

BIOL 410 Population and Community Ecology

Competition

Lotka-Volterra models

Lotka-Volterra models

- Logistic population models

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \quad \frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right)$$

- Solutions at equilibrium $\frac{dN}{dt} = 0$

$$\widehat{N}_1 = K_1 - \alpha N_2$$

$$\widehat{N}_2 = K_2 - \beta N_1$$

- Equilibrium population values

$$\widehat{N}_1 = \frac{K_1 - \alpha K_2}{1 - \alpha\beta}$$

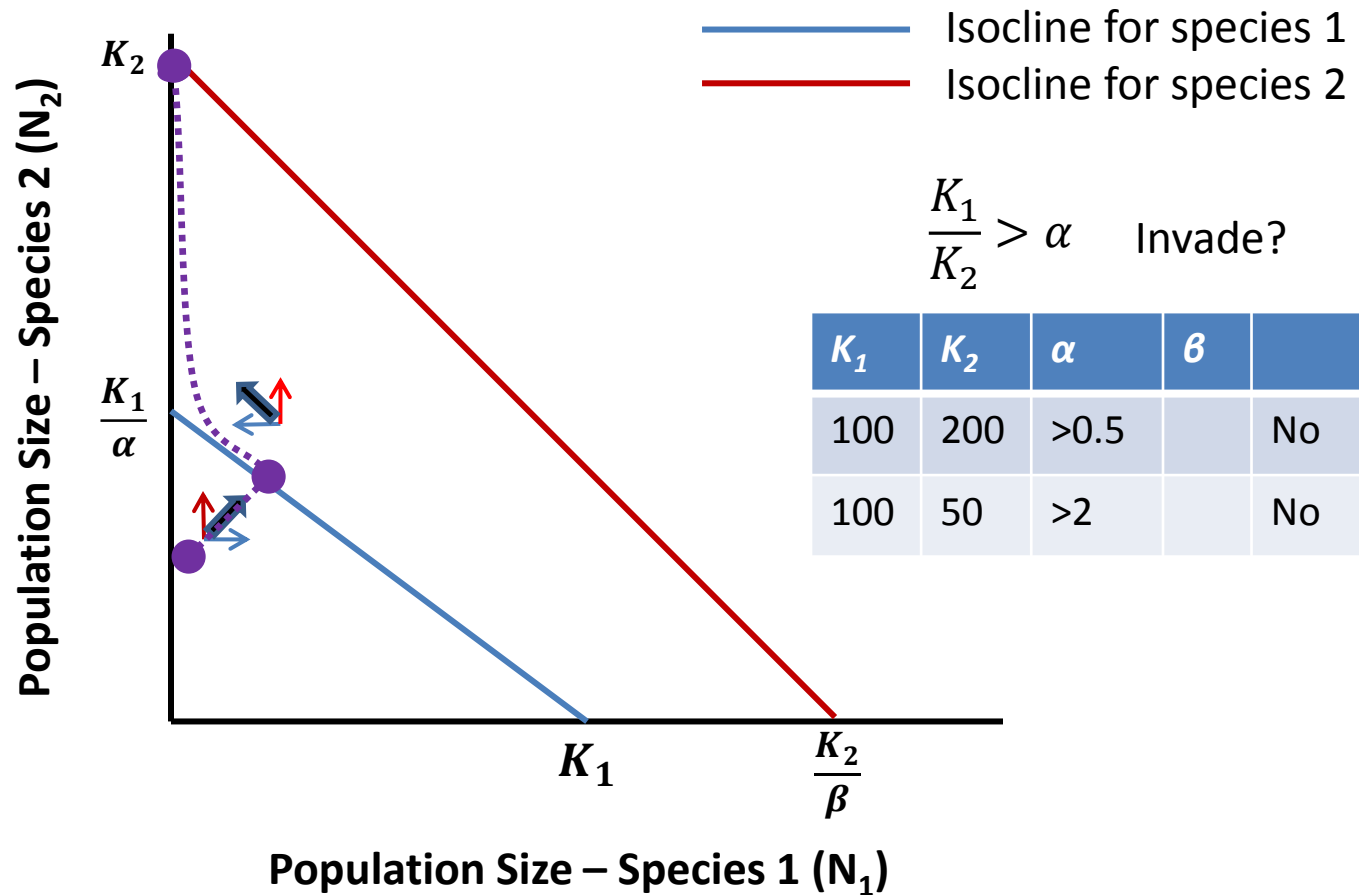
$$\widehat{N}_2 = \frac{K_2 - \beta K_1}{1 - \alpha\beta}$$

Can species invade?

- Species 1 can invade when $\frac{K_1}{K_2} > \alpha$
- Likewise, species 2 can invade when $\frac{1}{\beta} > \frac{K_1}{K_2}$

Interspecific competition

- Can species 1 invade?



Interspecific competition

- Can species 1 invade?

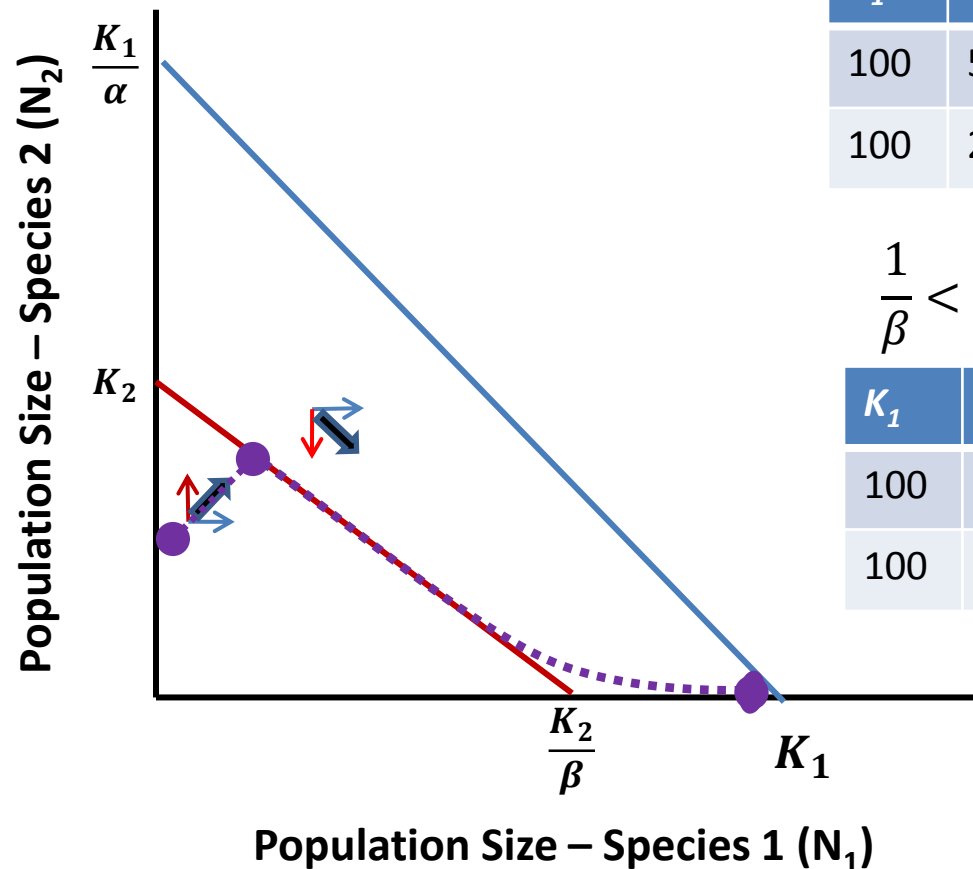
— Isocline for species 1
— Isocline for species 2

$$\frac{K_1}{K_2} > \alpha \quad \text{Invade?}$$

K_1	K_2	α	β	
100	50	<2		Yes
100	200	<0.5		Yes

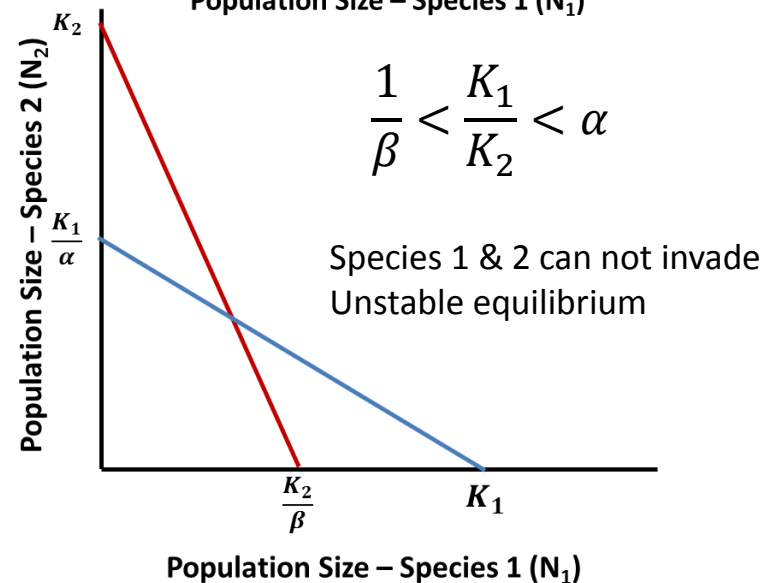
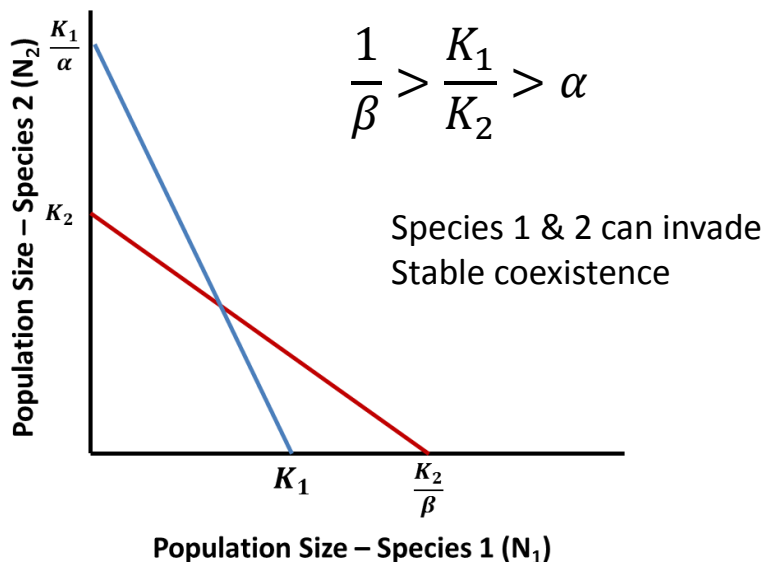
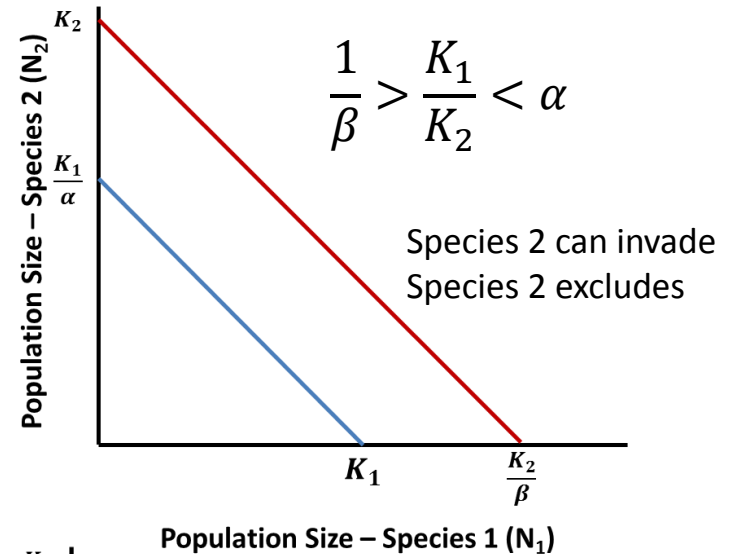
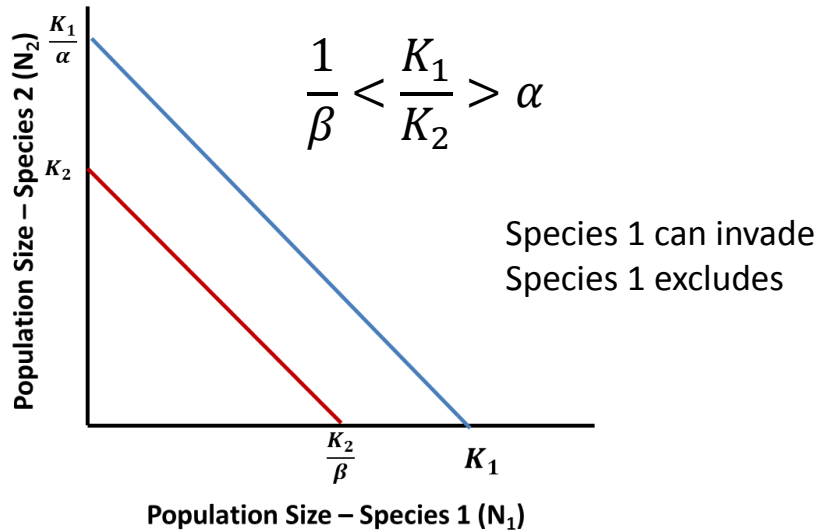
$$\frac{1}{\beta} < \frac{K_1}{K_2} \quad \text{Exclude?}$$

K_1	K_2	α	β	
100	50		>0.5	Yes
100	200		>2	Yes



Four outcomes of competition

Stability? Invasion capability?



Model Assumptions

- Logistic model assumptions – no age or genetic structure, no migration, no time lags...
- Additional Assumptions:
 1. Resources are in limited supply
 2. Competitive coefficient (α/β) and carrying capacities (K_1 / K_2) are constants.
 3. Density dependence is linear

Are Lotka-Volterra dynamics observed?

- Stable coexistence between competing species?
- Competitive exclusion when species compete?

Competitive exclusion principle

- **Gause's Law of Competitive Exclusion**
 - In a stable environment, two species cannot coexist if they use exactly the same resources
- **Gause (1934):** If two species, with the same niche, coexist in the same ecosystem, then one will be excluded from the community due to intense competition.
- The niche of a species consists of its role in the ecosystem (herbivore, carnivore, producer etc), its tolerance limits (e.g. soil pH, humidity) and requirements for shelter, nesting sites etc etc, all varying through time.

Principle of Competitive Exclusion

- Complete competitors can not co-exist
 - Two species with extremely similar ecology and physical attributes will have high competitive effects on each other (α and β are each close to 1)

INTERSPECIFIC COMPETITION \approx INTRASPECIFIC COMPETITION

- As species diverge to utilize less overlapping resources (Resource Partitioning), their competitive effect on each other is lessened (α and β are both closer to zero).

INTERSPECIFIC COMPETITION $<$ INTRASPECIFIC COMPETITION

Competitive exclusion

Georgyi Frantsevitch Gause

- Russian microbiologist
- Paramecium growing in controlled environment (1934)



Paramecium aurelia



Paramecium caudatum



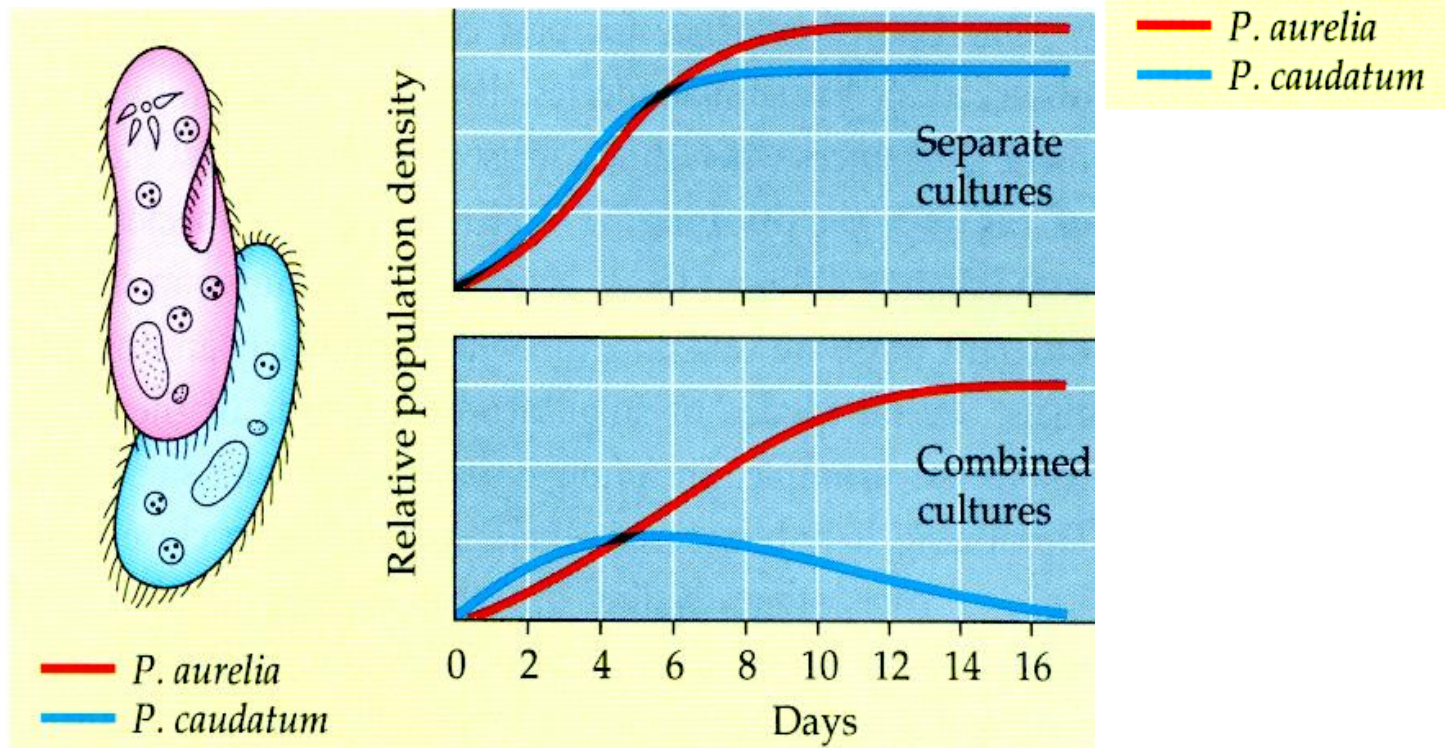
Paramecium aurelia



Paramecium caudatum



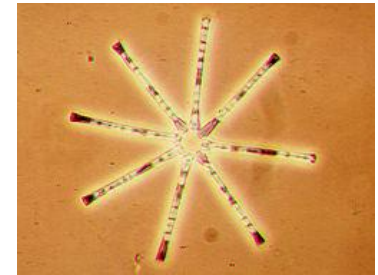
Competitive exclusion



- Gause (law of competitive exclusion)

Competitive exclusion

- Competition between freshwater diatoms
 - *Asterionella formosa*
 - *Synedra ulna*
- *Silica skeleton*
- *Silicate is the limiting nutrient*

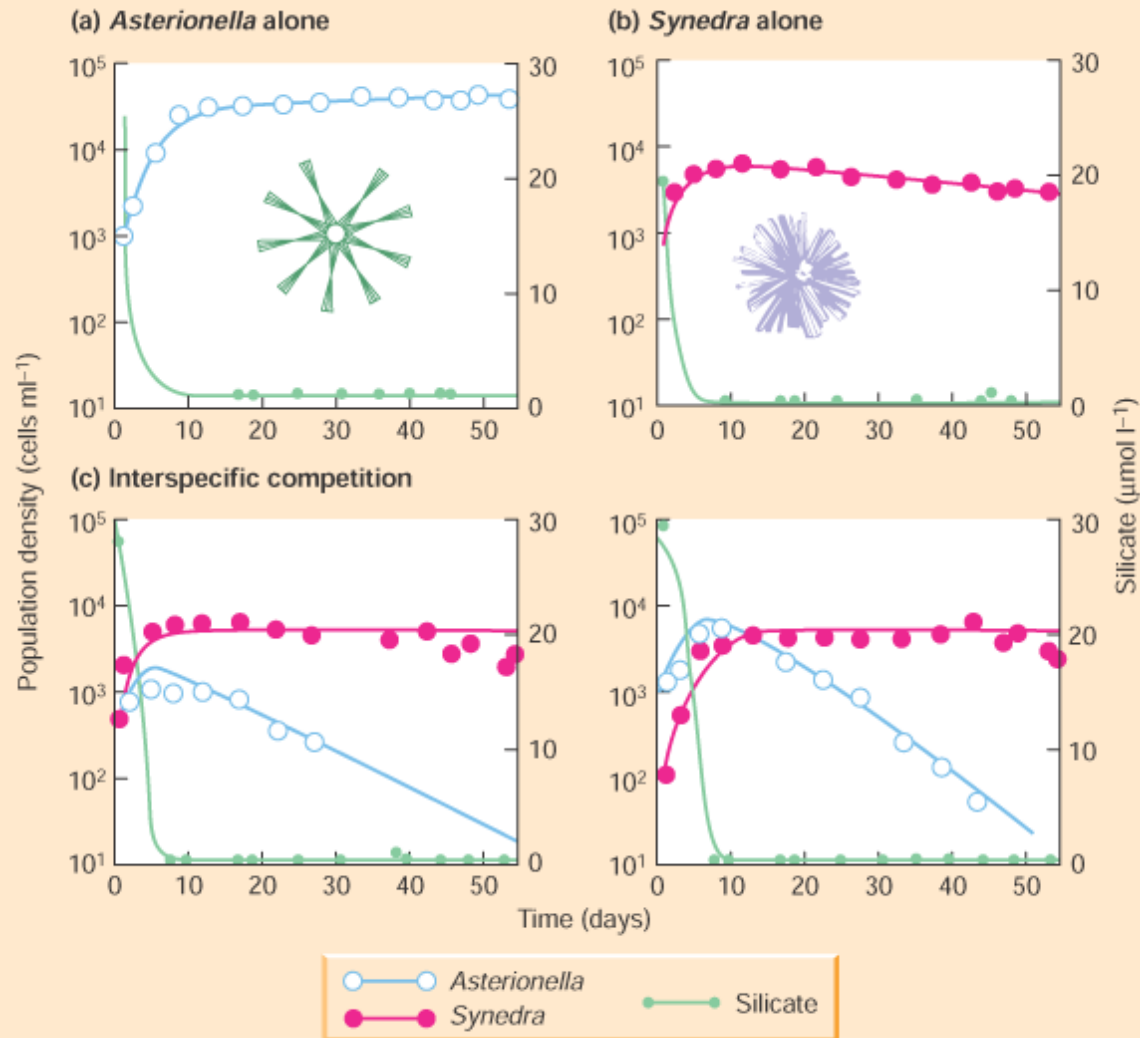


Limnol. Oceanogr., 26(6), 1981, 1020–1033

Competition and nutrient kinetics along a temperature gradient:
An experimental test of a mechanistic approach to niche theory¹

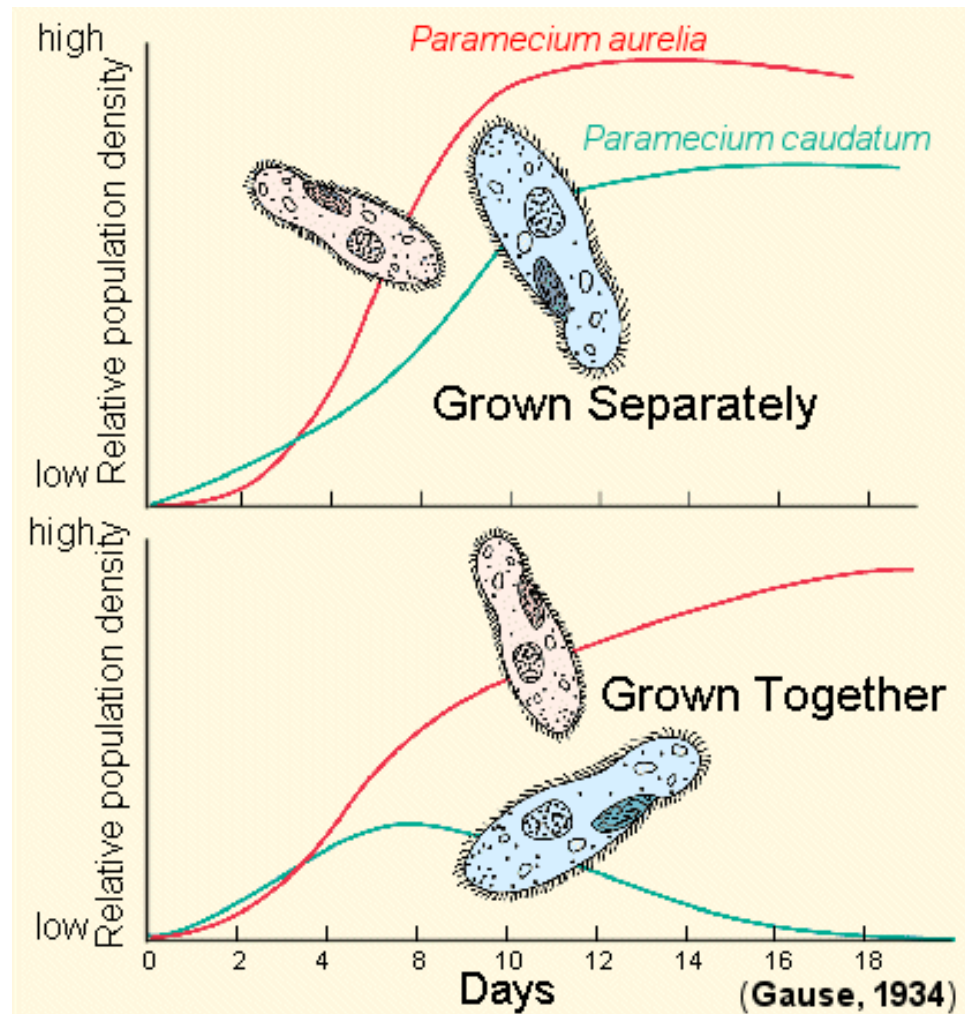
David Tilman, Mark Mattson, and Sara Langer

Competitive exclusion



- Controlled experiment
- Single limiting resource

Competitive exclusion



Exploitation competition or
Lower minimum resource needs?

Competitive exclusion

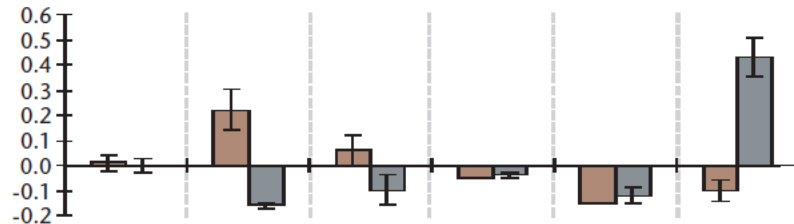
- Ecological examples?
- Red and Grey squirrels in Brittan
 - Red squirrels: native to European boreal forests
 - Grey Squires: native to NA hardwood and mixed forests.



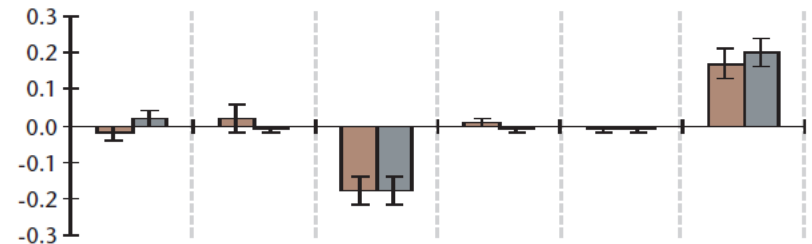
Red and Grey squirrels

Core area selection within study area

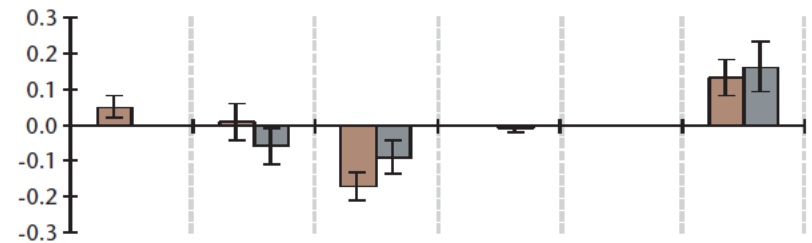
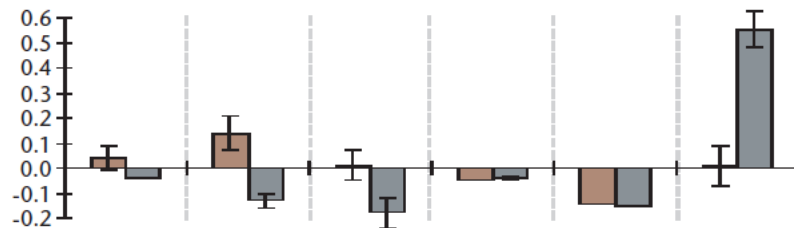
Autumn



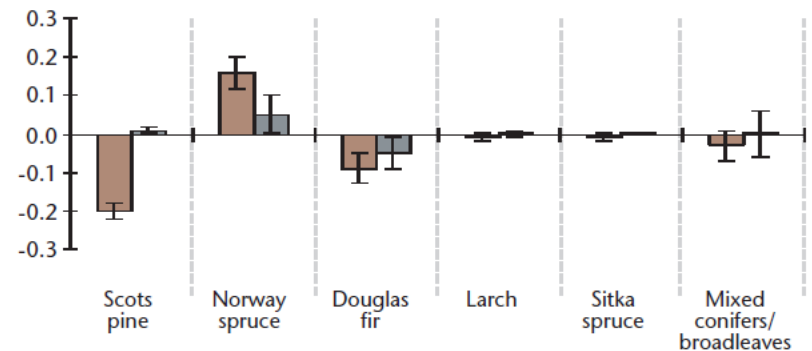
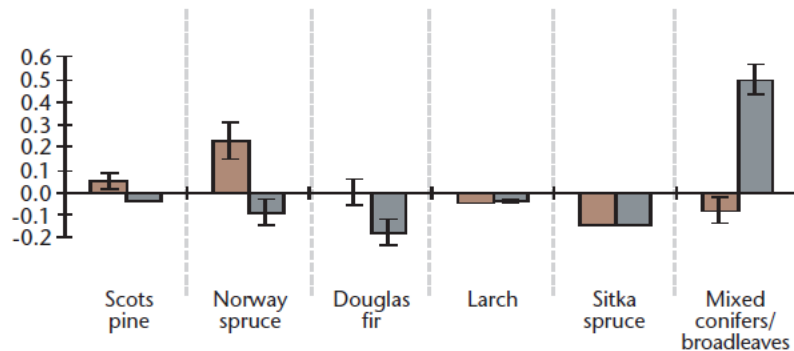
Tree species selection within total home range



Over-winter

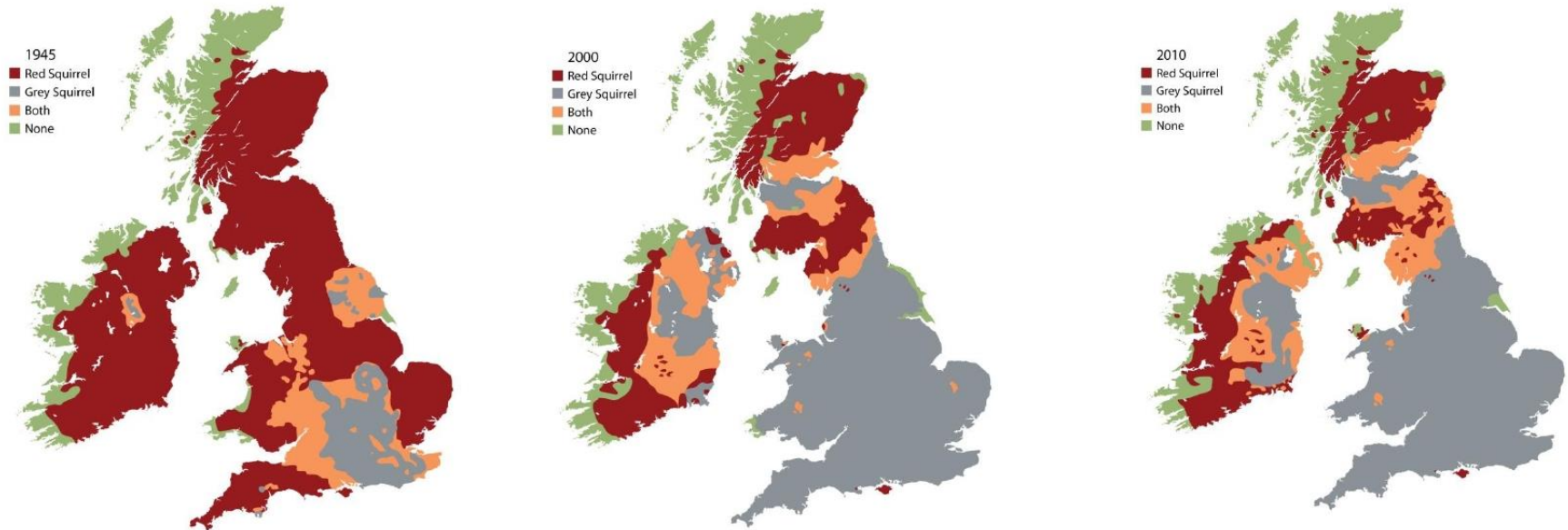


Spring



Red and Grey squirrel competition

Squirrel Distribution Maps 1945-2010



- Grey squirrels introduced in ~30 sites between 1876 and 1929
- Red squirrel decline
 - Complete exclusion
 - Disease, disappearance of hazel coppices and mature conifer forests

Stable coexistence

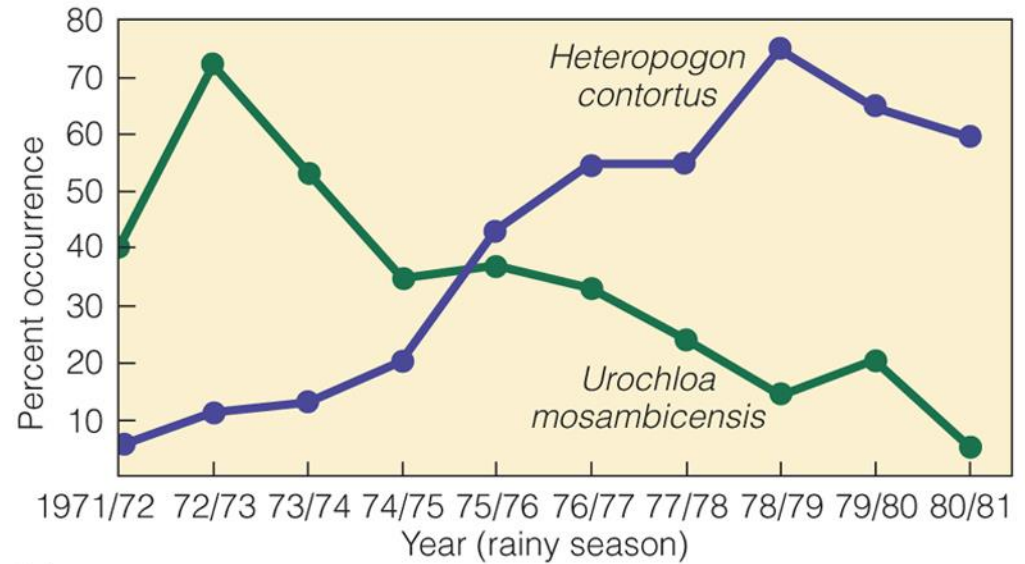
- Non-static relative competitive ability
 - Competition coefficients variable through time
 - Competition coefficients variable through space
- Non-identical resource needs
 - Avoid competition in space
 - Avoid competition in time
 - Use different resources (use resources differently)

Competition coefficients variable through time

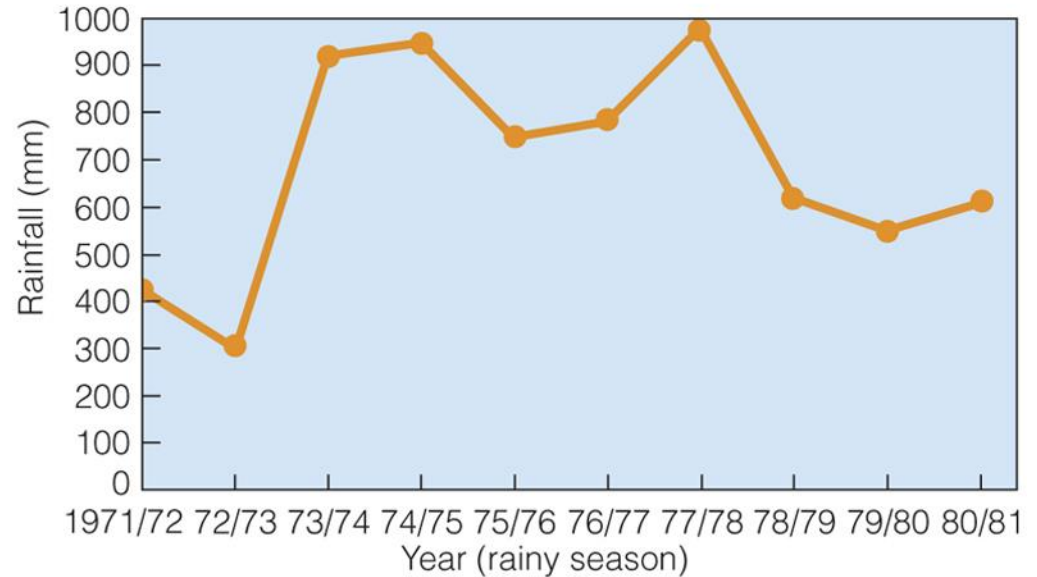


H. contortus
Perennial tussock
grass

U. mosambicensis
Buffalo grass



(a)



(b)

Over time, access to
resources can
change- shifting the
competitive balance
between two species

Competition coefficients variable in space



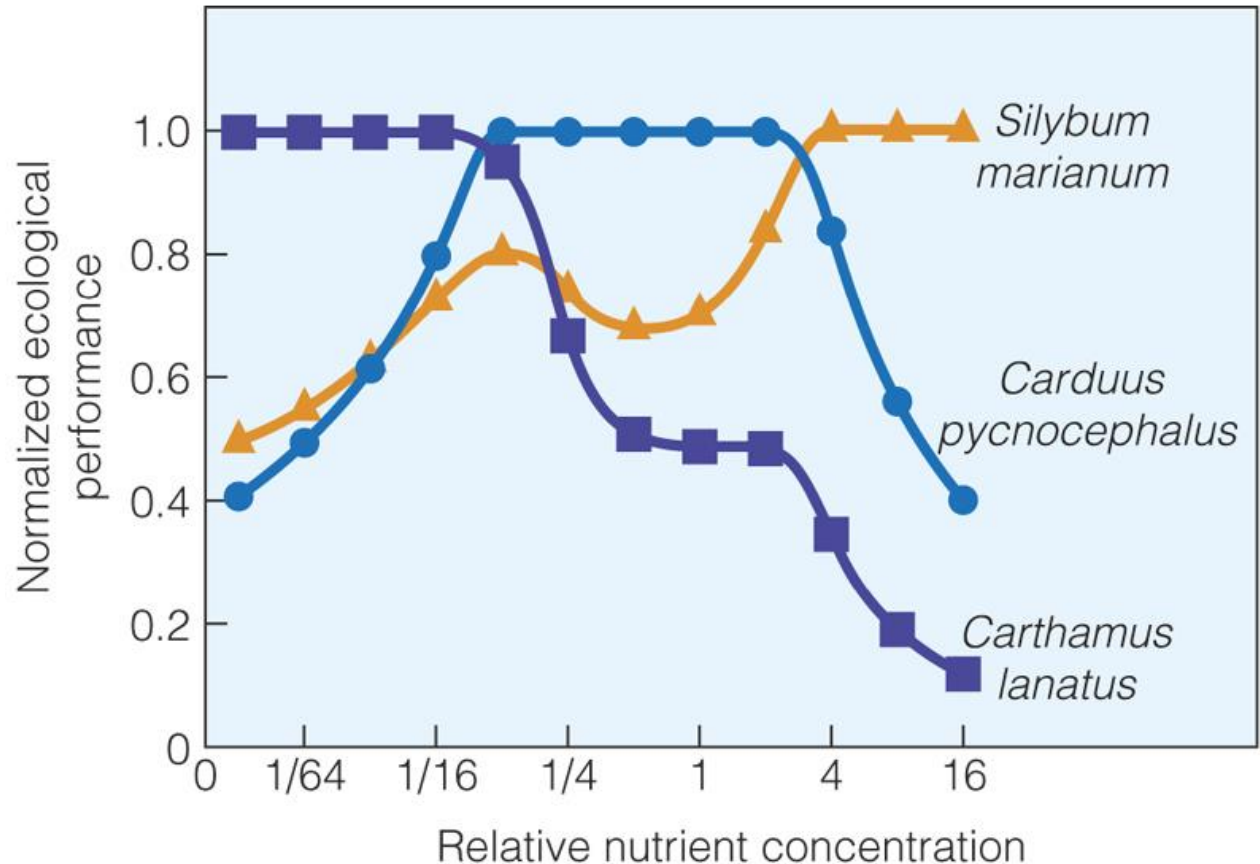
Milk
thistle



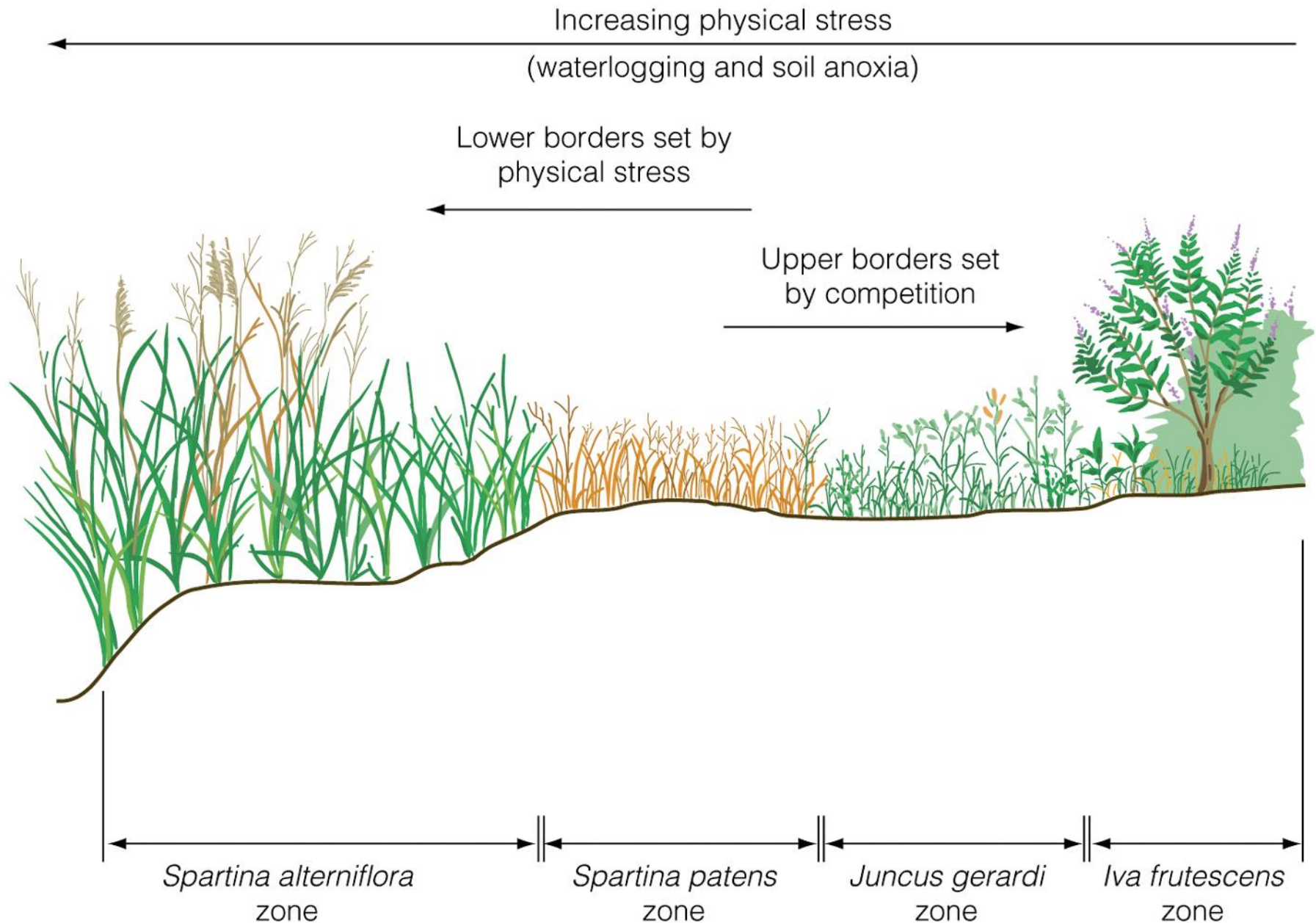
Italian
thistle



Woolly
dastaff
thistle



The competitive balance among species can be shifted along resource gradients

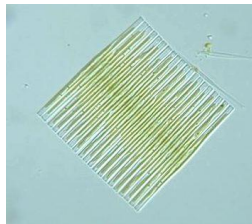


Gradients often represent a spectrum of stress tolerance and competitive ability

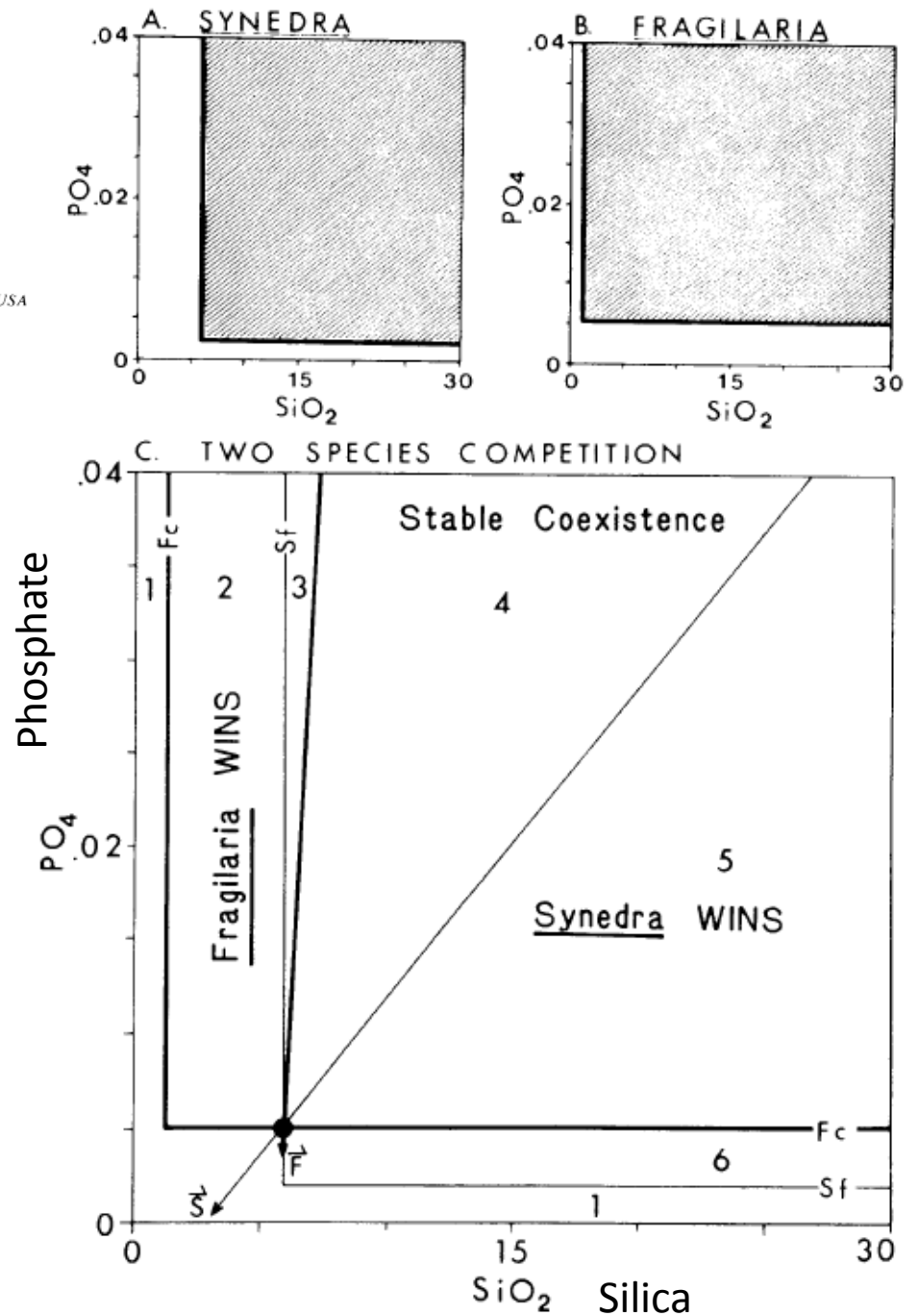
TESTS OF RESOURCE COMPETITION THEORY USING FOUR SPECIES OF LAKE MICHIGAN ALGAE¹

DAVID TILMAN

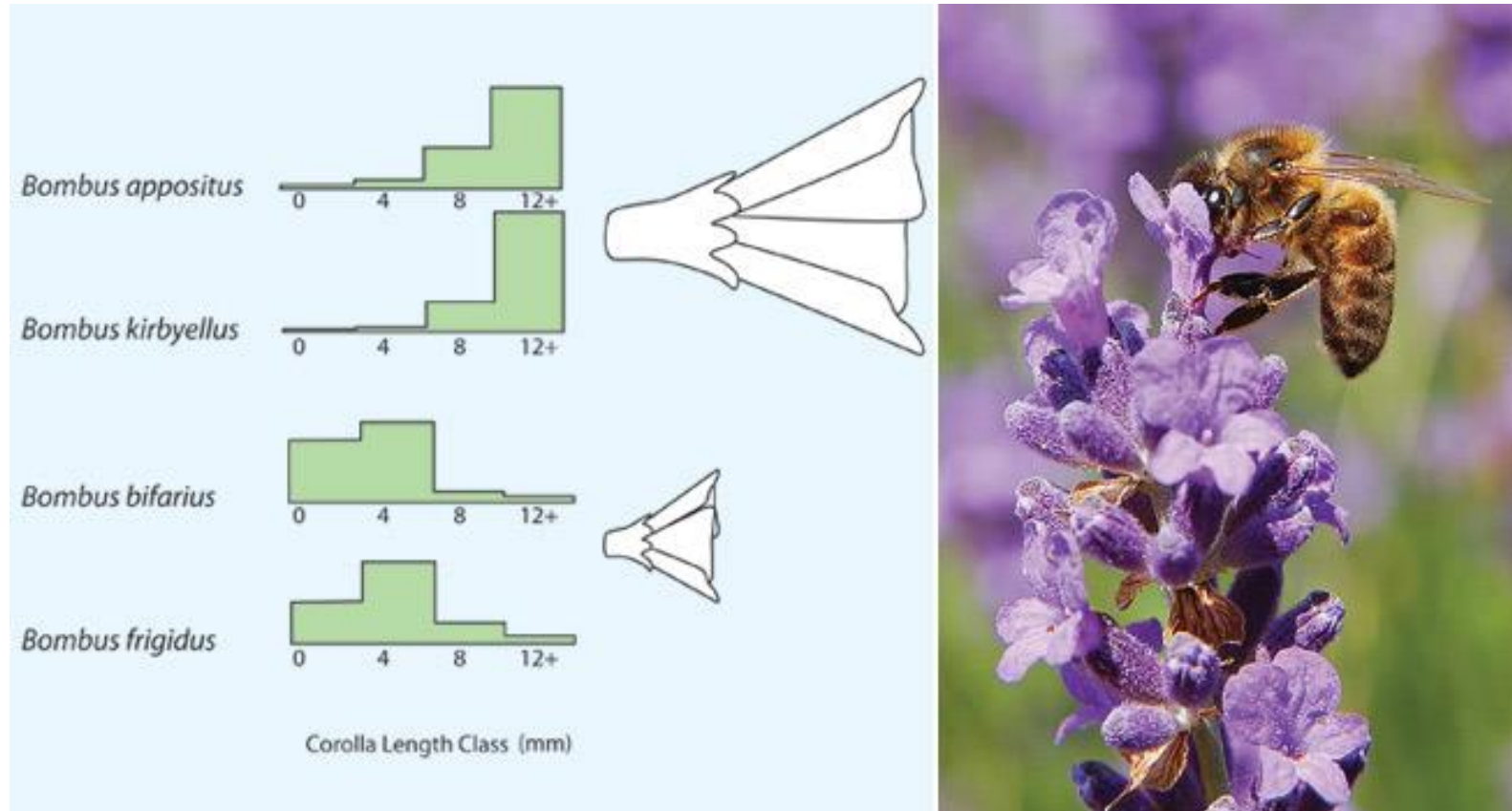
Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455 USA



Diatom competition

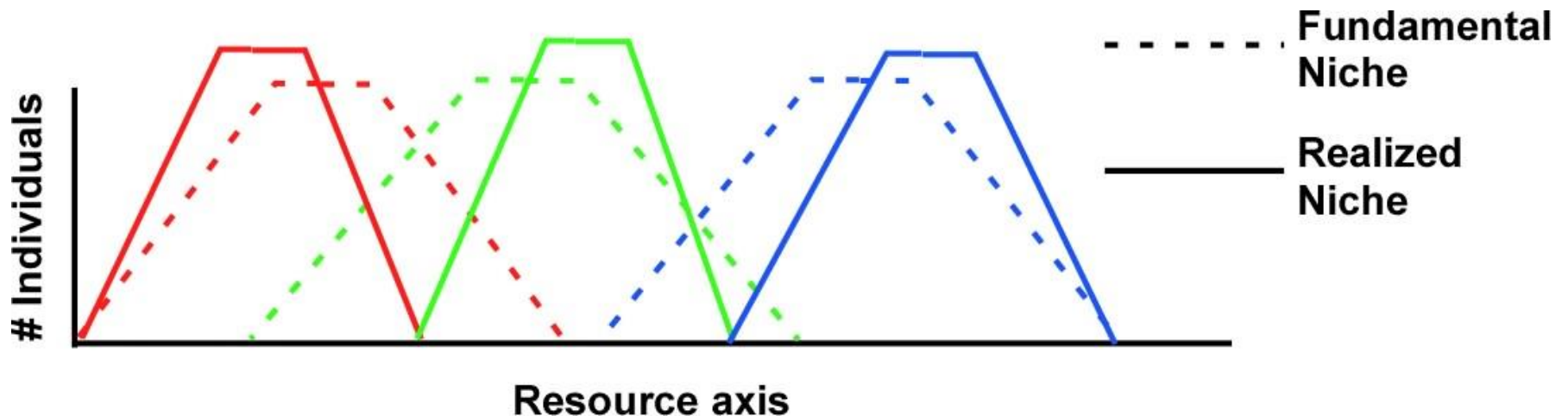


Resource partitioning

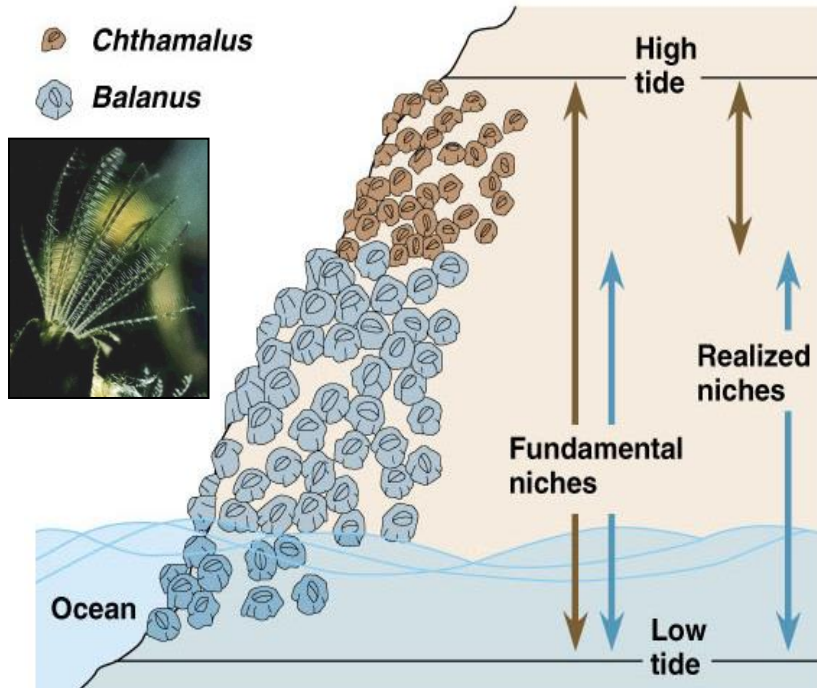


Resource partitioning

- Partitioning of resources, differentiation of realized niches
 - Potential niche
 - Fundamental niche
 - Realized niche



Niche differentiation and competitive exclusion



Chthamalus

- tolerates a broad range of exposure to air
- Poor space competitor



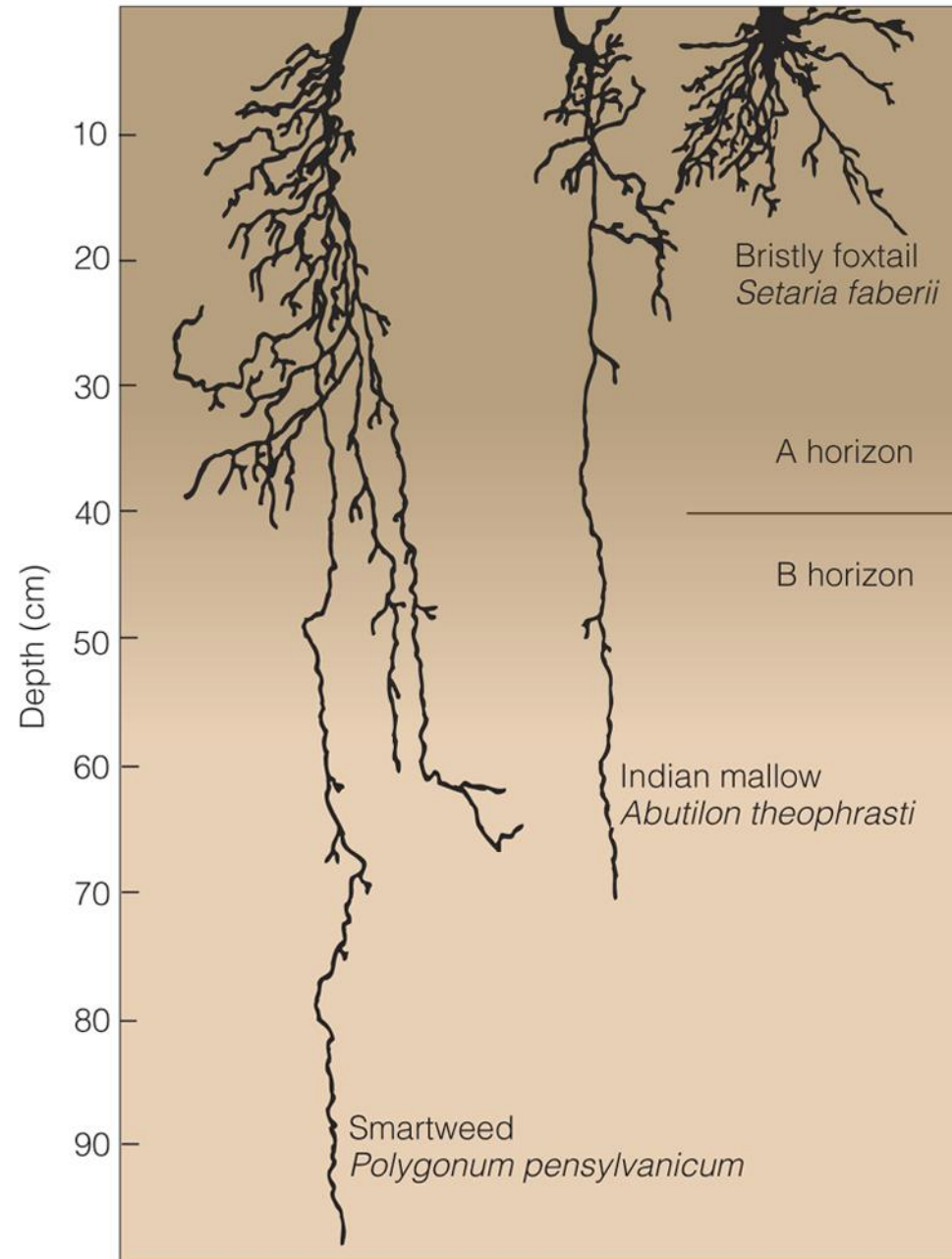
Balanus

- cannot tolerate long exposure to air
- but in lower inter-tidal, is very aggressive - pries off *Chthamalus*.

Niche partitioning ~ trade-offs

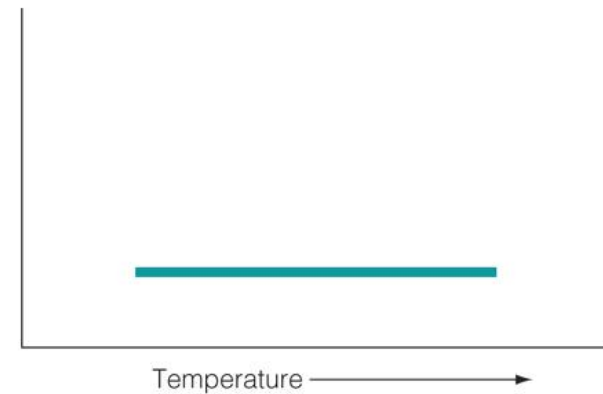
Niche differentiation

- Using resources differently
 - Accessing resources differently
 - Competing for resources differently

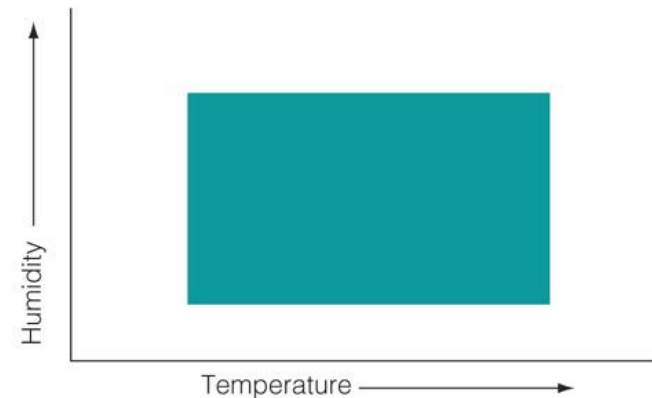


Niche

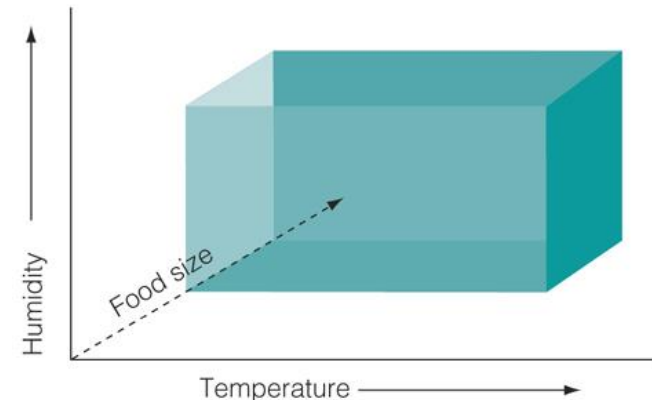
- **Niche** is a multidimensional
- An organisms niche is defined by many features of the environment dictate whether an organism is successful
- i.e. likelihood that two organisms share exactly the same niche space is potentially less
- Therefore, if two organisms share exactly the same requirements for some resource or environmental feature- they can still coexist as long as some other feature differs.



(a) One dimension

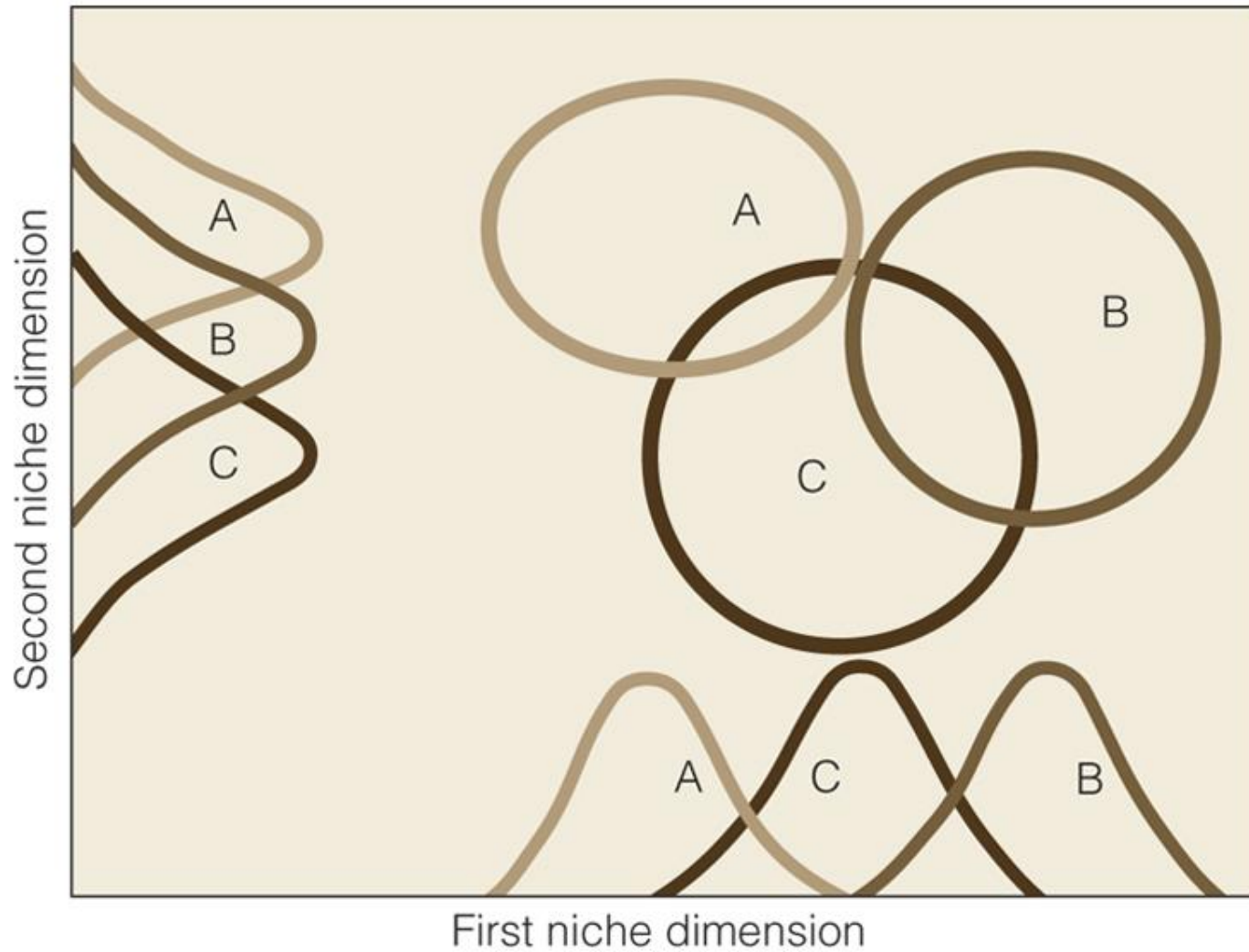


(b) Two dimensions



(c) Three dimensions

Niche differentiation



Competitive exclusion principle (restated)

If two competing species coexist in a stable environment, then they do so as a result of niche differentiation. If, however, there is no such differentiation, then one competing species will eliminate or exclude the other.

Begon et al. 1996

Ecology: From Individuals to Ecosystems

Spatial niche differentiation

POPULATION ECOLOGY OF SOME WARBLERS OF NORTHEASTERN CONIFEROUS FORESTS¹

ROBERT H. MACARTHUR

Department of Zoology, University of Pennsylvania

Ecology, Vol. 39, No. 4 (Oct., 1958), pp. 599-619

Resource Partitioning

**Blakburnian
Warbler**



**Black-throated
Green Warbler**



**Cape May
Warbler**



**Bay-breasted
Warbler**

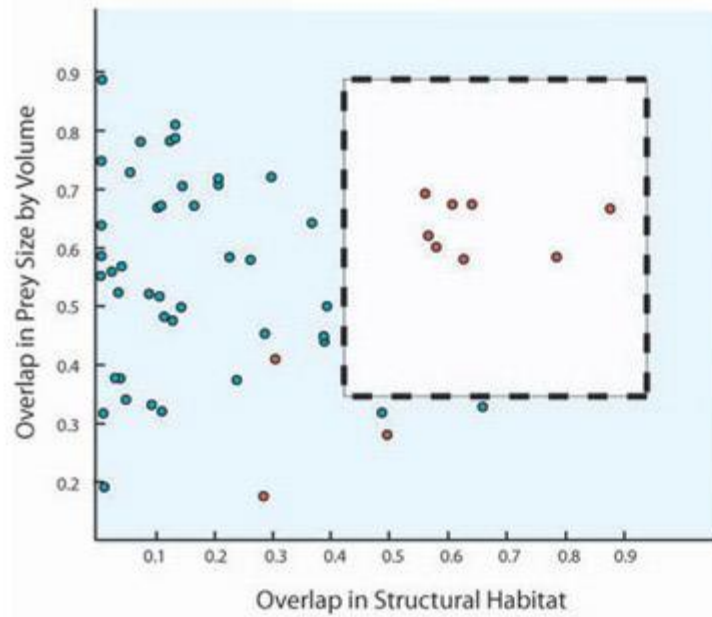


**Yellow-rumped
Warbler**



Spatial niche partitioning

- Caribbean *Anolis* lizards
 - Forage in the same place (thickness of branch)
 - Forage on the same prey items (prey size)

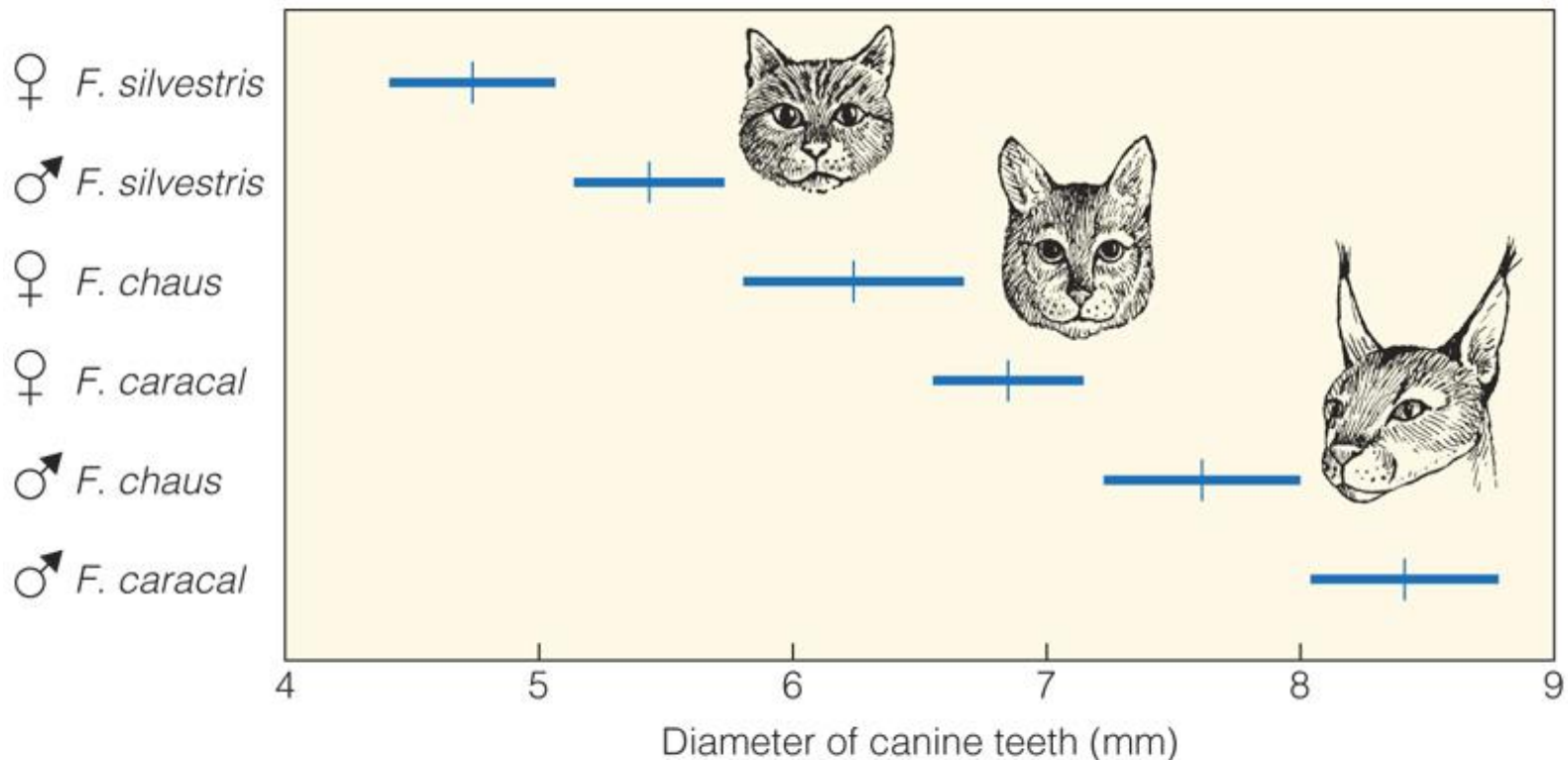


Competition

- Competitive exclusion
 - When niche is very similar and constant
- Stable coexistence
 - Niche differentiation
 - Dynamic environment (dynamic competition coefficients)

Niche differentiation

- Realized through changes in biology
- Niche separation between species, and sexes



Intraguild Predation

- Occurs when one species not only competes with its heterospecific guild member, but also occasionally preys upon it.
- Species 1 – Competitor & Occasional Predator
- Species 2 – Competitor & Occasional Prey



Intraguild Predation

- Species 1 – competitor and predator

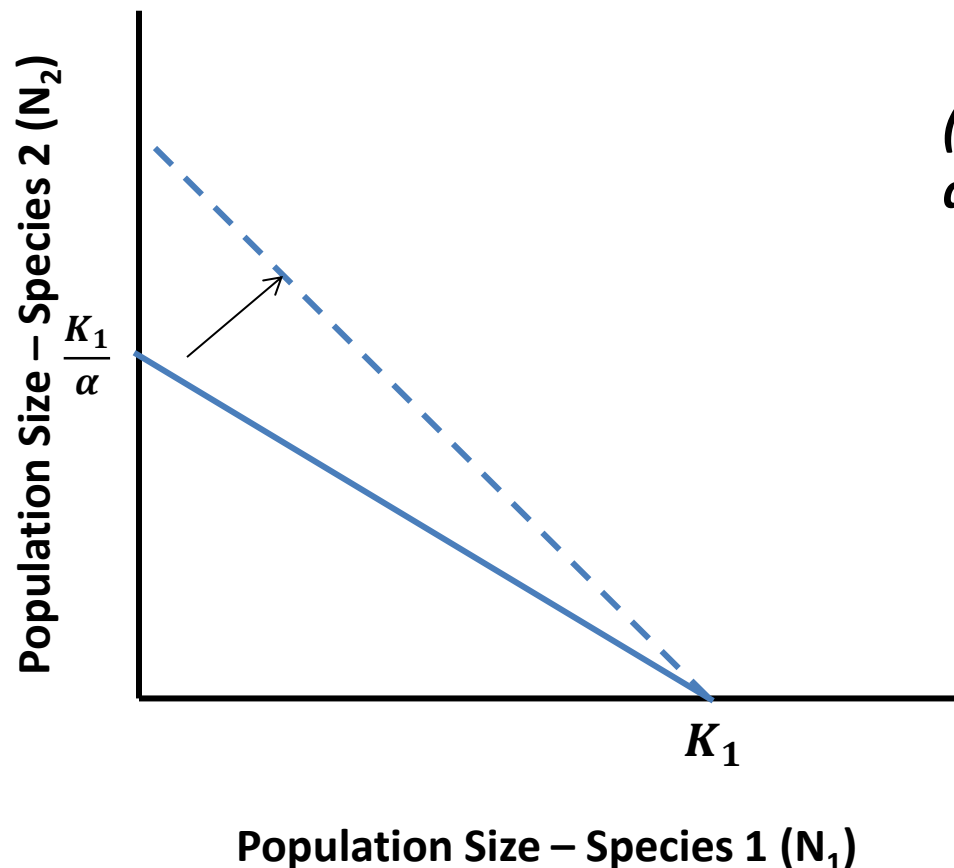
- $$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right) + \gamma N_1 N_2$$

- Species 2 – competitor and prey

- $$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right) - \delta N_1 N_2$$

Intraguild Predation and Isoclines

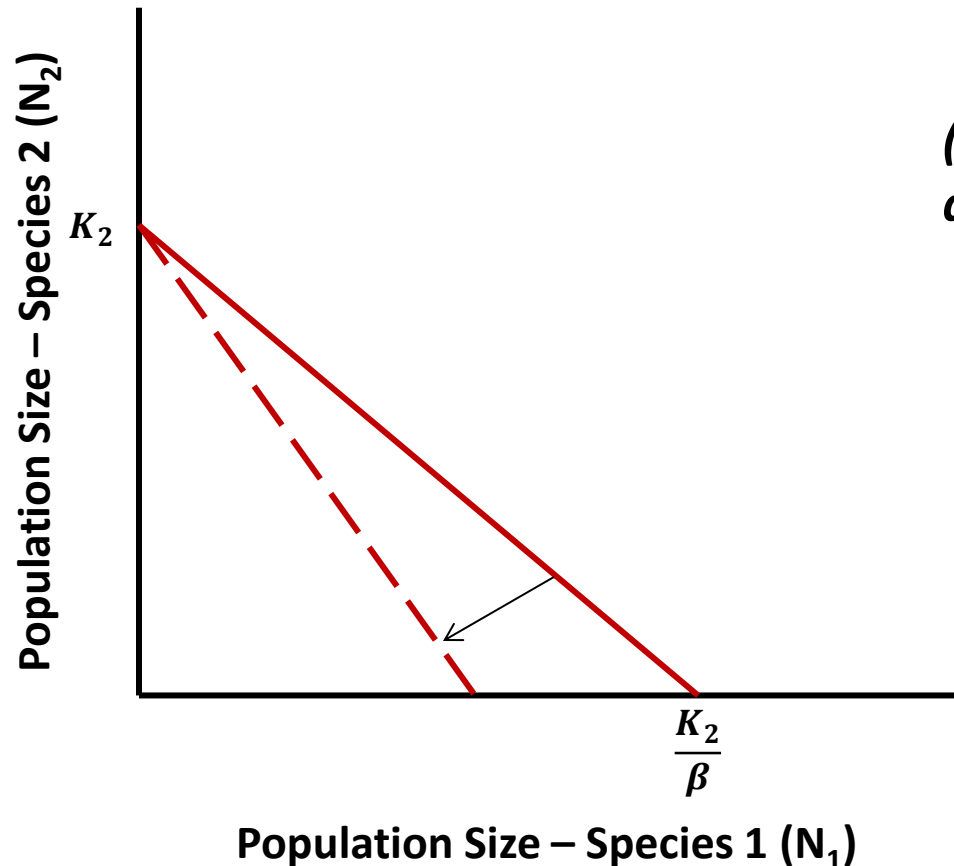
- Species 1 Isocline - Number of species 2 required to drive species 1 to extinction EXCEEDS K_1/α , as Species 2 losses individuals to predation.



(Isocline rotates, but K_1 and K_1/α do not change)

Intraguild Predation and Isoclines

- **Species 2 Isocline** - Number of species 1 required to drive species 2 to extinction is LESS THAN K_2/β , as Species 1 both competes and preys on species 2.



(Isocline rotates, but K_2 and K_2/β do not change)

Intraguild Predation and Isoclines

- Adding this dynamic can now change the anticipated outcomes of state-space models

