

Module 4: Community structure and assembly

Class	Topic	Reading(s)
Day 1 (Thu Nov 2)	Intro, definitions, some history. Messing around with a simple dataset in R.	
Day 2 (Tue Nov 7)	Paper discussion 1: Niches across scales	Chase and Myers (2011)
Day 3 (Thu Nov 9)	Paper discussion 2: Can we begin to infer community assembly processes from patterns?	Leibold and Mikkelsen (2002)
Day 4 (Tue Nov 14)	Paper discussion 3: do communities actually exist?	Half the class will read Ricklefs (2008) and half will read Brooker <i>et al.</i> (2009).
Day 5 (Thu Nov 16)	3 datasets, 3 groups (TBD). 'Elements of metacommunity Structure' approach applied to datasets using R package <i>metacom</i> .	
Day 6 (Tue Nov 21)	Brief group presentations and discussion. Is the world Clementsian/Gleasonian/neutral/other?	

From the course webpage:

“This will not be a survey of Ecology”

- How do we quantify diversity across scales?
- What does it tell us about community assembly?
- Today: a bit of historical context

Clementsian vs. Gleasonian succession

Cowles (1899) -> succession in Lake Michigan dune communities

Clements (1916) -> communities as “super-organisms”, succession as analogous to development – climax state

Gleason (1926) -> “individualistic model”: species interact during succession, but not in an integrated fashion

Horn (1975) and the Institute Woods

Table 1. Transition matrix for Institute Woods in Princeton: percent saplings under various species of trees

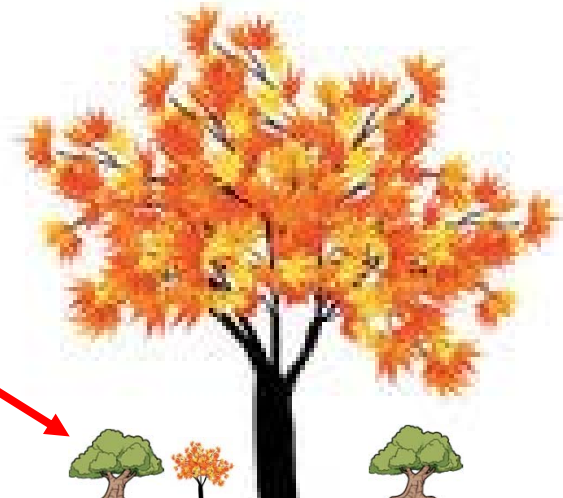
	Sapling species (%)											Total
	BTA	GB	SF	BG	SG	WO	OK	HI	TU	RM	BE	
Canopy species												
Big-toothed aspen	3	5	9	6	6	—	2	4	2	60	3	104
Gray birch	—	—	47	12	8	2	8	0	3	17	3	837
Sassafras	3	1	10	3	6	3	10	12	—	37	15	68
Blackgum	1	1	5	20	9	1	7	6	10	25	17	80
Sweetgum	—	—	16	0	31	0	7	7	5	27	7	662
White oak	—	—	6	7	4	10	7	3	14	32	17	71
Red oaks	—	—	2	11	7	6	8	8	8	33	17	266
Hickories	—	—	1	3	1	3	13	4	9	49	17	223
Tuliptree	—	—	2	4	4	—	11	7	9	29	34	81
Red maple	—	—	13	10	9	2	8	19	3	13	23	489
Beech	—	—	—	2	1	1	1	1	8	6	80	405

Horn's table in cartoon form...

Sassafras



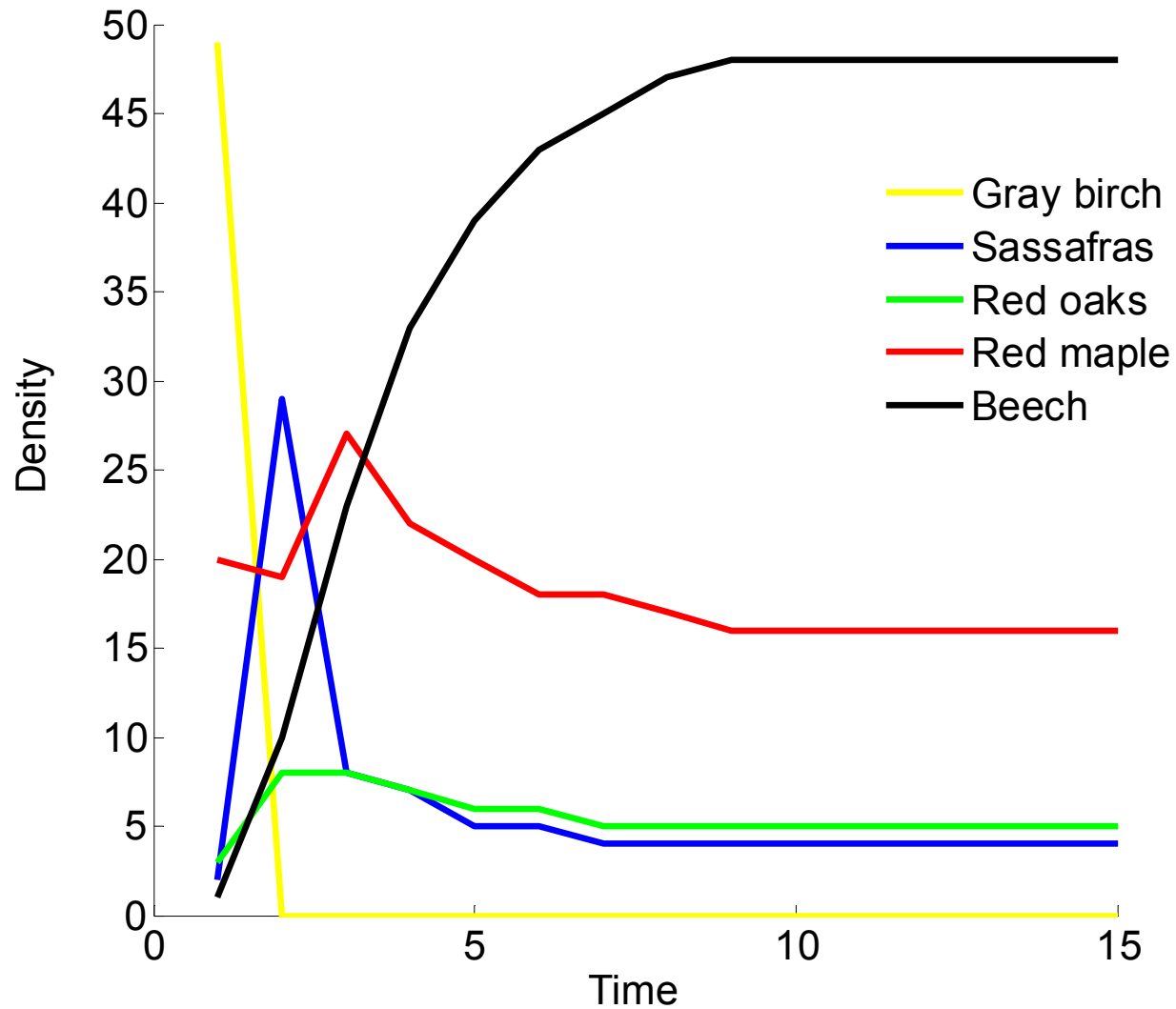
Red maple



Beech



A simulation of succession based on Horn's overstory/understory data



Models of succession (Connell and Slatyer 1977)

Disturbance creates colonization opportunities

Facilitation: first species change conditions to **allow** later species to colonize. Implies high level of community integration.

Tolerance: later species take time to disperse, grow, and establish. They grow **despite** the presence of early-successional species, and eventually **out-compete** them.

Inhibition: early-successional species **inhibit** colonization by all others. Late successional species are those that are able to survive better.

Climax

Silvertown *et al.* invasion probabilities

Table 1. Rates of replacement (p_{ij}) used in the cellular automaton models. Species along the top are the native species, and those along the side are the invaders. Numbers are the proportion by biomass of the invader found in the native plot 18 months after the experiment was set up (from Thórhallsdóttir 1990)

Invader	Native species					Sum
	<i>Lolium</i>	<i>Agrostis</i>	<i>Holcus</i>	<i>Poa</i>	<i>Cynosurus</i>	
<i>Lolium</i>	—	0.02	0.06	0.05	0.03	0.16
<i>Agrostis</i>	0.23	—	0.09	0.32	0.37	0.81
<i>Holcus</i>	0.06	0.08	—	0.16	0.09	0.39
<i>Poa</i>	0.44	0.06	0.06	—	0.11	0.67
<i>Cynosurus</i>	0.03	0.02	0.03	0.05	—	0.13
Sum	0.76	0.18	0.24	0.58	0.60	

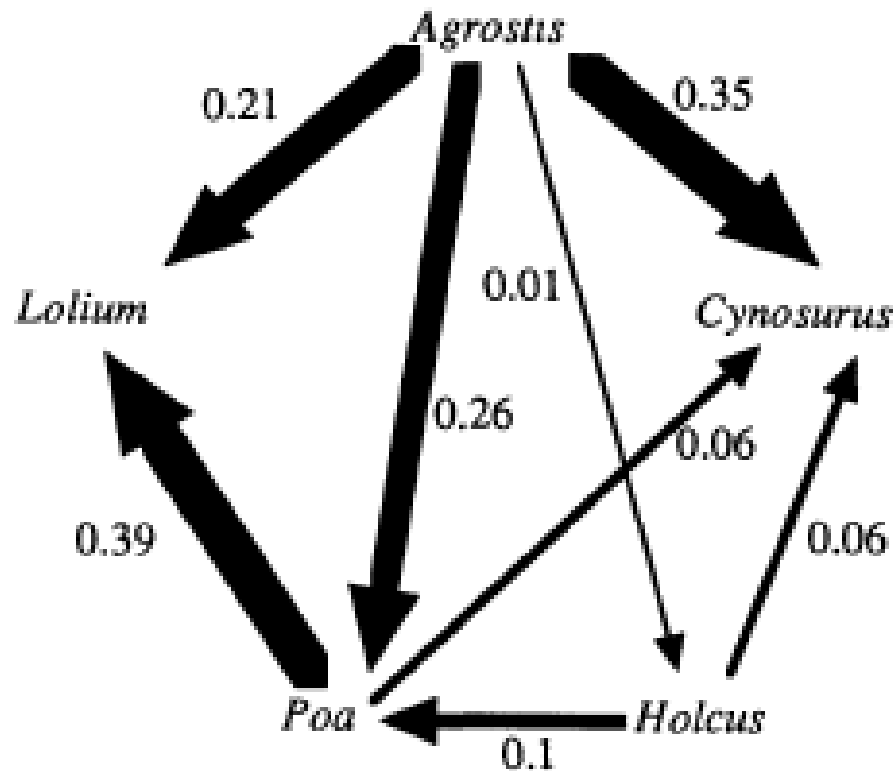


Fig. 1. Net rates of invasion by species ($p_{ij} - p_{ji}$) in Thórhallsdóttir's (1990) experiment, calculated from transitions (p_{ij}) shown in Table 1. Arrows point from the invading species to the invaded species.

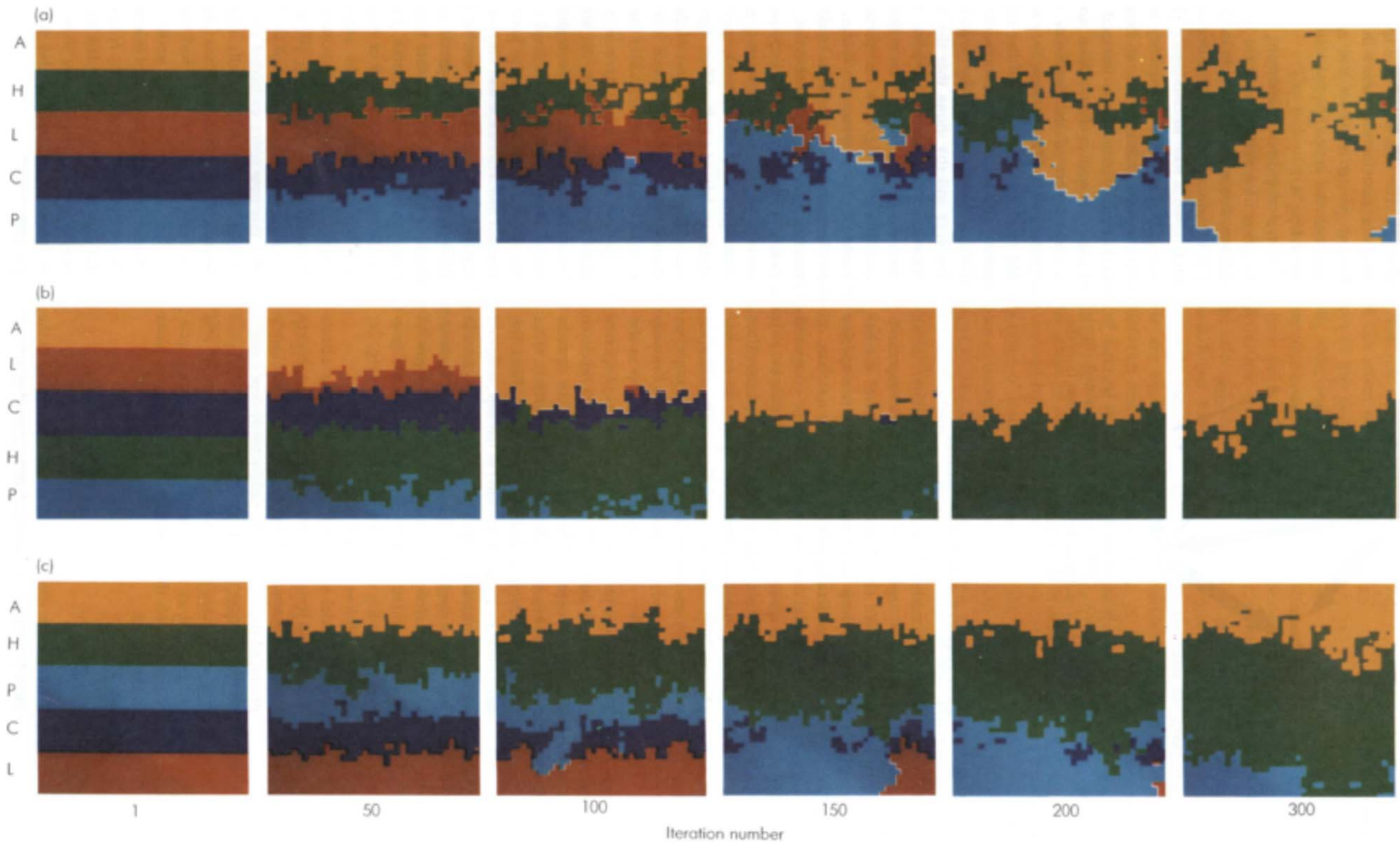
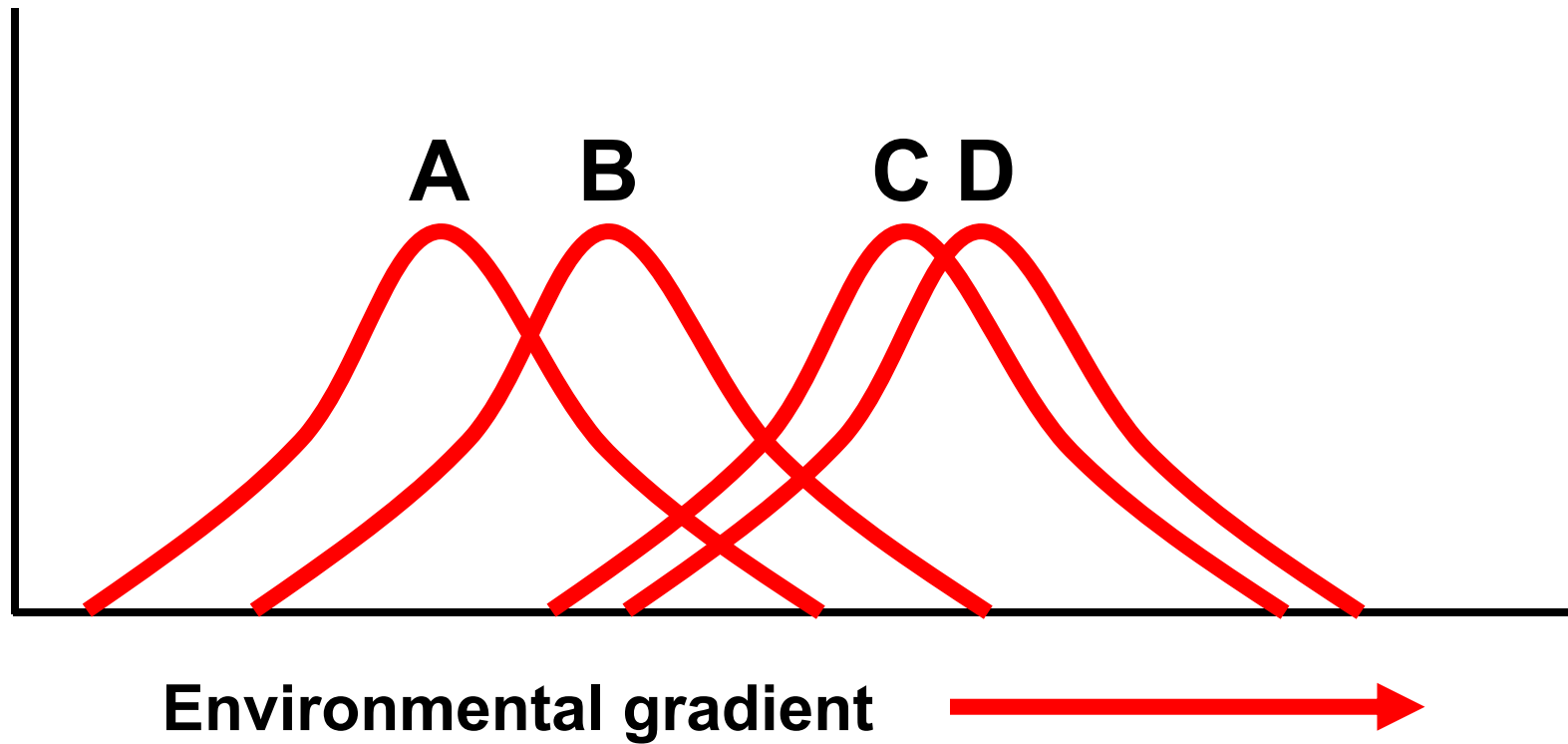


Fig. 2. Initial arrangement of *Agrostis* (yellow), *Holcus* (green), *Lolium* (red), *Cynosurus* (dark blue) and *Poa* (light blue) in the aggregated model and species' distributions at iterations 1, 50, 100, 150, 200, 300; (a) *Agrostis*, *Holcus*, *Lolium*, *Cynosurus*, *Poa*; (b) *Agrostis*, *Lolium*, *Cynosurus*, *Holcus*, *Poa*; (c) *Agrostis*, *Holcus*, *Poa*, *Cynosurus*, *Lolium*.

The previous examples represented longitudinal datasets

How much can we infer about process when we examine static patterns?

Species distributions form successive Gaussian envelopes along environmental gradients



Whittaker (1965, 1967)

Woodland communities along the catena

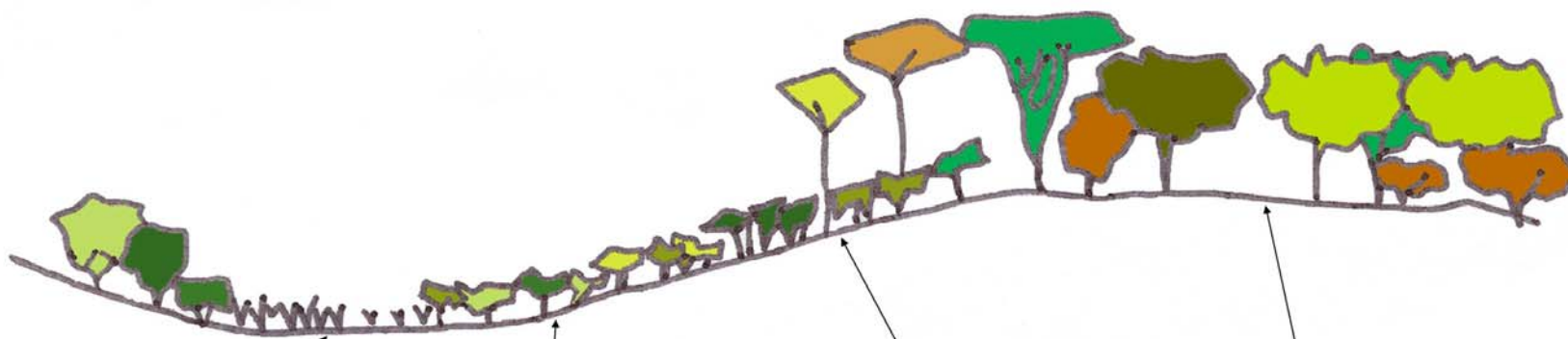
Dete vlei

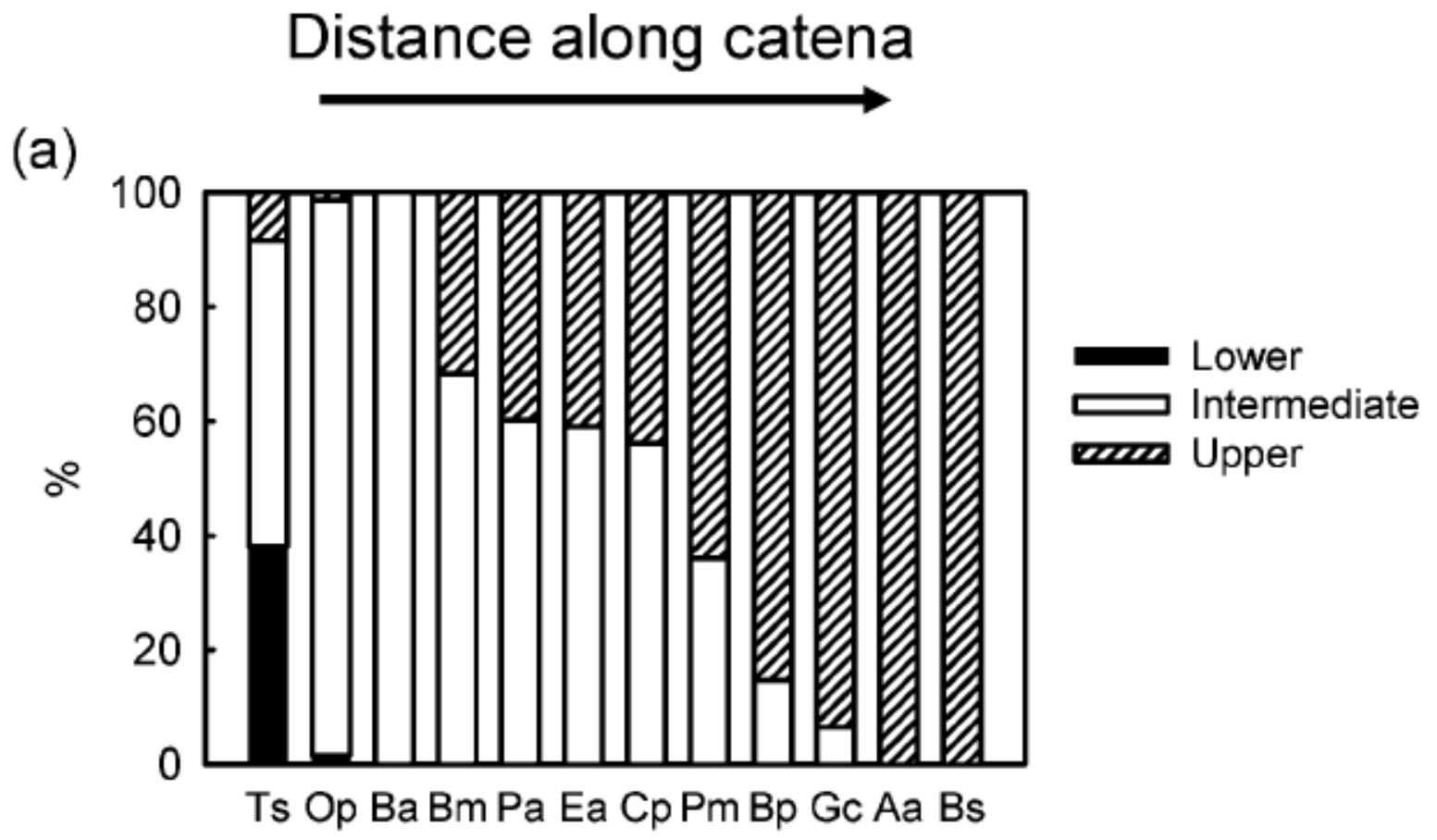
Lower

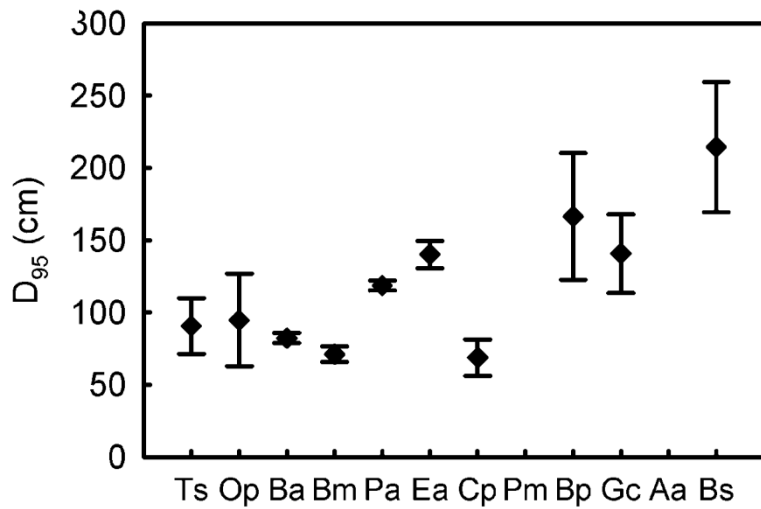
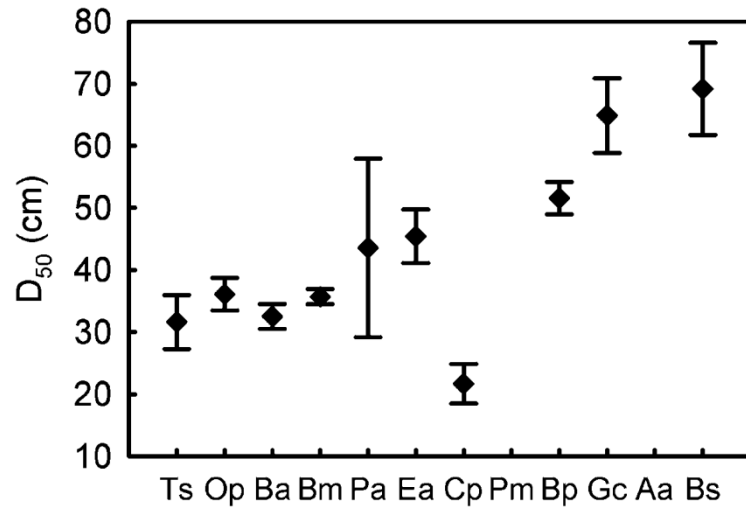
Mid

Upper

200 m transect



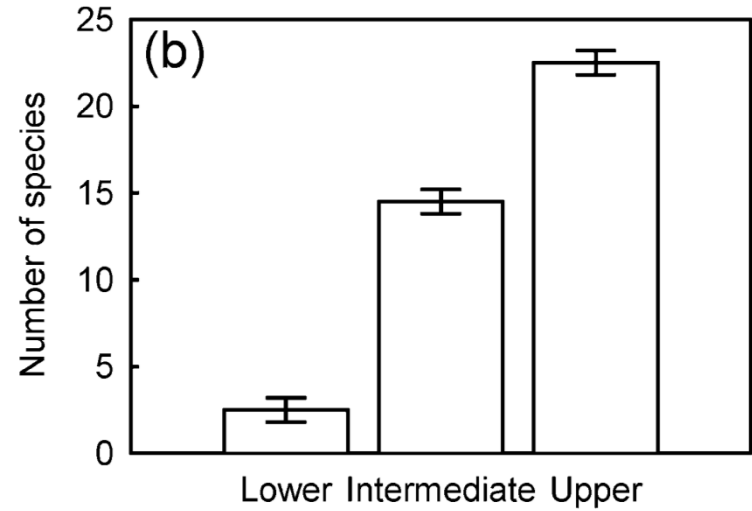




Species



Species richness increases up the catena



Holdo & Timberlake (2008)

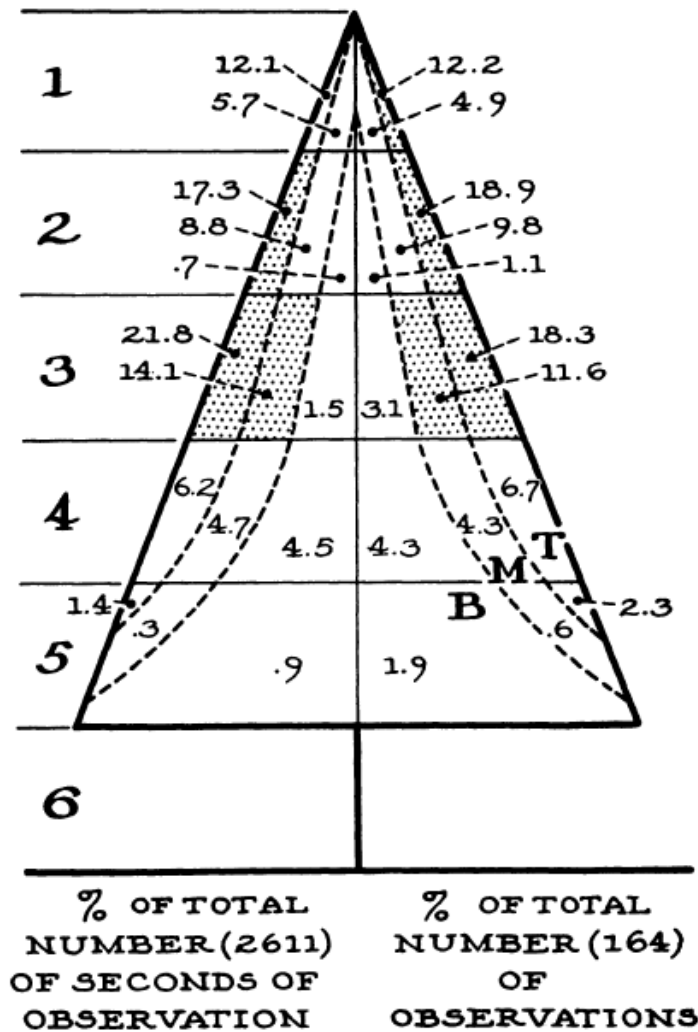
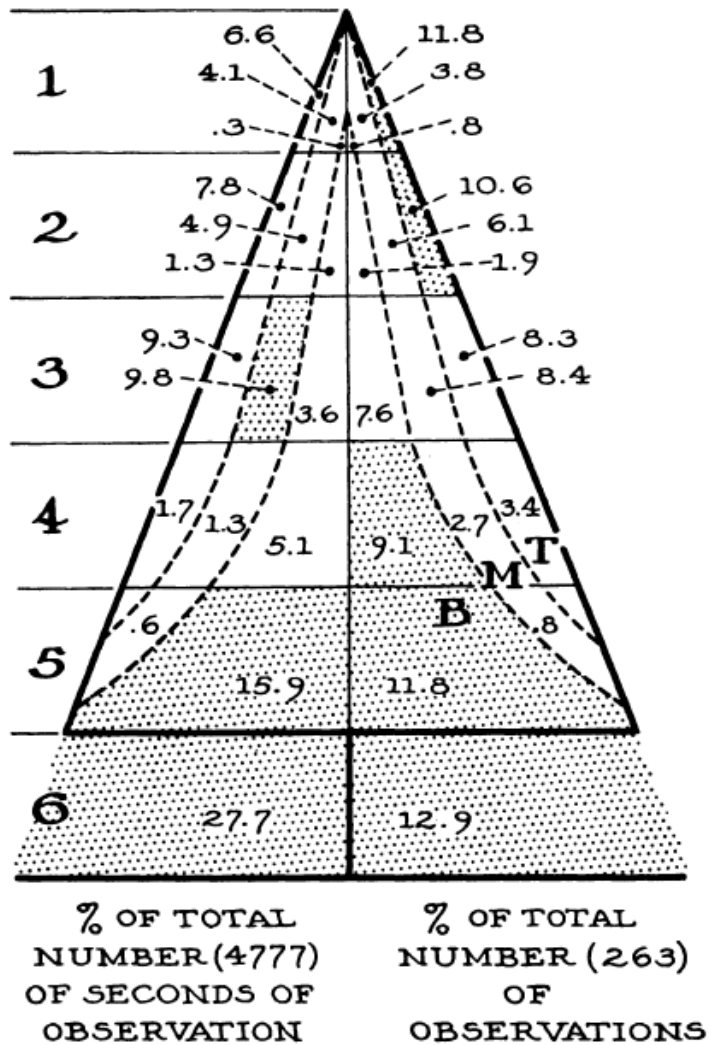
The niche concept and competition

- Grinnellian niche (Grinnell 1917)
- Eltonian niche (Elton 1927)
- Niche is “n-dimensional”, maps population dynamics onto environmental space (Hutchinson 1957)
- Competitive exclusion principle (Hardin 1960)
- MacArthur and Levins (1967): limiting similarity

Feeding positions

Myrtle warbler

Black-throated green warbler



MacArthur (1967)

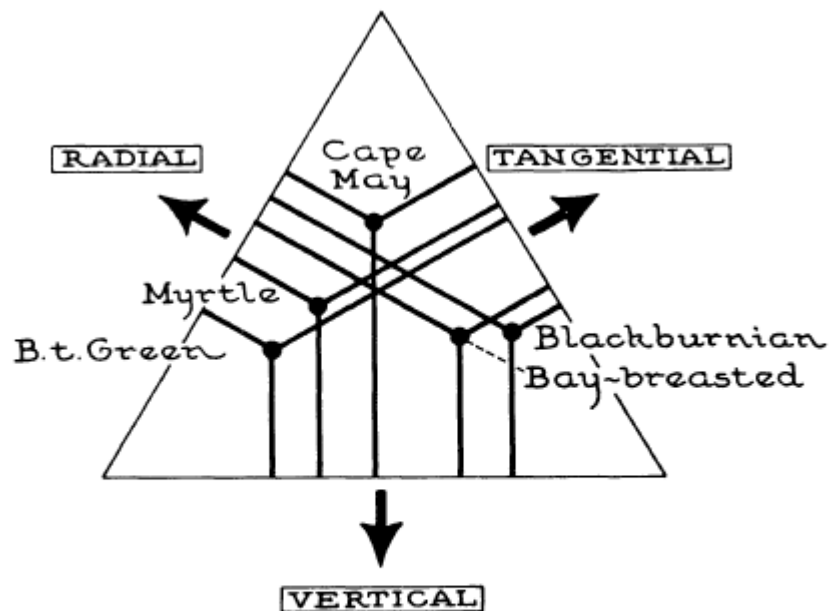


FIG. 7. Components of Motion. From the dot representing a species, lines are drawn to the sides of the triangle. The lengths of these lines are proportional to the total distance which the species moved in radial, tangential, and vertical directions, respectively.

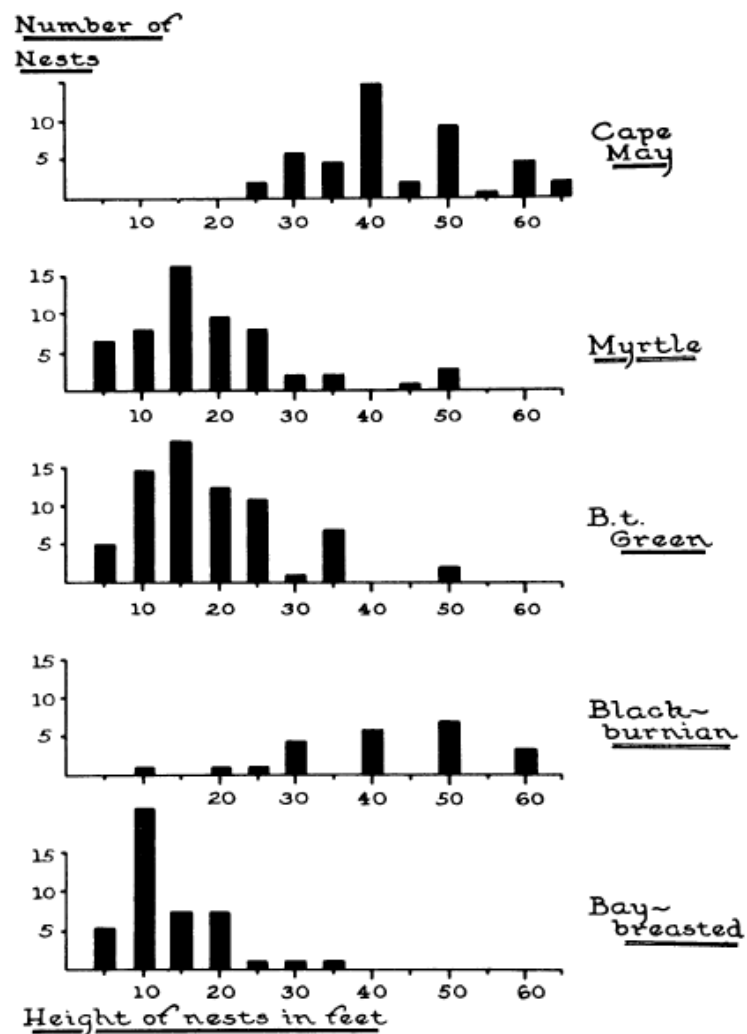


FIG. 8. Nesting heights of warblers.

Competition

A.G. Tansley (1917):
demonstrated competition
between closely related
species.

Galium saxatile found in
acid, peaty soils

G. sylvestre found on
limestone (calcareous)
hills, pastures



Galium saxatile

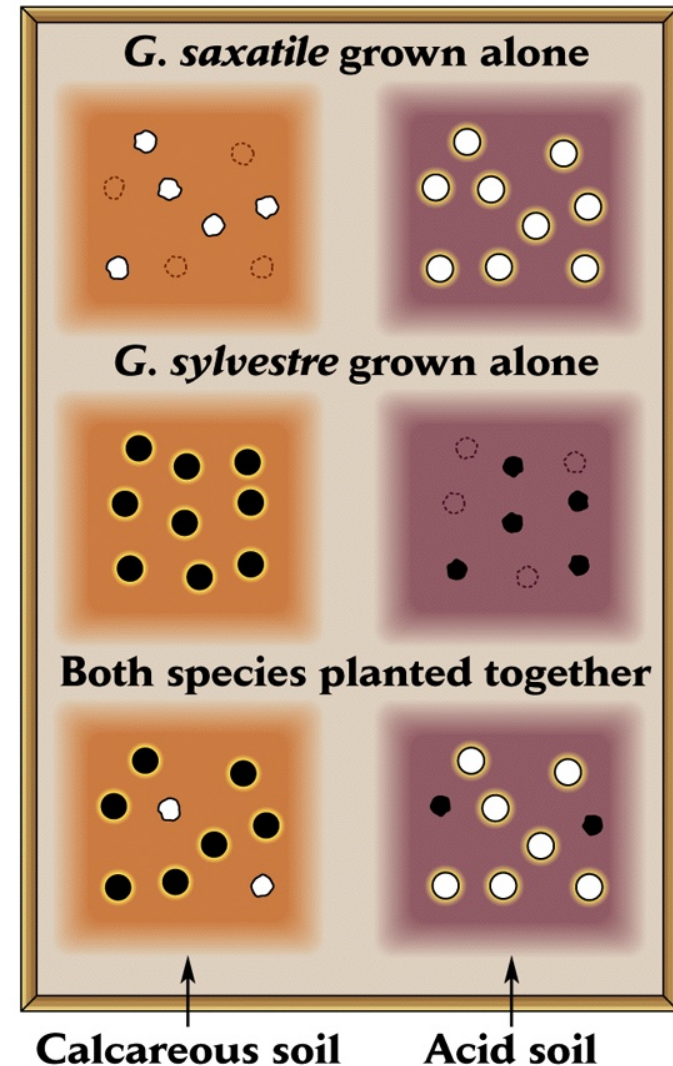


Galium sylvestre

Image/fig from Cain *et al.* (2014)

To investigate interactions between these closely related species, Tansley conducted a **common garden experiment**

**Experimental common garden
(equal sun, rain, temperature
for each group of plants)**



Image/fig from Cain *et al.* (2014)

Tansley's classic experiment

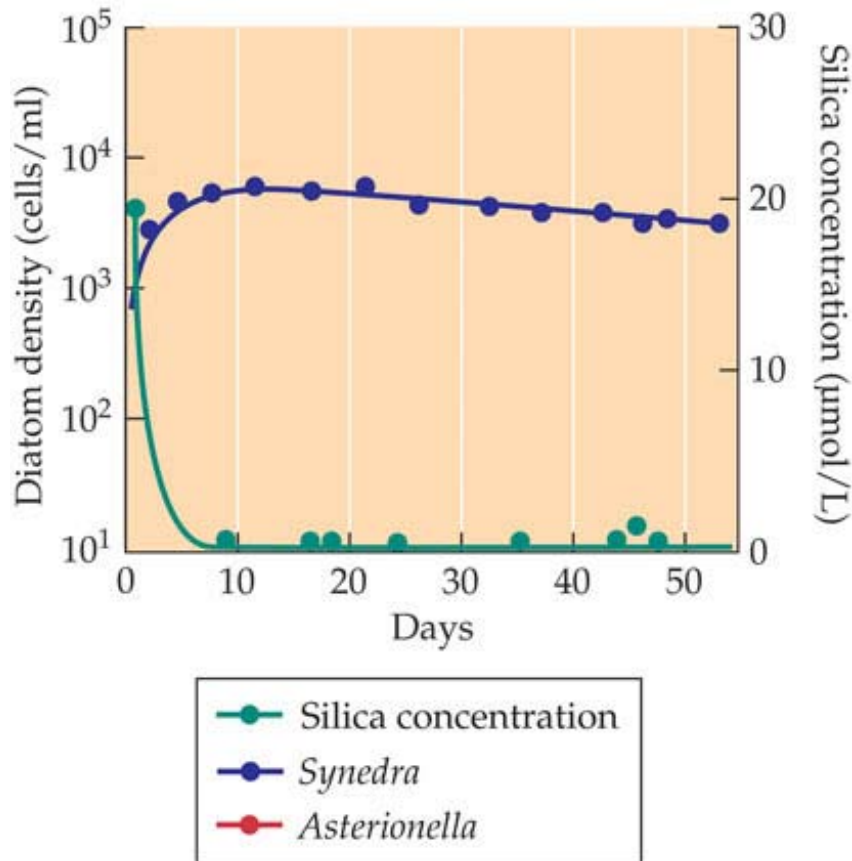
- Presence or abundance of one species can affect another species
- Competitive outcomes can depend on underlying environmental conditions
- Present ecological segregation of species might be the result of past competition



Image/fig from Cain *et al.* (2014)

Resource consumption often leads to resource depletion

(A) *Synedra* alone



ECOLOGY 3e, Figure 12.4 (Part 1)
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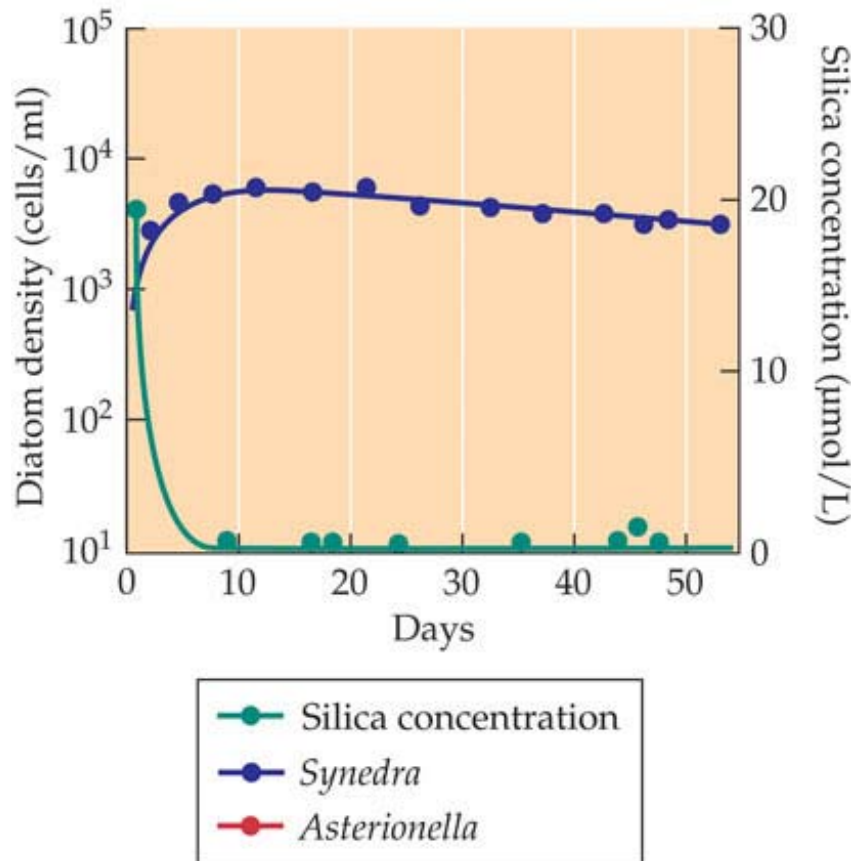
- The ability of a species to maintain itself in a community is determined by the limiting resource level (R^*) that results in zero net population growth (ZNPNG).
- This depends on the supply and consumption rates of the resource and the reproduction and mortality rates of the consumer species.

Image/fig from Cain *et al.* (2014)

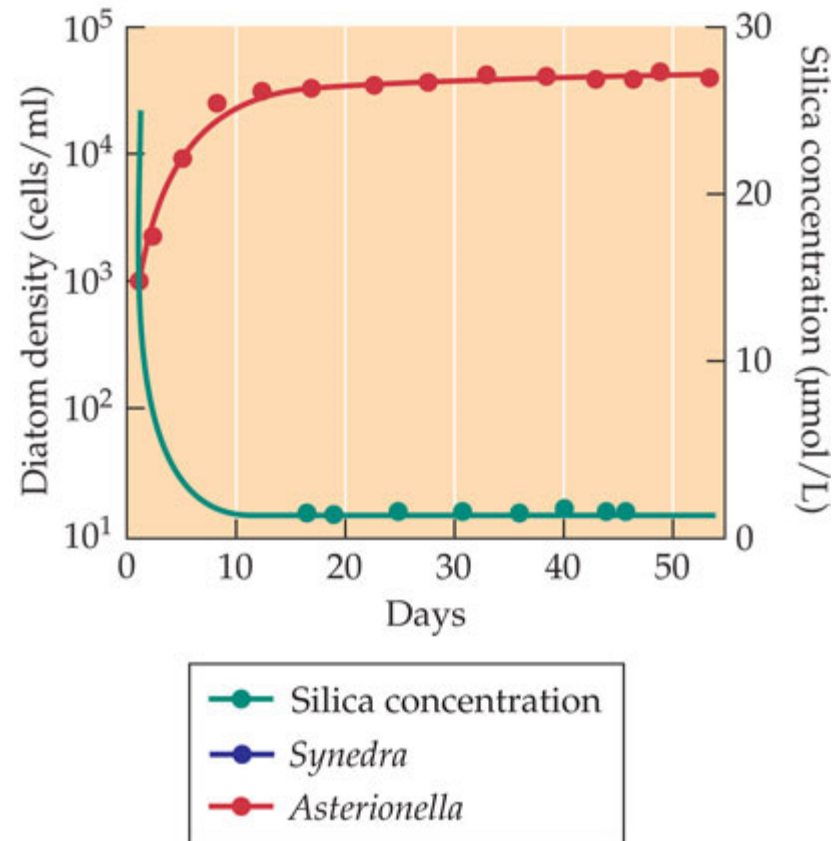
Tilman (1980); Tilman *et al.* (1981)

Two species may have different R^* values corresponding to their respective ZNPG states

(A) *Synedra* alone



(B) *Asterionella* alone



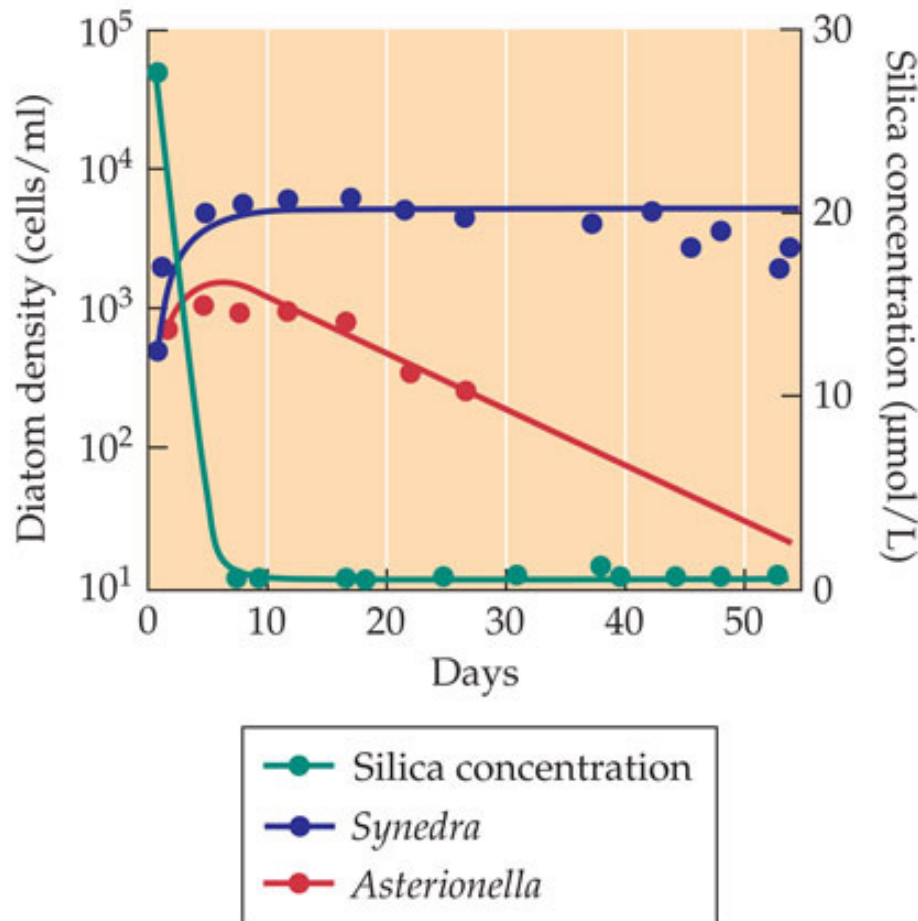
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Image/fig from Cain *et al.* (2014)

In competition, *Synedra* has a lower R^* , and outcompetes *Asterionella*

(C) Interspecific competition



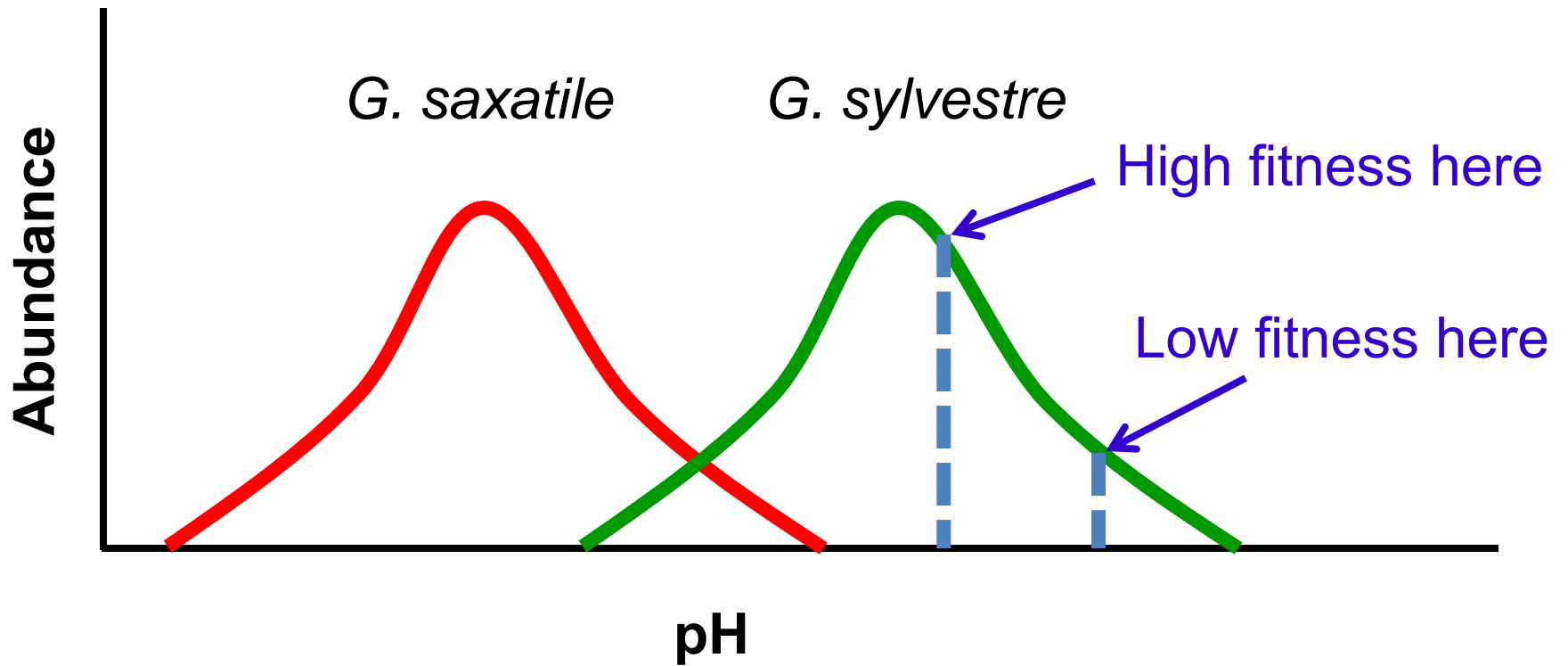
ECOLOGY 3e, Figure 12.4 (Part 3)
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R^* represents the level of the resource that will allow a species to persist

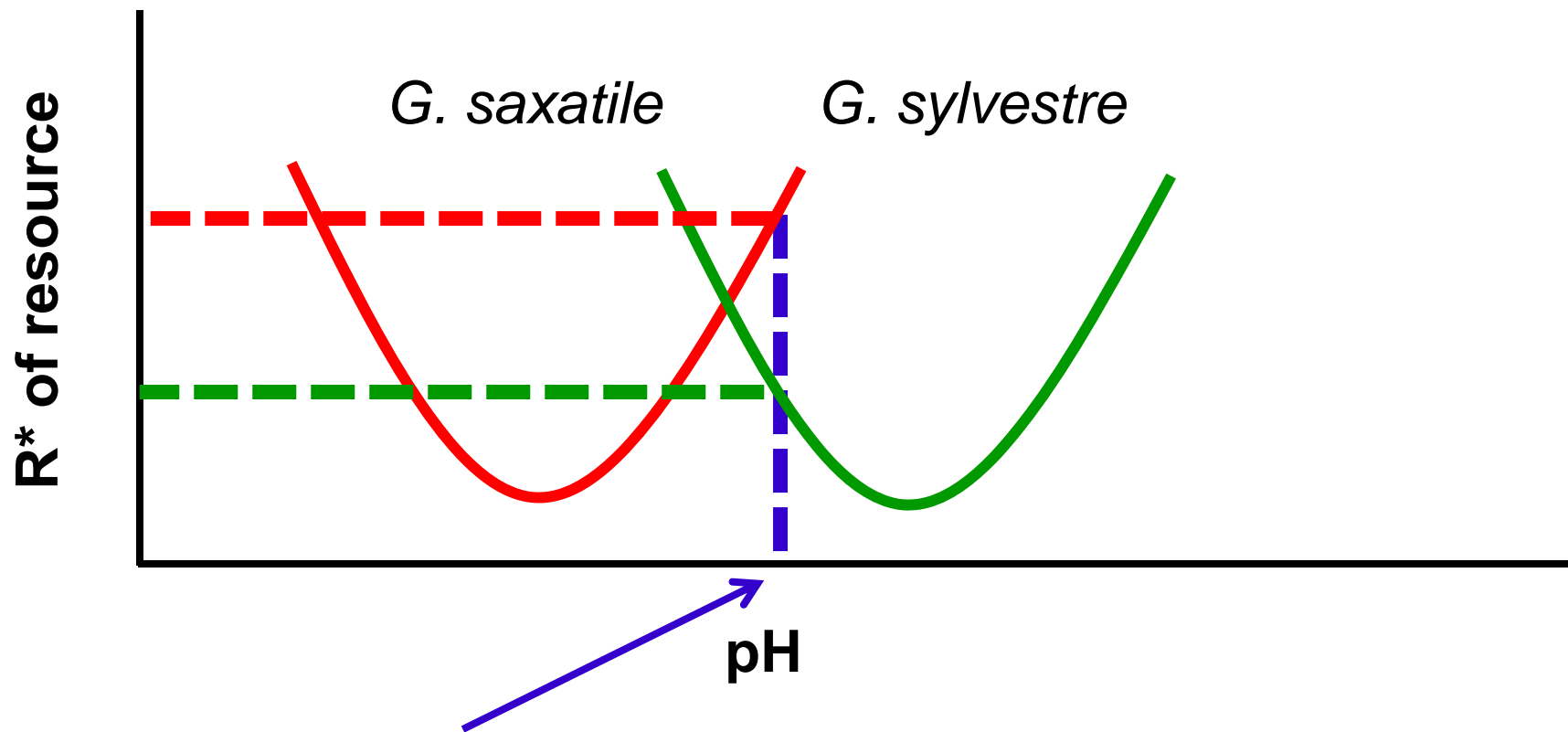
If R^* is low, the resource is being used efficiently

Image/fig from Cain *et al.* (2014)

A plausible (but hypothetical) interpretation of the Tansley data...

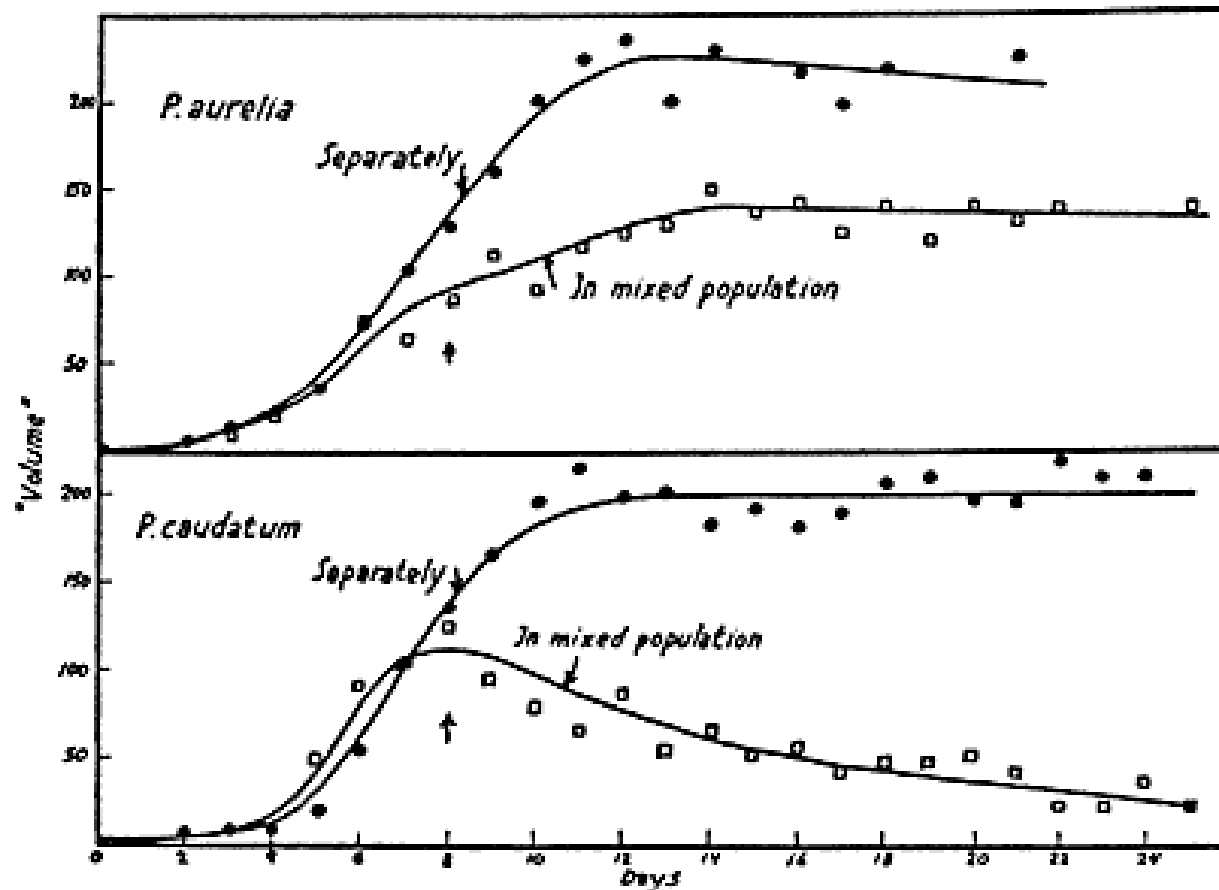


...and what it might mean in terms of resource acquisition ability



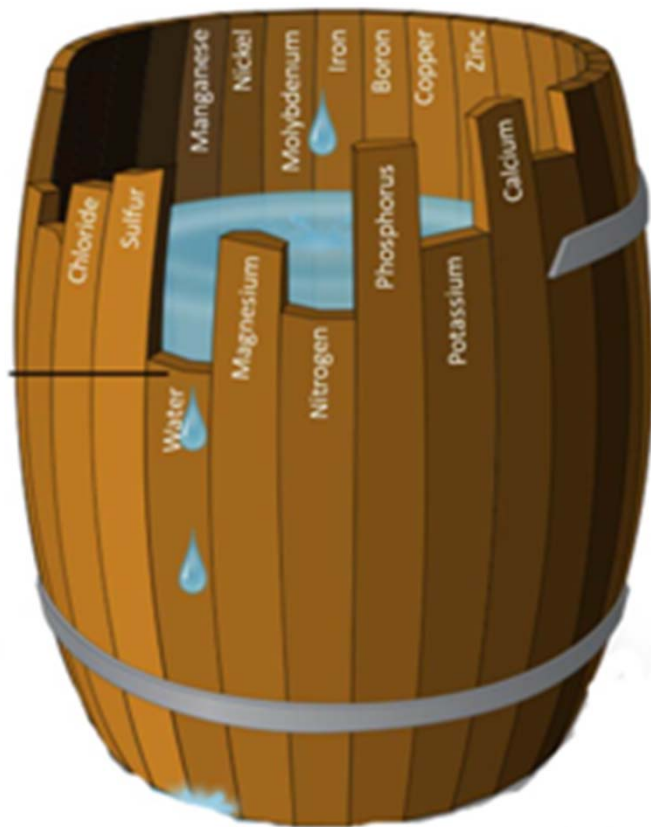
At this pH, *G. sylvestre* has a lower R^* and can outcompete *G. saxatile*

Gause's *Paramecium* experiments and competitive exclusion



Gause (1934)

What happens when there are multiple resources?



<http://corn.osu.edu/>

von Liebig's Law of the Minimum: yield is proportional to the amount of the most limiting nutrient in the soil

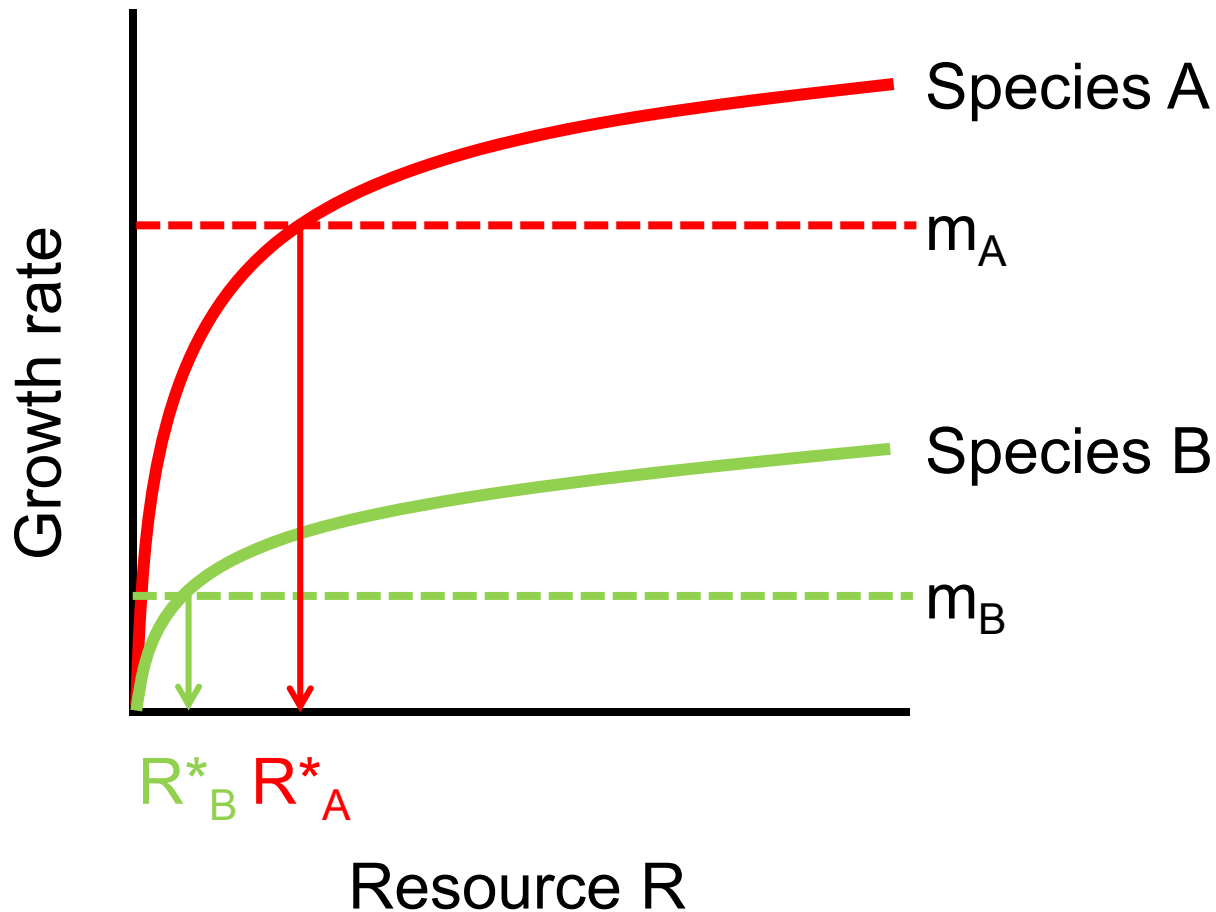
A population will grow until one resource becomes limiting for further growth

Organisms need many resources – but von Liebig suggested that at any given time **only one is limiting**

Image/fig from Cain *et al.* (2014)

All plants need similar resources – how do so many species coexist?

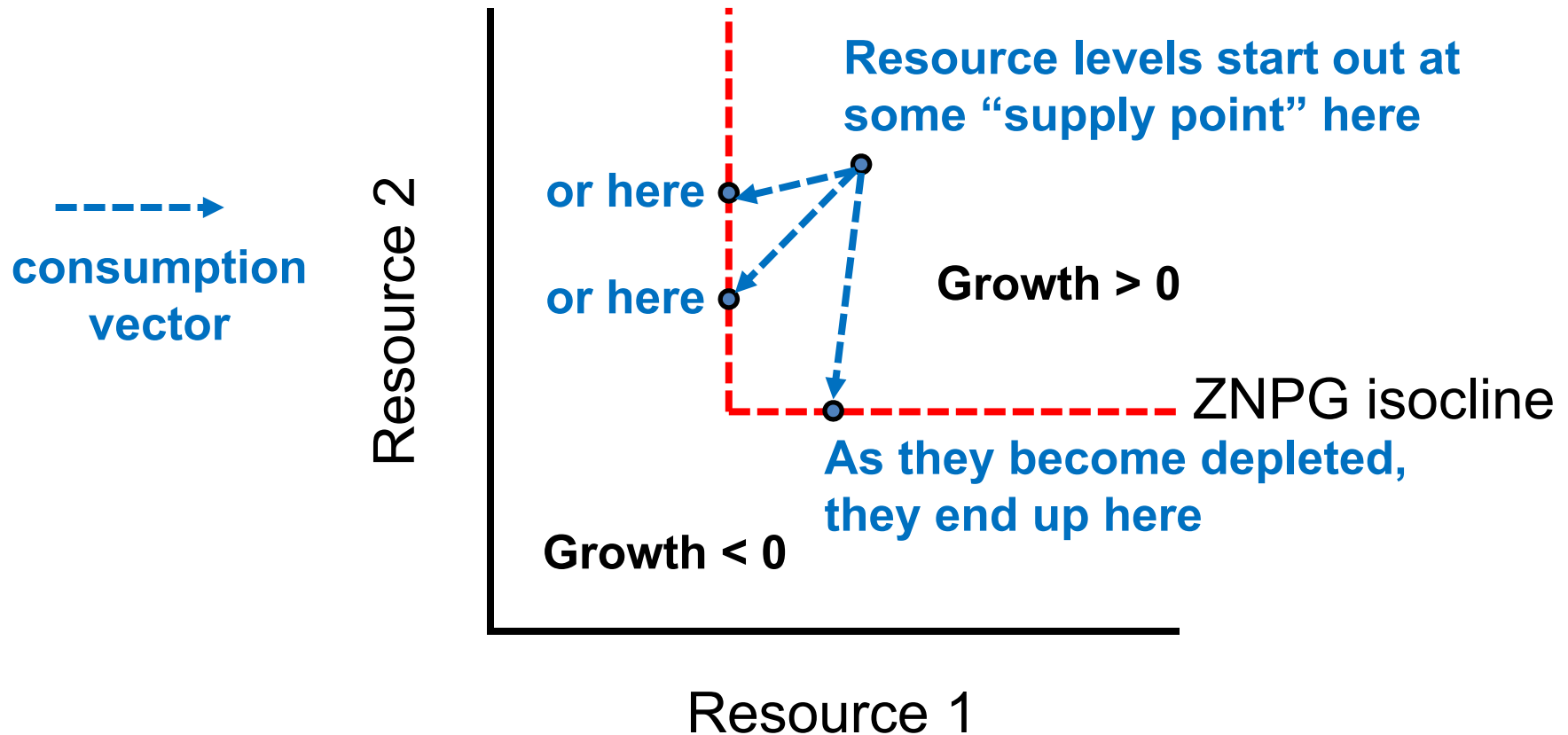
Tilman's R^* provides a mechanism for understanding competitive exclusion and coexistence in terms of population dynamics



Two species,
one resource
– who wins?

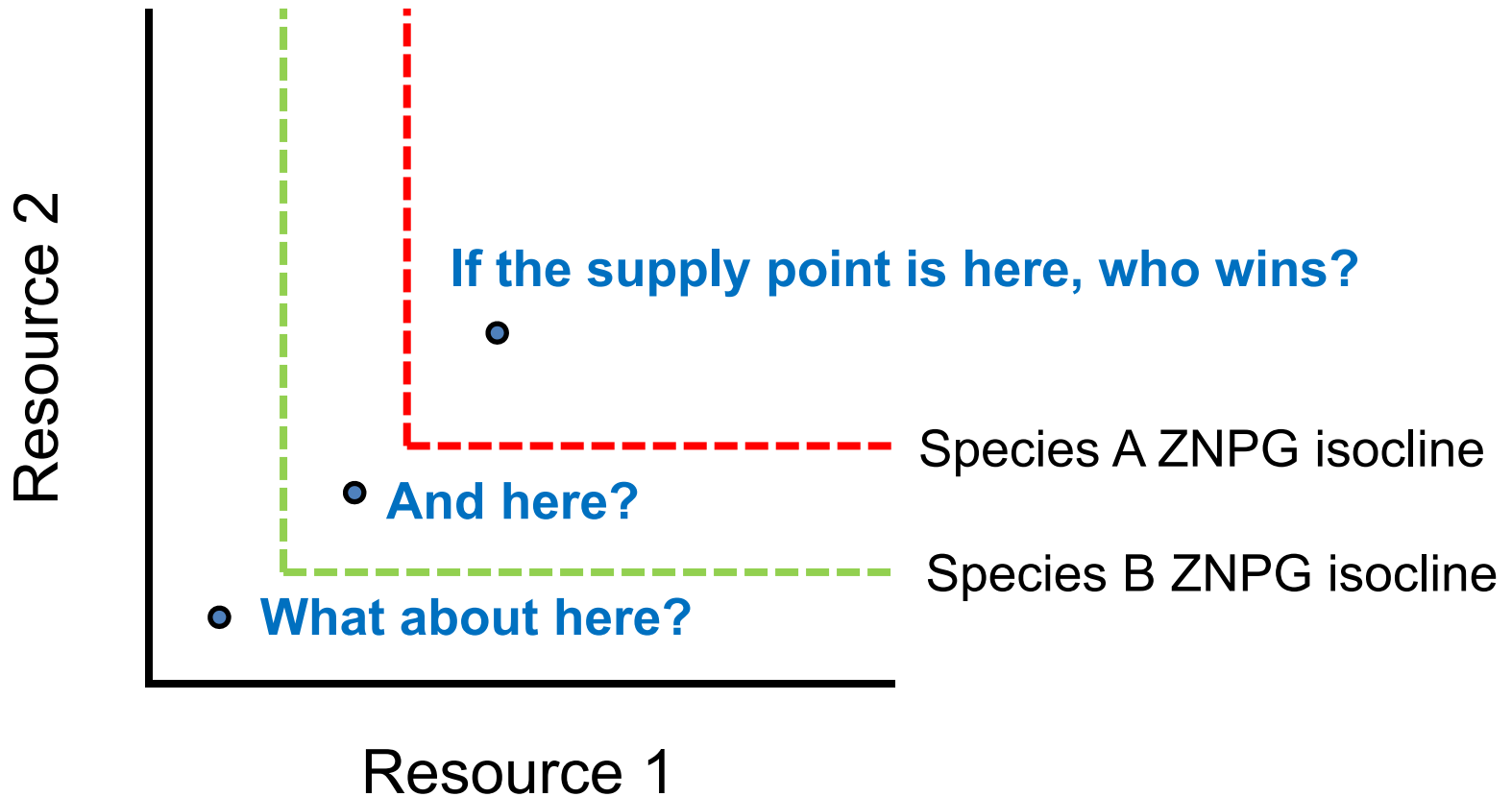
What happens when there are two potentially limiting resources?

Now we have two resources 1 and 2, and any given species has R^* values for each of these

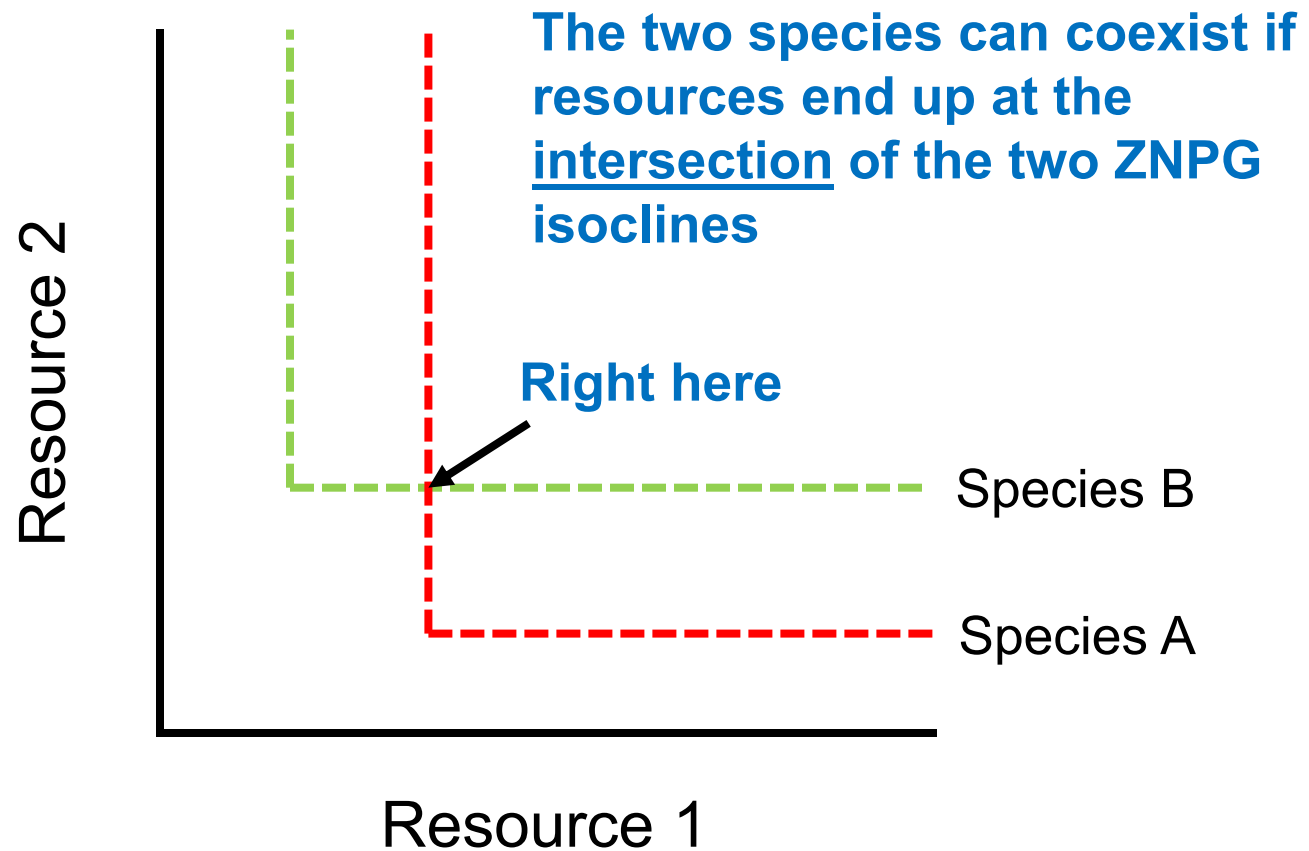


The **ratio** of resource 1 to resource 2 and the consumption vector will affect which resource ultimately becomes limiting

Now let's add a second species



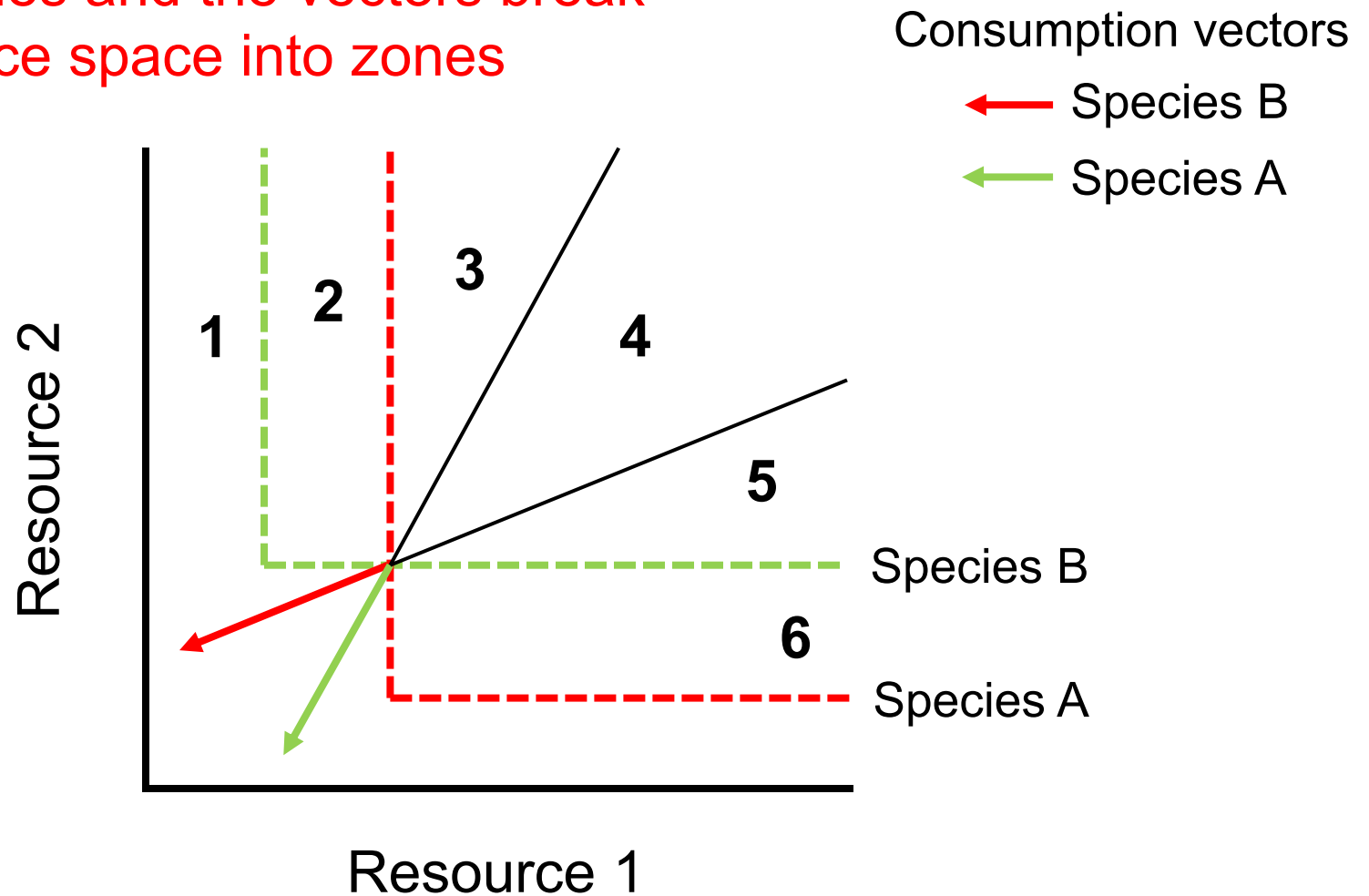
What happens if we have a tradeoff, with each species being most efficient at using different resources?



How can we get there?

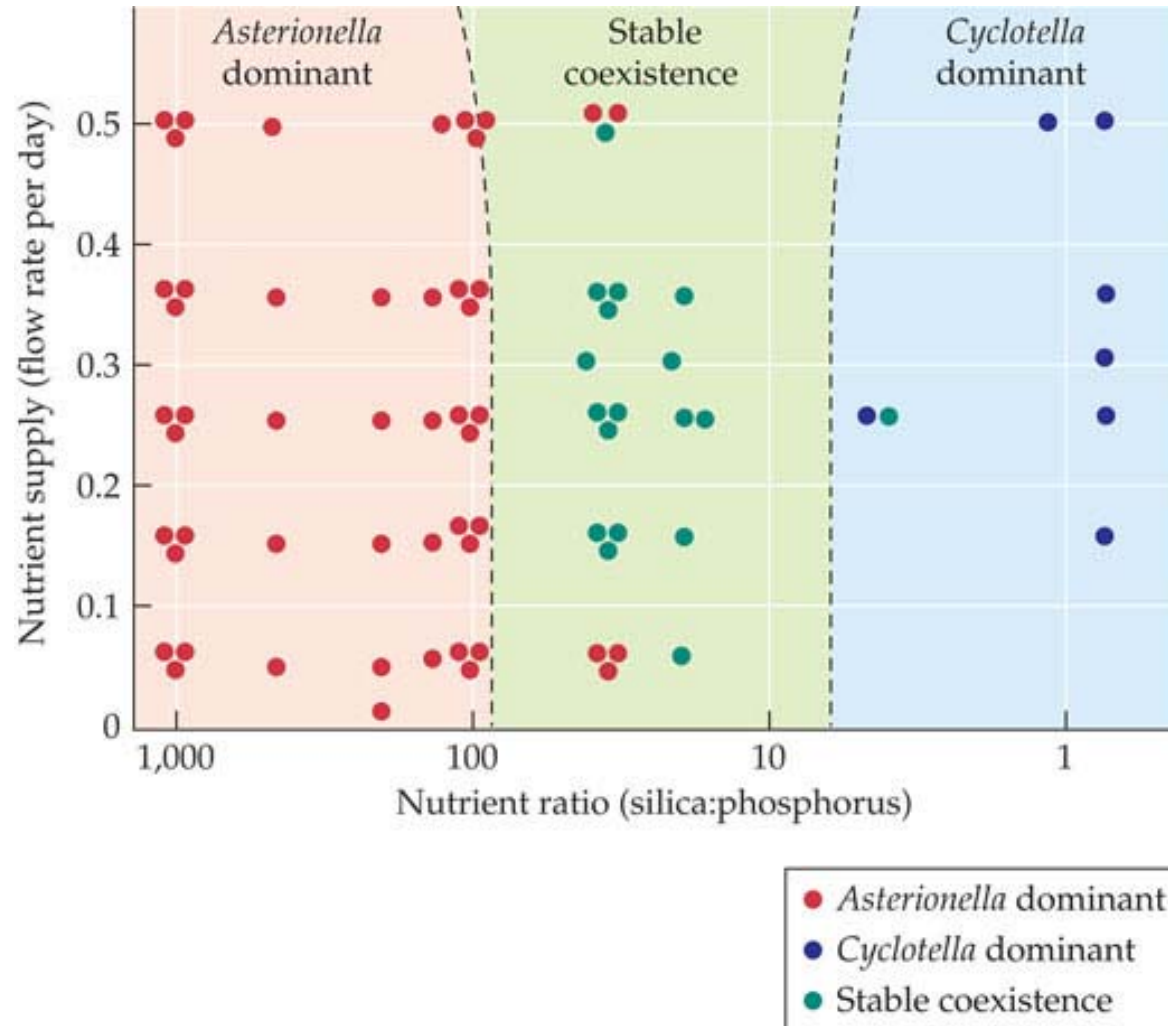
First, we need to add consumption vectors for each species

The isoclines and the vectors break the resource space into zones



Only a resource supply in zone 4 will lead to the coexistence point, but this shows that conditions exist that allow coexistence

Tilman showed experimentally that certain combinations of resource ratios and nutrient supply rates allowed stable coexistence between two diatom species

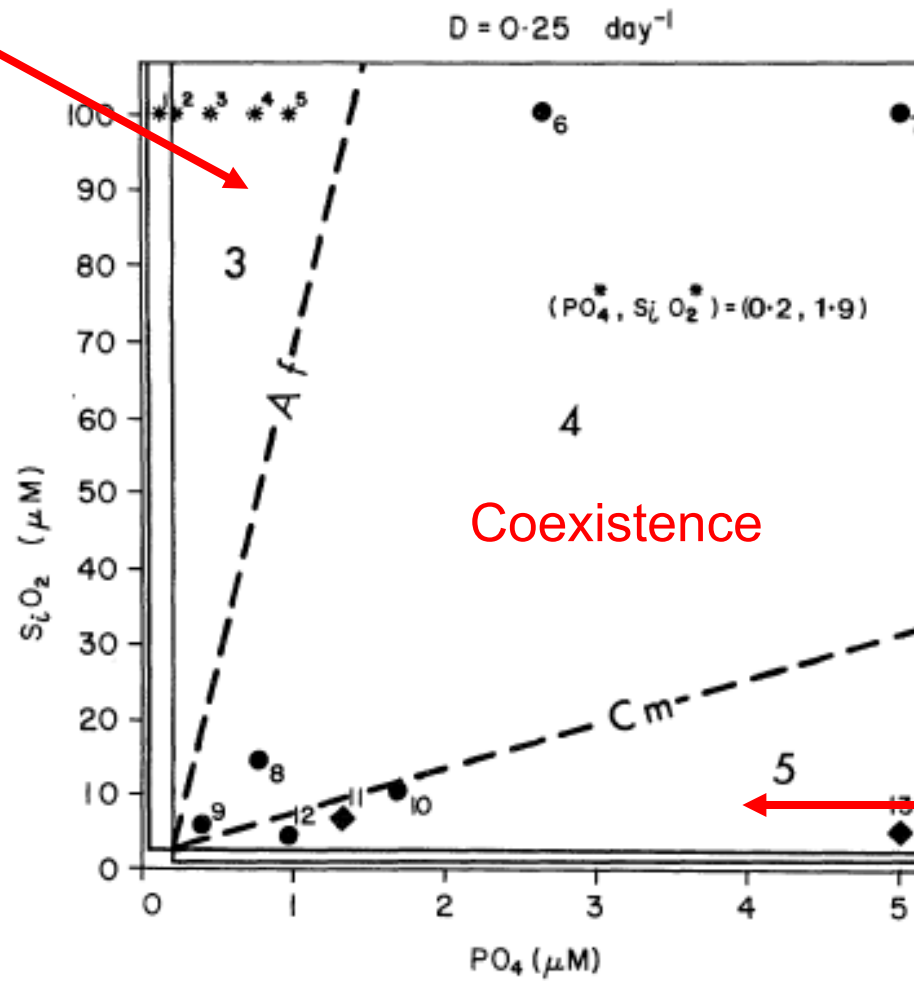


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Image/fig from Cain *et al.* (2014)

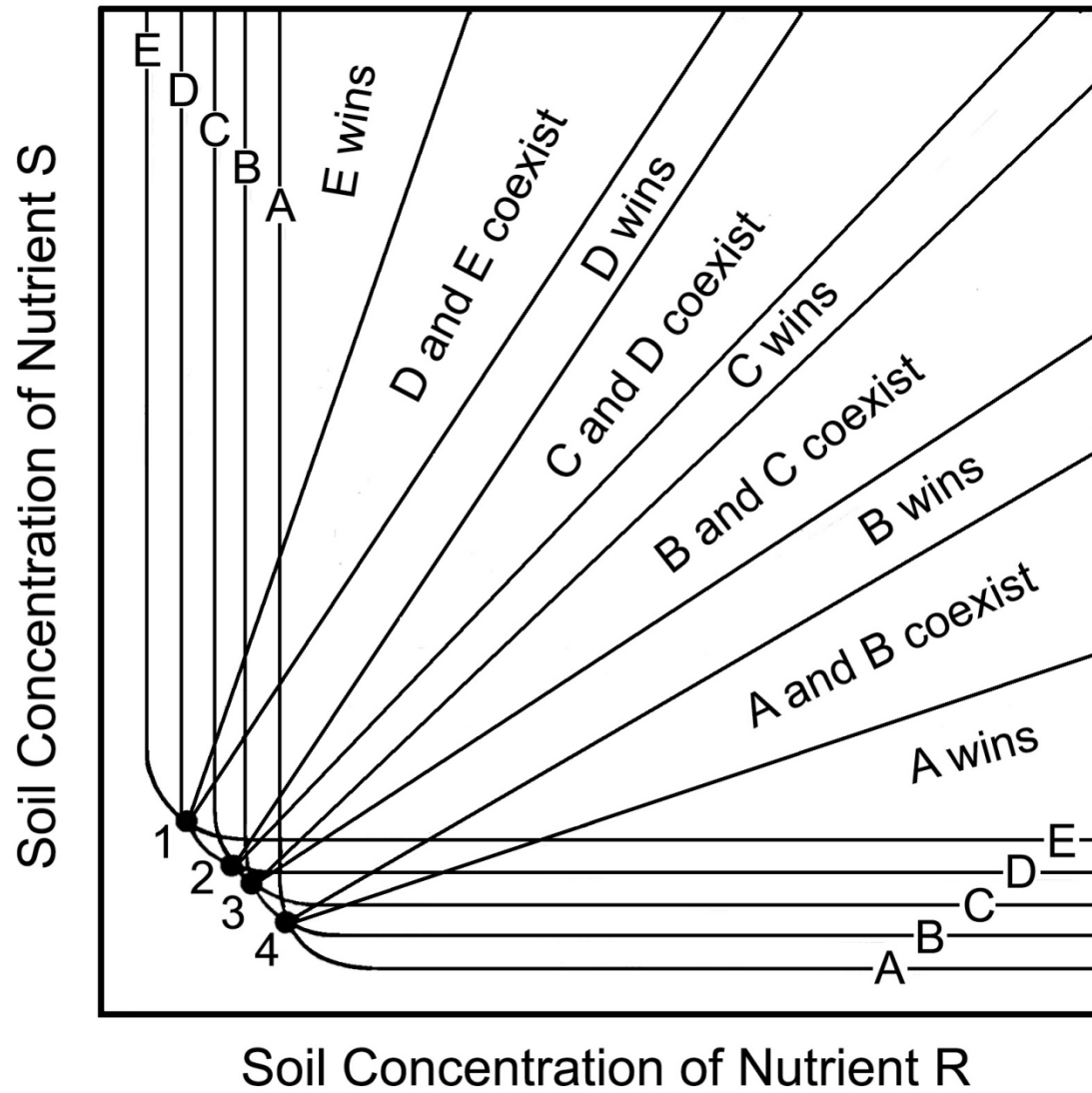
Experimental results from Tilman (1980)

Asterionella dominant



Cyclotella
dominant

Tilman (1988) expanded this idea to incorporate many species



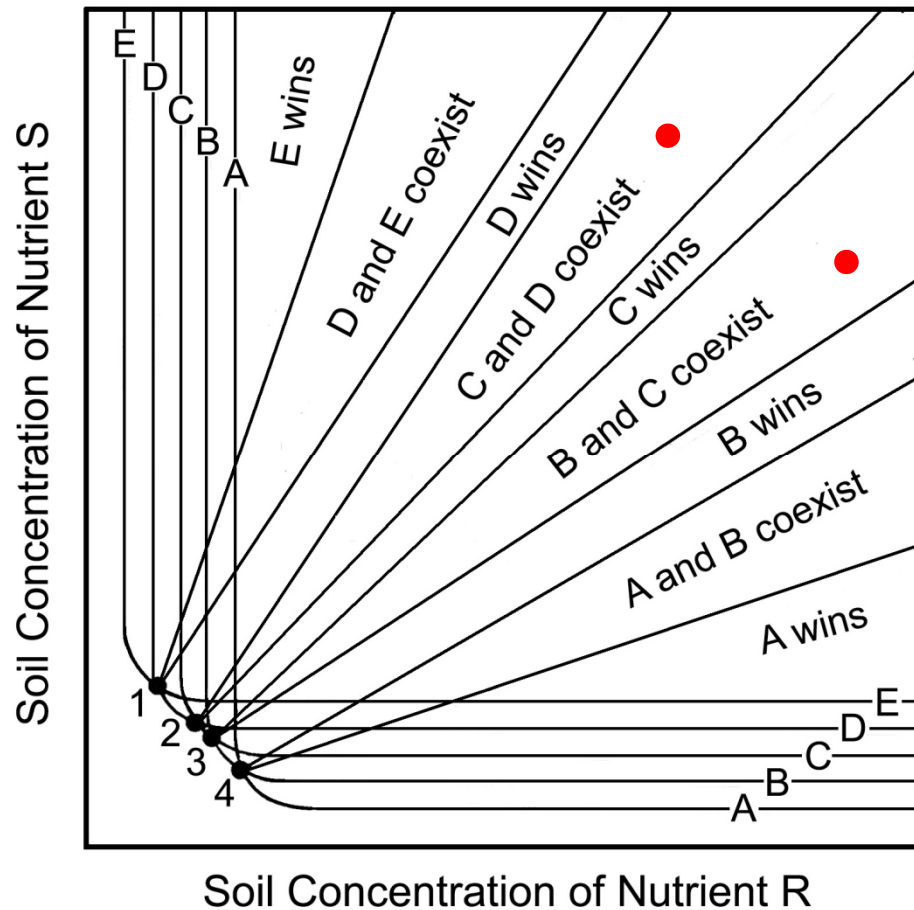
At any given point in space, two species can coexist when there are two limiting resources

It follows that if there are n limiting resources, n species can theoretically coexist

BUT – there are only so many resources...

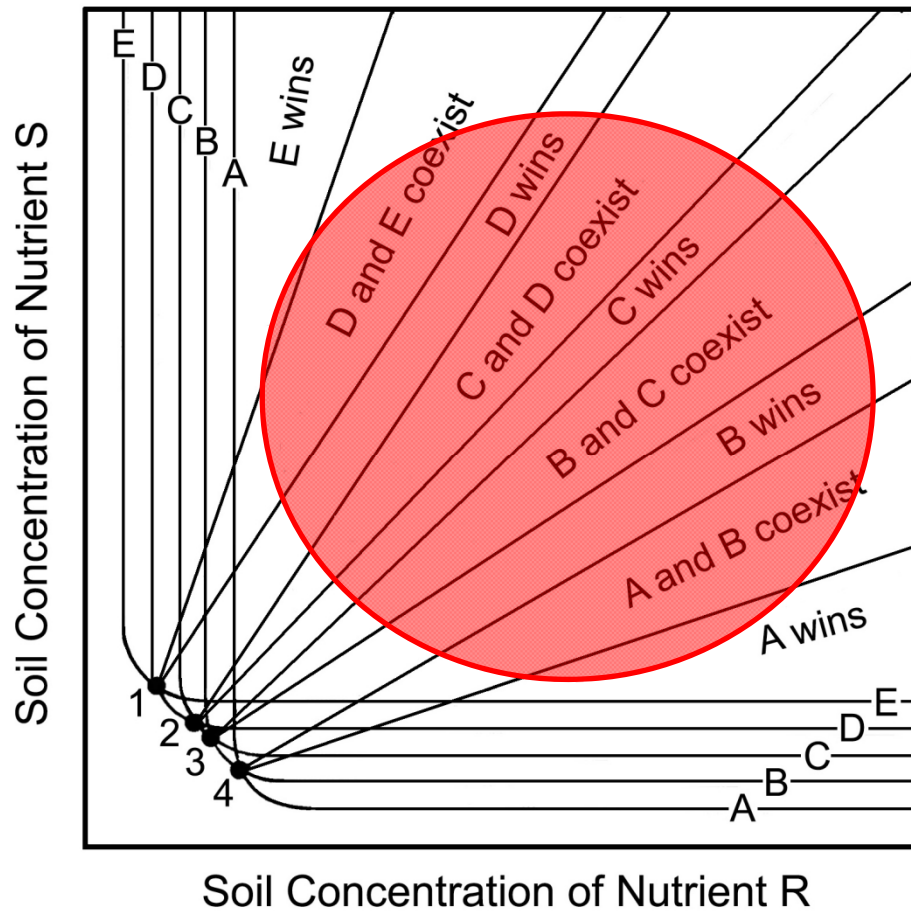
Hutchinson (1961), in “The paradox of the plankton” asked, how do $n+1$ species coexist on n resources?

One way -> if there is spatial variation in resource supply rates



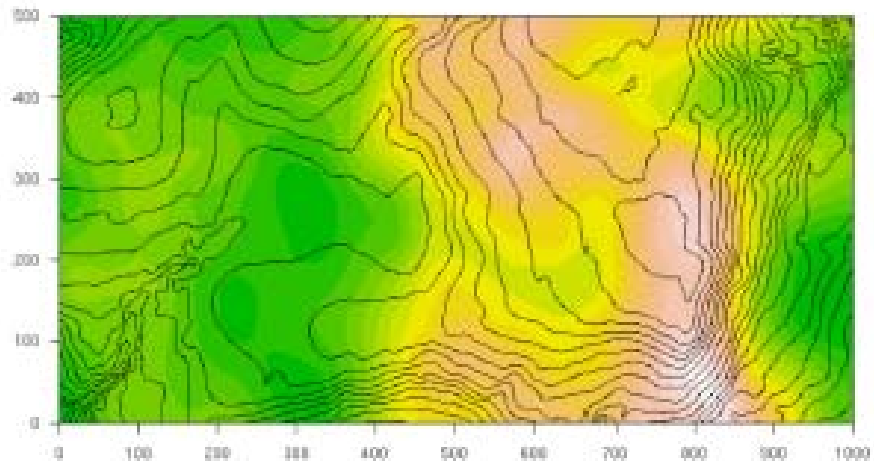
If the environment is homogeneous, we can think of the supply point as exactly that – a point, and only two species coexist

But if we have substantial spatial heterogeneity in supply rates and resource ratios, many species can coexist

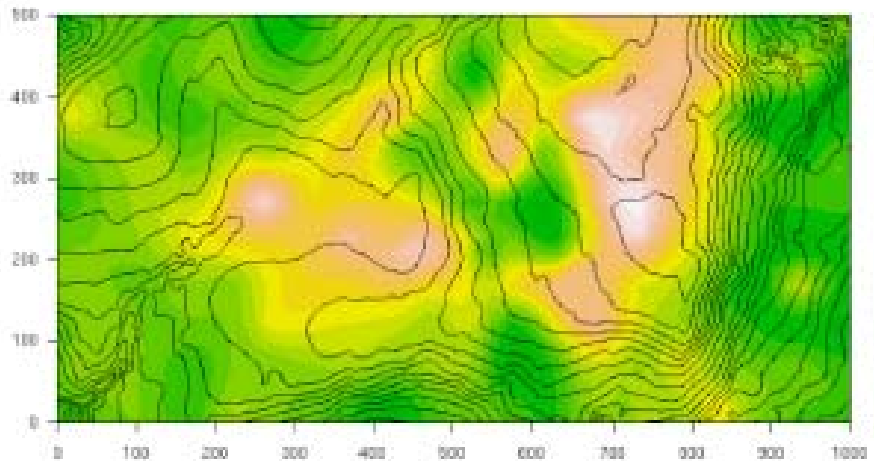


Tilman (1988)

Another example: soil N and P in Barro Colorado Island (BCI), Panama



Soil N



Soil P

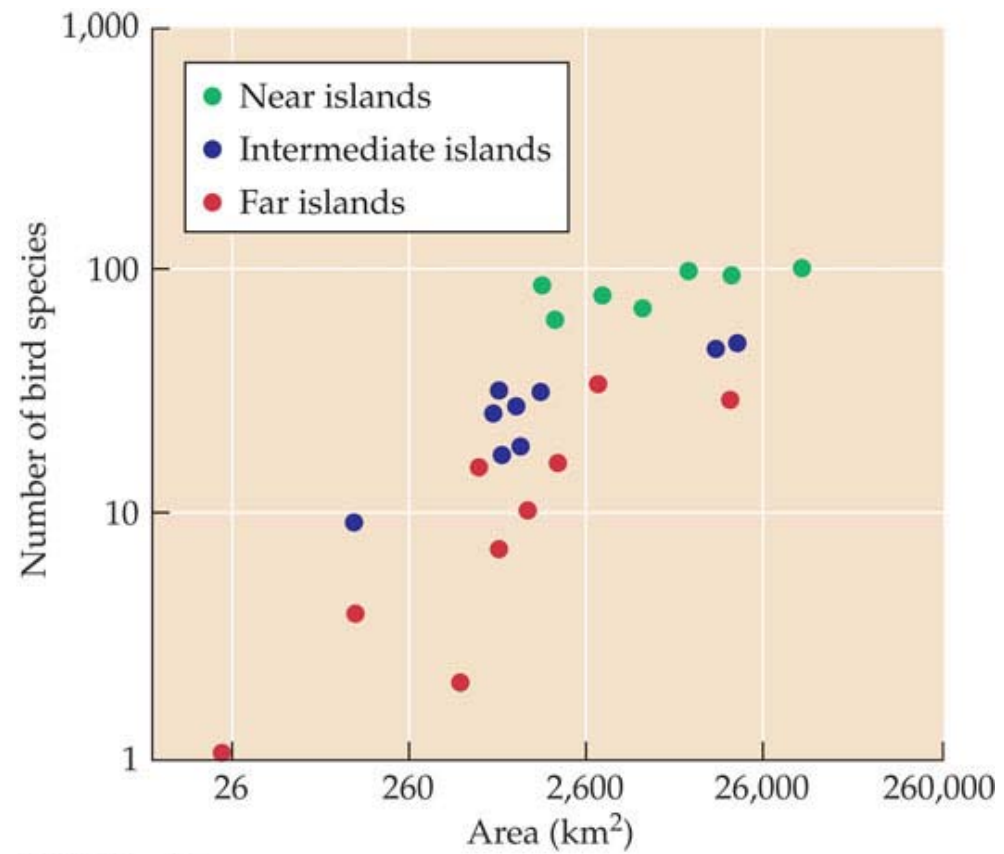
Some mechanisms that may explain local species richness:

- Resource ratios
- Spatial heterogeneity in resource ratios
- Hutchinson (1961): Non-equilibrium

Theory of Island Biogeography (MacArthur and Wilson 1967)

Area and distance (=isolation) influence rates of immigration (recolonization) and extinction

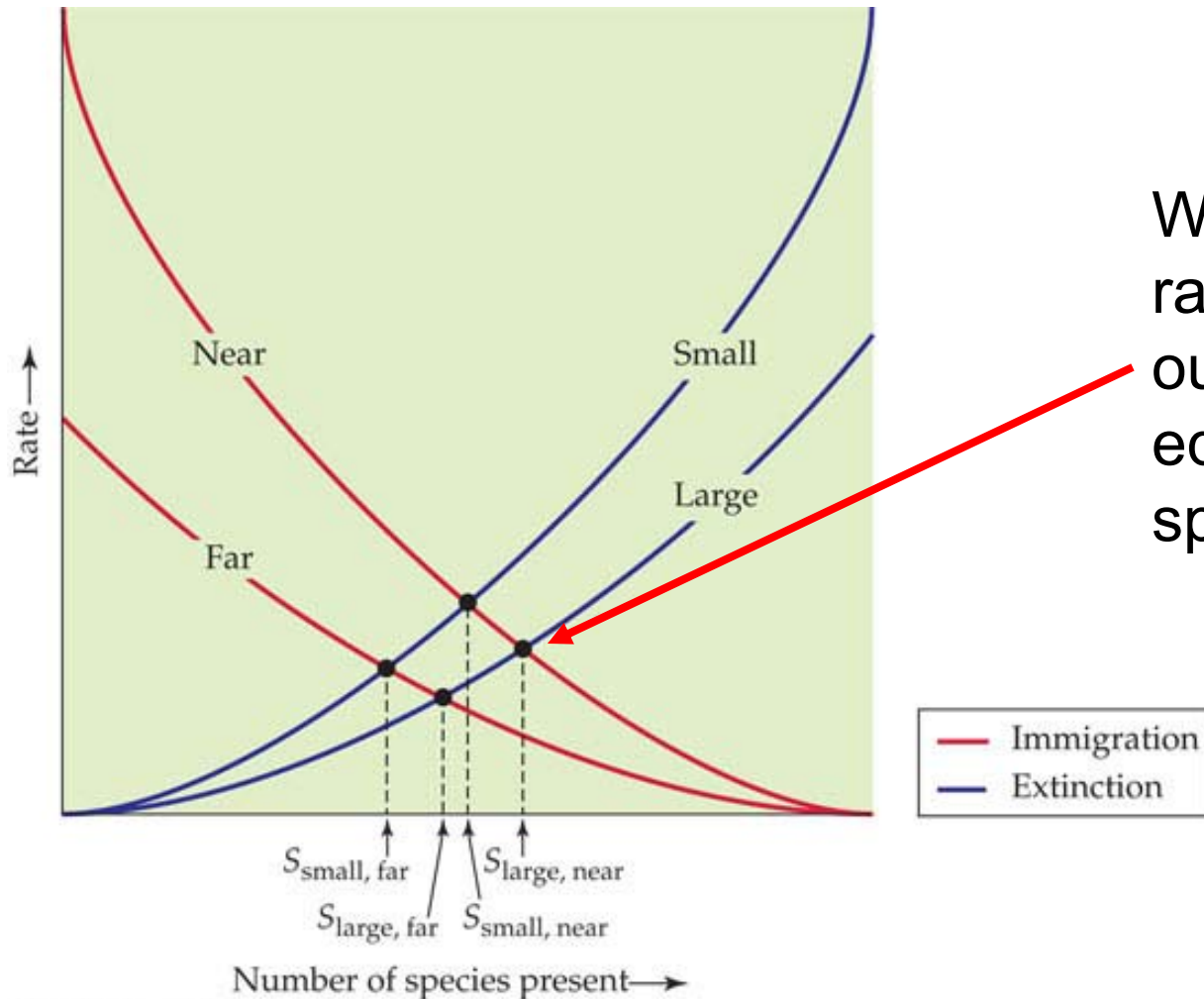
Effect of area and distance on New Guinea bird species richness



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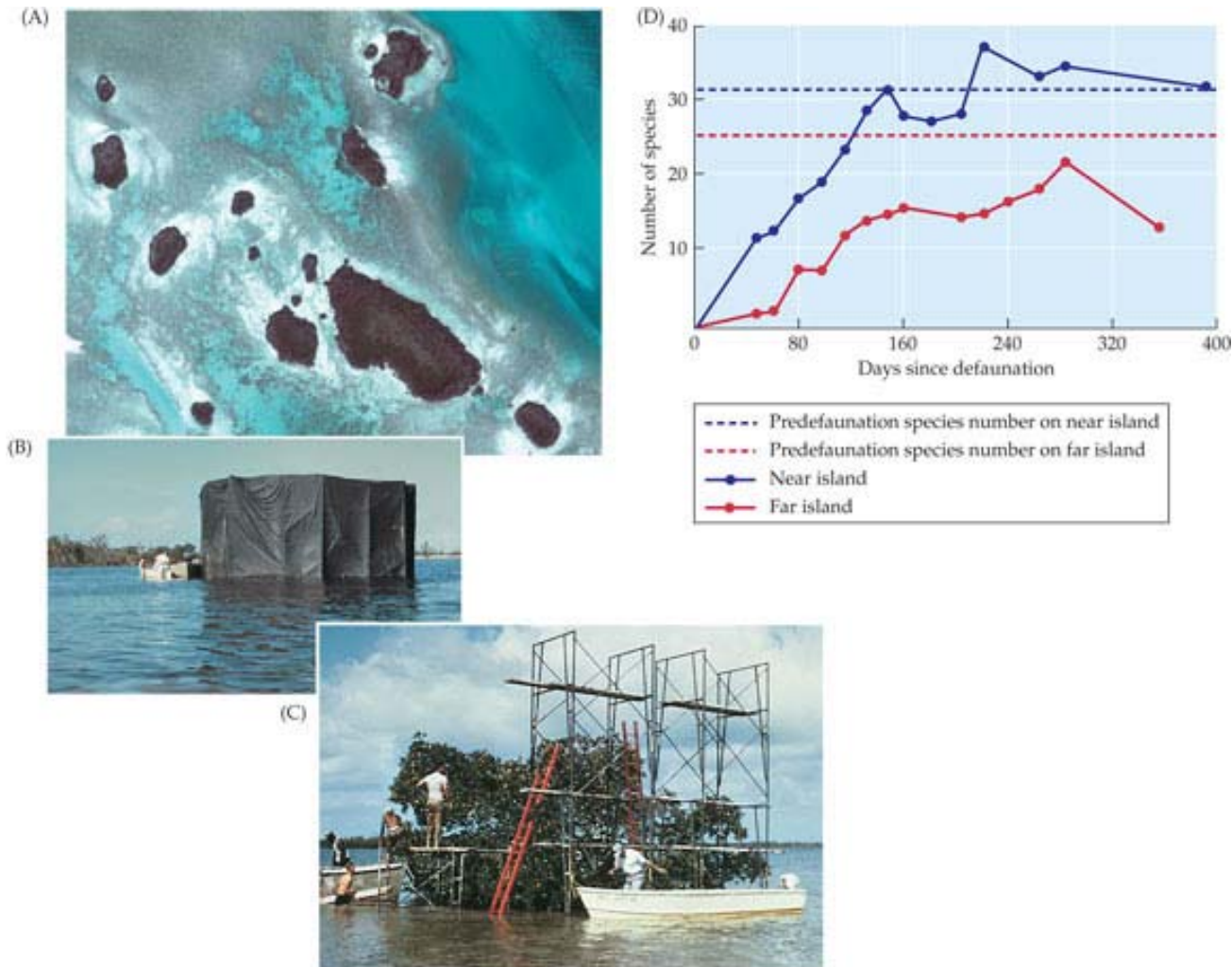
Image/fig from Cain *et al.* (2014)

Area drives extinction rates and distance drives immigration rates



Where the two rates balance out, there is an equilibrium species richness

The theory was tested by Simberloff and Wilson (1969) on mangrove islands



ECOLOGY 3e, Figure 18.23
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Image/fig from Cain *et al.* (2014)

Enter Hubbell (1997 and 2001): A unified theory of biogeography and relative species abundance

- Focuses on two scales: local community dynamics and regional metacommunity dynamics. Generalization of IB to include speciation
- Local communities are ‘saturated’ and no births or immigration occurs until spaces are vacated by deaths
- They can be recolonized by reproduction by the local species pool or by immigration from the regional pool
- No need for niches – species are identical, wide range of species relative abundance distributions explained by this model, which only has 3 parameters θ , J and m
- Dispersal limitation is the key

The fundamental biodiversity number θ

$\theta = 2J_M v$, where J_M = metacommunity size and v = speciation rate

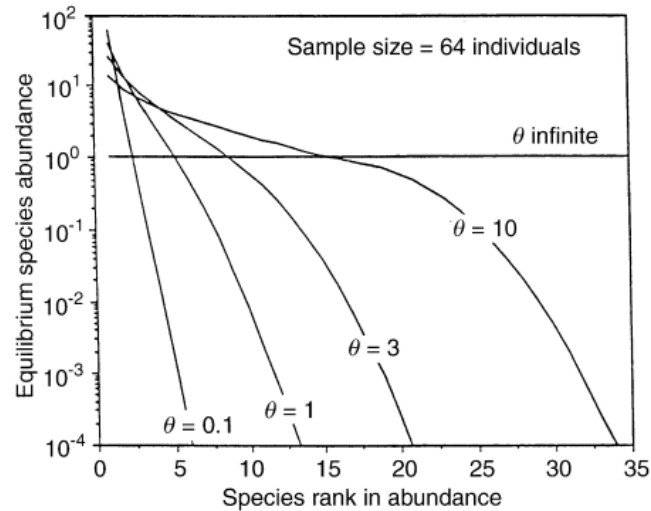


Fig. 4. Expected metacommunity dominance-diversity distributions for a random sample of 64 individuals from the metacommunity, for various values of the fundamental biodiversity number θ

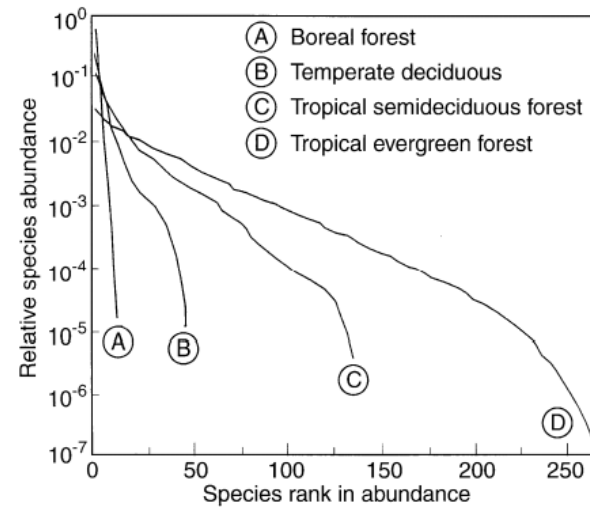
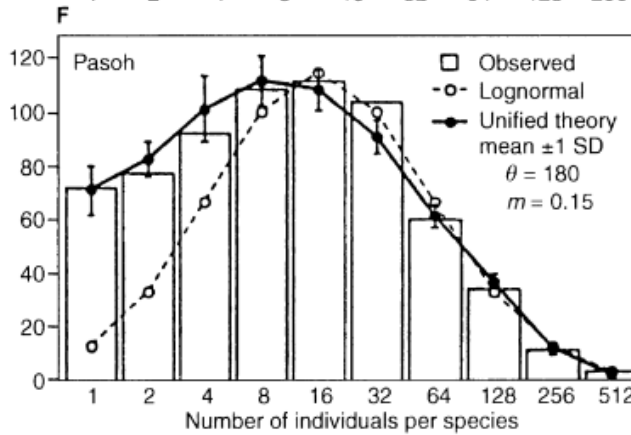
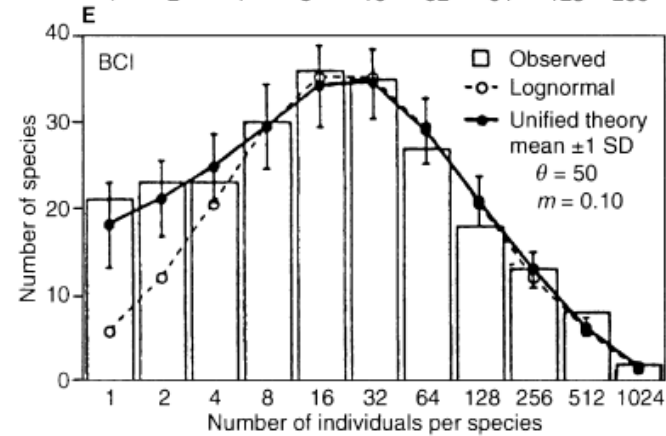
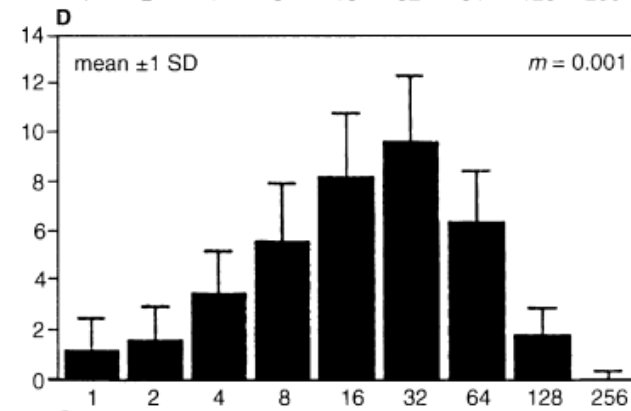
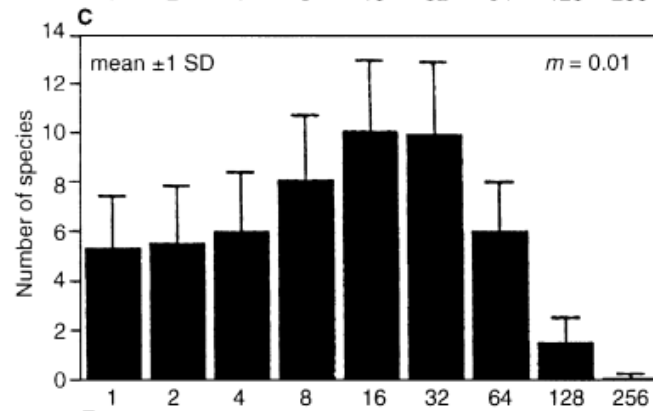
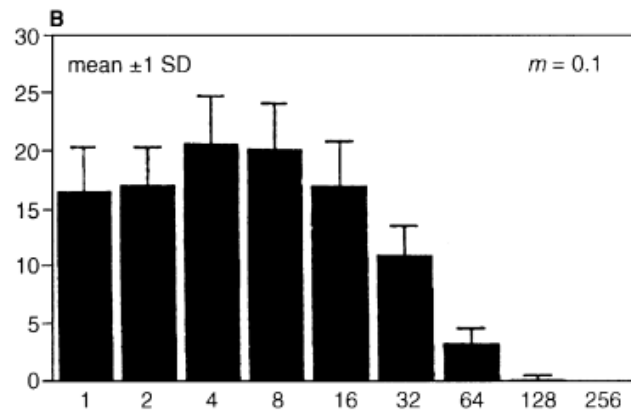
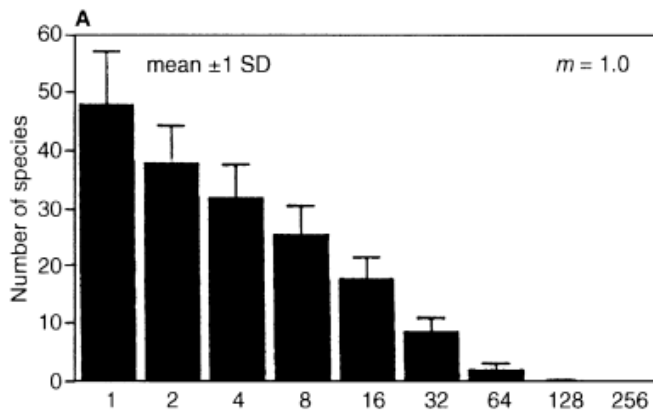


Fig. 5. Dominance-diversity distributions for four closed-canopy tree communities spanning a large latitudinal gradient, from boreal forest to equatorial Amazonian forest, after Hubbell (1997)

When $\theta = 1$, there is 1 monodominant species

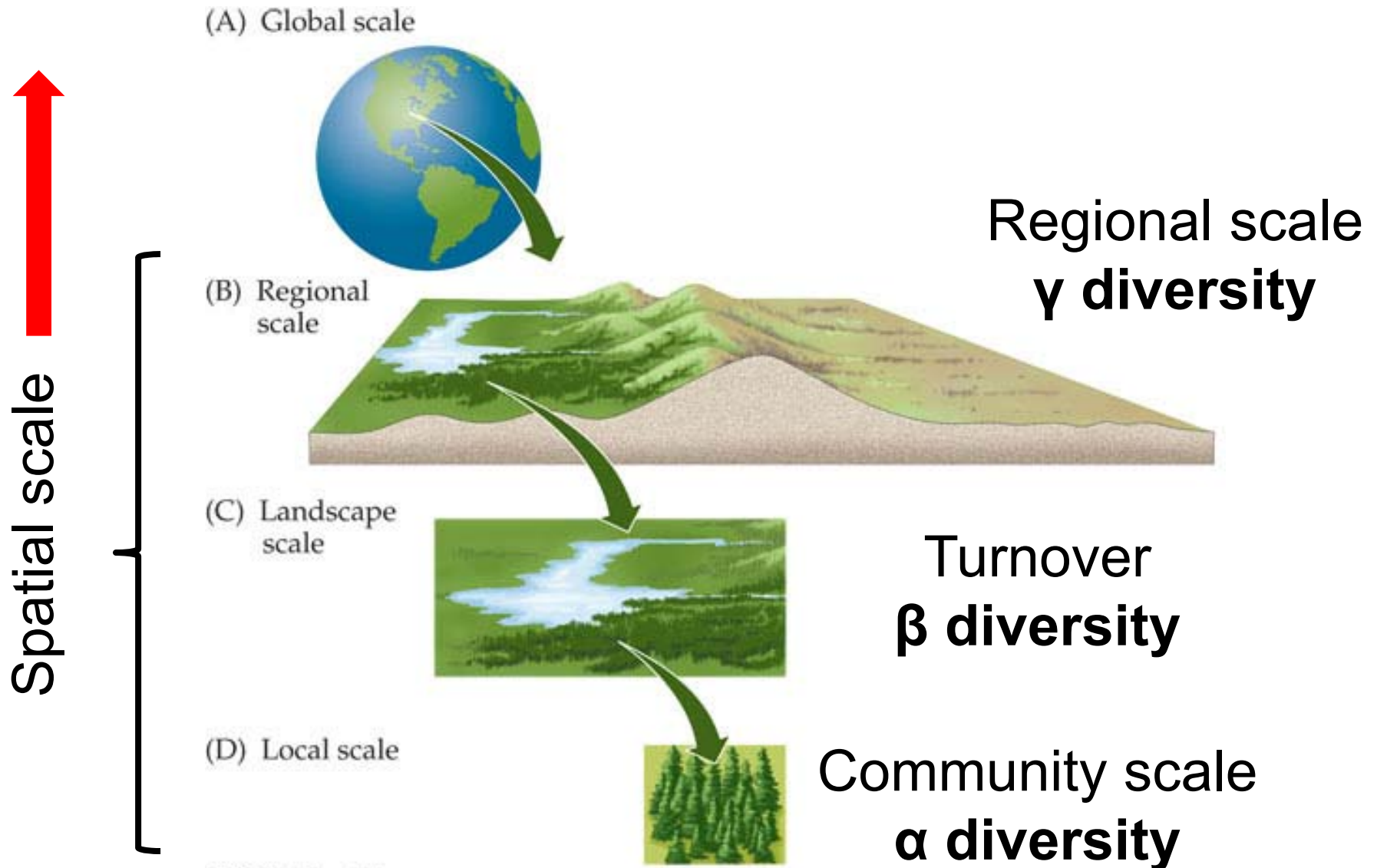
When $\theta = \infty$, there is infinite diversity (every individual is a new species)



Hubbell (1997)

- So how do niche principles “scale up”?
- According to Hubbell, not very well
- Neutral model can explain observed patterns very well
- Homogeneous environments can be occupied by diverse communities of effectively identical species (in terms of niches)
- Hubbell acknowledges that species do have niches, but they don't matter at large scales

Diversity across scales

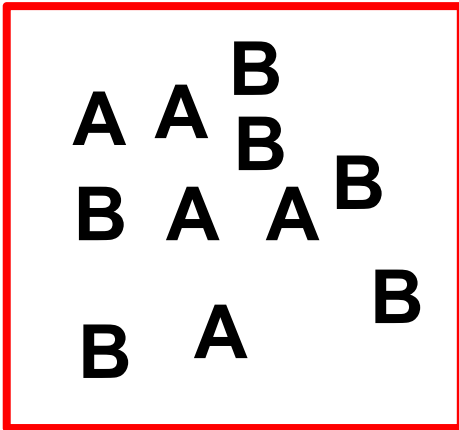


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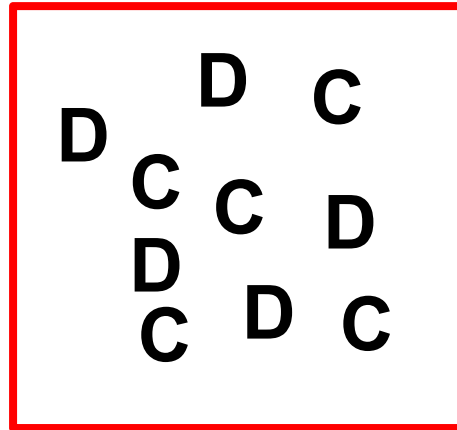
Image/fig from Cain *et al.* (2014)

A cartoonish, non-quantitative example

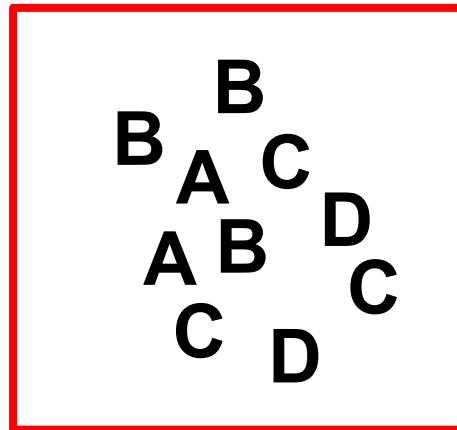
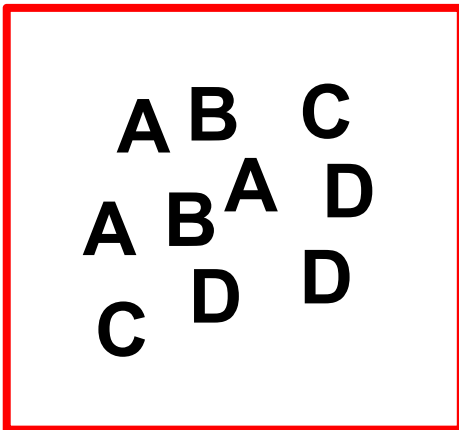
Plot 1



Plot 2



Example 1
Low α , High β



Example 2
High α , Low β

Going forward

- What do neutral and niche models have to say about α and β diversity?
- What do patterns of α , β diversity tell us about the mechanisms of community assembly?
- Is the world niche or neutral, or some of both?
- If species differences matter, are communities Gleasonian or Clementsian?

How do we quantify β diversity?

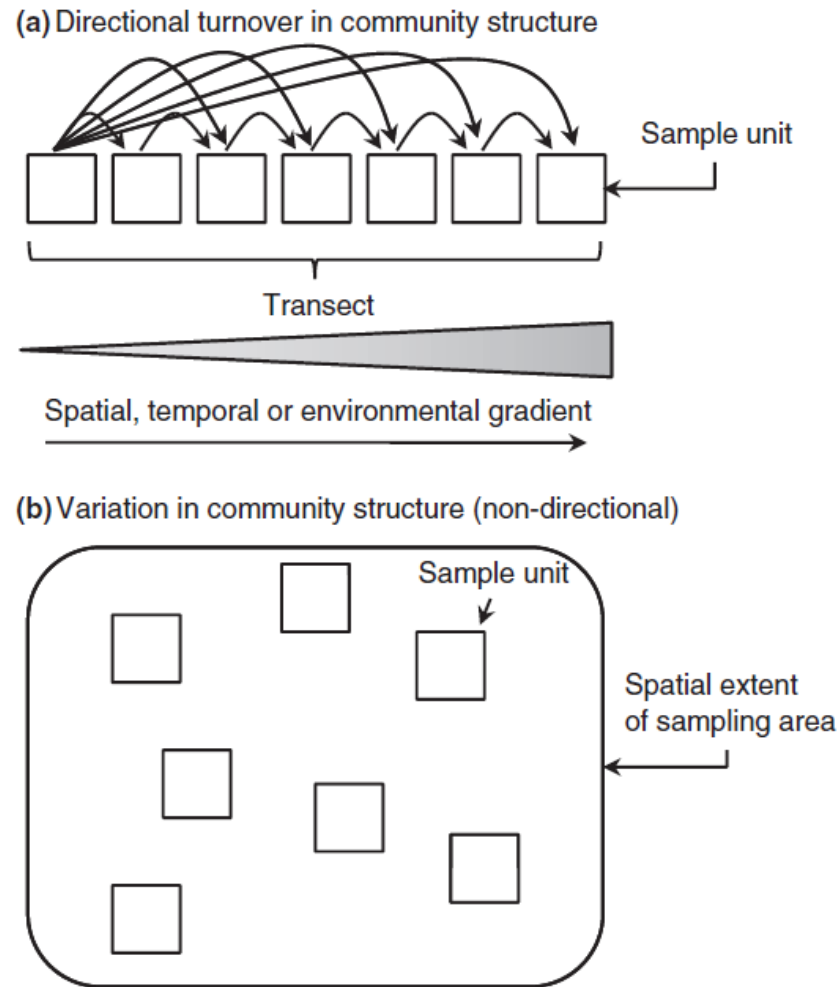


Figure 2 Schematic diagram of two conceptual types of β diversity for ecology: (a) turnover in community structure along a gradient and (b) variation in community structure among sample units within a given area.

A common metric of Beta diversity: Bray-Curtis dissimilarity between two sites i and j

$$d^{BCD}(i, j) = \frac{\sum_{k=0}^{n-1} |y_{i,k} - y_{j,k}|}{\sum_{k=0}^{n-1} (y_{i,k} + y_{j,k})}$$

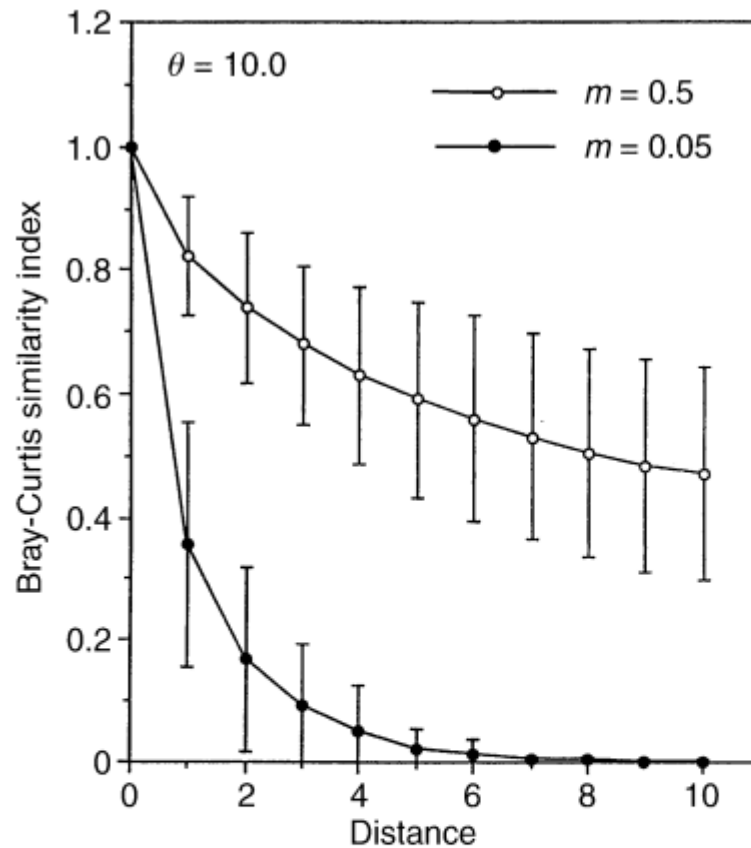


Fig. 15. Bray-Curtis index of community similarity as a function of distance separating the compared local communities in a model metacommunity consisting of 41×41 local communities each of size $J = 16$. The upper curve is the case for a high dispersal rate ($m = 0.5$), and the lower curve is for a low dispersal rate ($m = 0.005$). These couplings also change as a function of local community size J . As J gets larger, the Bray-Curtis similarity index remains higher and falls more slowly with distance