Mechanistic models of competition

Cedar Creek, Minnesota

Volterra models summary

Competition term added to logistic term in growth equation
Species 1: $dN_1/dt = r_1N_1((K_1\text{-}N_1\text{-}\alpha_{12}N_2)/K_1)$

Coexistence predicted if interspecific competition weaker than intra-specific (within species) competition ($\alpha < 1$)

Nature of resource limitation unexplored -- what resources limit growth?

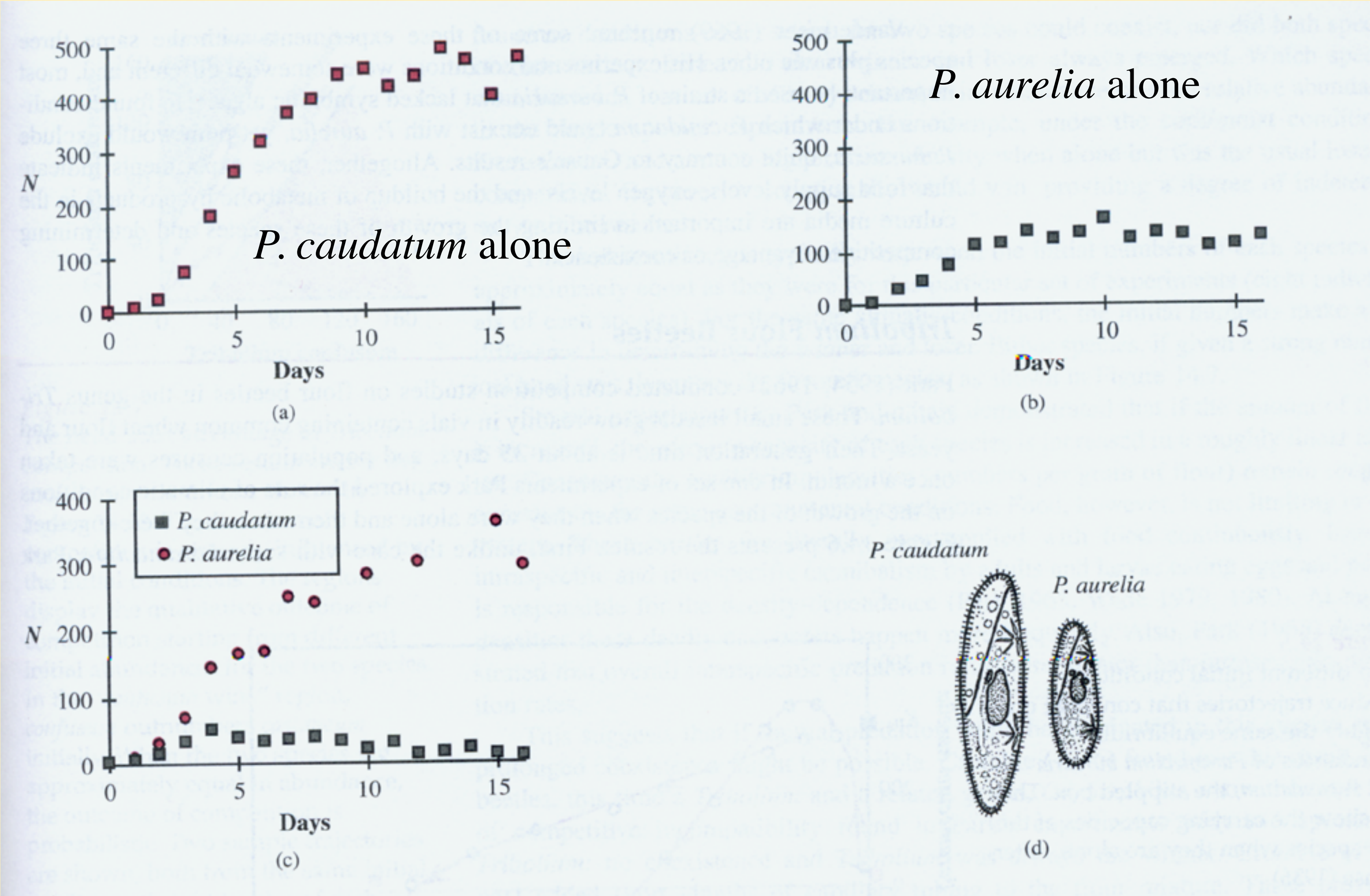
Volterra assumptions

- No age or genetic structure, no time-lags, no migration
- Competition coefficients are fixed and carrying capacities are constants
- No density-dependent effects (linear isoclines) see Rosenzweig (1981)
- Individuals interact with the entire population of competitors (no spatial structure)

Testing the Volterra model

Gause (1934): Application of Volterra model to population dynamics of two *Paramecium* species

- species independently showed logistic growth curves grown in media containing *Bacillus subtilis* food
- estimating α is problematic… Gause looked at the relative size of the two *Paramecium* species to estimate biomass produced under non-limiting conditions
- competition coefficients predicted stable coexistence



Oh dear… larger *P. caudatum* excluded, even though Gause inferred a higher α for *P. caudatum*

- Gause did find that large *P. caudatum* could coexist with small *P. bursaria*.

But…

P. bursaria has symbiotic algae that allowed this protozoan to sit at the bottom of the test-tube in O_2 depleted zone.

Coexistence of Protozoa revisited by Vandermeer (1969). Found *P. caudatum* and *P. aurelia* coexist (and predicted 4 species competition effects).

Food supply, O_2, metabolic waste all probably important in determining coexistence

Mechanistic competition models

- Express competition coefficients and carrying capacities as rates of utilization/renewal of resources (MacArthur 1972)

- Use differences in the ability of species to grow at various levels of two or more resources to predict conditions under which species will coexist (Monod 1950; Tilman 1977, 1982)

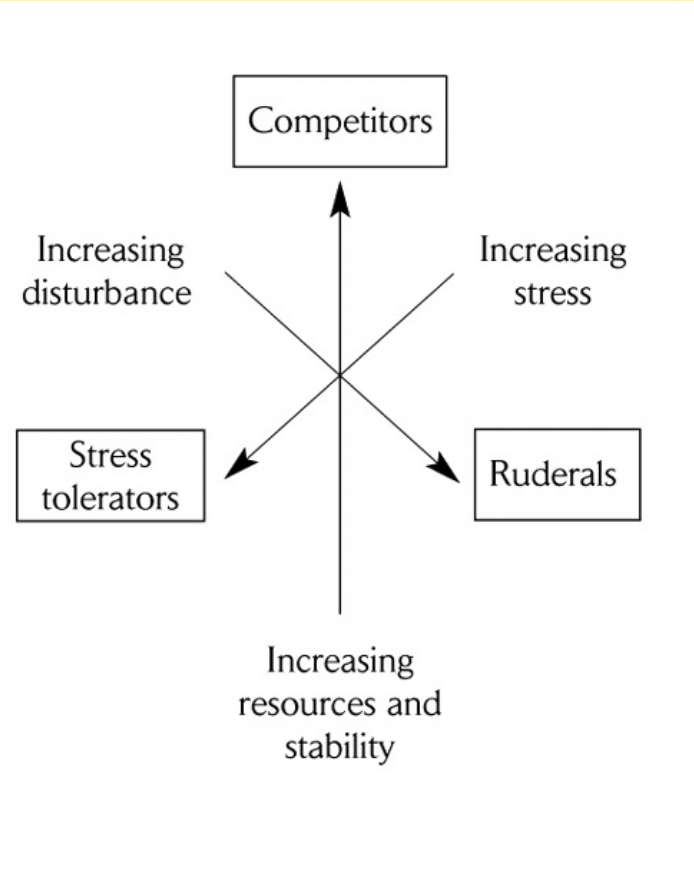
- Examine fecundity and survival of sessile organisms as a function of the abundance of their immediate neighbours (‘neighborhood models’ Pacala and Silander 1985)

Grime vs. Tilman and the nature of competition

Grime: Plants have "strategies" competitors, stress tolerators or ruderals

Tilman: Competition important everywhere. Spp differ in ability to acquire different resources

Grime's trait triangle



A general classification of plant traits

Some tolerate "stress"

"Ruderals" colonize disturbed areas

"Competitors" good at occupying space and acquiring resources from neighbors?

Grime argued that stress and disturbance most important in structuring resource *poor and rich* environments *respectively* (see Functional Ecology 1: 297-315)

Tilman's R^* (resource ratio) model

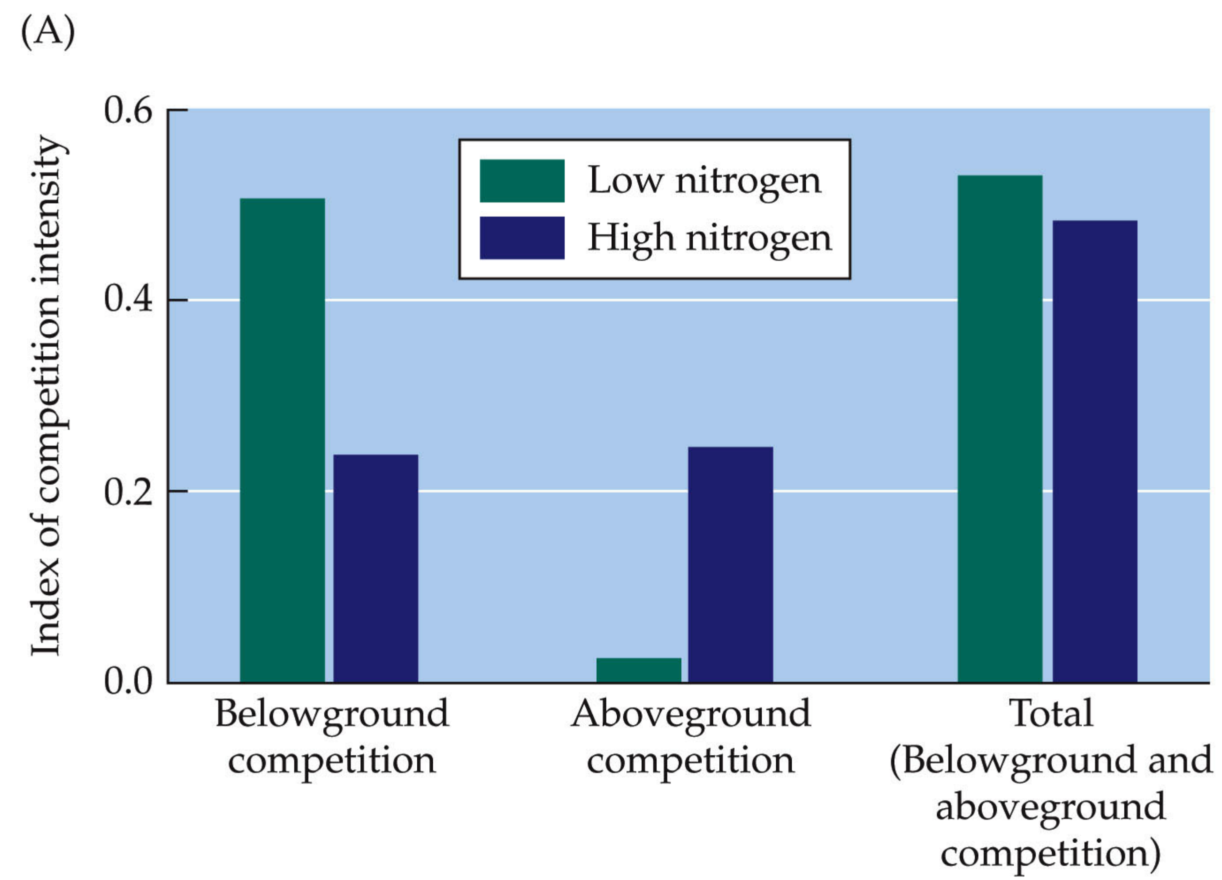
Dissatisfied with Grime's predictions that competition is most intense in resource rich environments.

Grime argument: A strong competitor is a species that is leafy, grows rapidly *and* fills the soil volume with roots. *A strong competitor for light should also be a strong competitor for nutrients*.

In a stressed (resource poor) environment a plant cannot fill the soil and canopy. Competition should therefore be less important.

How would you show experimentally that competition is intense in resource poor environment??

Tilman and Wilson (1993) Changed N availability (limiting resource in the Cedar Creek grassland)



ECOLOGY, Figure 11.5 (Part 1)

Competition Index: proportional reduction in growth rate in presence of neighbors vs. neighbor root or shoot removed

Tilman built R* model based on insights about competition

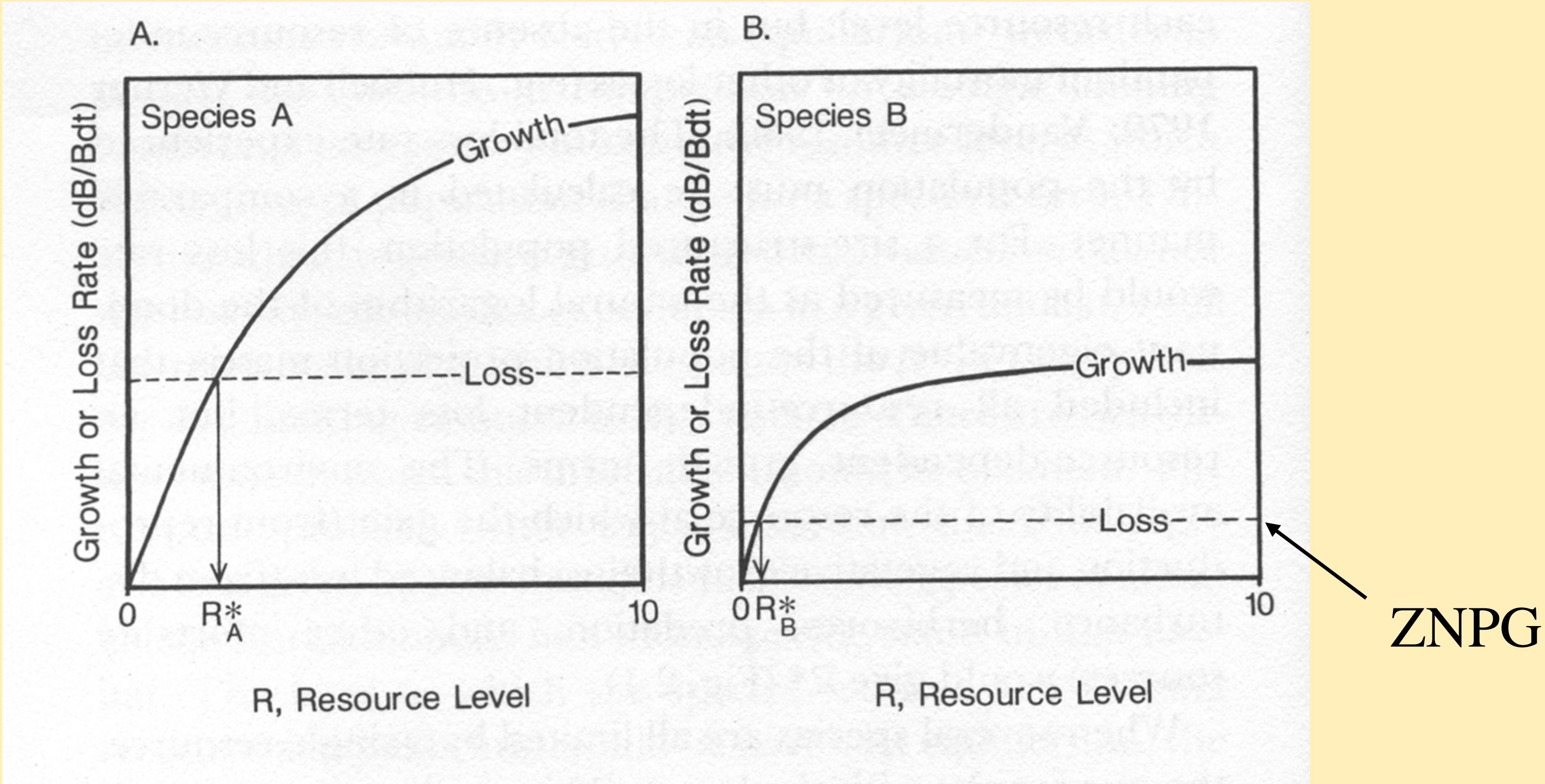
1. Optimal foraging. *Organisms can only be limited by one resource at a time* (Liebig's law of the minimum), Acquiring excess of non-limiting resources will not increase fitness. Organisms should therefore balance resource acquisition so that all resources are equally limiting.

Liebig's barrel

Tilman built R* model based on insights about competition

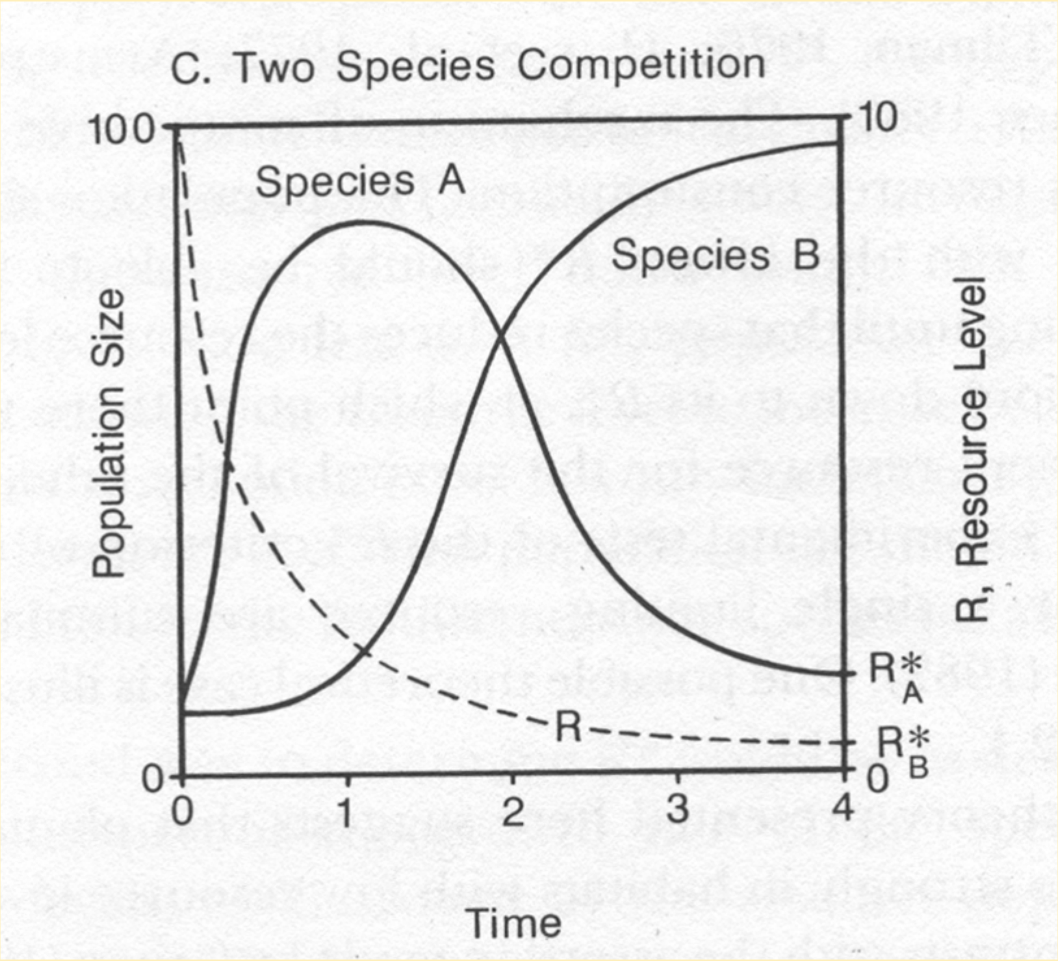
2. A species ability to maintain itself in a community will be determined by the *level of the limiting resource that results in zero net population growth* (ZNPG). This depends critically on the supply rate and consumption rate of the resource (collectively the resource level) and the reproduction and mortality rate of the the species (collectively the population growth rate).

Species coexistence on a single limiting resource



R* represents the resource level at which *population* growth is balanced by population loss (mortality or biomass loss in plants). At resource levels *below* the R* population growth is negative.

Species coexistence on a single limiting resource



2 species - one limiting resource
What is the outcome of competition?

Is there a scenario where these two species could coexist on a single limiting resource?

What about 2 species and 2 resources?

Grime argument: Strong competitor for one resource strong for all.

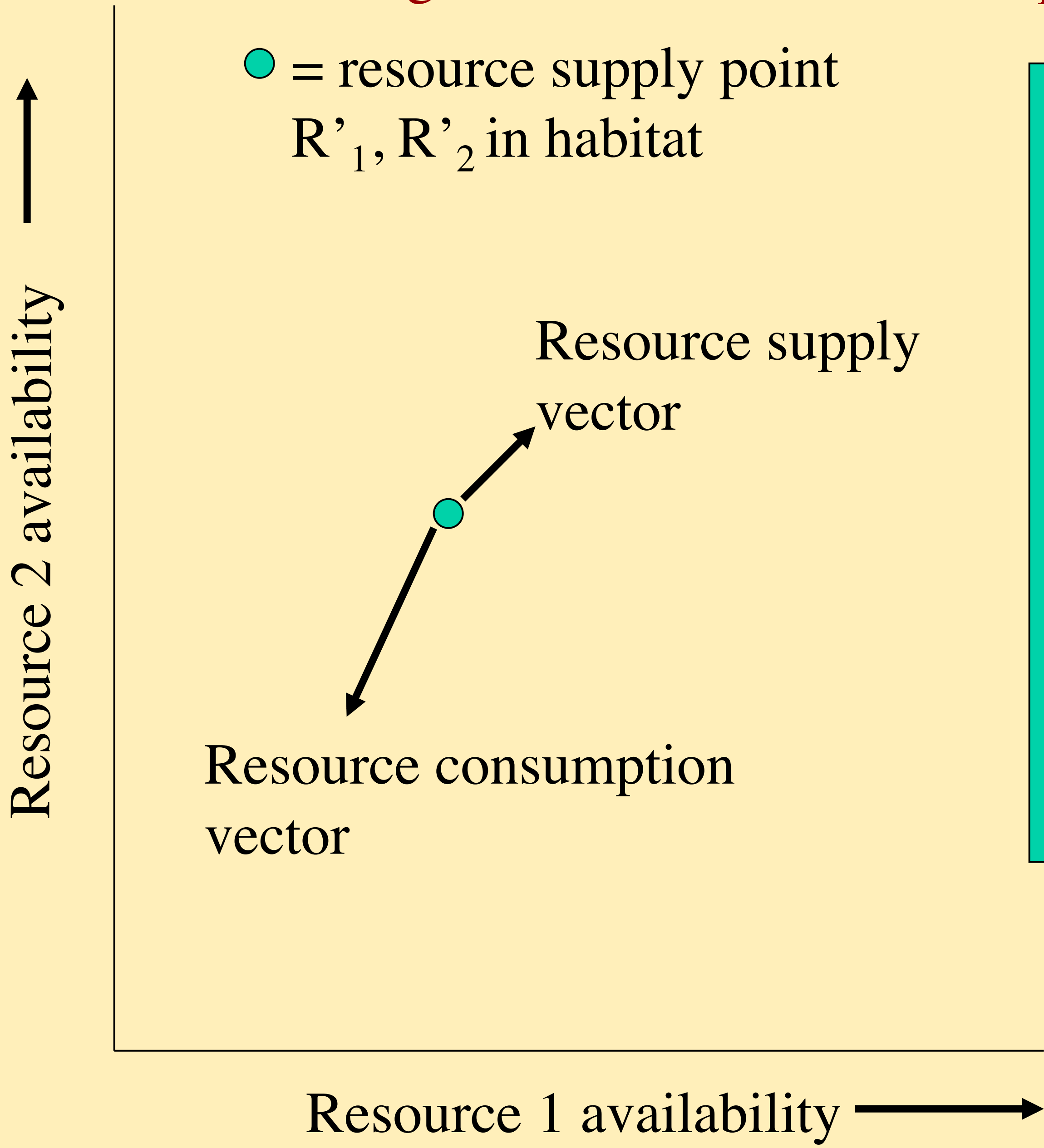
Tilman argument: Resource allocation **trade-offs** mean that strong competitive ability for one resource = poor ability for another.

If there is spatial variation in the availability of potentially limiting resources, then species may therefore differ in their R^* values for the same resources

Resource allocation trade-off:

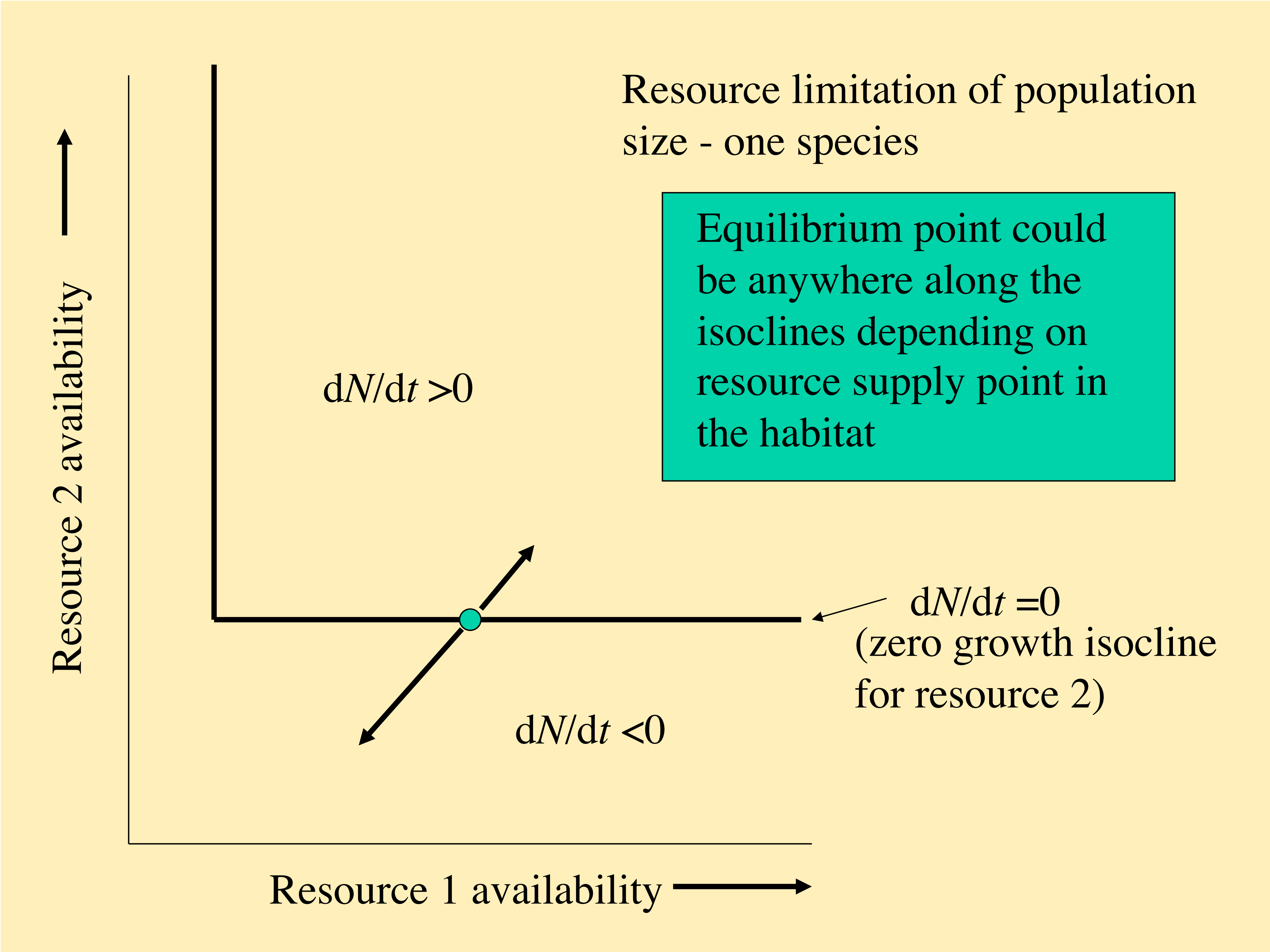
More resources allocated to light capture means less resources available for soil-borne resource capture

Adding a second resource to competition models



Resource level will depend on resource supply and resource consumption rates.

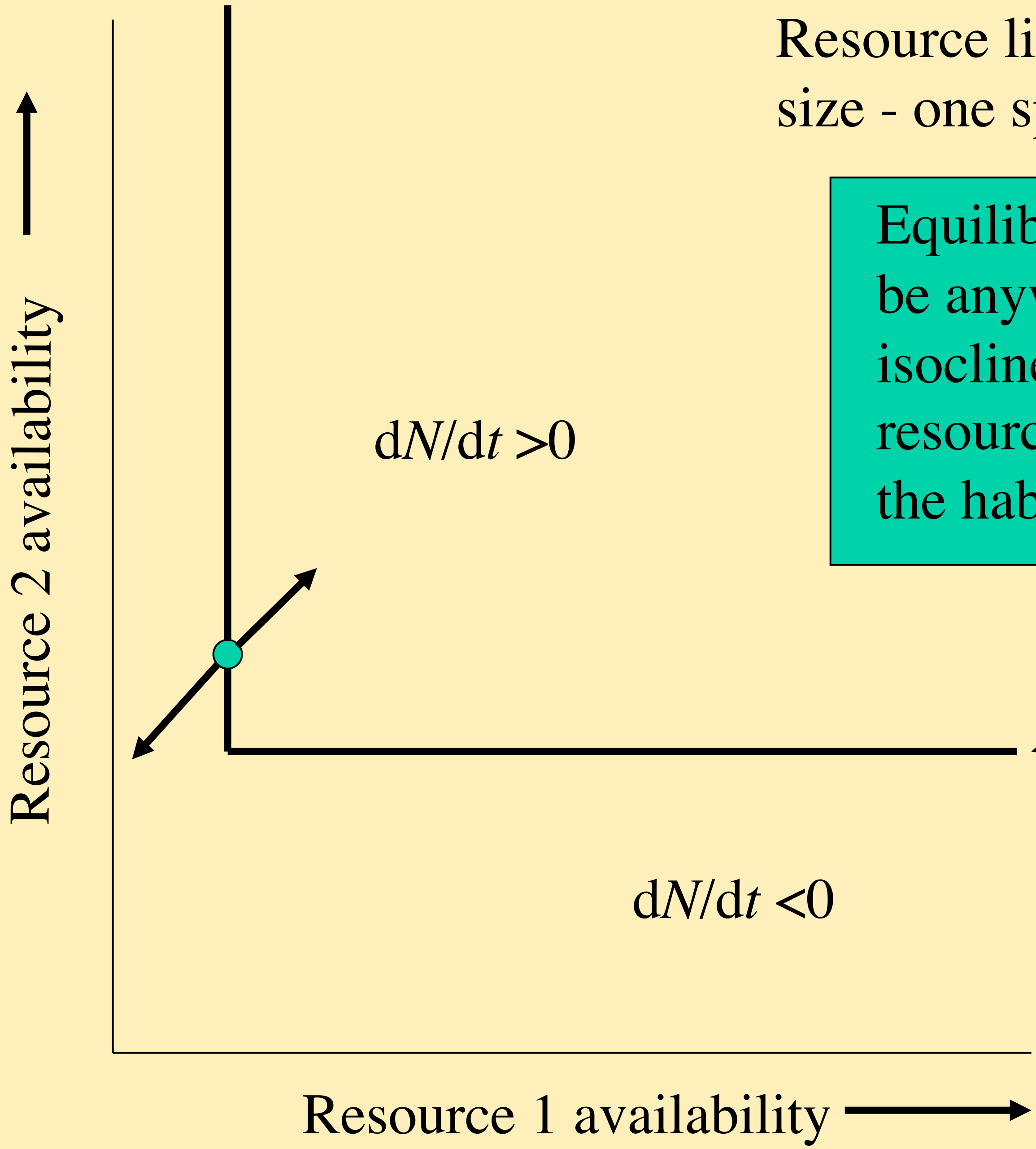
Direction of the consumption vector - results from trade-offs in resource uptake



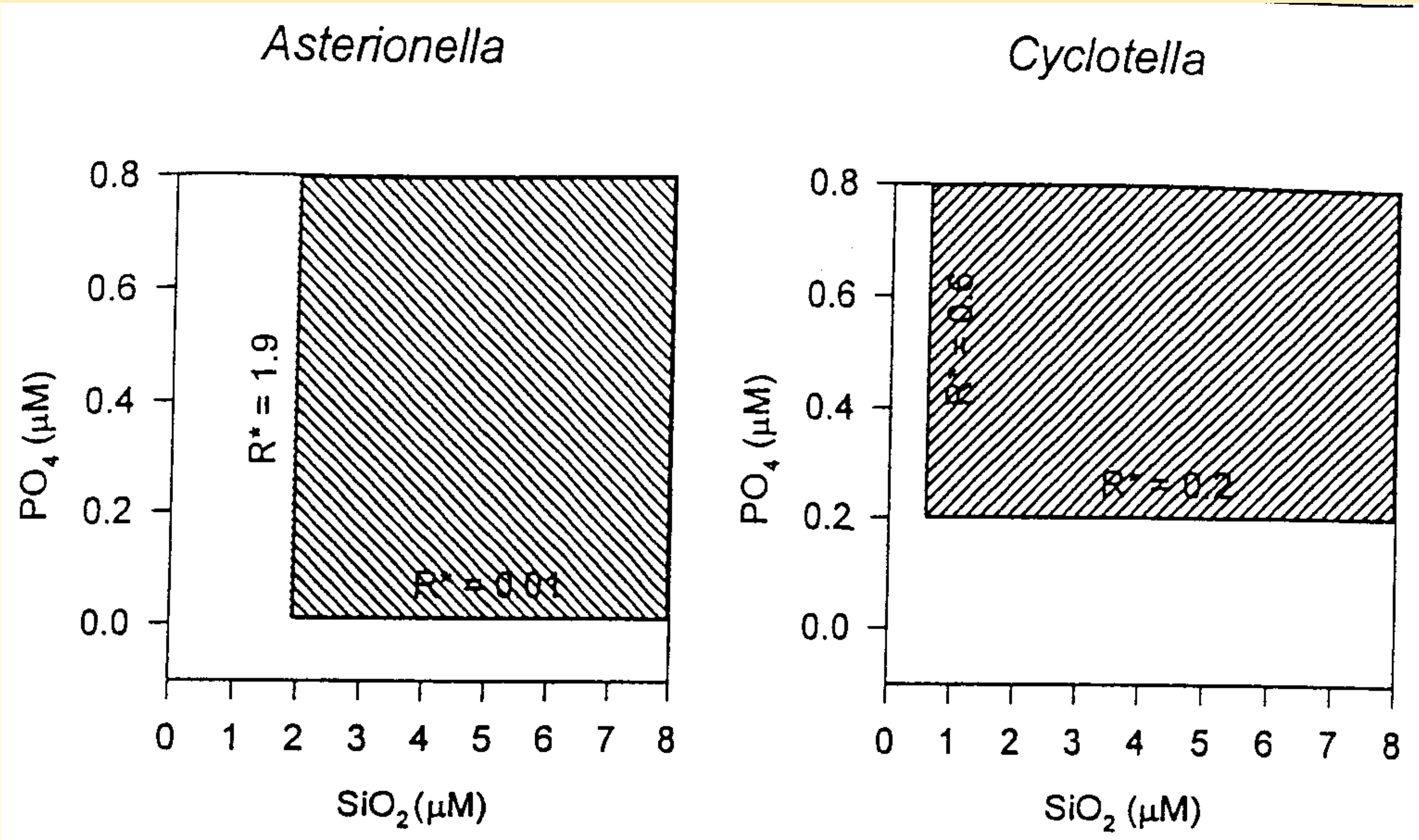
Resource limitation of population size - one species
Equilibrium point could be anywhere along the isoclines depending on resource supply point in the habitat
dN/dt >0
dN/dt =0
(zero growth isocline for resource 2)
dN/dt <0
Resource 2 availability
Resource 1 availability

Resource limitation of population size - one species

Equilibrium point could be anywhere along the isoclines depending on resource supply point in the habitat



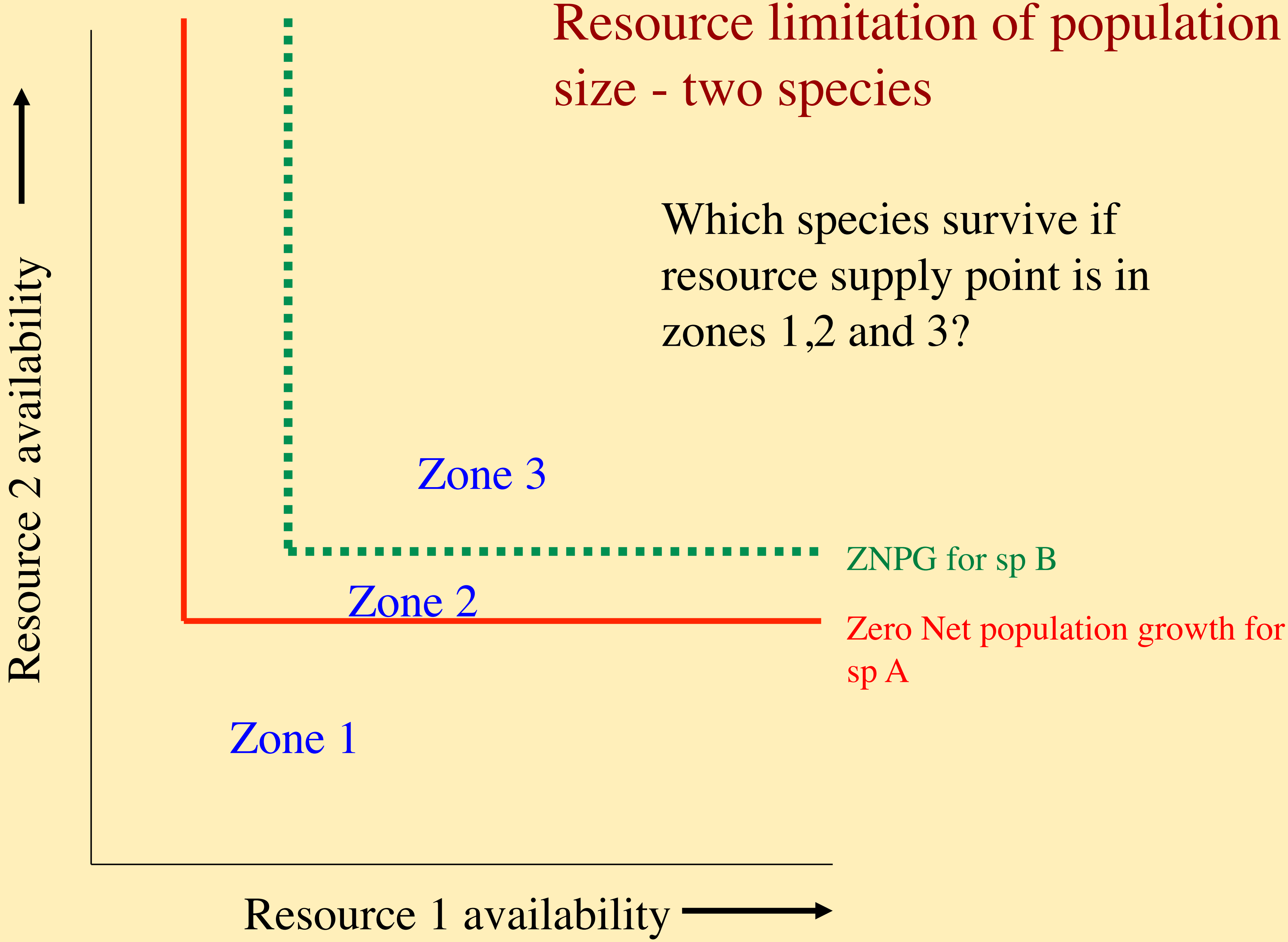
Experimentally determined R* values for algae (from Morin)



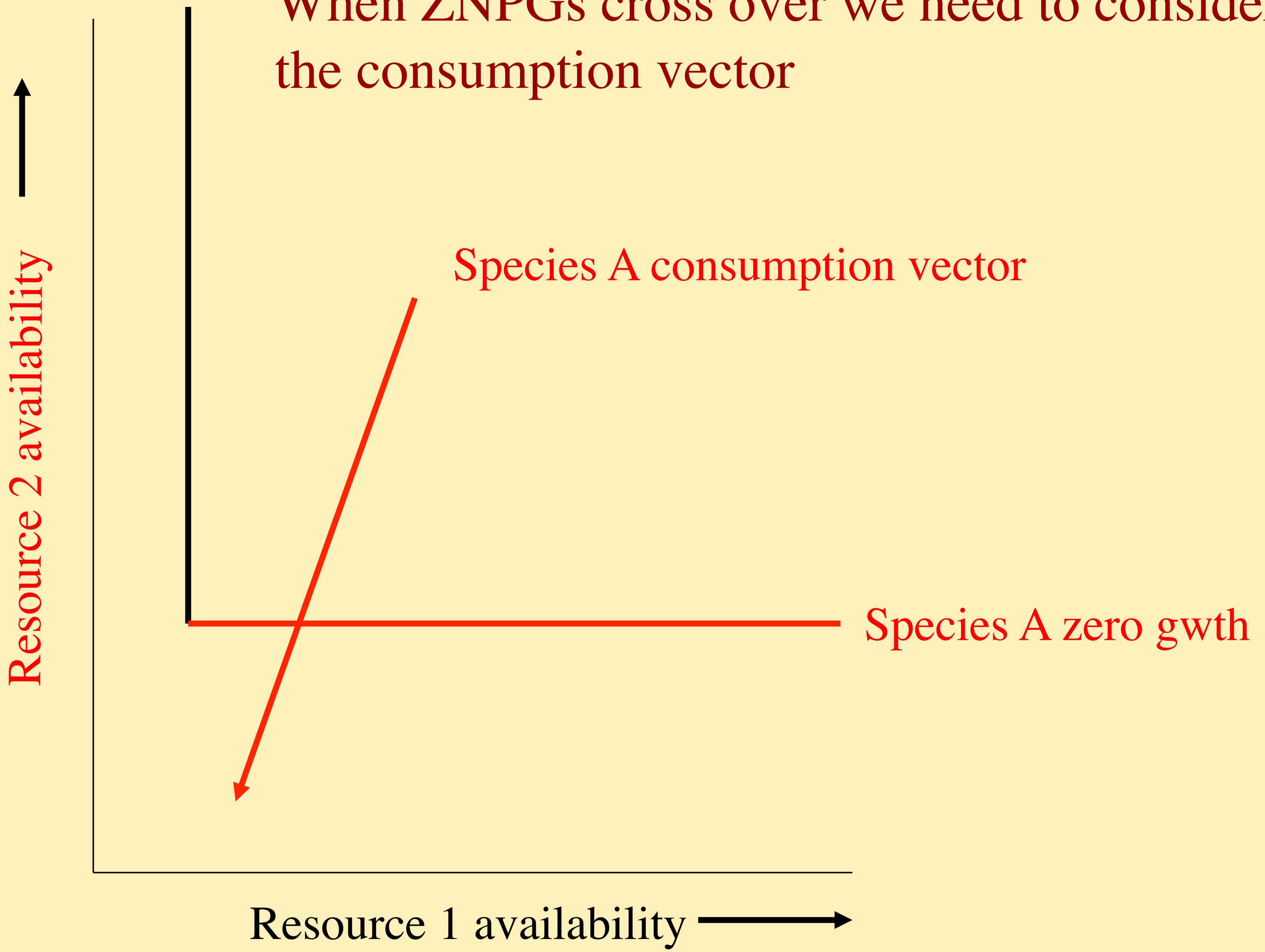
(notice there is a trade-off here in R* values)

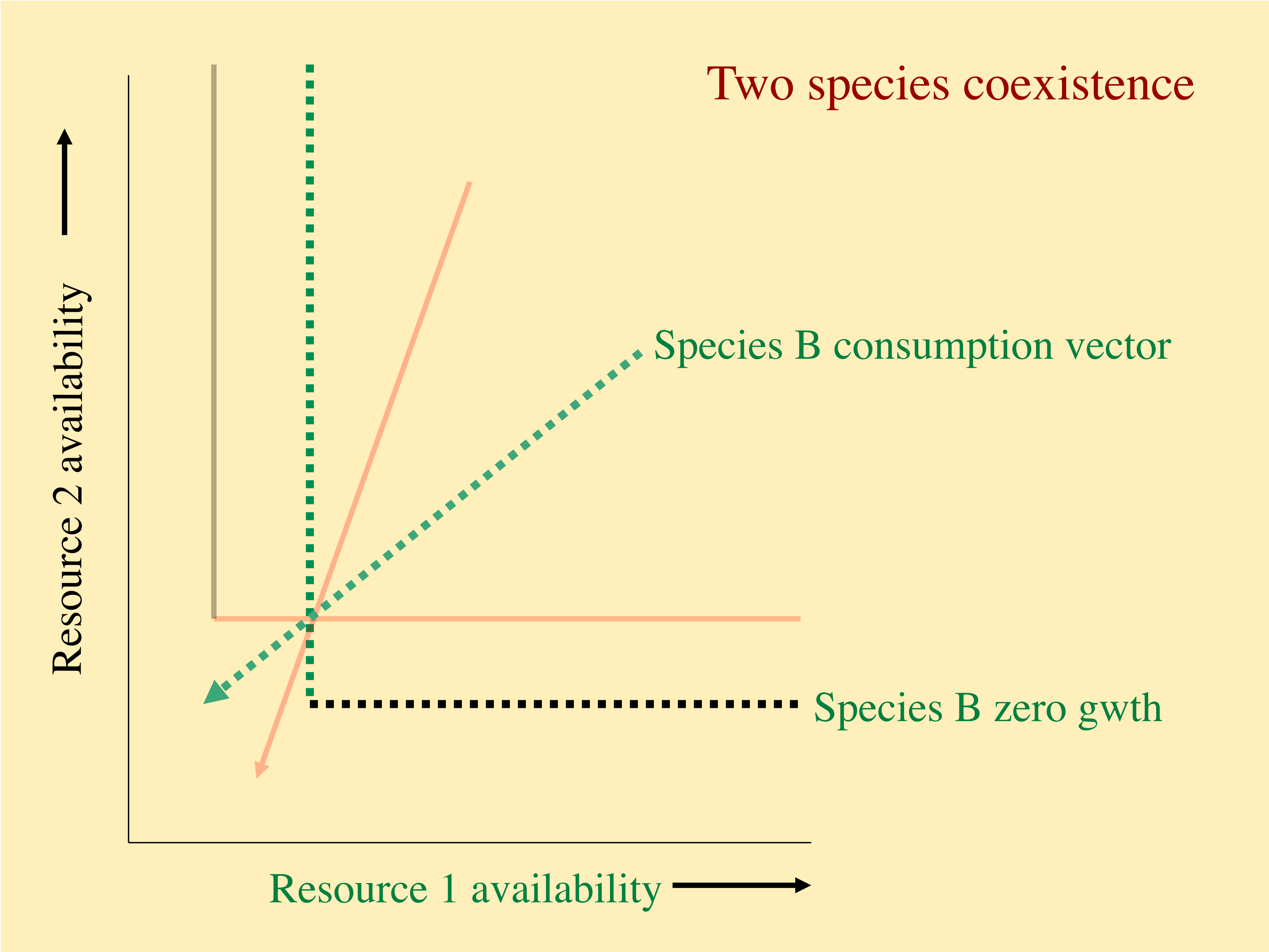
Resource limitation of population size - two species

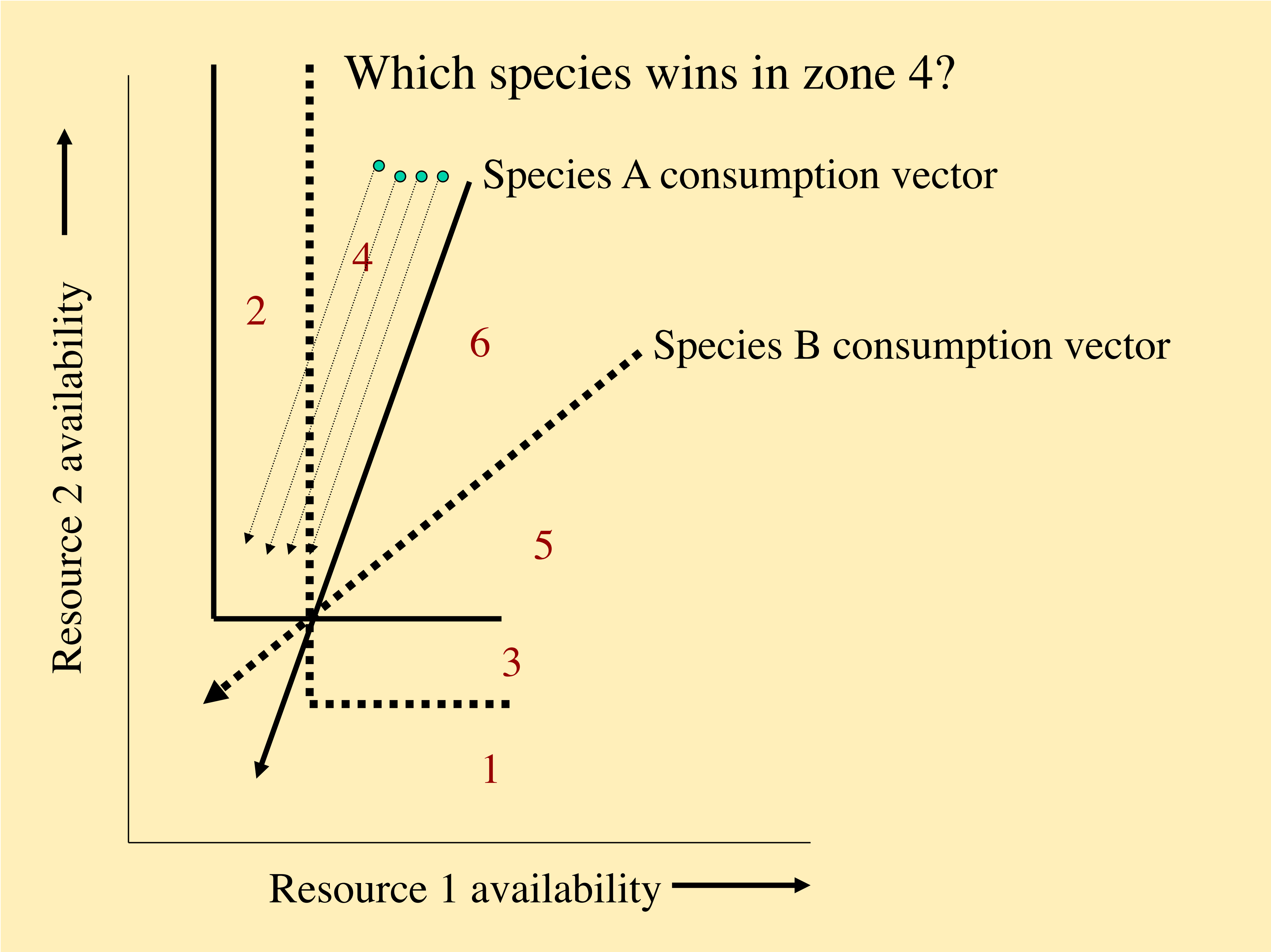
Which species survive if resource supply point is in zones 1,2 and 3?



When ZNPGs cross over we need to consider the consumption vector

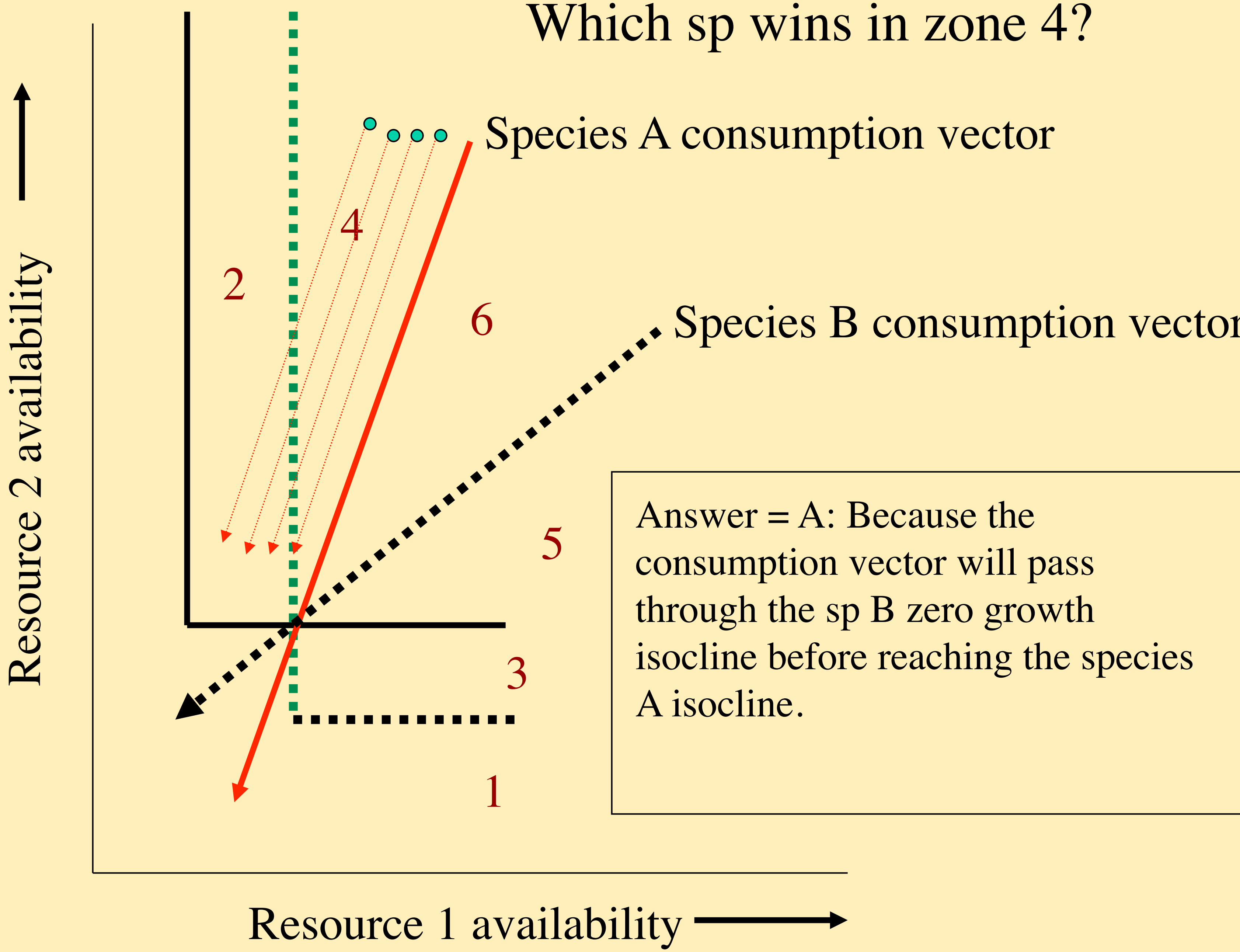



Two species coexistence
Species B consumption vector
Species B zero gwth
Resource 2 availability
Resource 1 availability

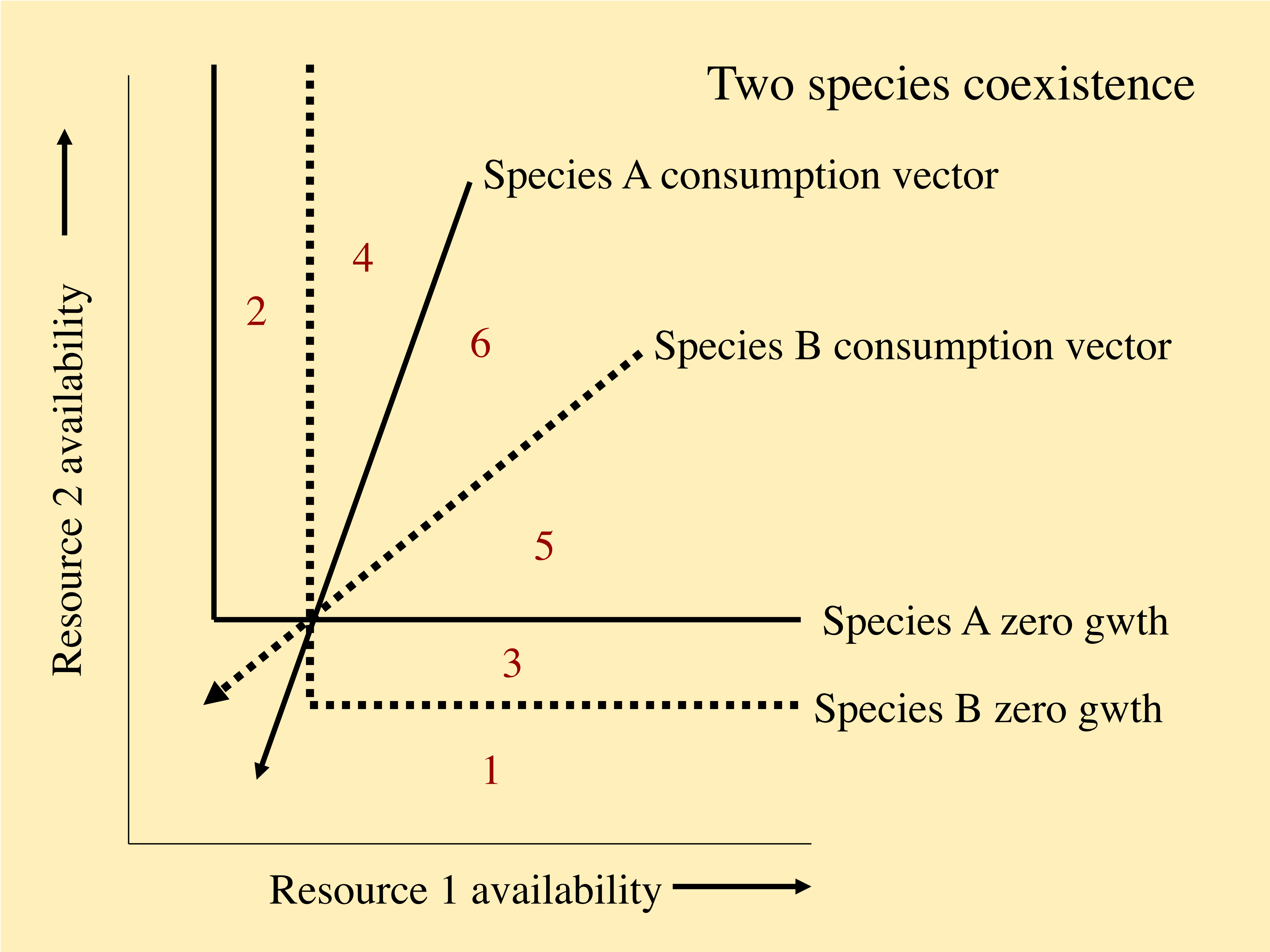


Which species wins in zone 4?
Species A consumption vector
Species B consumption vector
Resource 2 availability
Resource 1 availability
2
4
6
5
3
1

Which sp wins in zone 4?



Answer = A: Because the consumption vector will pass through the sp B zero growth isocline before reaching the species A isocline.


Two species coexistence
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Resource 2 availability
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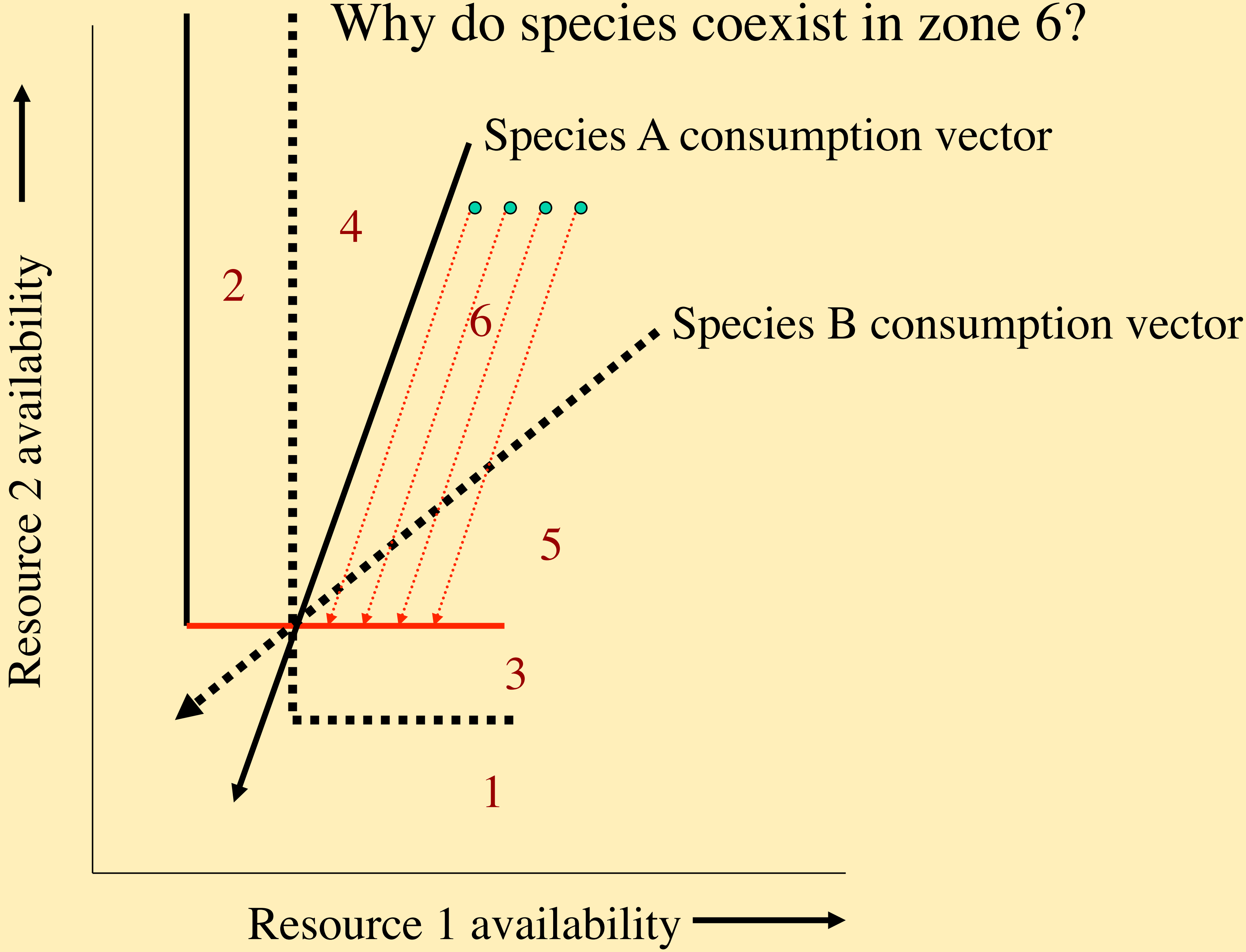
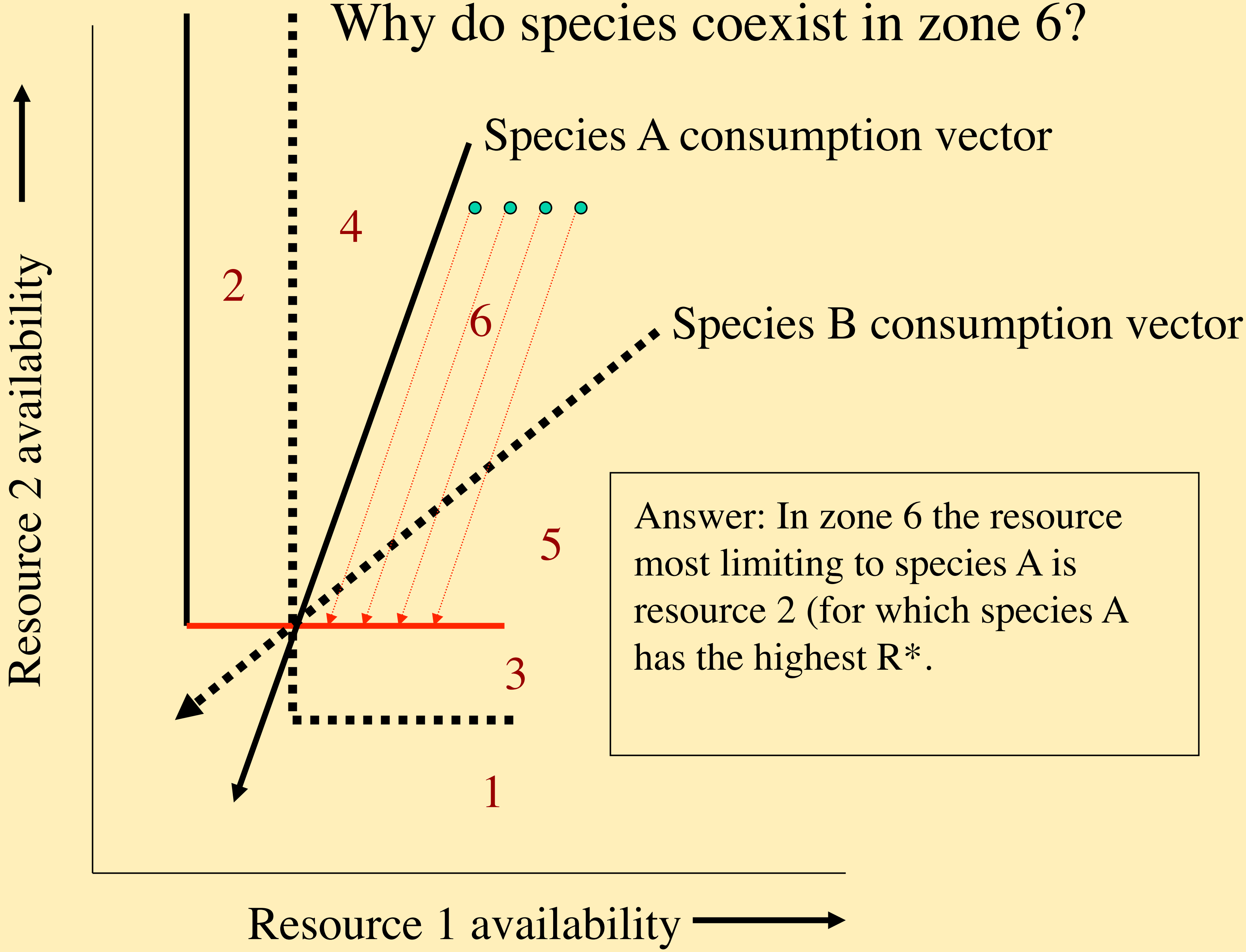
Why do species coexist in zone 6?

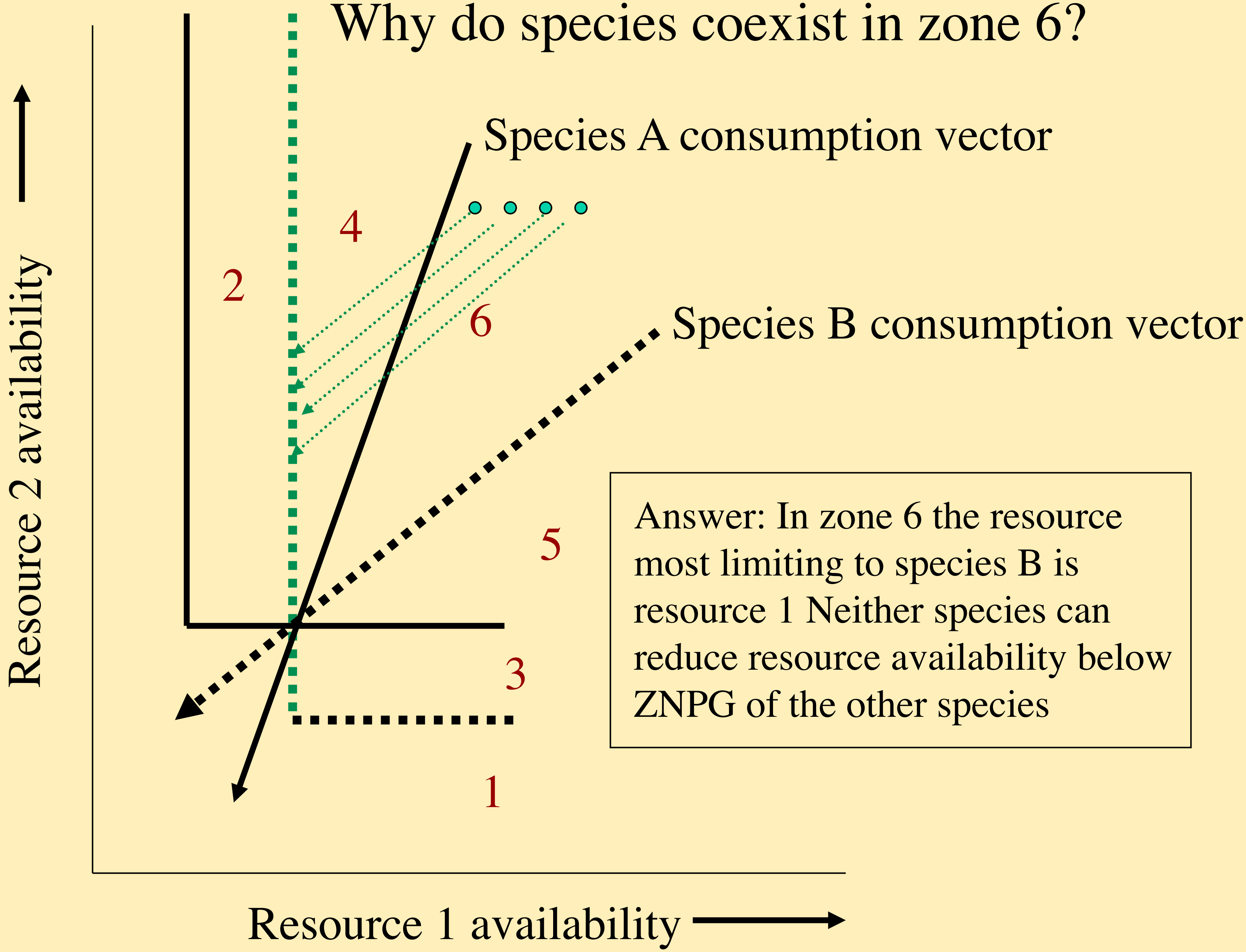


Why do species coexist in zone 6?



Answer: In zone 6 the resource most limiting to species A is resource 2 (for which species A has the highest R*.

Why do species coexist in zone 6?



Answer: In zone 6 the resource most limiting to species B is resource 1 Neither species can reduce resource availability below ZNPG of the other species

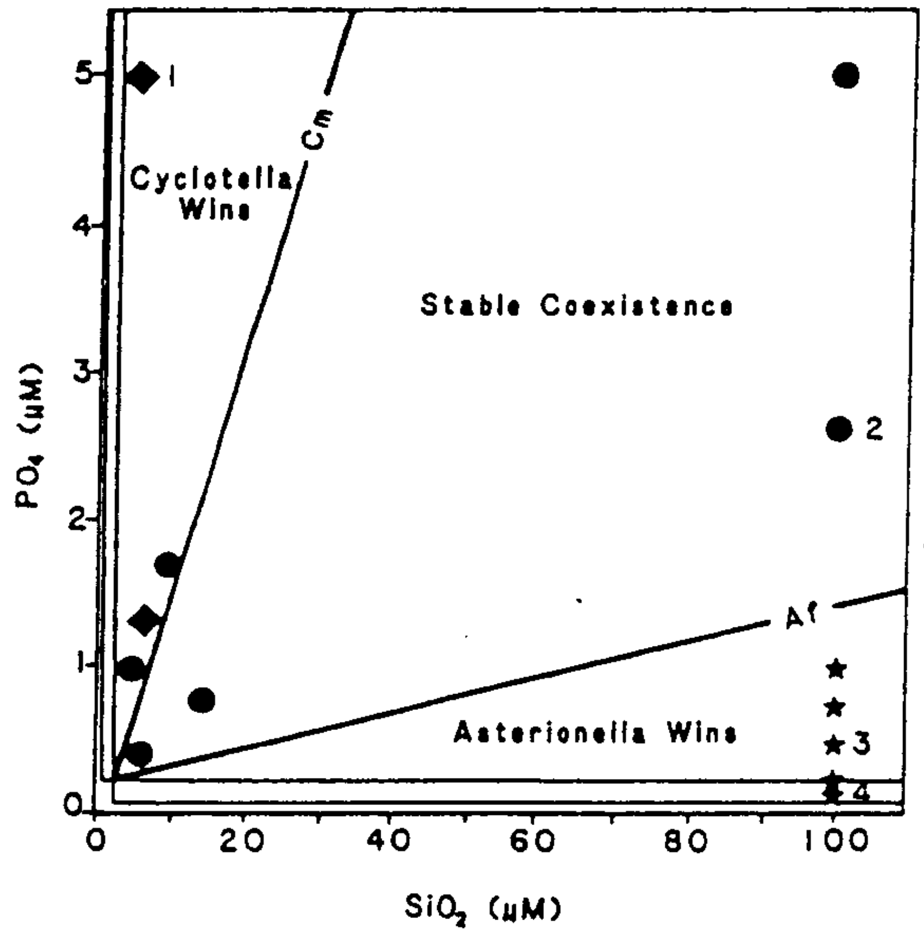
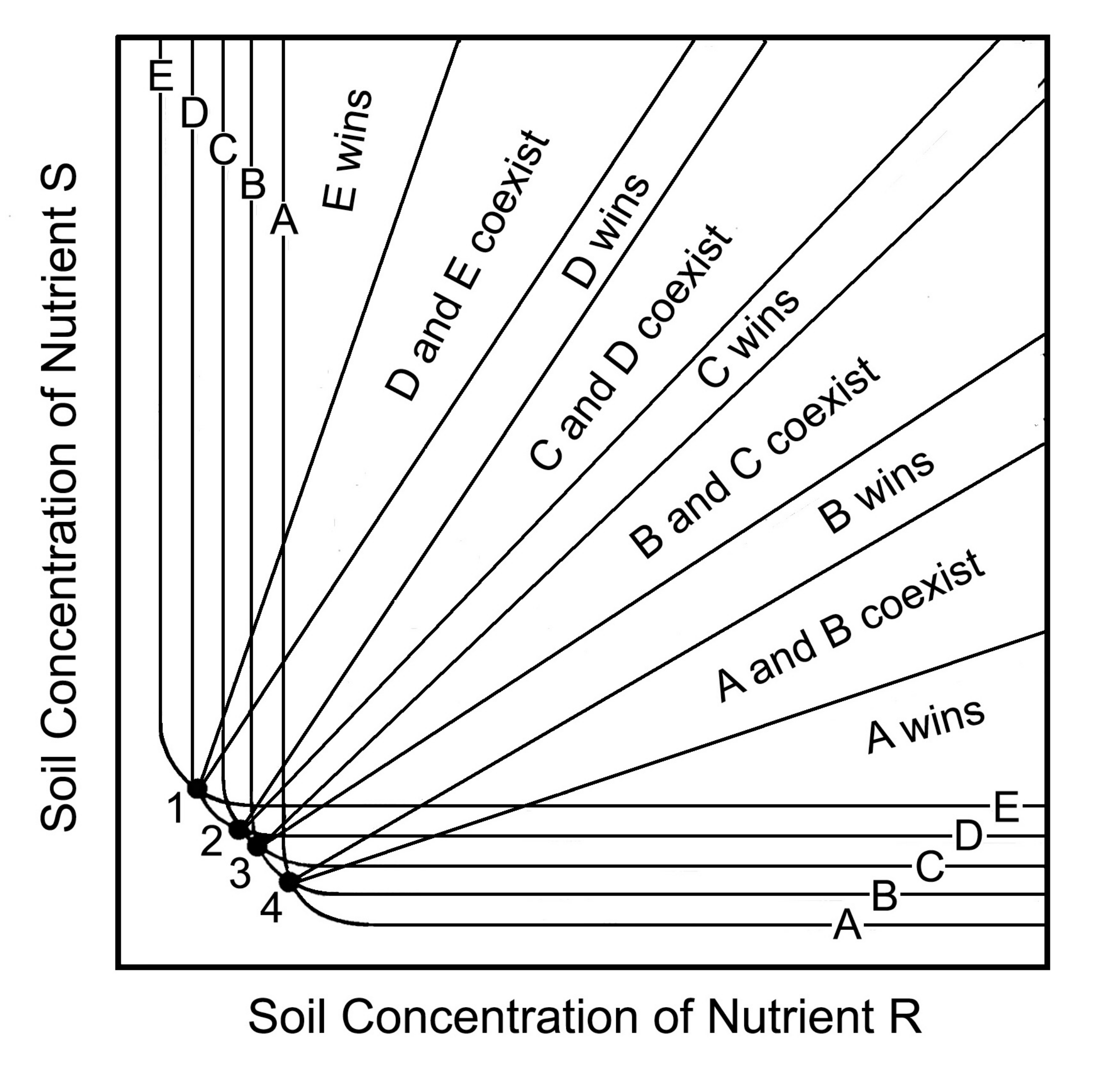


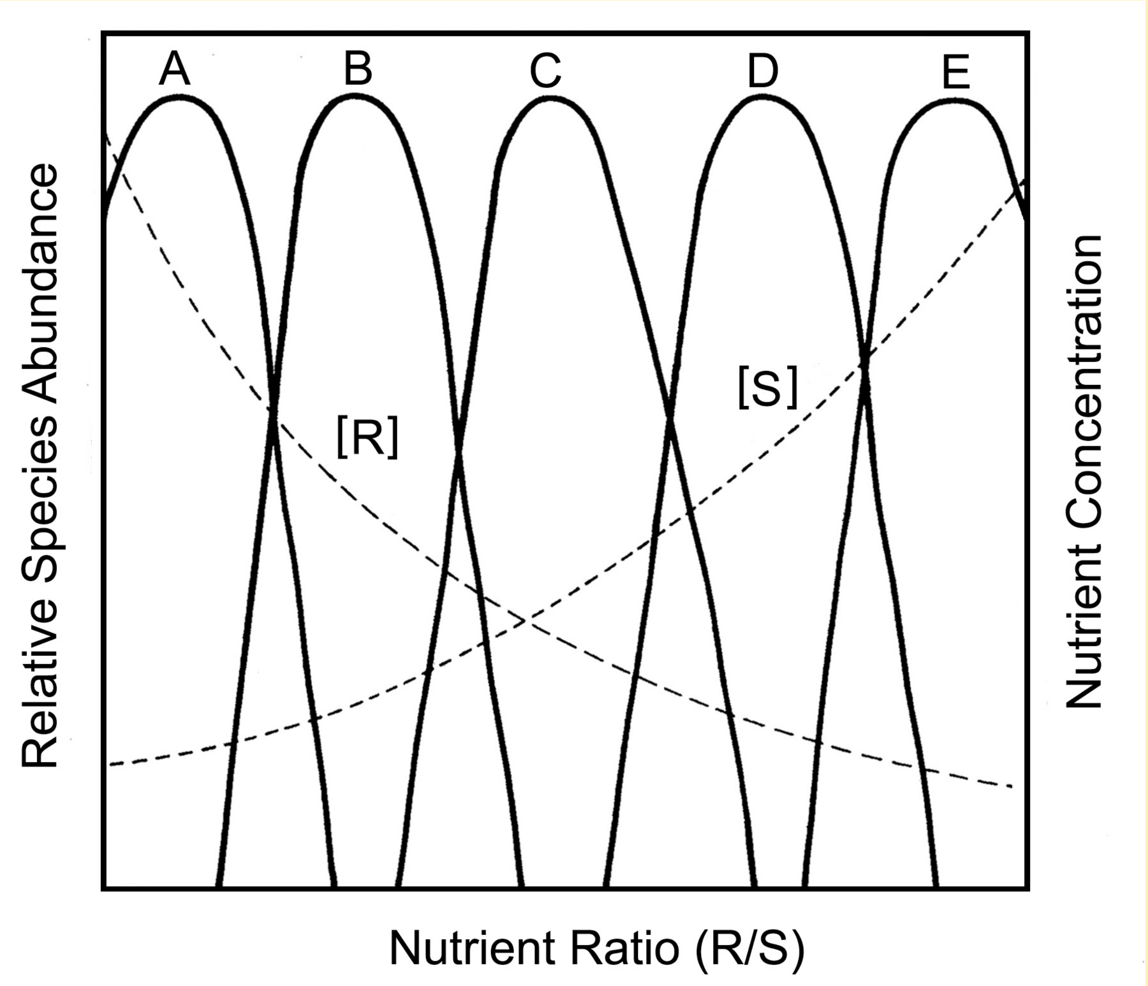
FIGURE 2.6. *(B) Top: Examples of zero-growth isoclines for SiO_2 and PO_4 for two algal species,* Asterionella *and* Cyclotella. *Within the shaded region each species can increase in population size. Note that the lowest* R* *for each species is for a different resource. Bottom: The outcome of competition between these species is described well by the isoclines and consumption vectors. Diamonds =* Cyclotella *wins; dots = stable coexistence; stars =* Asterionella *wins. (Adapted with permission from Tilman, D.* Resource competition and community structure. *© 1982 by Princeton University Press.)*

Can R* promote multi-species coexistence?



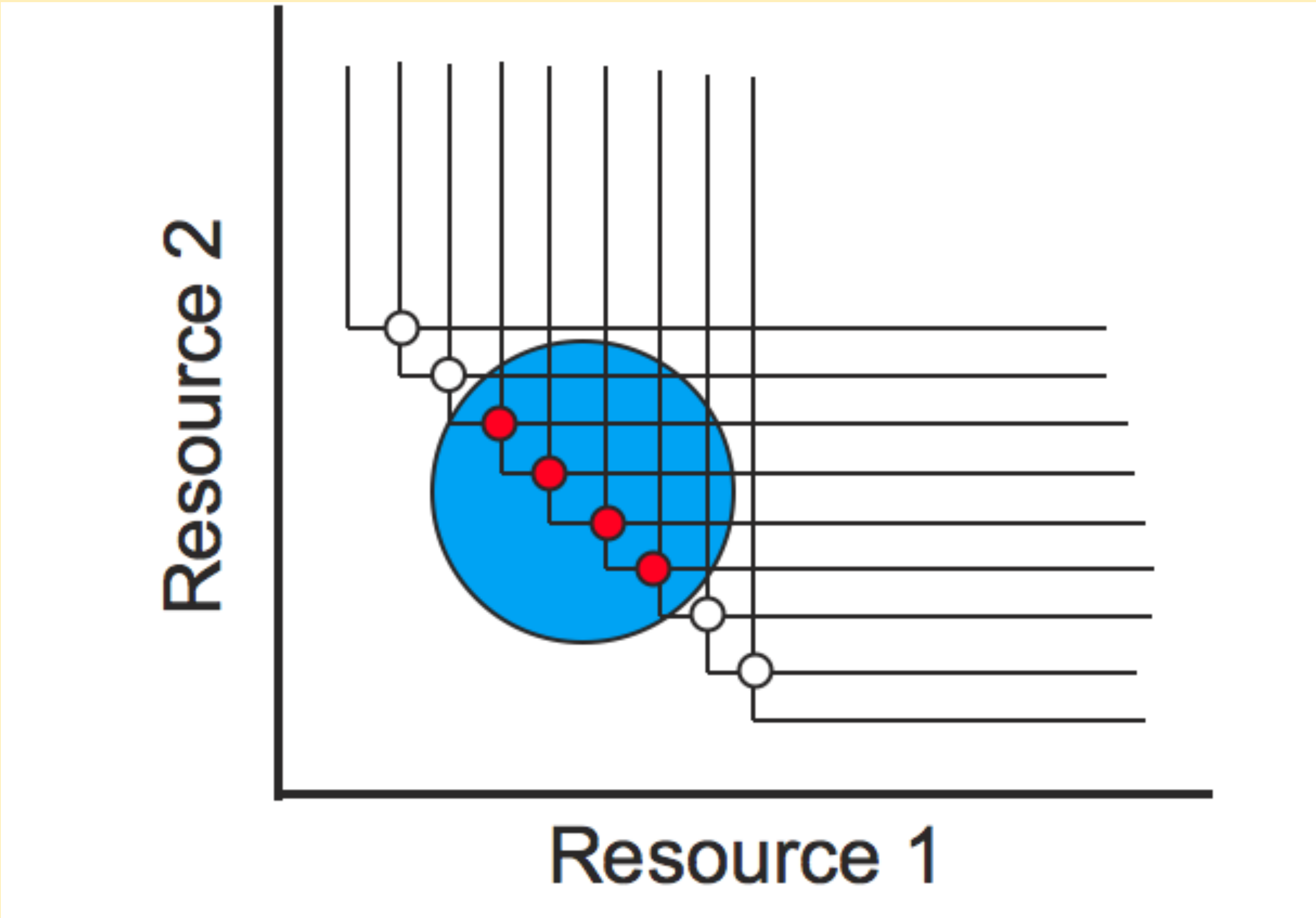
Tilman (1988) Fig. 2.10a

Can R* promote multi-species coexistence?

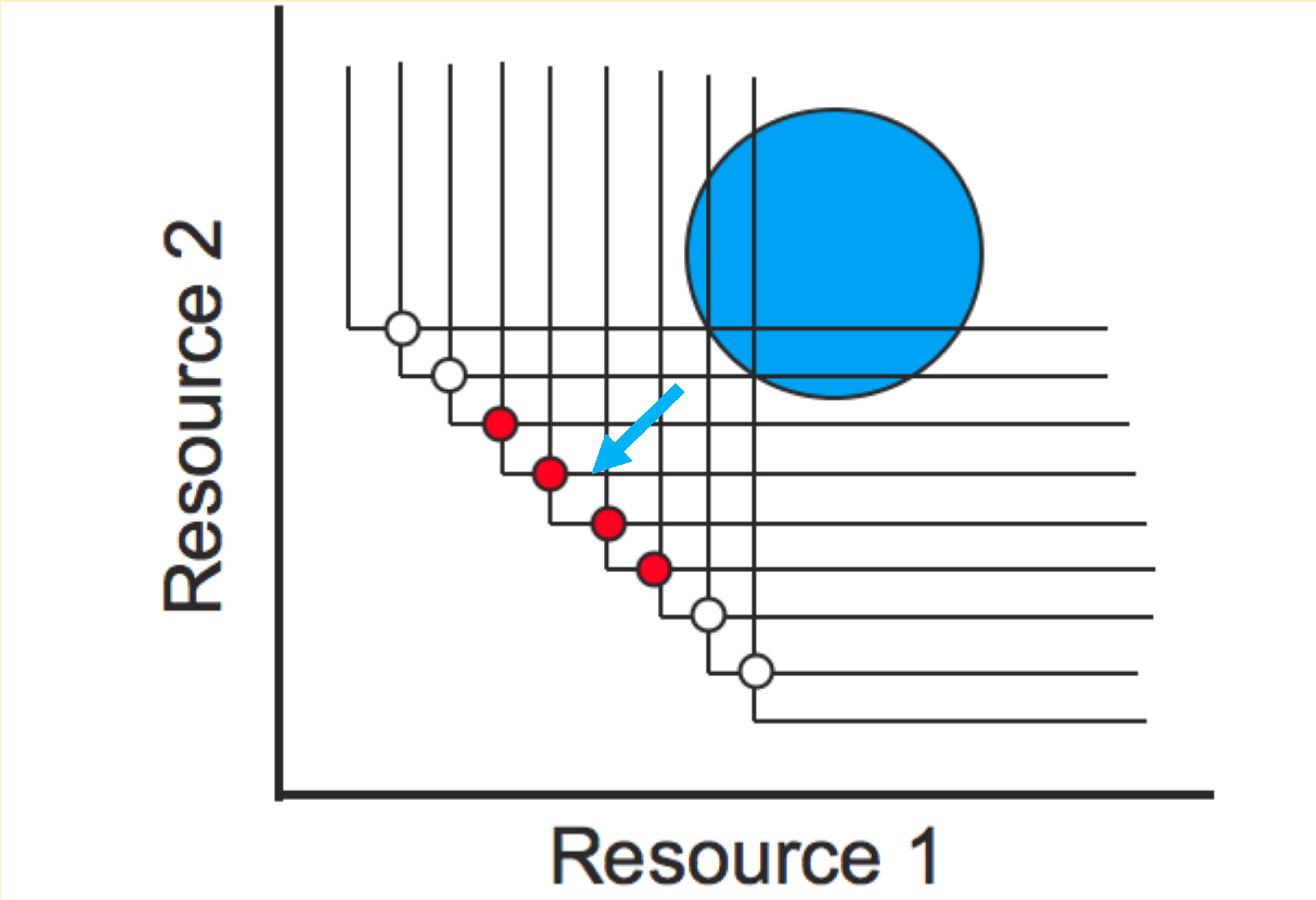


Species differences in R* across gradients of resource availability

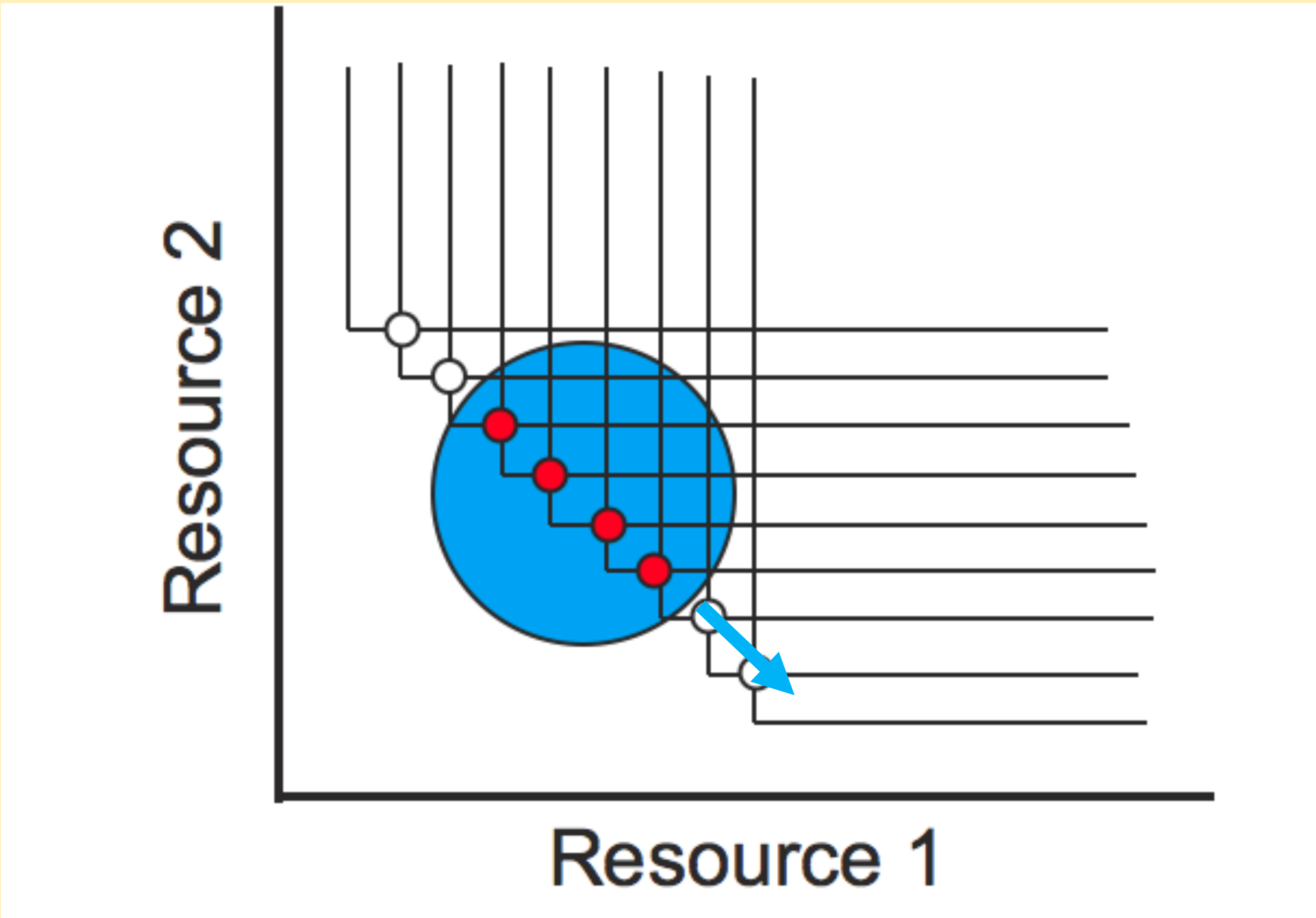
Multispecies coexistence if there is sufficient variation in resource ratios across the landscape



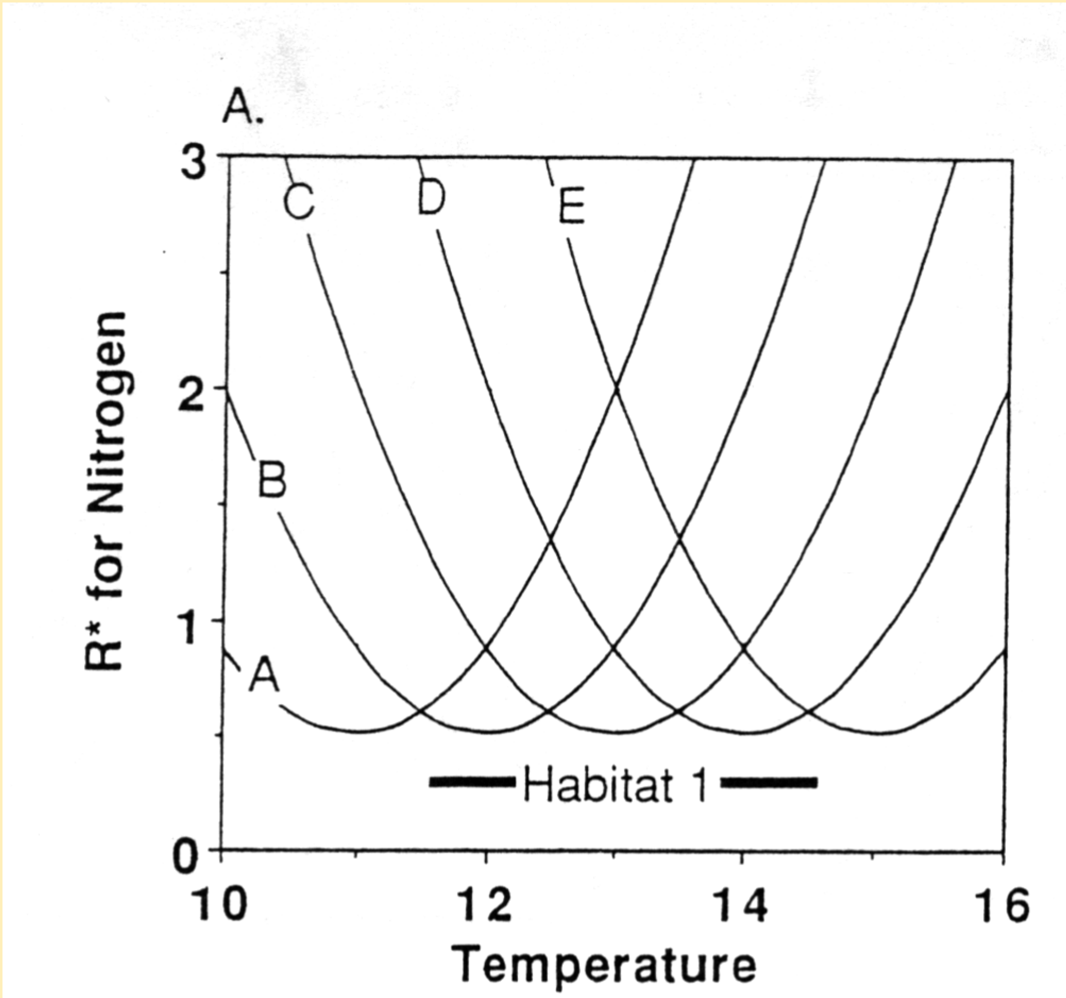
Even if initial resource supply rates are high…



Might also account for successional change?



Factors might also modify a species R* value?



Temperature effects on
R* values for N?

How much evidence is there for R* Theory 'in the wild'??

Miller et al. (2005) reviewed tests of R* theory:

1,333 citations of R* theory papers

26 tests of at least one R* prediction (42 tests total)

31 tests supported prediction (11 not)

37 of 42 tests in freshwater/marine systems

Only 5 studies with terrestrial plants

3 supported R*

ALL carried out at Cedar Creek, Minnesota by Tilman and collaborators

So, why are we calling this a theory?

Why so few tests?

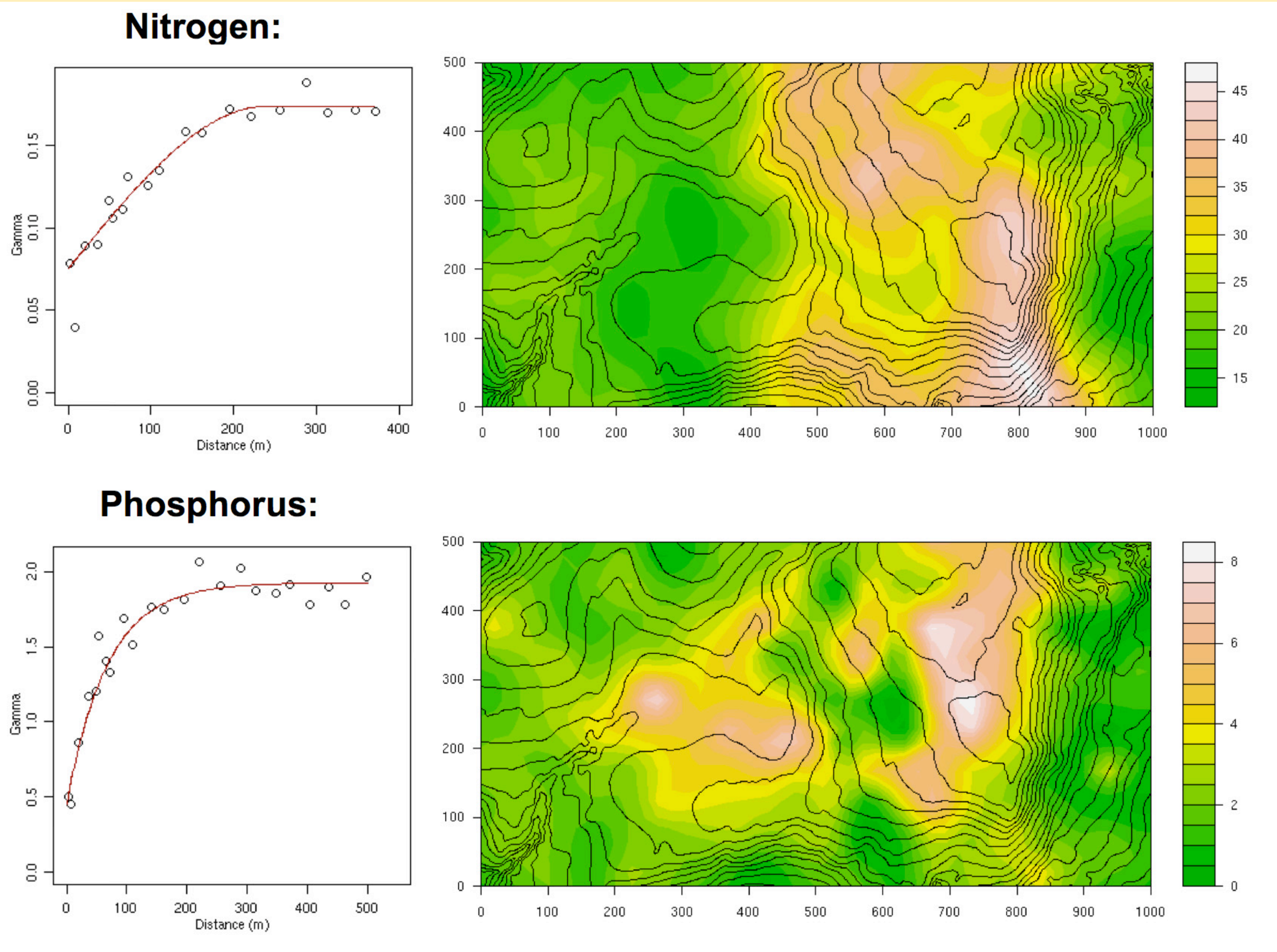
Hard to measure R* values (hard to manipulate nutrients, water, light effectively and retain mycorrhizae, soil structure etc)

If you can do it, then it is expensive to replicate R* measurements for multiple species

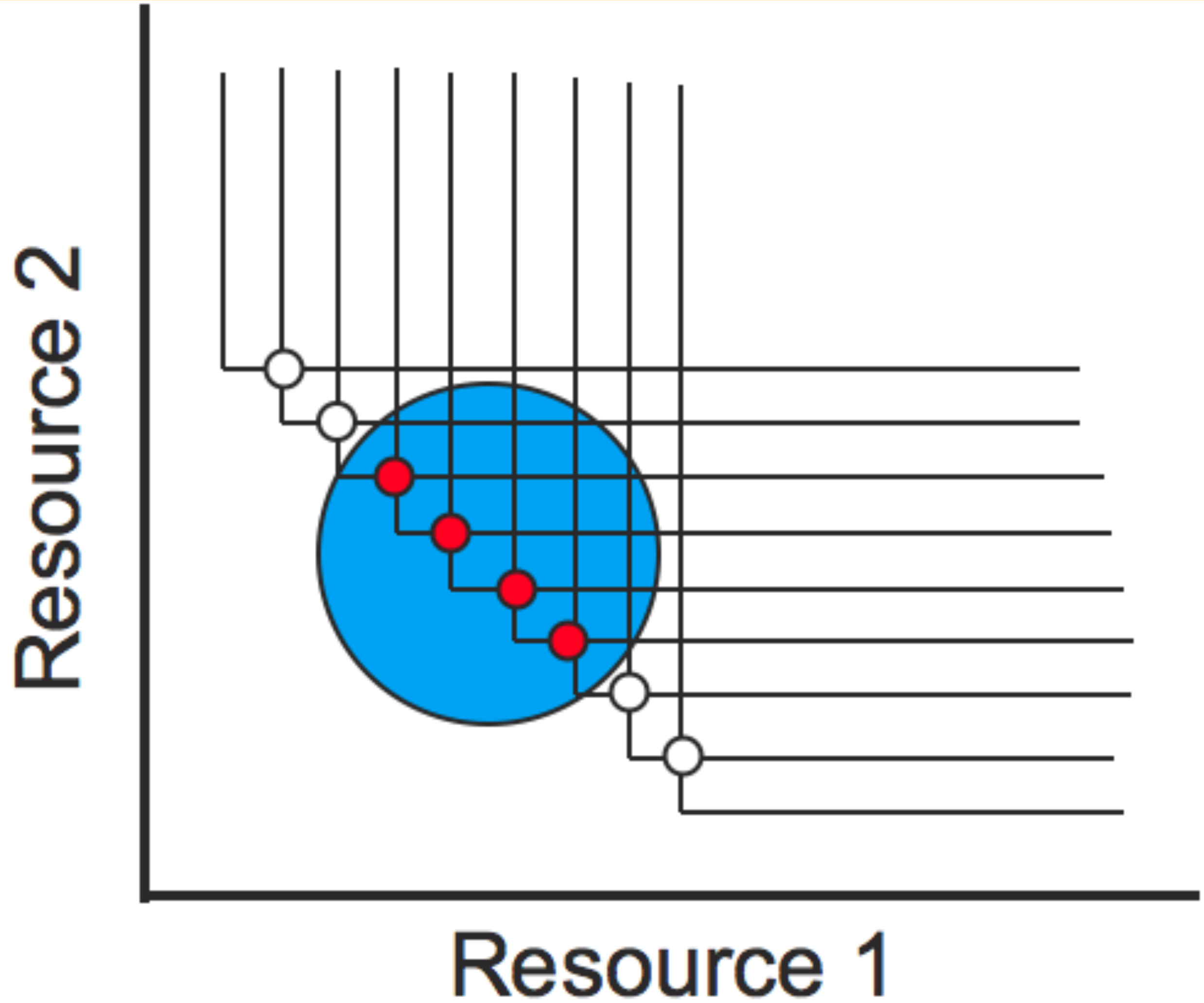
Expensive to measure resource availability in the field at the scale of individual plants.

Proposal reviewers doesn’t seem to be interested?!

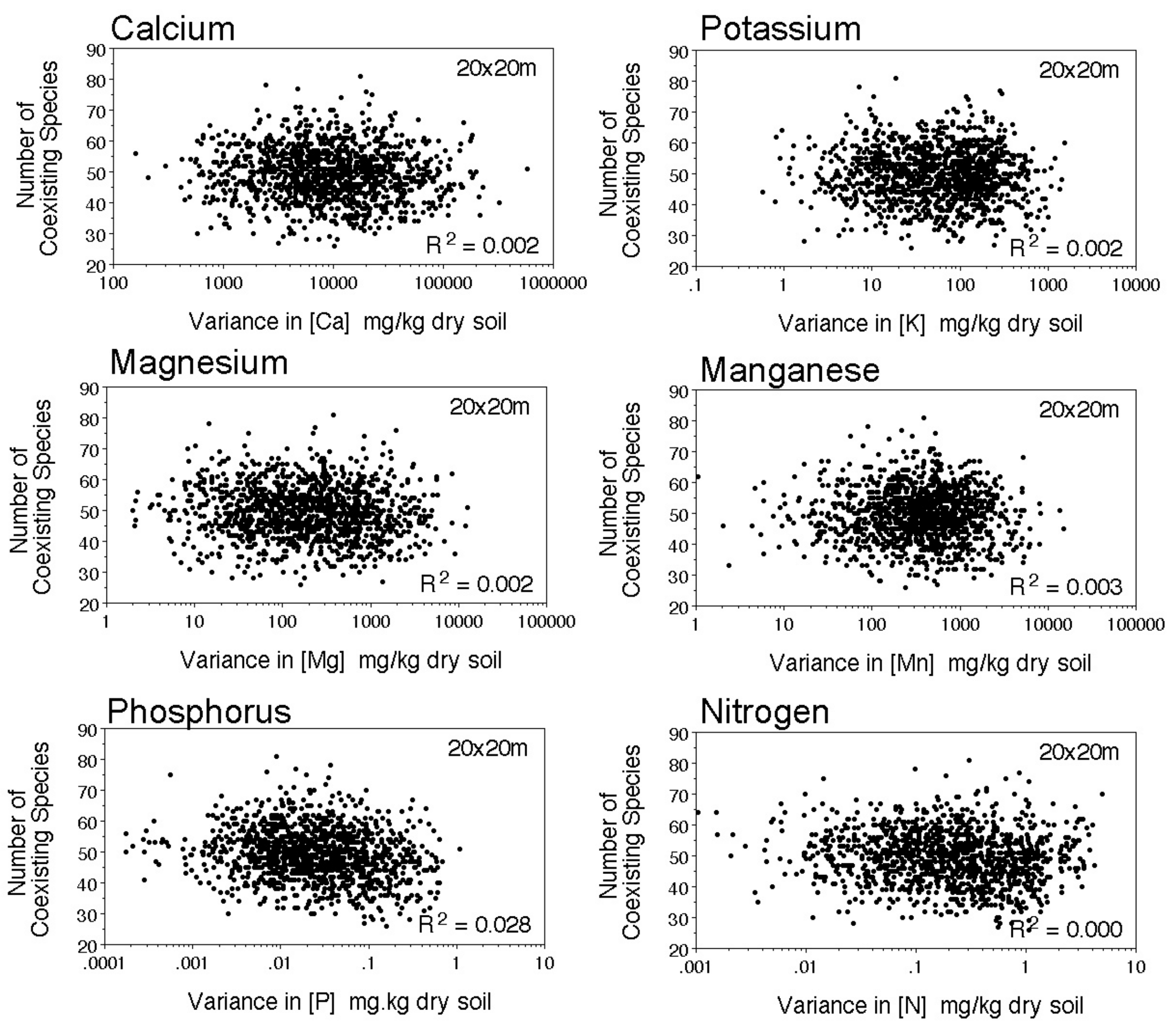
Variation in soil nutrient availability in the BCI forest, Panama



Multispecies coexistence if there is sufficient variation in resource ratios across the landscape



No evidence that variance in nutrient concentrations is related to local species richness in the plot



Plot of number of species present in a 20 x 20 m plot versus variance in nutrient concentrations in the plot

Hubbell et al. unpubl.