R with TILMAN1 "Tilman_1species.R"

- Present the program
- iso-growth
- Consumption vectors
- Supply Vectors
- Equilibrium points (show that supply below ZNGI prohibits survival)

Competition

2 Species : competition
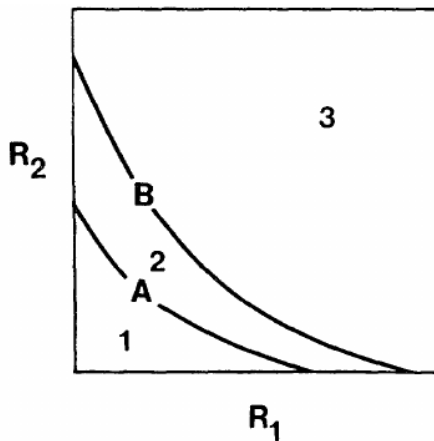
Question

What's the outcome of supply point in 1, 2, 3 ?

2 Species : competition
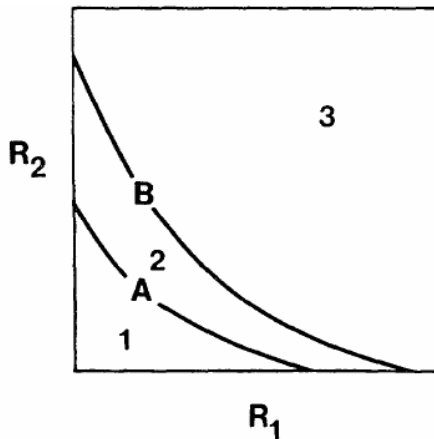
1 Neither species able to survive
2 Only A can survive
3 A removes B by competion

2 Species : competition
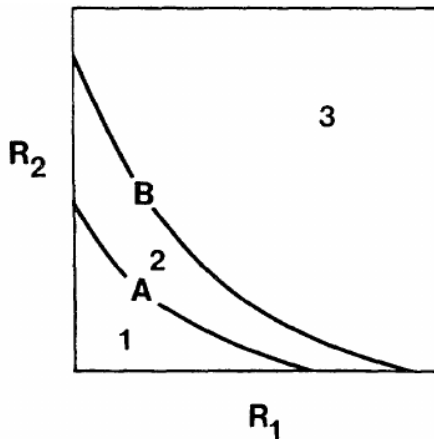
Question

Which condition for coexistence ?

2 Species : competition
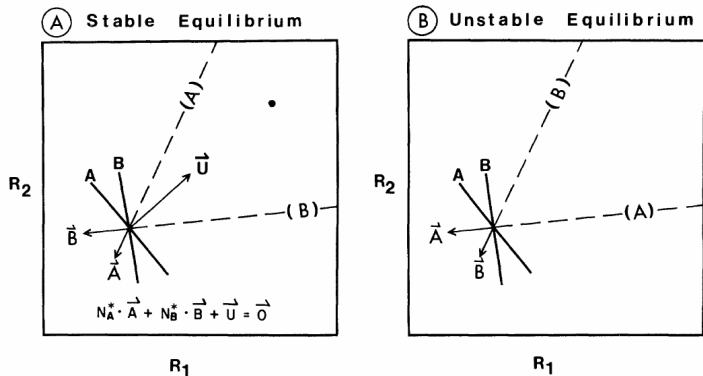
- Crossings of the ZNGI defines cohabitation equilibrium point
- Might be stable or unstable

2 Species : competition
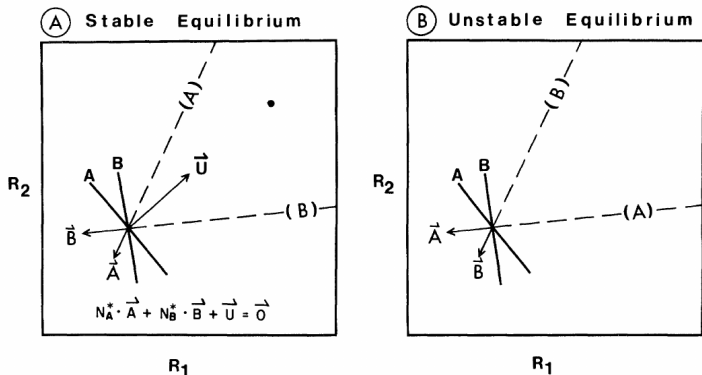
Trade-offs

In resource poor environments, organisms allocate resource for efficiency on one resource → less efficiency regarding other resources.
Example : Leaves or roots ?

2 Species : competition
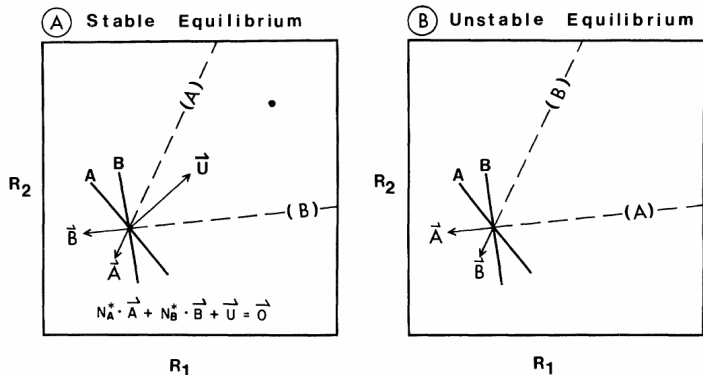
Stable if

1. Each species consumes proportionately more of the resources that limits its own growth
2. The amounts of resource consumed by individual changes only slightly in response to small changes in R_j

2 Species : competition

Case 1: A dominant

Case 2: B dominant

Case 3: Stable Equilibrium

Case 4: Unstable Equilibrium
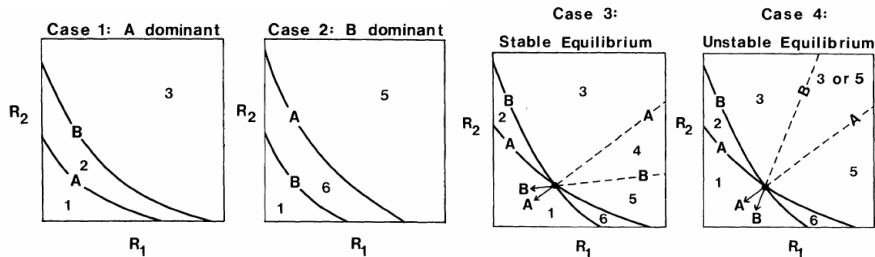
1 Neither species able to survive

2 Only A can survive

3 A removes B by competition

4 Coexistence

5 B removes A by competition

6 Only A can survive

2 Species : Competition
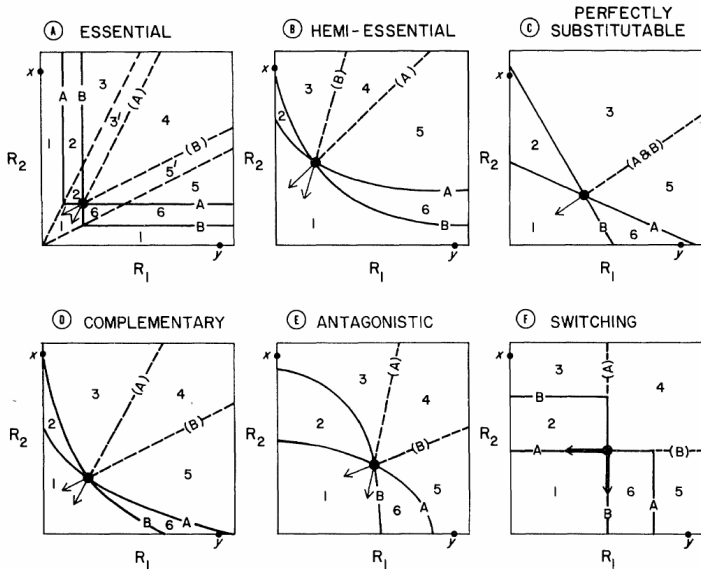
2 Species : Competition

Examples in R with TILMAN1 "Tilman_2species.R"

- Trajectories
- Equilibrium points (show that cohabitation conditions depends on resource supply point)

Resource spatial gradients
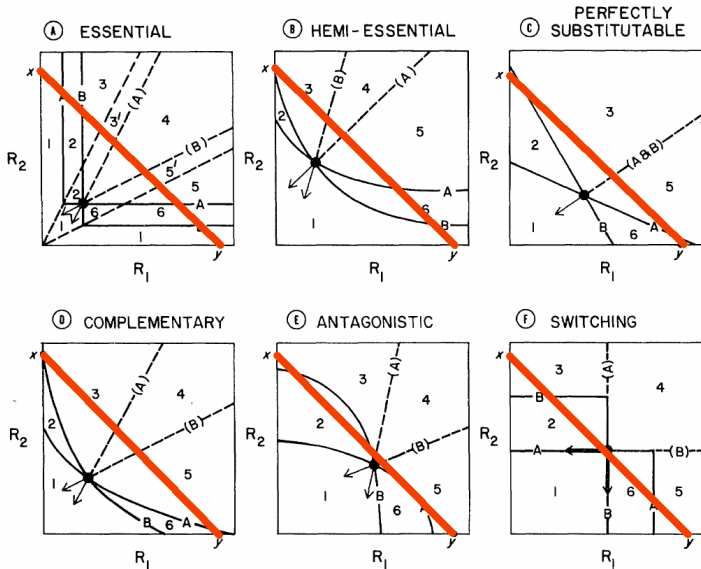
Resource spatial gradients
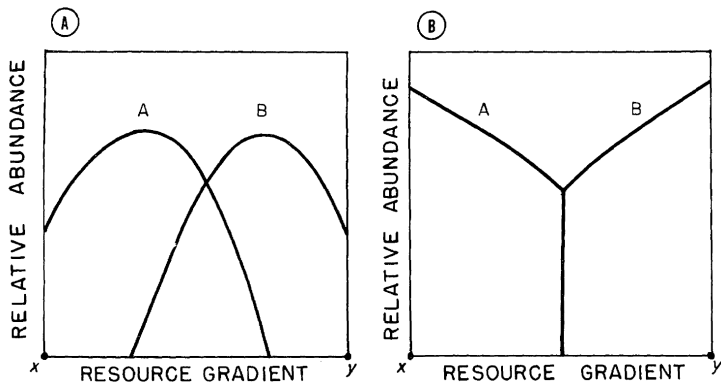
Mixed Resource types
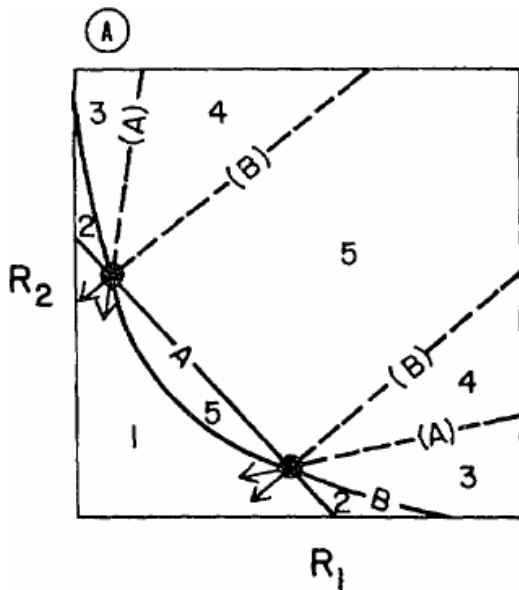
Mixed Resource types
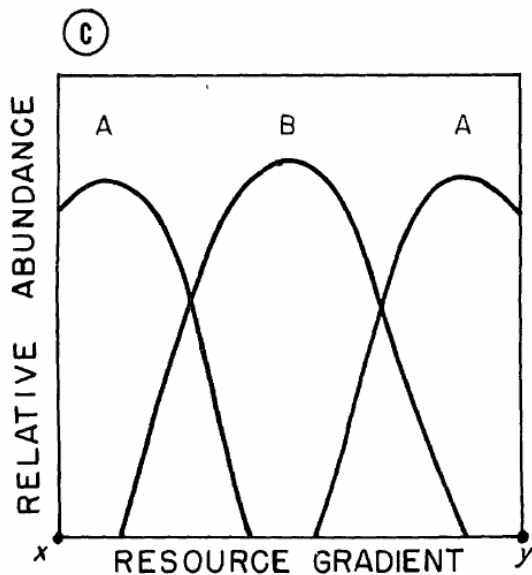
Multi Species
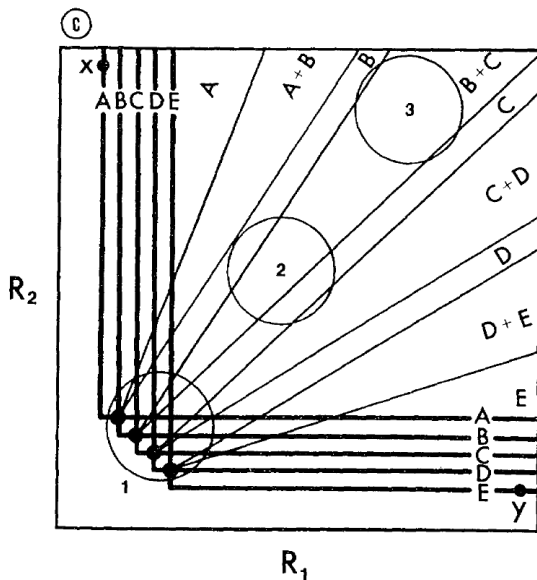
Multi Species
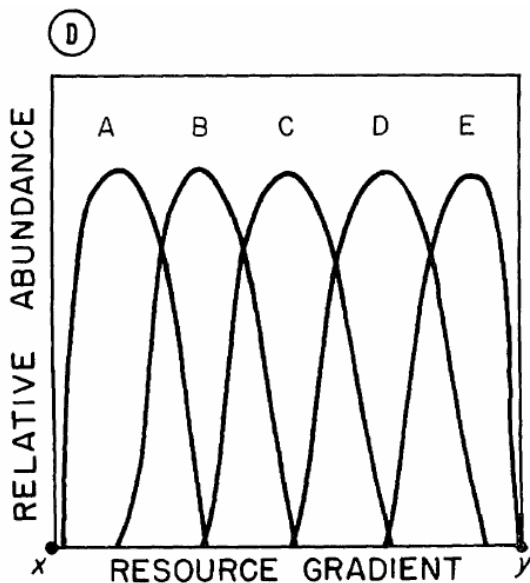
Multi Species
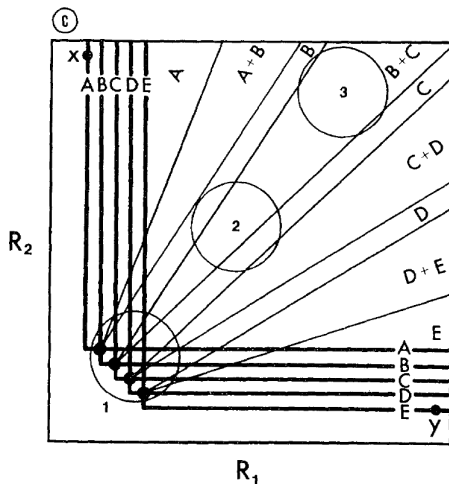
Heterogeneity

Variations in resource RATIOS supports species variety

Experiments

A Critical Review of Twenty Years' Use of the Resource-Ratio Theory

Thomas E. Miller,[1,*] Jean H. Burns,[1,†] Pablo Munguia,[1,‡] Eric L. Walters,[1,§] Jamie M. Kneitel,[1,∥] Paul M. Richards,[1,#] Nicolas Mouquet,[2,**] and Hannah L. Buckley[1,††]

Table 1: Predictions from the resource-ratio theory, based on studies that cite Tilman (1980, 1982)

Prediction

1. The species that can survive at the lowest levels of a limiting resource will be the best competitor for that resource
2. Species dominance varies with the ratio of the availabilities of two resources
3. The number of coexisting species is less than or equal to the number of limiting resources
4. The vector describing the resource supply rate to an environment will affect whether competing species coexist and, if not, which species will competitively exclude the other
5. The vectors describing the consumption rates of resources for two species will determine whether competing species coexist or, if not, which species will dominate competitively
6. Trade-offs in resource use must occur for species to coexist along a gradient of ratios of the availabilities of two resources
7. The highest diversity of competing species will occur at an intermediate ratio of the availabilities of two resources

Table 2: Number of individual tests of the seven predictions of the resource-ratio theory listed in table 1

Prediction number	Test adequate?			
	Yes; prediction supported?		No	Total
	Yes	No		
1	8	5	9	22
2	13	3	31	47
3	1	1	1	3
4	5	1	5	11
5	2	0	1	3
6	2	1	2	5
7	0	0	10	10
Total	31	11	59	101

Note: The 101 overall tests were published in 68 different articles. Tests were classified as adequate if a clear and sufficient experimental design and appropriate replication were used. Studies were classified as supporting the prediction on the basis of our interpretation of the results presented in the corresponding article.

Experiments
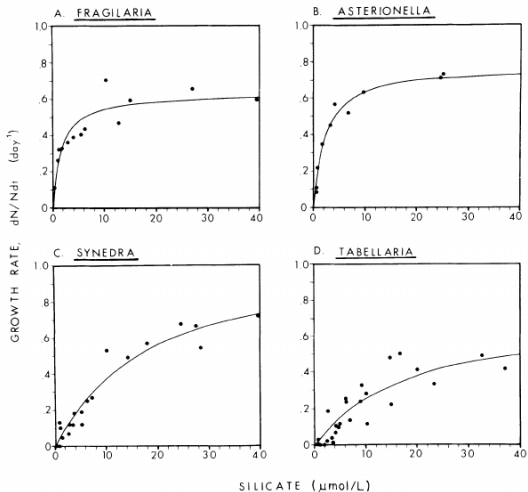
Experiments

TABLE 1. Silicate and phosphate kinetic parameters for four Lake Michigan diatoms. K is the half saturation constant; r the maximal growth rate; Q the quotient; and R^* the calculated amount of nutrient required to grow at $D = 0.25$ d^{-1}. The 95% confidence intervals are in parentheses.

| Species	r (d^{-1})	K (μmol/L)	Q (μmol/cell)	R^* (μmol/L)
Silicate-limited experiments				
Fragilaria	0.62 (.54–.70)	1.5 (.7–2.5)	9.7×10^{-7}	1.0 (.7–1.5)
Asterionella	0.78 (.72–.84)	2.2 (1.6–2.9)	1.5×10^{-6}	1.0 (.8–1.3)
Synedra	1.11 (.87–1.36)	19.7 (12.7–30.3)	5.8×10^{-5}	5.7 (4.0–8.3)
Tabellaria	0.74 (.44–1.04)	19.0 (9.0–41.7)	6.3×10^{-6}	9.7 (5.3–23.0)
Phosphate-limited experiments				
Fragilaria	0.80 (.72–.88)	0.011 (0–.024)	4.7×10^{-8}	.005 (.002–.008)
Asterionella	0.59 (.53–.64)	0.006 (.002–.011)	2.6×10^{-8}	.004 (.003–.007)
Synedra	0.65 (.61–.69)	0.003 (0–.015)	1.1×10^{-7}	.002 (.001–.006)
Tabellaria	0.36 (.30–.43)	0.008 (0–.04)	1.9×10^{-7}	.02 (.006–.07)
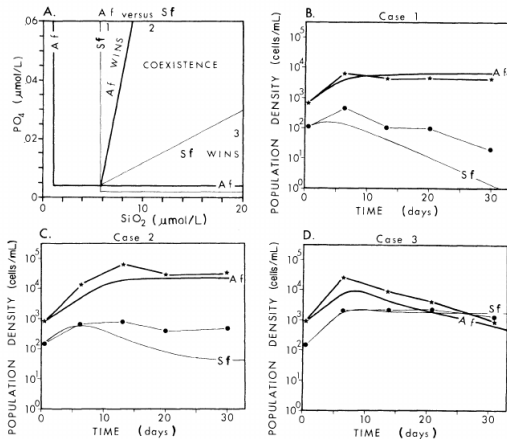
Experiments

FIG. 4. (A) The predicted outcomes of resource competition between *Asterionella formosa* (Af) and *Synedra filiformis* (Sf).

(B) Observed results of competition experiments for Case 1 (low silicate) are shown with stars for Af and dots for Sf. A broken line joins the observed points. The continuous thick line, labeled Af, and the continuous thin line, labeled Sf, show the predicted population dynamics.

(C) The same notation as above is used for Case 2 (intermediate concentrations of SiO₂ and PO₄).

(D) The same notation as above is used for Case 3 (low PO₄ experiments).
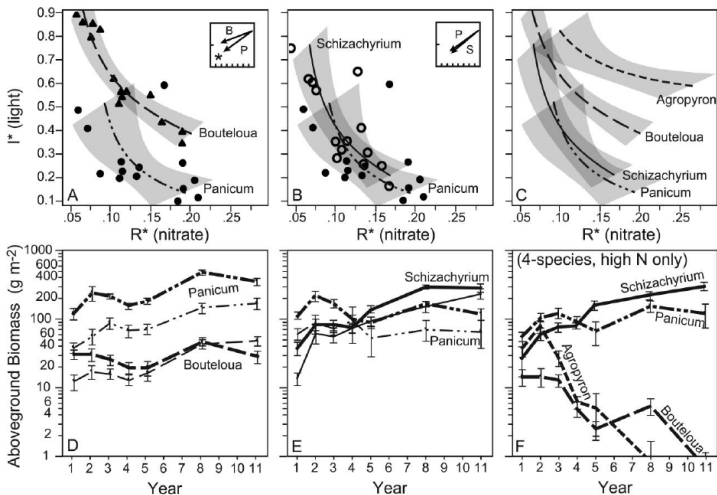
Experiments

Figure 3: Ray Dybzinski and David Tilman, 2007, *The American Naturalist*

Propositions of investigations

- Extend R framework for two species, illustrate cases, Monte Carlo to visualize coexistence.
- Mixotrophy/Allelopathy
- Heterogeneity
- Investigate Plankton dominance in BS model outputs
- Fit and identify growth parameters for various species.

RESOURCES: A GRAPHICAL-MECHANISTIC APPROACH TO COMPETITION AND PREDATION

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In such circumstances the question as to the causes of the victory of certain forms over others presents itself in the following aspect: By aid of what morphological and physiological advantages of the process of the individual does one plant suppress another? [G.F. Gause (1934)].

Recent application : http://www.biogeosciences.net/14/2877/2017/