

# Ecology 8310

## Population (and Community) Ecology



### Coexistence in a competitive guild

- Hutchinson
- Resource heterogeneity
- Patch dynamics / IDH
- Predation
- Resource fluctuations
- **Neutral Theory**
- Interference competition
- **Chesson: stabilizing and equalizing mechanisms**

# THE AMERICAN NATURALIST

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Vol. XCIII

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No. 870

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HOMAGE TO SANTA ROSALIA  
*or*  
WHY ARE THERE SO MANY KINDS OF ANIMALS?\*

G. E. HUTCHINSON

Department of Zoology, Yale University, New Haven, Connecticut



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The American Naturalist

May-June, 1961

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## THE PARADOX OF THE PLANKTON\*

G. E. HUTCHINSON

Osborn Zoological Laboratory, New Haven, Connecticut

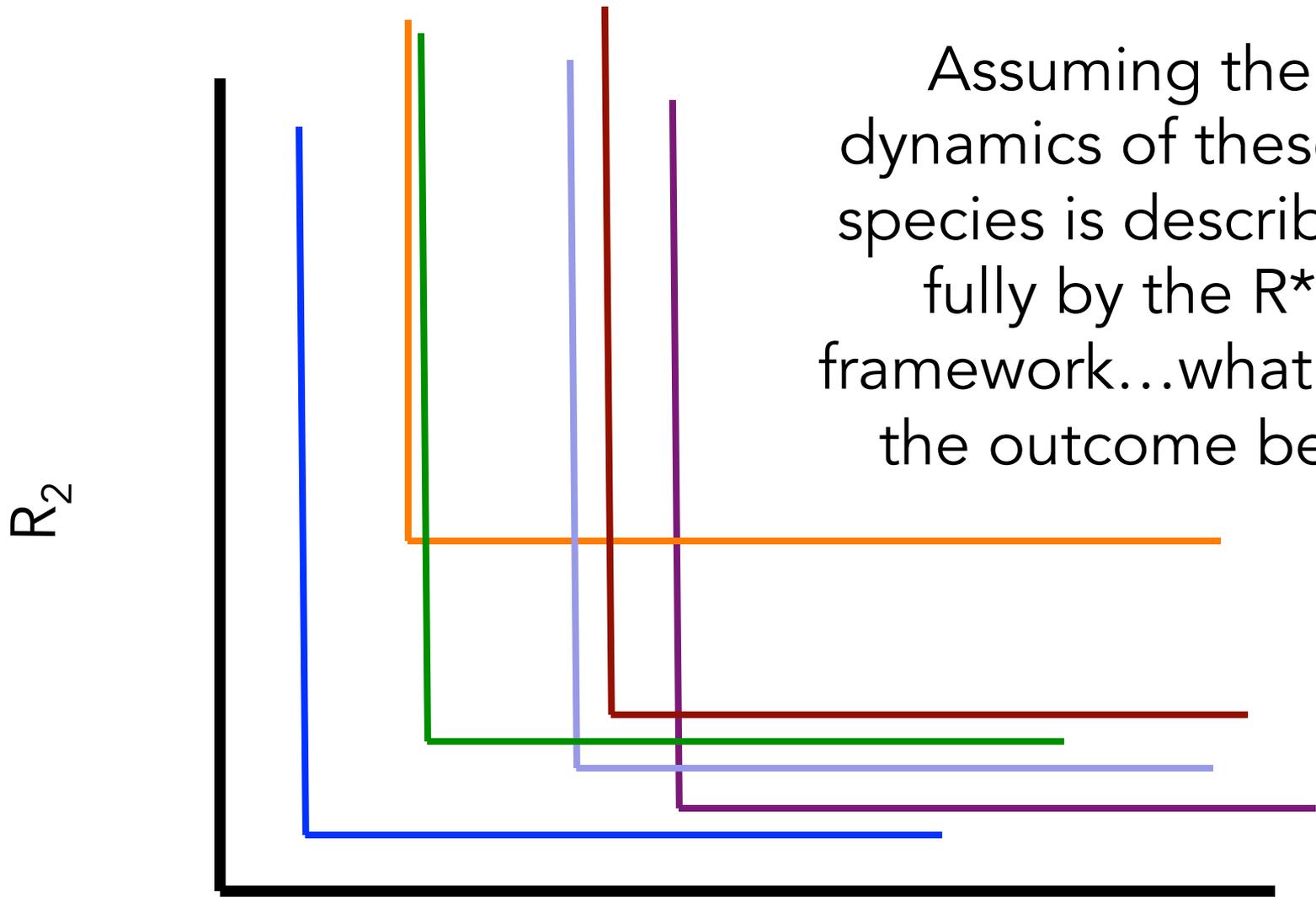


"Vast numbers of Corixide were living in the water .... These ideas finally prompted the very general question as to why there are such an enormous number of animal species."

Let's explore a few of those issues for a guild  
of competitors...

- 1) Resource partitioning (niche divergence):  
"intra>inter"
- 2) Environmental heterogeneity
- 3) Disturbance
- 4) Interference competition

# Many competitors:



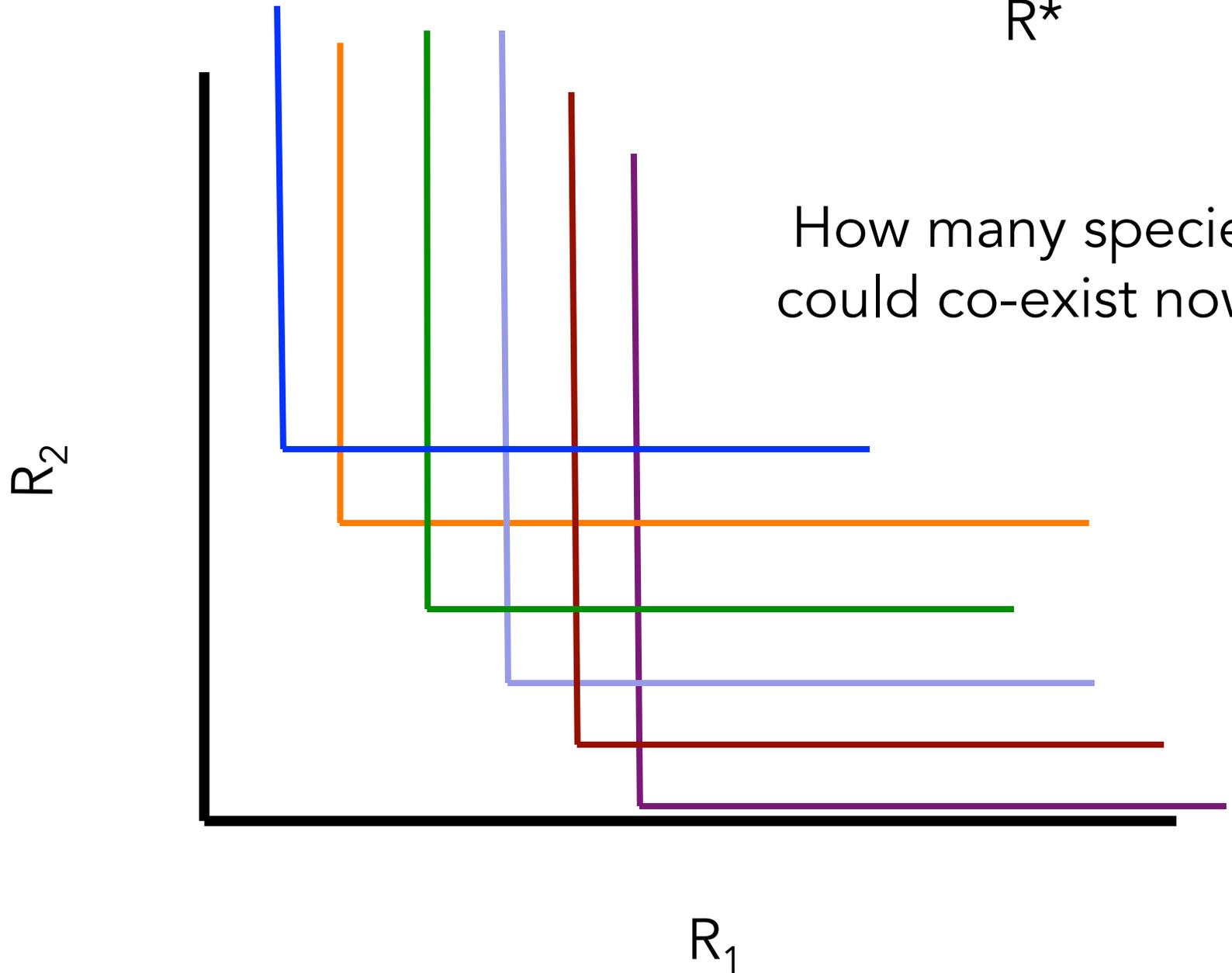
Assuming the dynamics of these 6 species is described fully by the  $R^*$  framework...what will the outcome be?

$R_1$

How can we modify this picture to facilitate coexistence?

Many competitors:

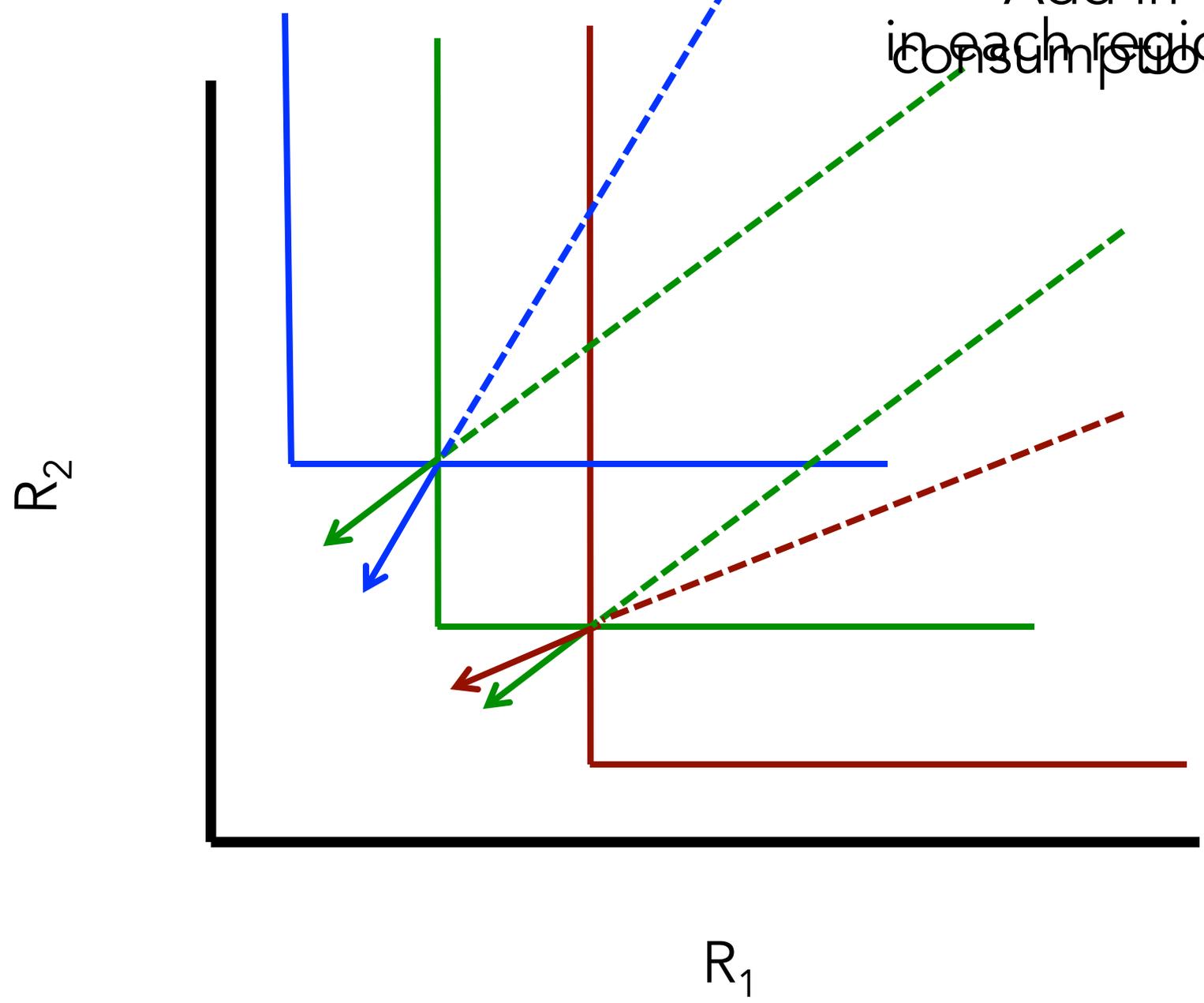
Assume a trade-off in  $R^*$



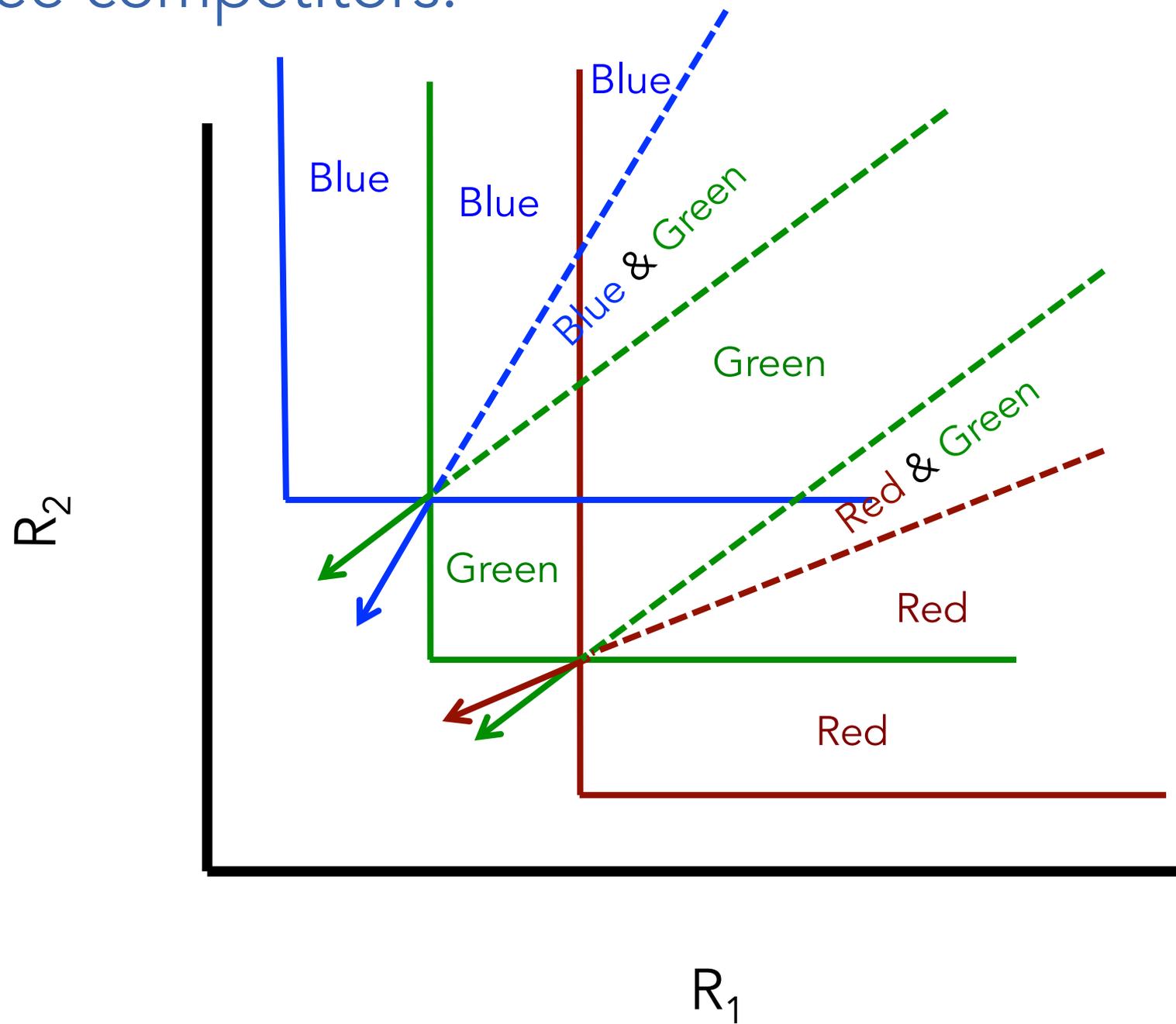
We need to specify consumption (and supply)

Three competitors:

What is the outcome  
Add in  
in each region?  
consumption..?

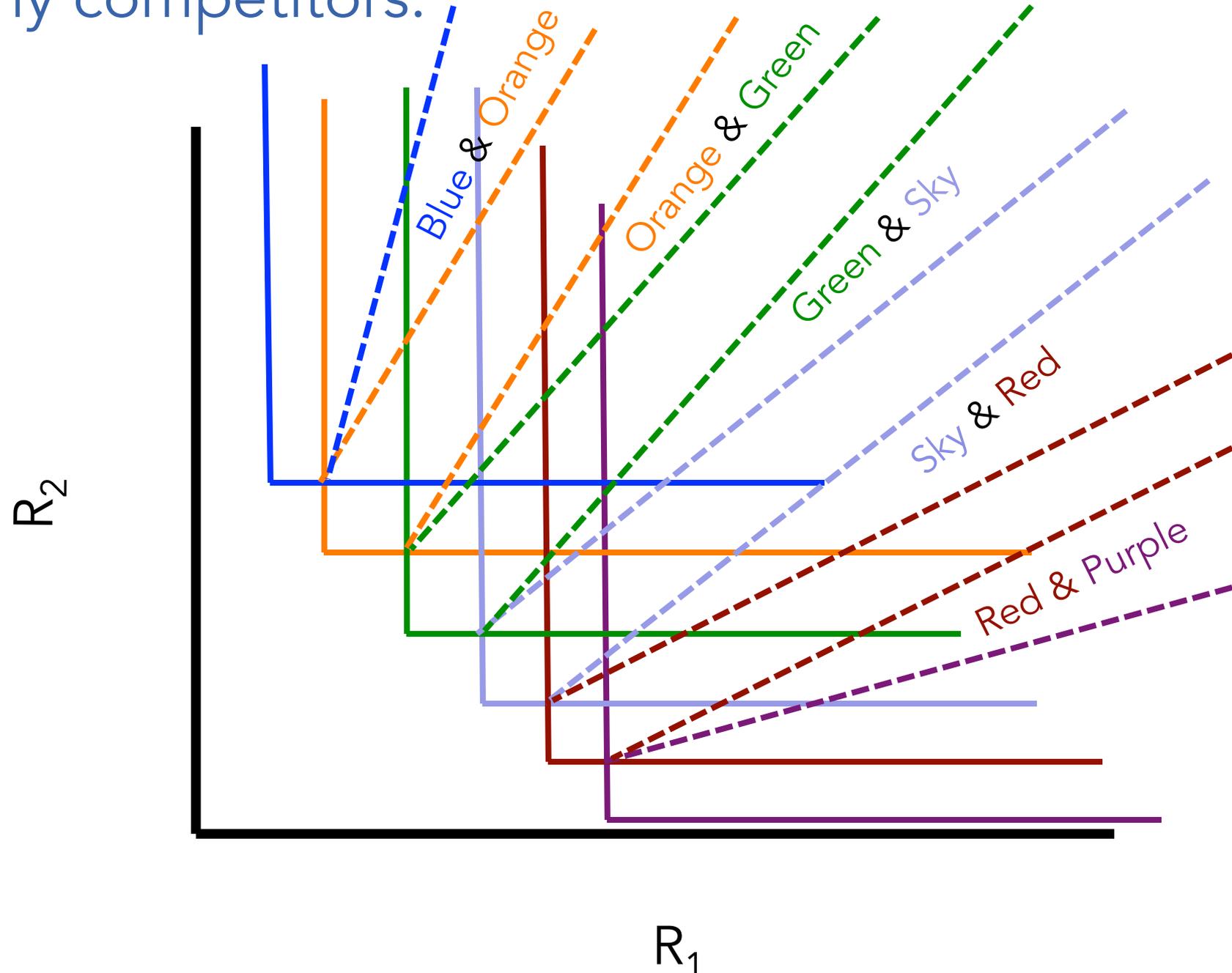


Three competitors:



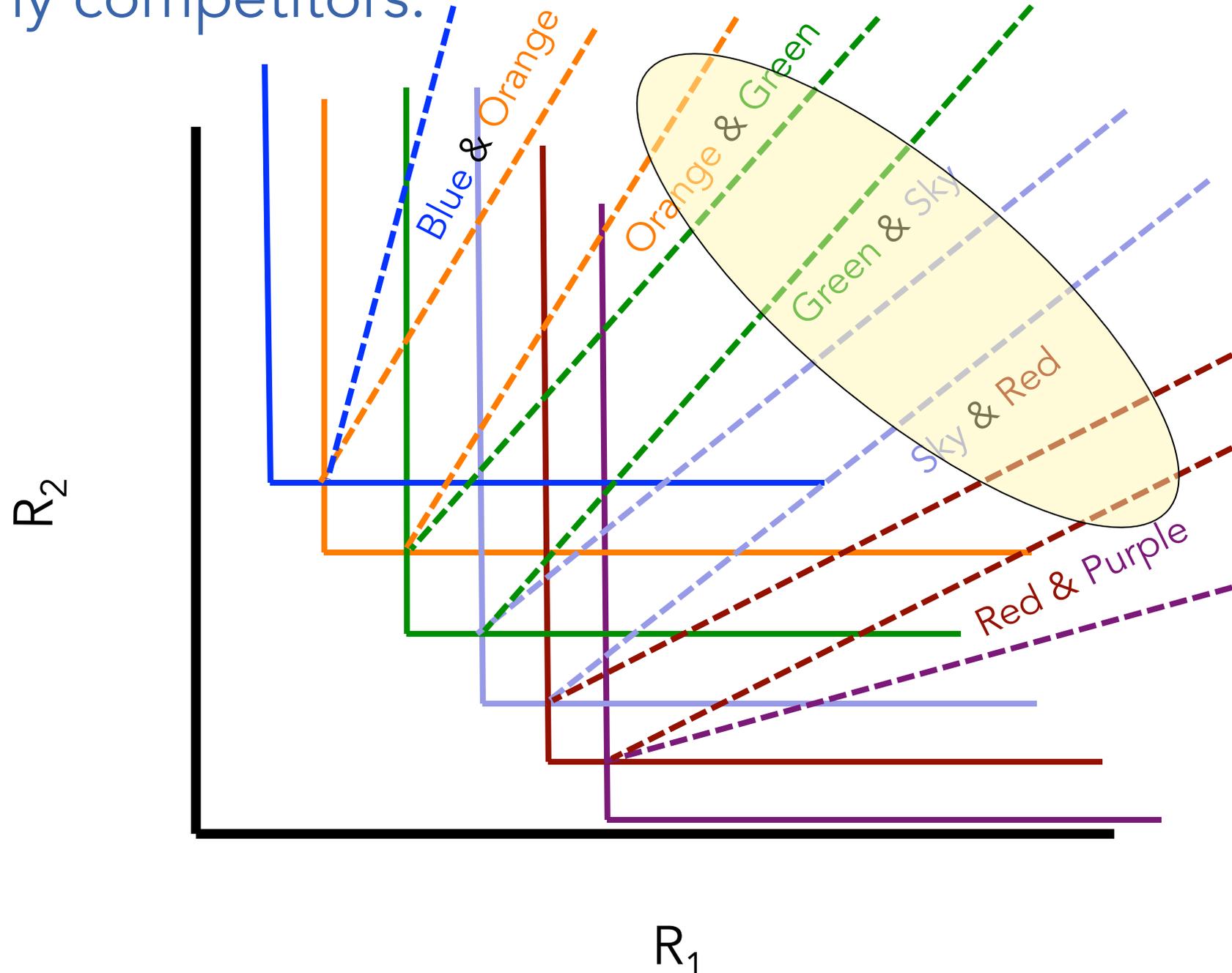
- Trade-off in  $R^*$ s
- Correlation between  $R^*$ s and consumption  
(i.e., better competitor for a resource,  
consumes relatively less of that resource)
- But, still only get (at most) 2 coexisting  
consumers

Many competitors:



What if a region is heterogeneous in  $S$ ?

Many competitors:



What if patches don't come to a competitive equilibrium?



Paradox:

1 limiting resource (Nitrogen)

Many species of plants (persisting together)

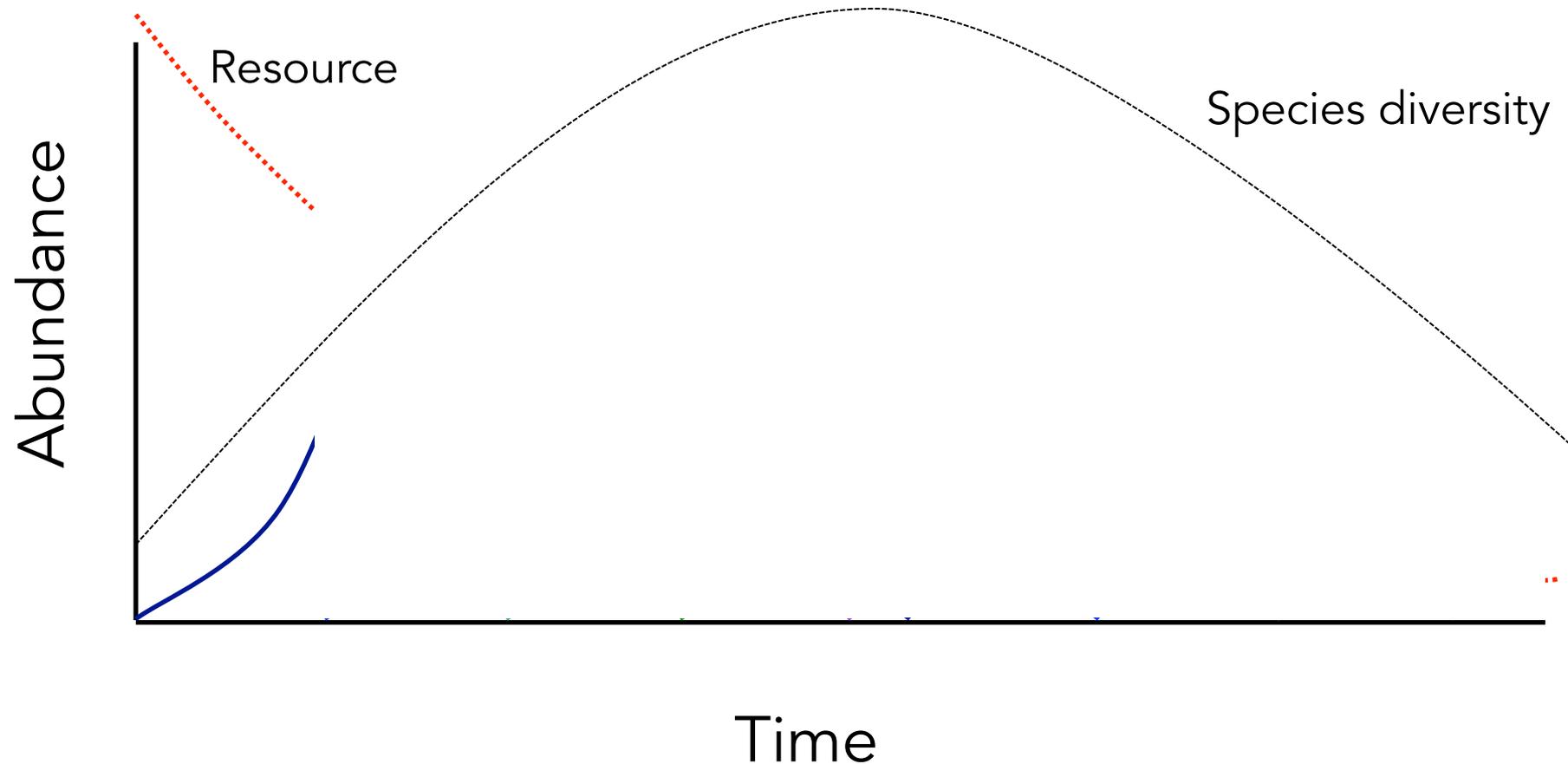
How is this possible?

# Patch dynamics:

1. Disturbances open up space.
  2. Good colonizers arrive first.
  3. Competition occurs as others colonize.
  4. One species wins (within that patch).
  5. "Losers" persist by colonizing recently disturbed sites.
- Trade-off b/w ' $R^*$ ' and colonizing ability

# With-in Patch:

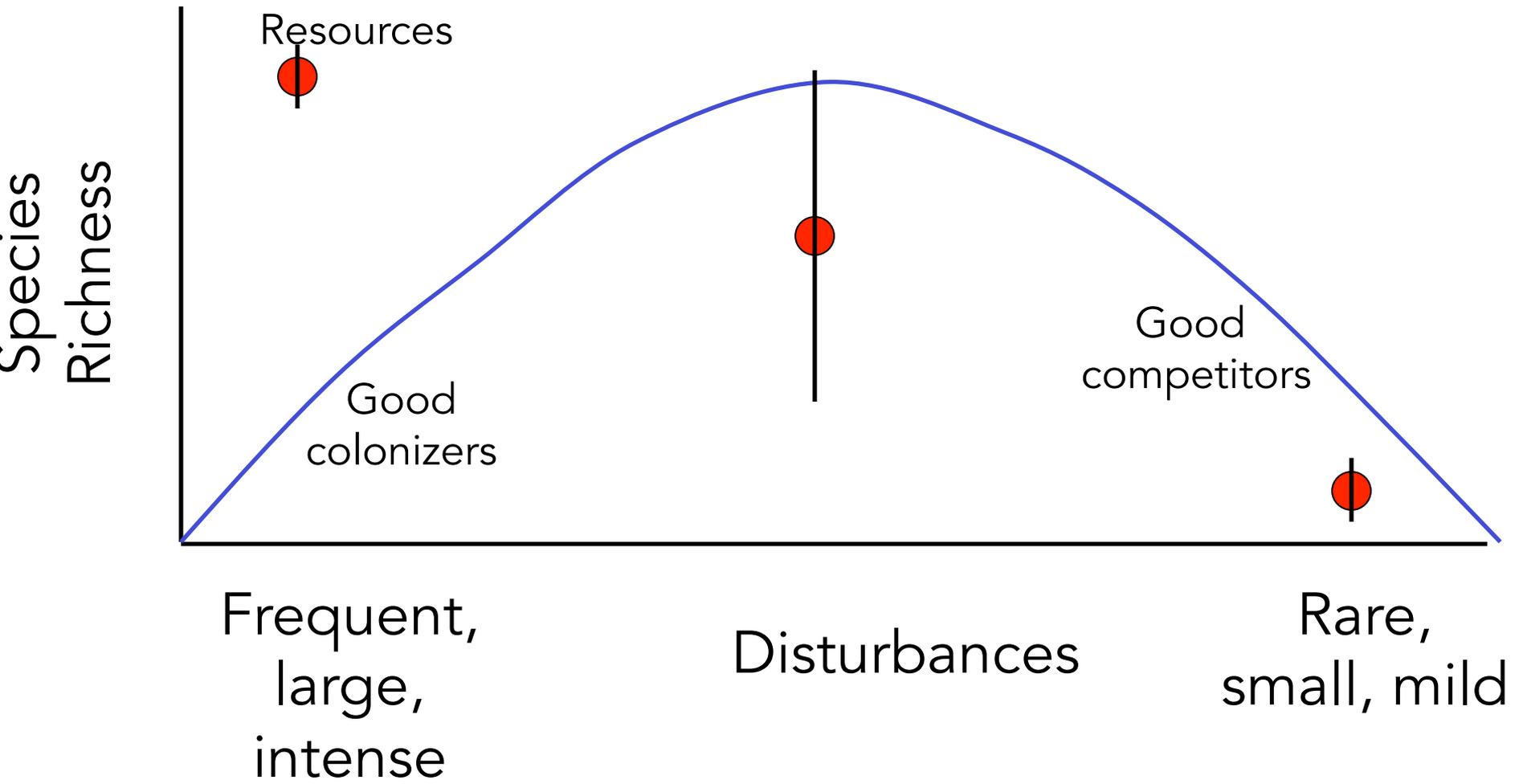
Let's look at one patch in detail:



Note: Richness increases then decreases with time

# Among-Patch:

Now look at a collection of patches (and vary disturbances) → mosaic:  
Intermediate Disturbance Hypothesis



Let's review Tilman's  
classic paper:

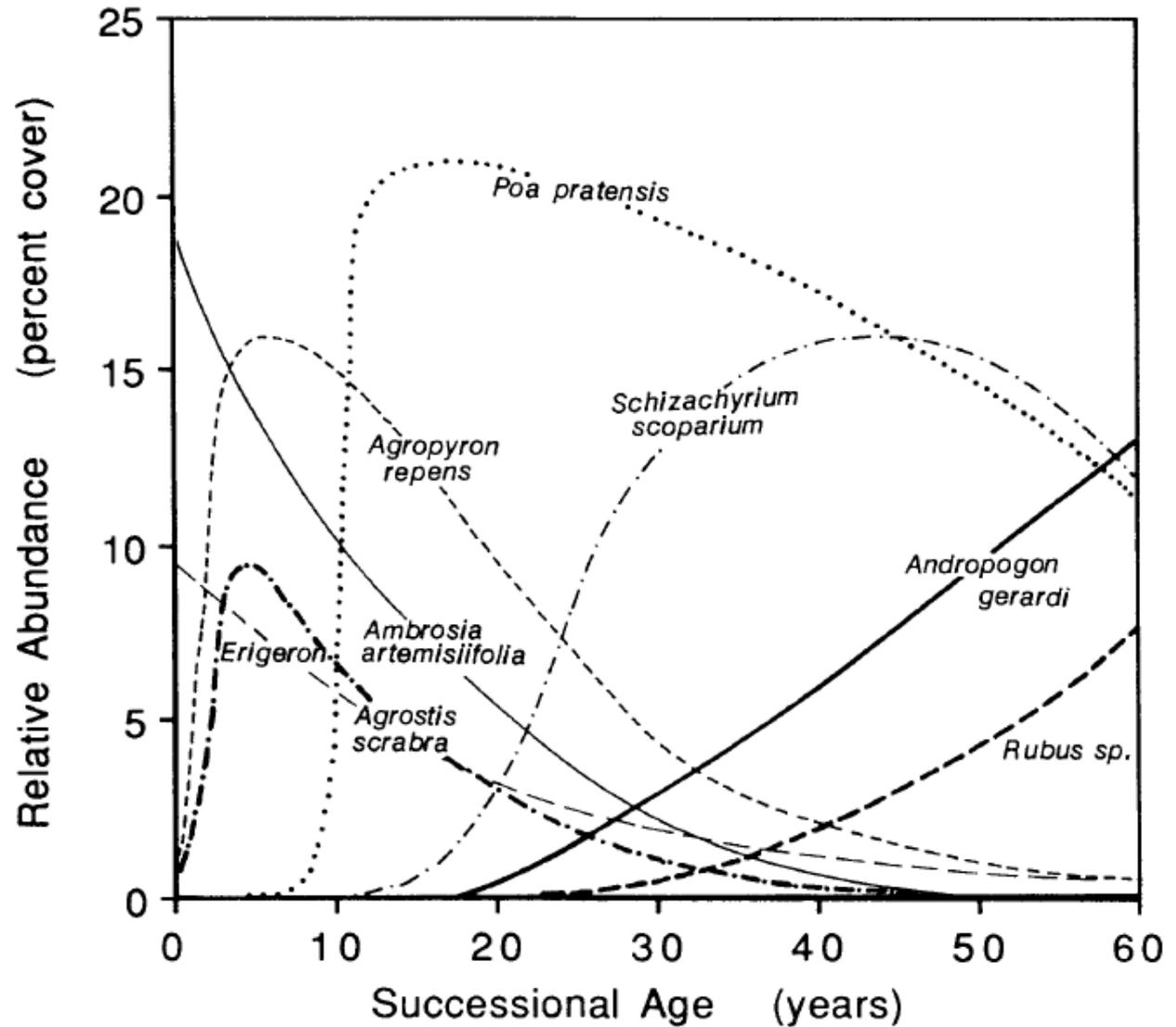
*Ecology*, 75(1), 1994, pp. 2–16  
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## COMPETITION AND BIODIVERSITY IN SPATIALLY STRUCTURED HABITATS<sup>1</sup>

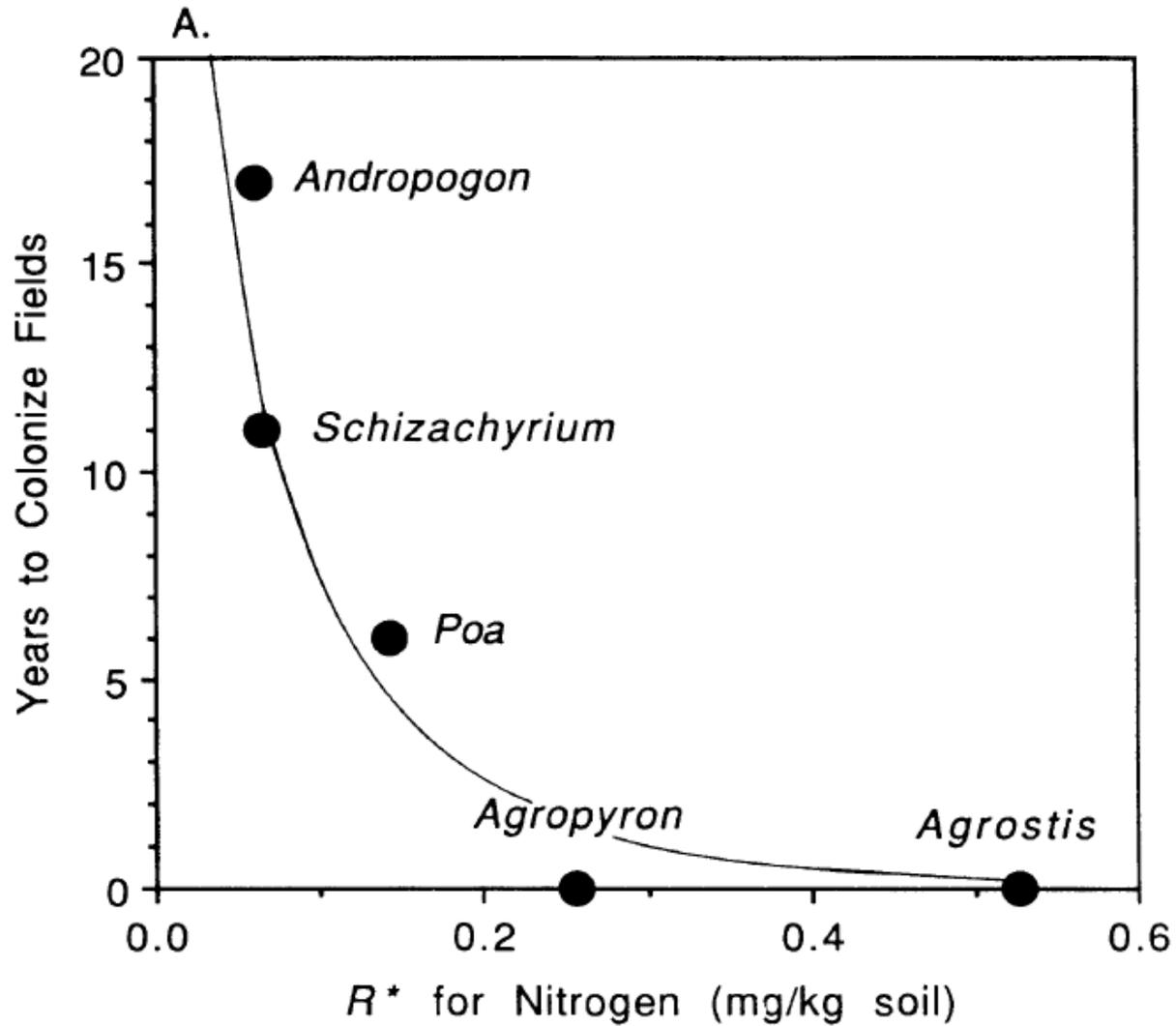
DAVID TILMAN

*Department of Ecology, Evolution, and Behavior, 1987 Upper Buford Circle,  
University of Minnesota, St. Paul, Minnesota 55108 USA*

# Successional patterns:

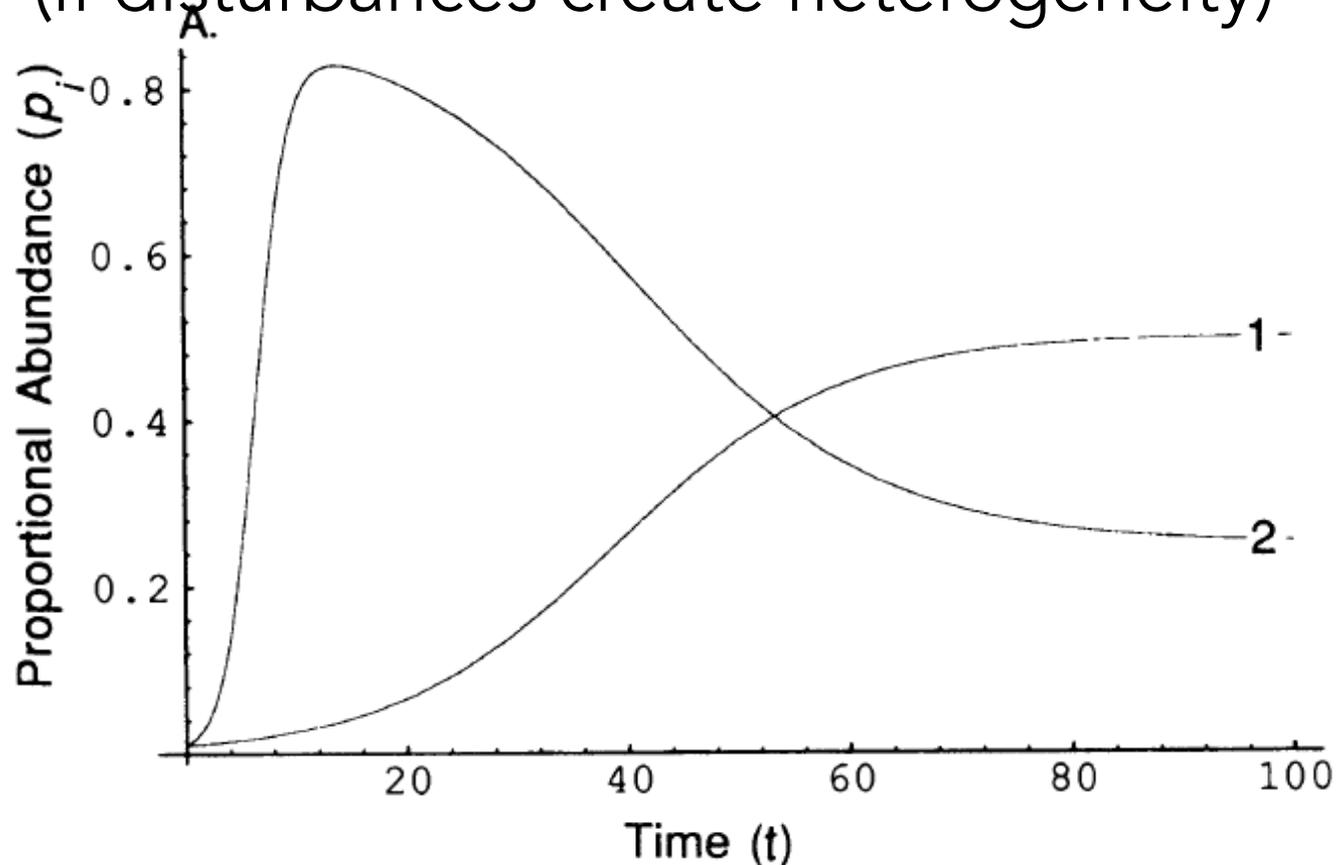


# Trade-off:



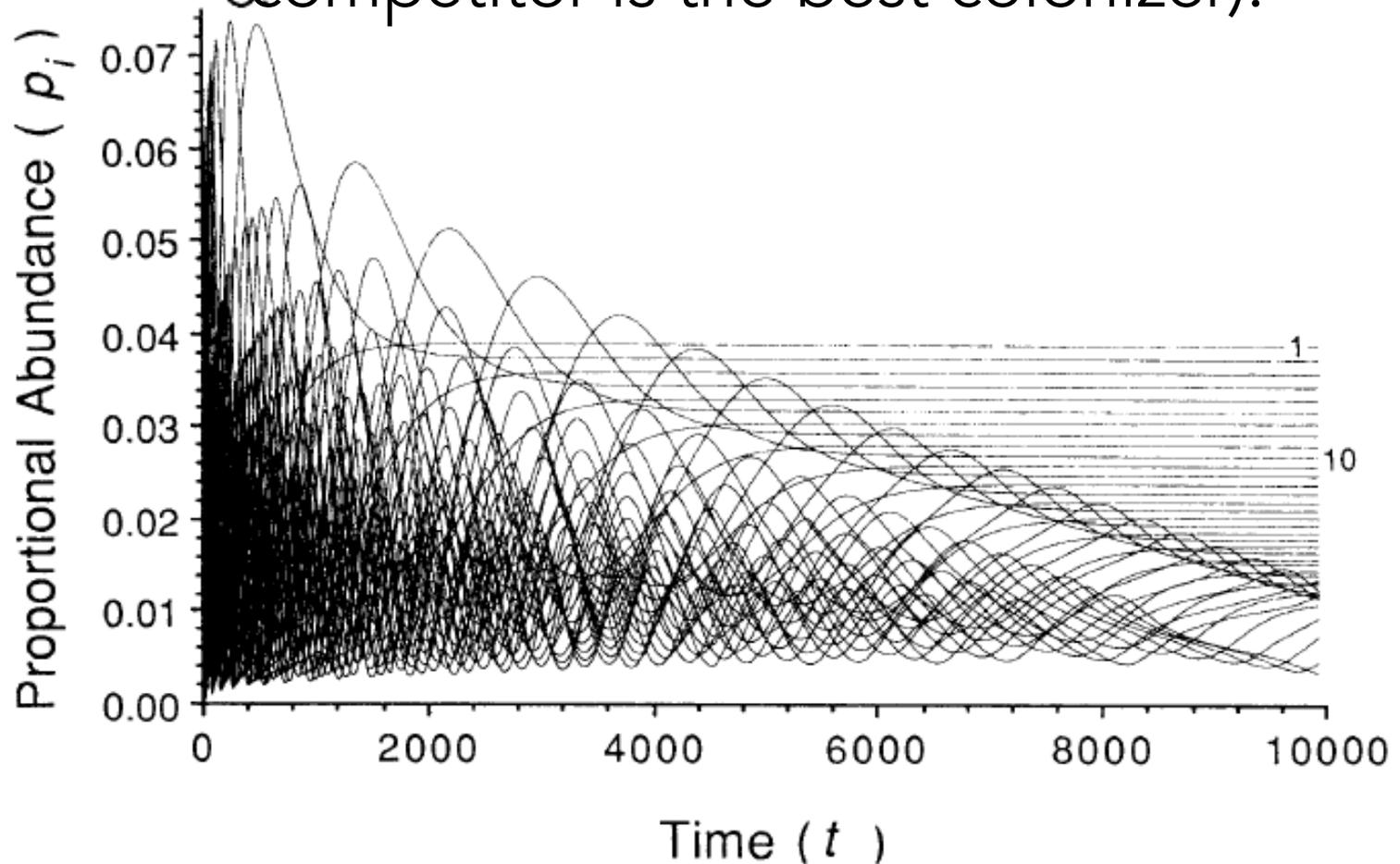
# Trade-off:

Two species can persist...on one resource, even when one species is best competitor (if disturbances create heterogeneity)



# Trade-off:

Many species can persist...on one resource (so long as the poorest  $\propto$  competitor is the best colonizer):



# Trade-offs



Possible trade-offs with competitive ability (that promote persistence of competitors):

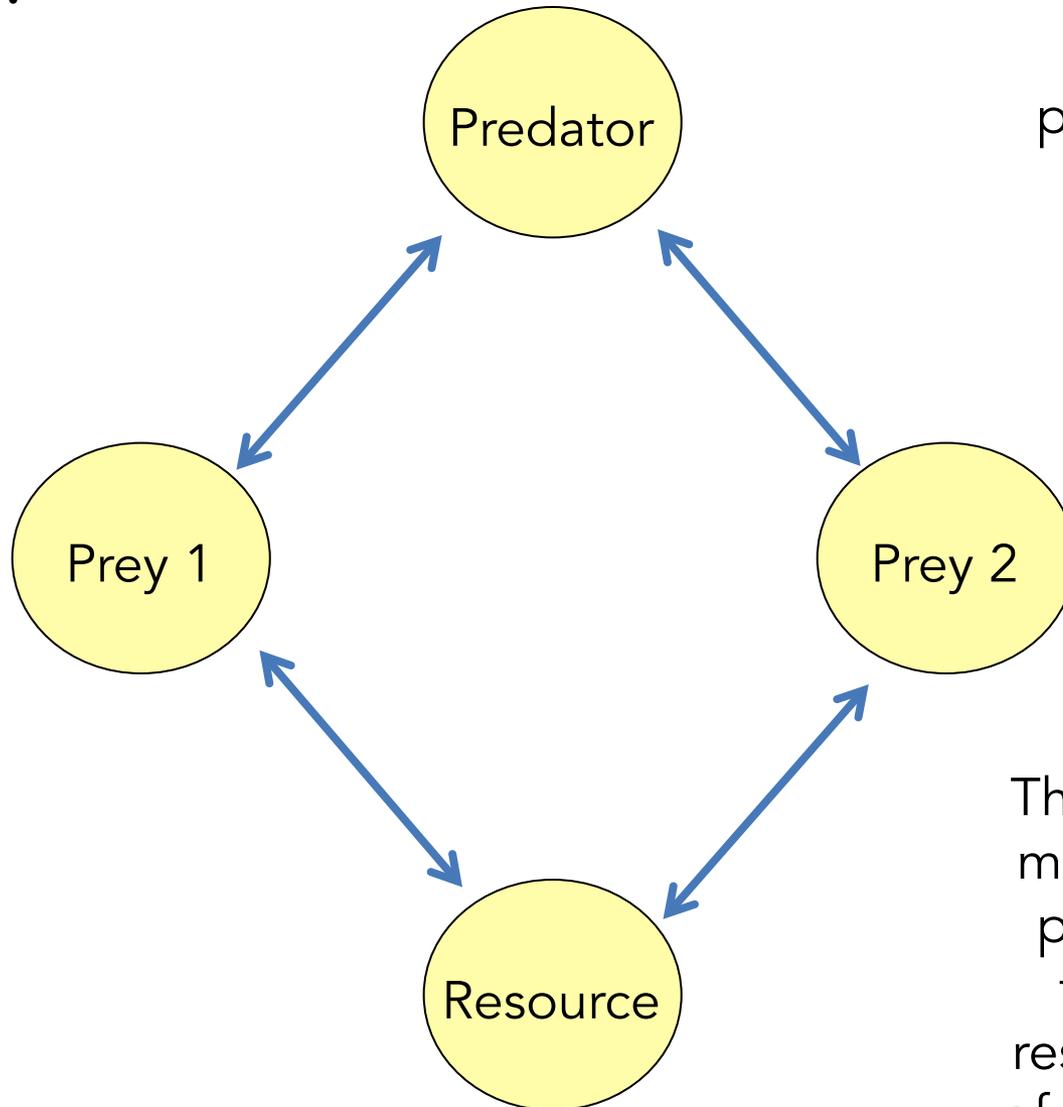
Colonizing ability

Vulnerability to disturbance

Vulnerability to predators

# Predators

# Diamond food web:



Coexistence possible if better competitor is preferred by predator

Thus one prey is more limited by predation and the other by resource (a form of "partitioning")

PLANT SPECIES DIVERSITY IN A MARINE INTERTIDAL  
COMMUNITY: IMPORTANCE OF HERBIVORE  
FOOD PREFERENCE AND ALGAL COMPETITIVE ABILITIES

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**Damselfish as Keystone Species in Reverse:  
Intermediate Disturbance and Diversity of Reef Algae**

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and Evolutionary Biology,  
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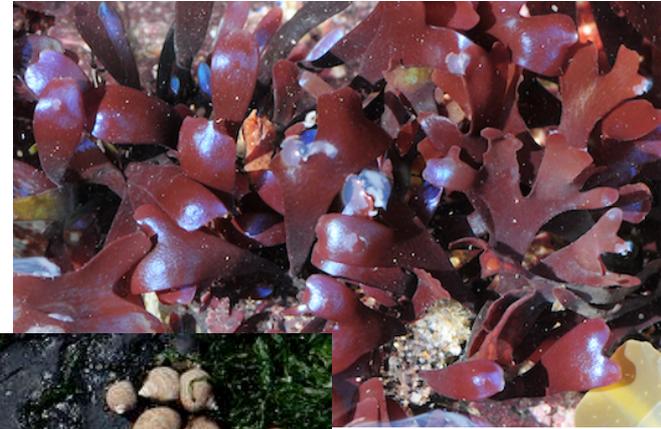
WILLIAM N. BROSTOFF

*Department of Botany,  
University of Hawaii, Honolulu 96822*

SCIENCE, VOL. 220

29 APRIL 1983

Avoided:  
*Chondrus*

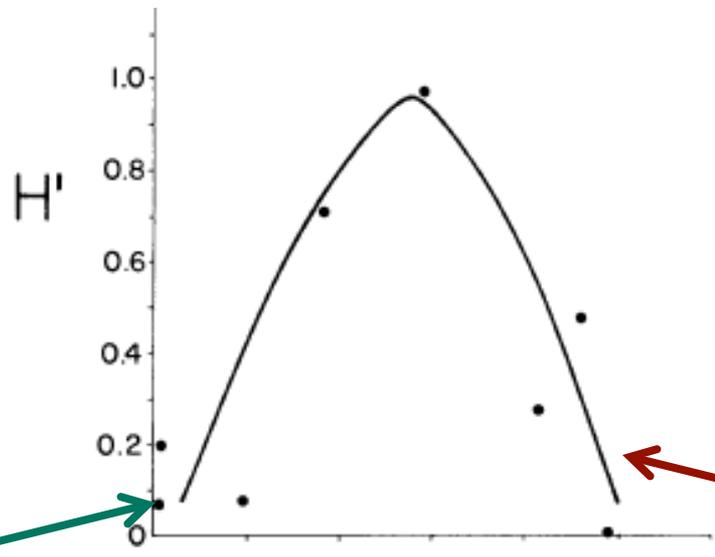


The grazer:  
*Littorina littorea*



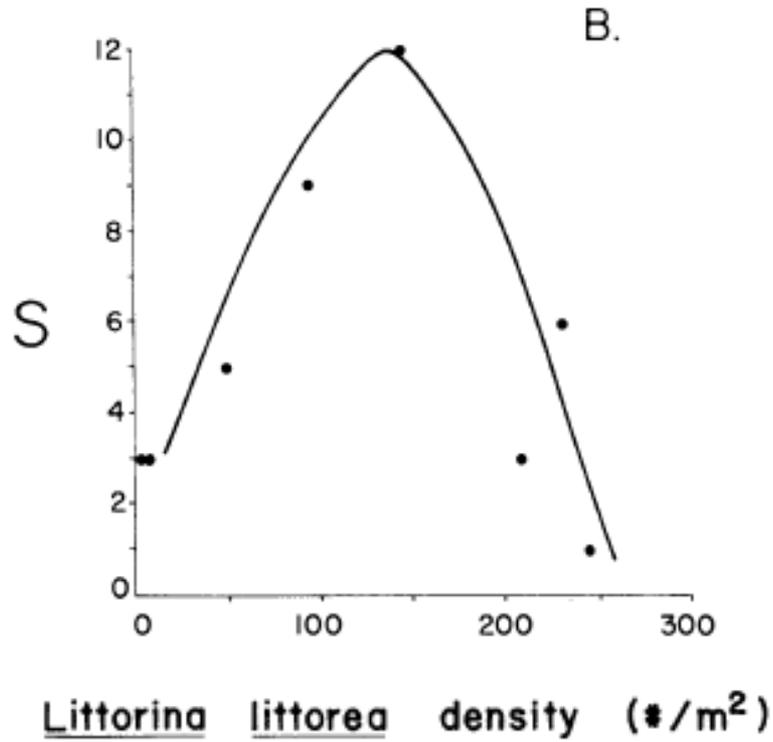
Preferred:  
*Enteromorpha*



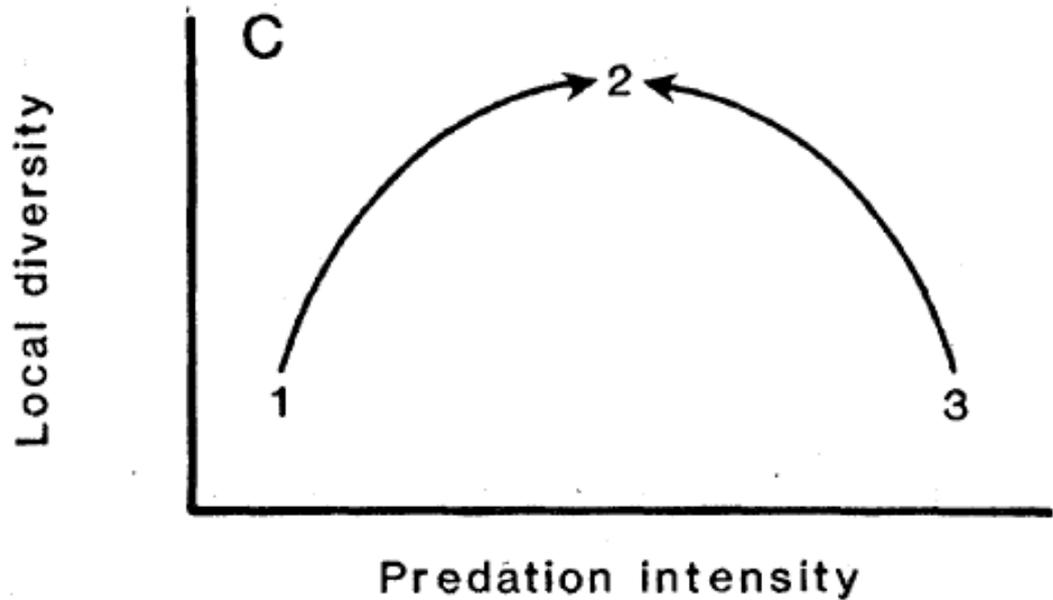
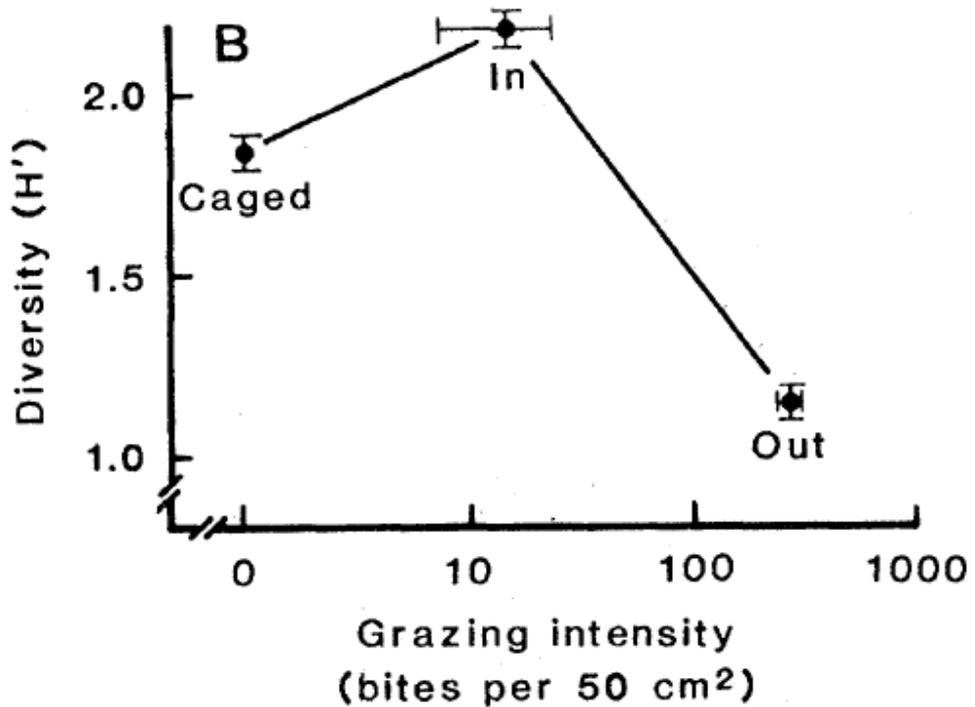
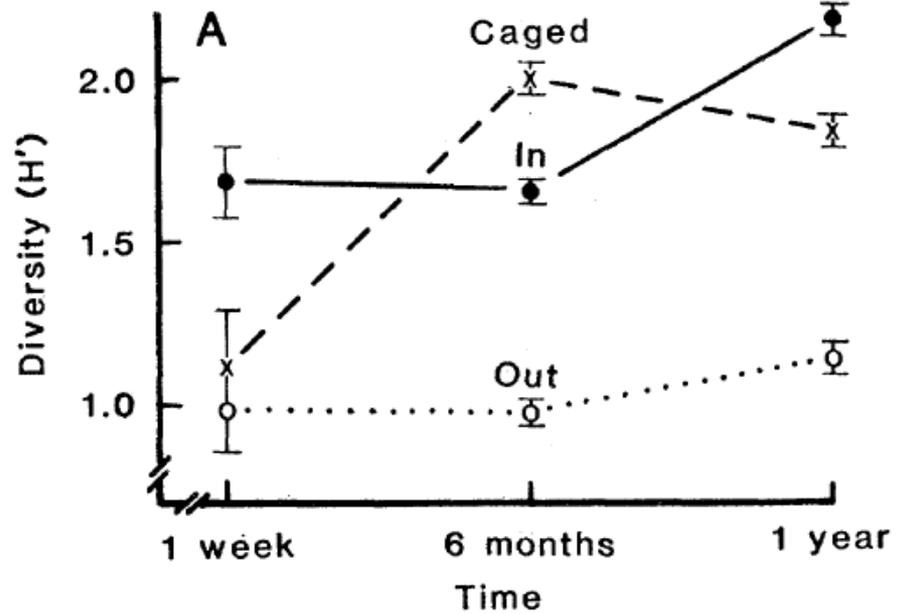


Inedible species dominates (Chondrus)

Competitive dominant wins (Enteromorpha)







# Resource fluctuations

COEXISTENCE IN A VARIABLE ENVIRONMENT

RICHARD LEVINS

Exogenous:

Mean vs. variance specialists

Endogenous:

Limit cycles

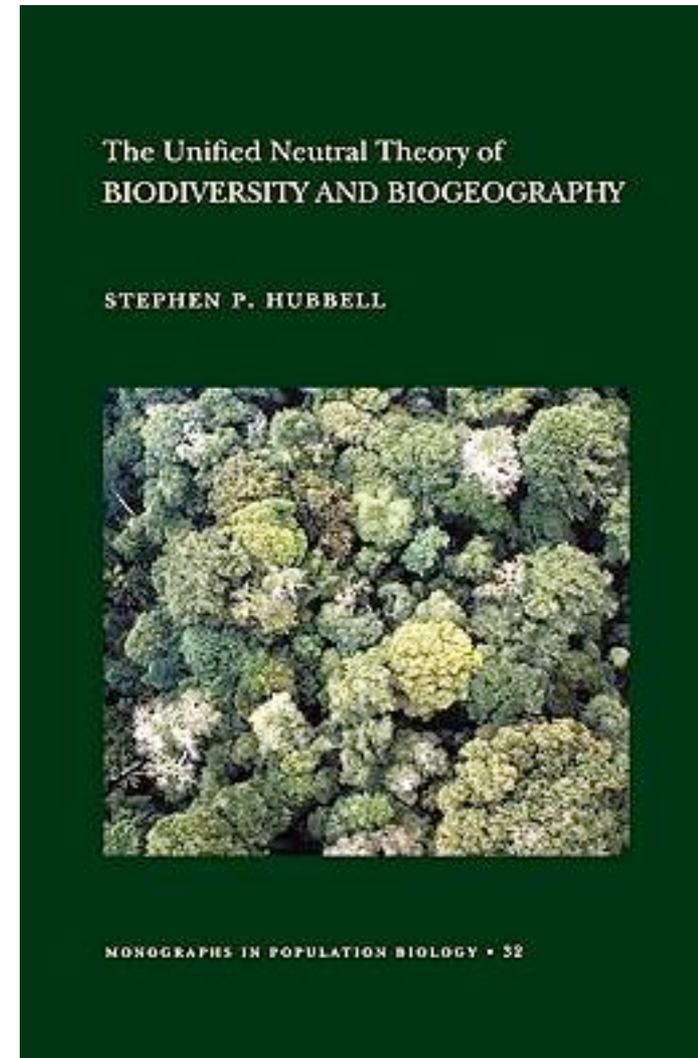
COMPETITIVE EXCLUSION

ROBERT A. ARMSTRONG\* AND RICHARD MCGEHEE

# Hubbell's Neutral theory:

A different perspective (analogous to Kimura's model neutral theory in evolution):

1. Species are identical: cf. niche theory
2. Systems are saturated
3. Random walk to extinction
4. Extinction balanced by speciation
5. Can achieve persistence of diverse communities (dynamic, no "winner")



What if competitors compete via exploitation  
AND interference?

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# Intraspecific density dependence and a guild of consumers coexisting on one resource

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Type II functional responses

Logistic growth

$$\frac{dR}{dt} = R \left( c - dR - \sum_{i=1}^n \frac{a_i N_i}{1 + a_i h_i R} \right)$$

Resource

$$\frac{dN_i}{dt} = N_i \left( \frac{b_i a_i R}{1 + a_i h_i R} - (f_i + g_i N_i) \right)$$

Consumer

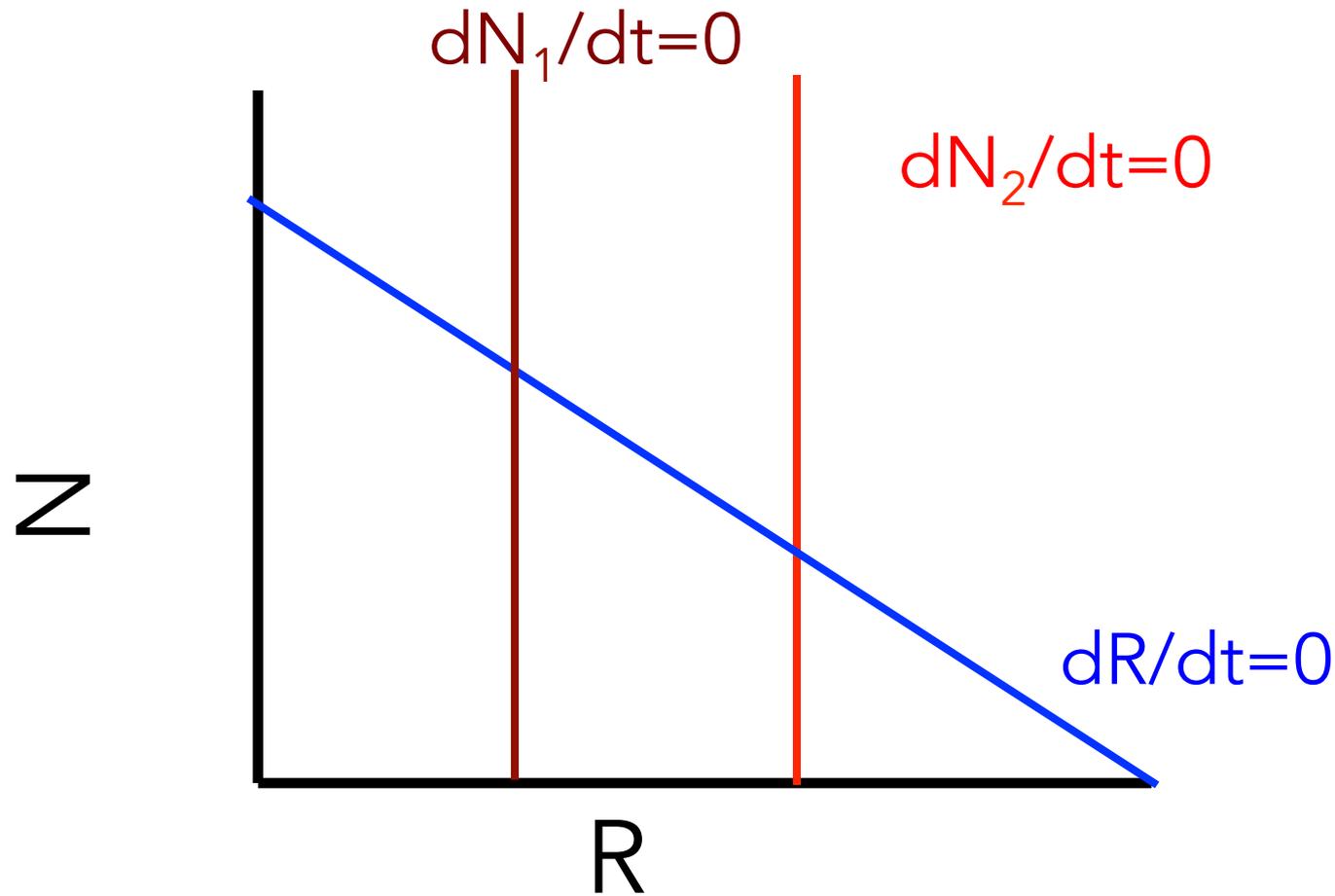
Mortality

Interference-mediated mortality

How does this change our basic 2-consumer model?

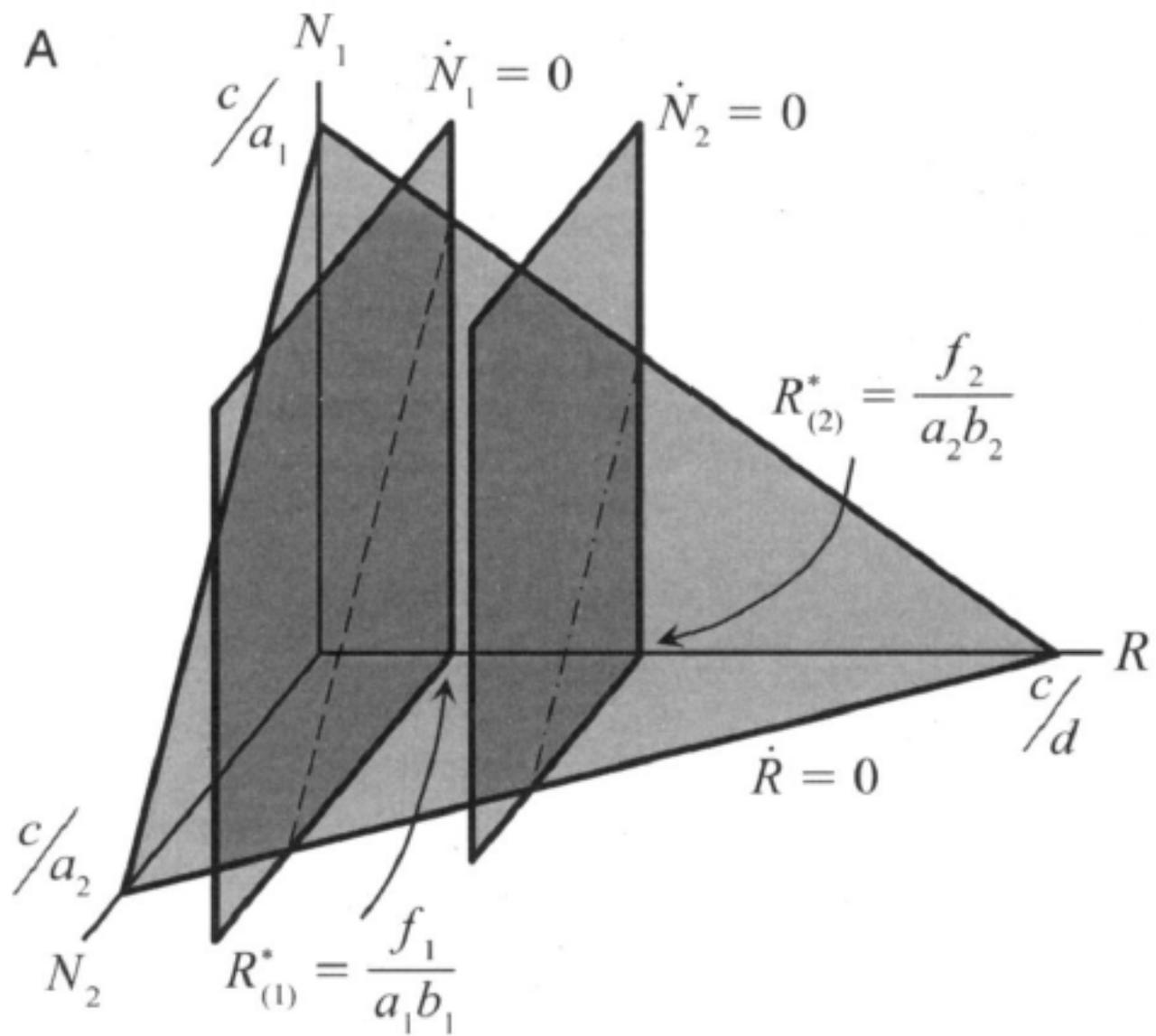
Consumer-  
resource phase  
plane:

Without interference  
( $g=0$ ) or handling costs  
( $h=0$ )



Who will "win"?

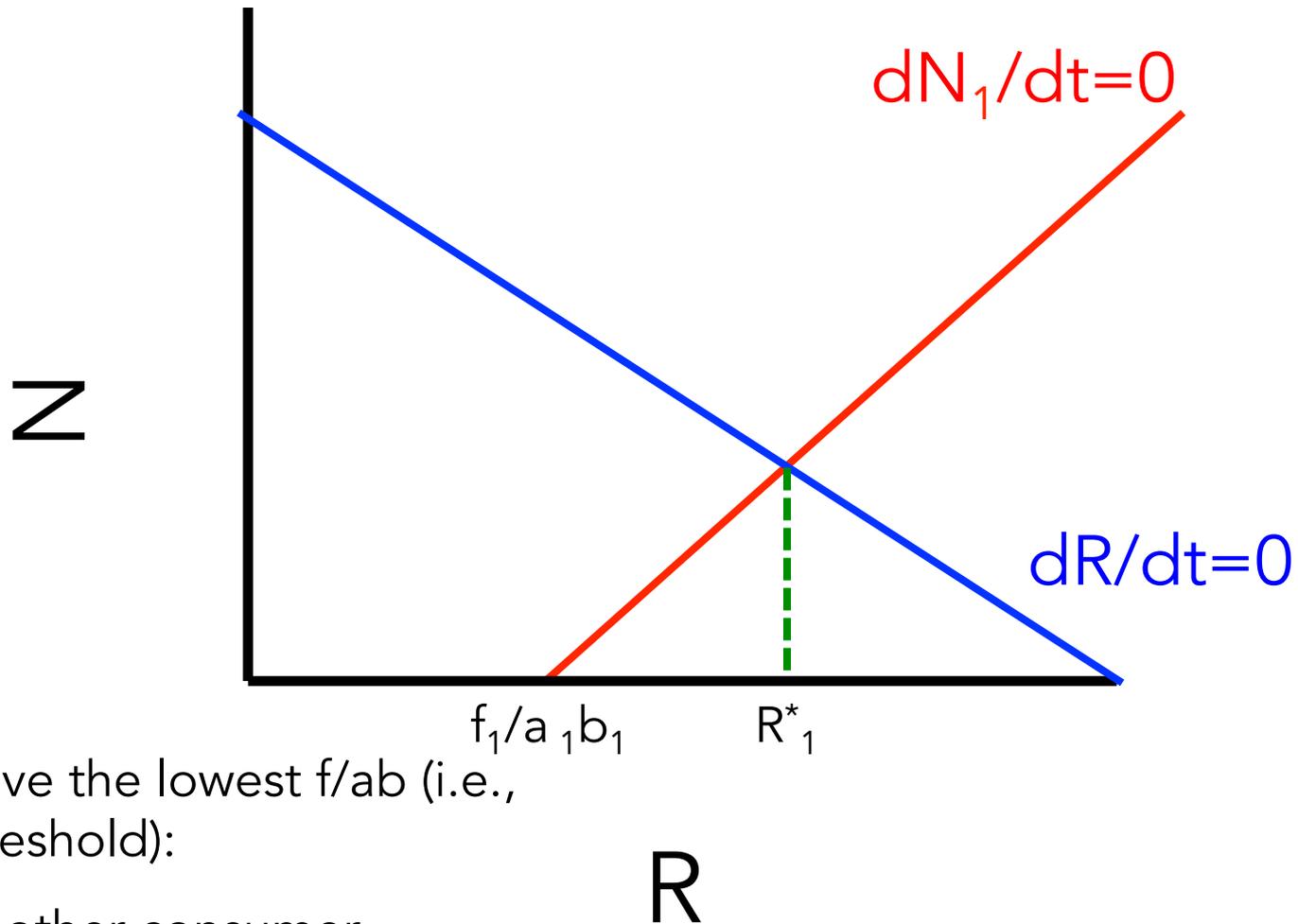
Our picture isn't sufficient – we really need a  
3-d phase plane...



Now let there be INTRAspecific  
interference...

# Consumer-resource phase plane:

With interference ( $g > 0$ ) but still no handling costs ( $h = 0$ ).

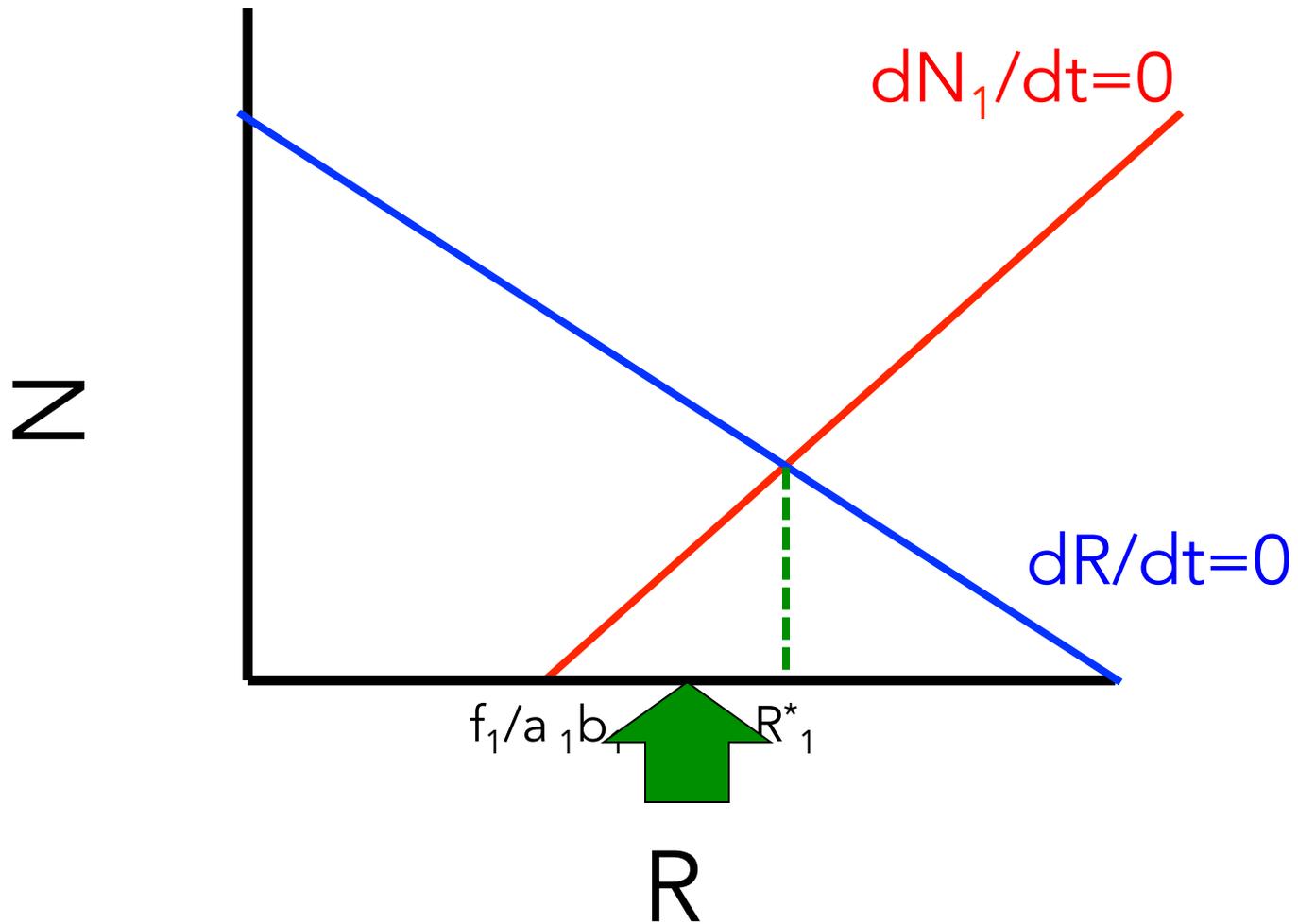


Let sp. 1 have the lowest  $f/ab$  (i.e., invasion threshold):

How can another consumer invade?

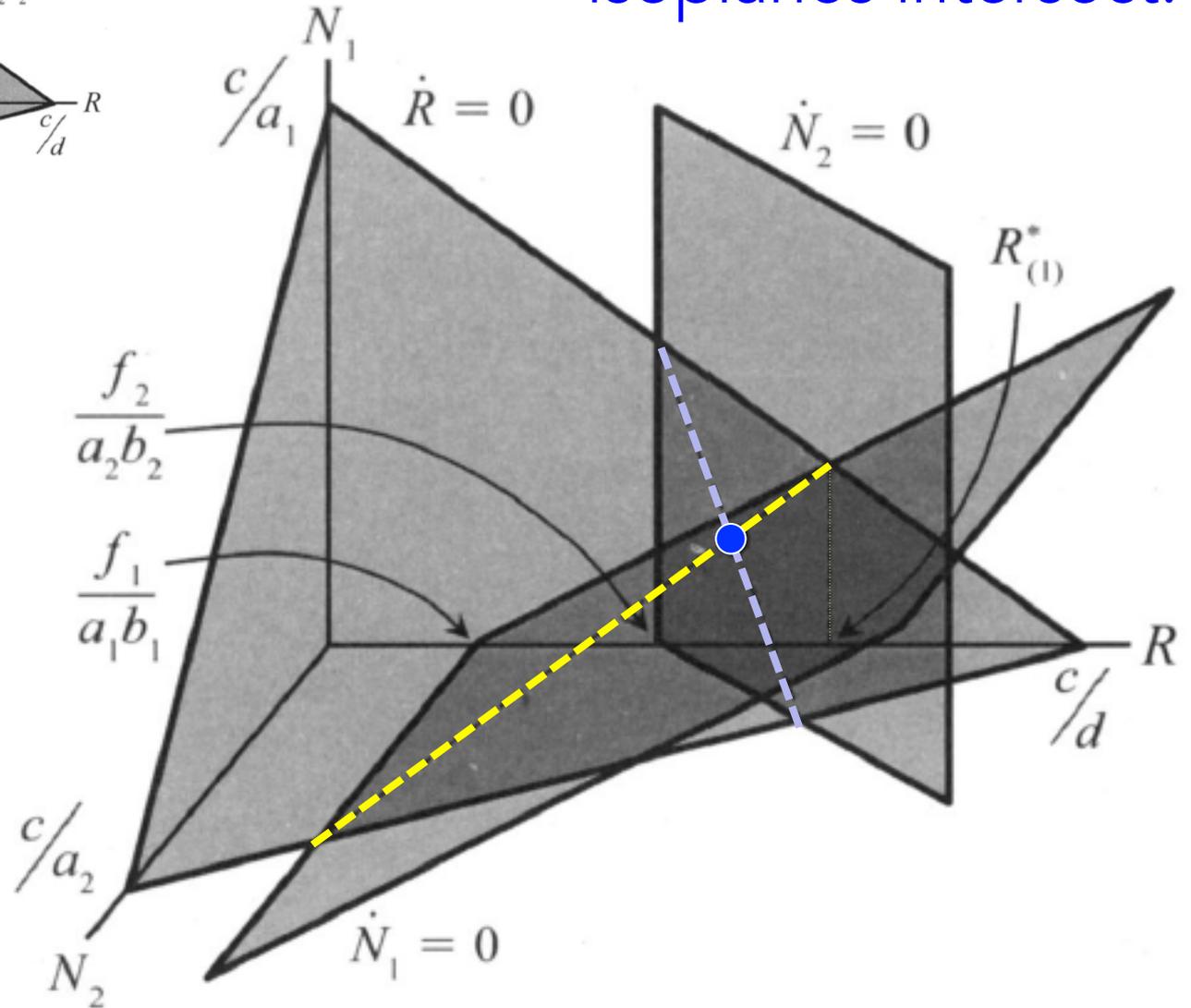
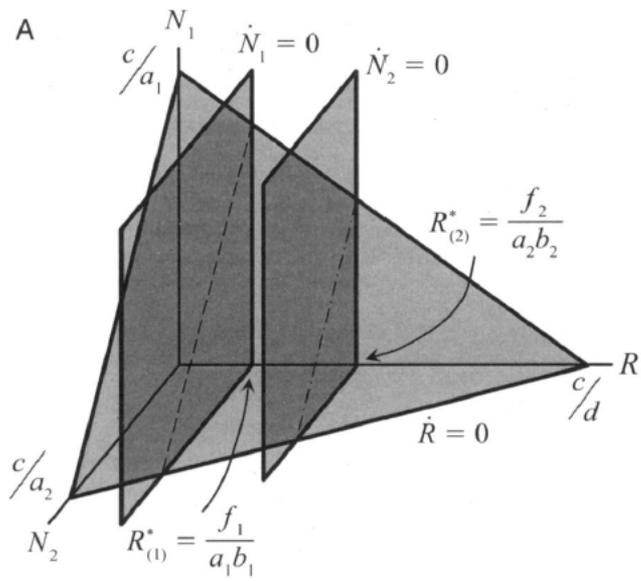
Consumer-  
resource phase  
plane:

For species 2 to invade:  $f_2/a_2b_2 < R^*_1$



Let's look at this in 3-d...

Three species equilibria where the isoplanes intersect:



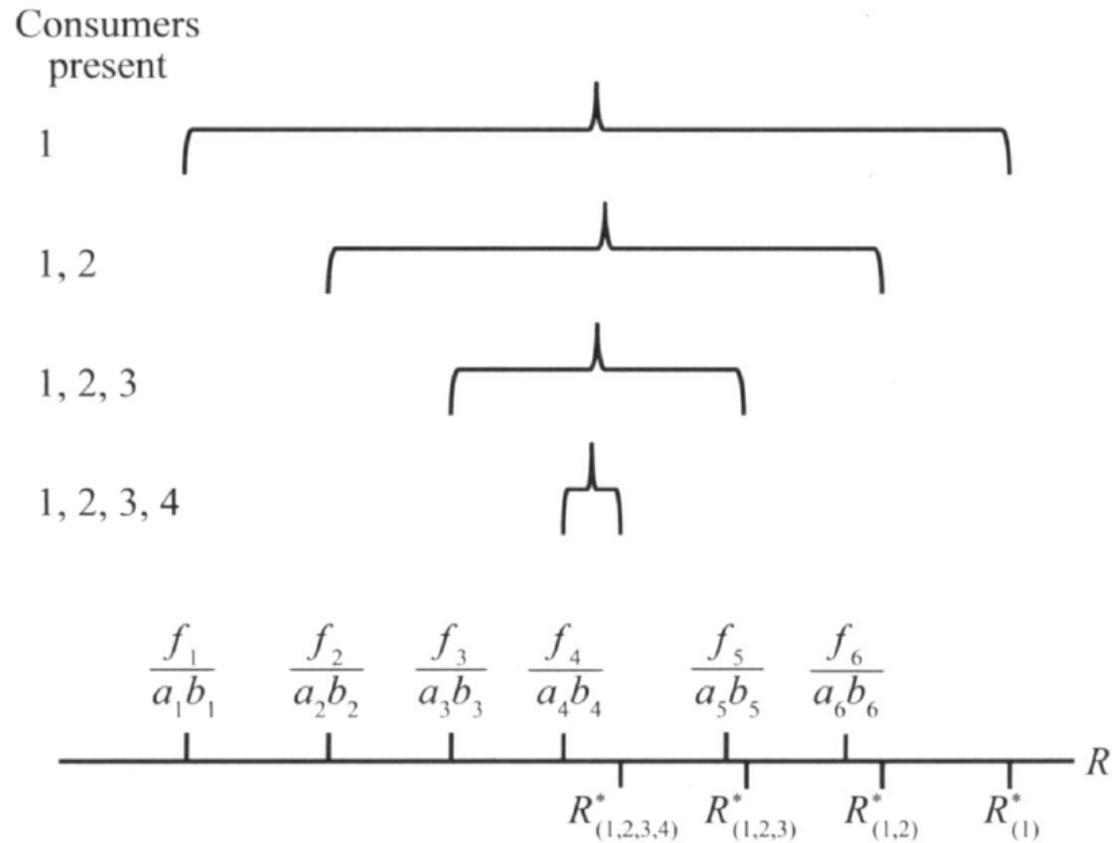


FIG. 2. An illustration focusing on the resource axis from Fig. 1 to show how adding additional species causes the window of critical ratios to become smaller as more consumers invade the system. With only consumer 1 (the species that can maintain a positive population growth rate at the lowest resource abundance) in the system, any species with  $f_1/(a_1 b_1) < f_i/(a_i b_i) < R_{(1)}^*$  can invade the system and coexist with consumer 1; with both consumer 1 and 2 (the two species that can maintain positive population growth rates at the lowest resource abundances) in the system, any species with  $f_2/(a_2 b_2) < f_i/(a_i b_i) < R_{(1,2)}^*$  can invade and coexist with them; and so on. In this specific case, consumers 1–4 could coexist with one another, but consumers 5 and 6 would be excluded. Note that consumer 5 could coexist in a community that contained consumers 1, 2, and 3 but lacked consumer 4, and that consumer 6 could coexist in a community that contained consumers 1 and 2 but lacked consumers 3 and 4.

Therefore, interference enables multiple consumers to coexist on a single resource

(creates "intra>inter"; analogous to each species having it's own unique resource (partitioning) or specialized predator (apparent competition))