Diversity & stability

ECOL 4000/6000

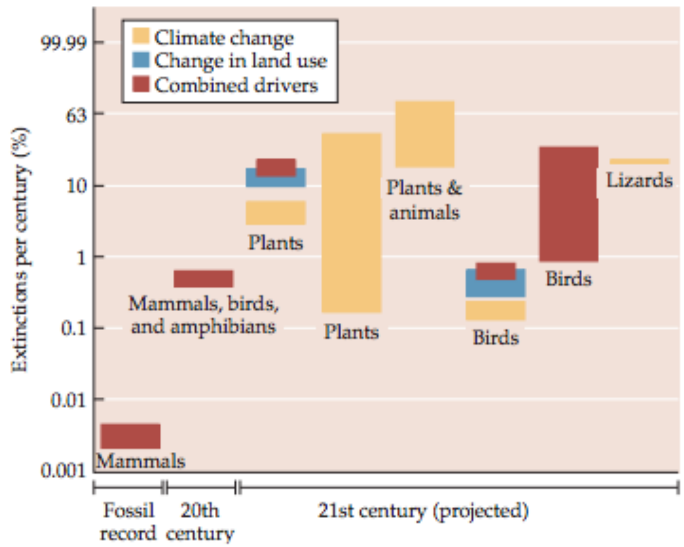
Quiz: According to the reading, variability in productivity may decline with species richness due to…(there are 3 correct answers)

- A) Portfolio effect
- B) Intermediate disturbance
- C) Insurance effect
- D) Positive covariance
- E) Negative covariance
- F) Allee effect

Diversity-Stability: Outline

- Loss of single species: knock-on effects (e.g. keystone species, trophic cascades)
- Diversity stability case study 1: fisheries
- Measures of stability (dynamic/resilience)
- General findings: diversity promotes stability
- May's counterpoint and challenges to it
- Diversity stability case study 2: eutrophication

Current species loss rate is high (growing?)



- If species richness affects ecosystem stability, then effects on ecosystems will increase in the future

Paine (1966) studied rocky intertidal zone's community structure

In one site he removed starfish (*Pisaster ochraceus*) and in neighboring control site he left it

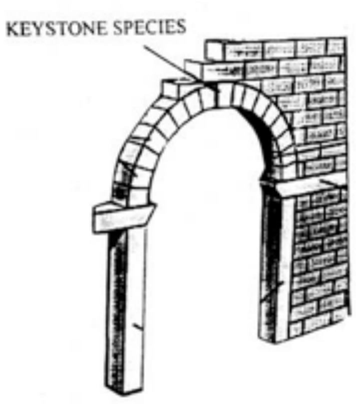
Community changed dramatically

- First barnacles occupied the space where starfish had been
- Later these were outcompeted by mussels
- ¾ of algae species were eliminated (lack of space)
- Browsing limpets and chiton moved out of site (lack of space & food)
- Number of species went from 15 to 8

A complete Pisaster!

Keystone species

- Removal of some species can have a significant effect on several others (extinction, large change in density) throughout the web
- We refer to them as keystone
- Originally referred to predators but now more widely used



Non-predator keystones

- In a study of Venezuelan streams, Flecker (1993) found that the detritivore *Prochilodus mariae* had a greater impact on the insect community than the insectivore fishes
- By grazing on detritus on stones they removed resources (detritus, algae) of insects
- Insectivore predation was compensated by rapid insect colonization (since resources were plentiful)

- Mycorrhizal fungi live in root tissue and soil
- Assist in nutrient uptake
- Many trees obligately associated
- Absence can slow reforestation

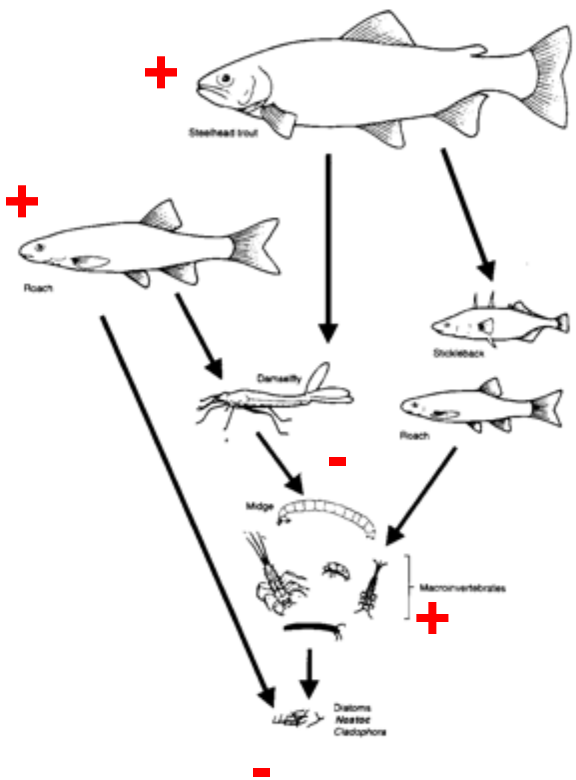
Keystone ecosystem engineers…

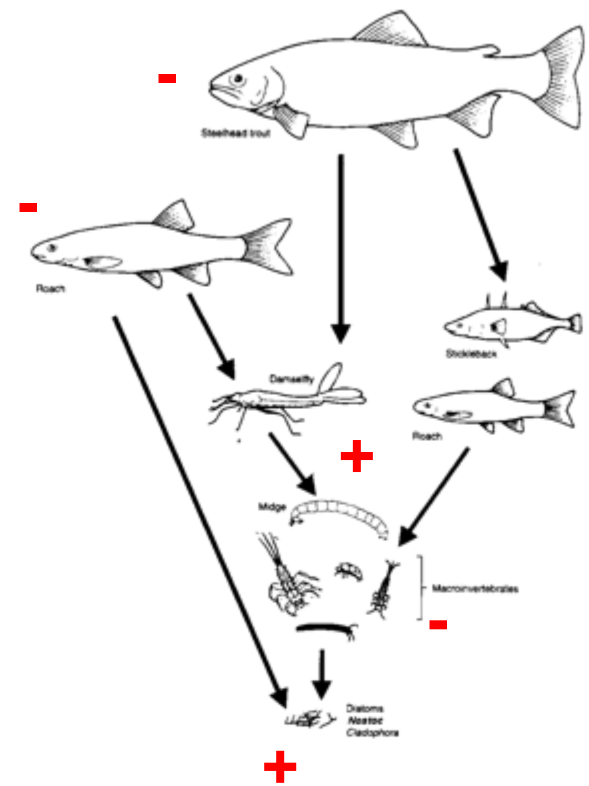
Generally speaking, keystone species…

- Occur in all major ecosystems and habitat types (intertidal, coral reef, freshwater, grasslands, woodlands, desert)
- Are not always top predators, but usually are at a high trophic level
- Are not always consumers – some are mutualists, competitors, habitat modifiers




Trophic cascade example



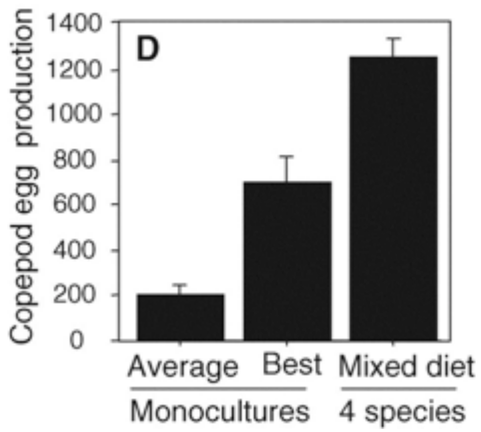


Presence of top predators in CA stream suppressed invertebrate predators allowing high densities of herbivores which suppressed the algae. Removing top predators had a cascading effect resulting in increased algal biomass

Power 1995, Power et al. 1985

Consequences of diversity (loss)

- Biodiversity & ocean ecosystem stability (fishery)
  - Diversity enhanced ecosystem ability to withstand recurrent perturbations in controlled experiments (a meta-analysis of 32 experiments)



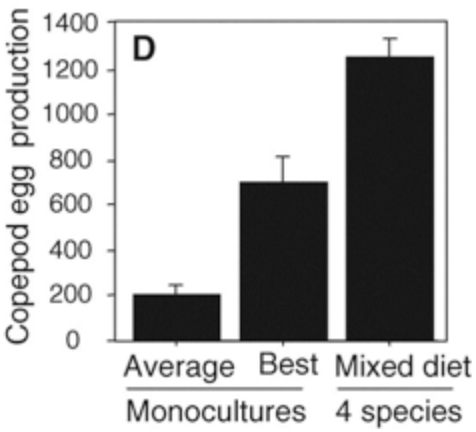
Worm et al 2006 *Science*

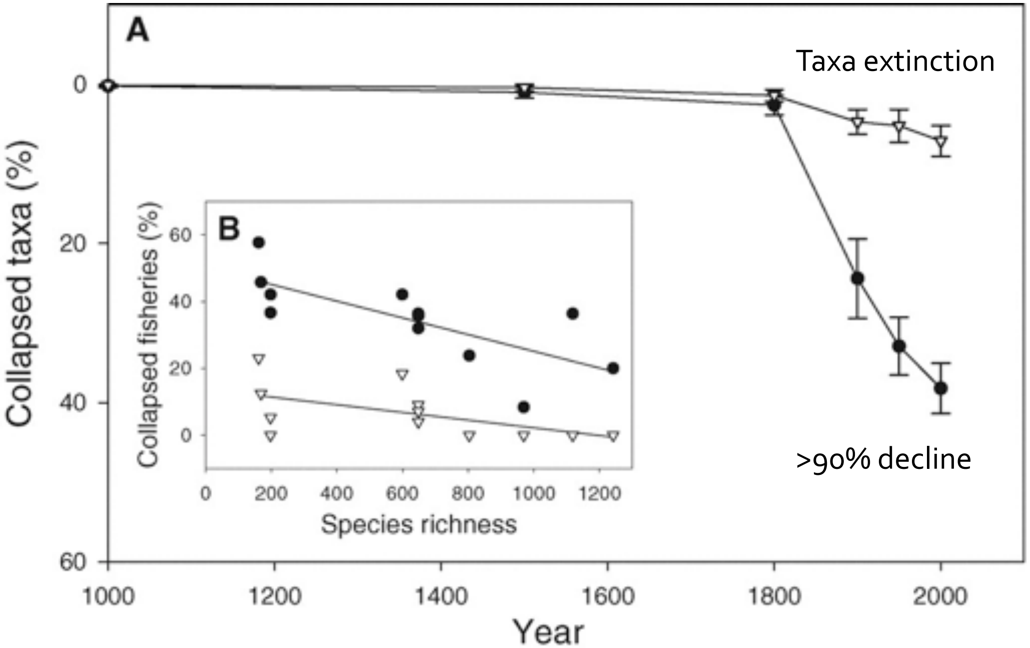
Consequences of diversity (loss)

- Biodiversity & ocean ecosystem stability (fishery)

Diet diversity enhanced reproductive capacity in zooplankton over both the average- and best-performing monocultures

(A) Trends of collapse (circles, >90% decline) and extinction (triangles, 100% decline) of species over the past 1000 years. Means and standard errors are shown (n = 12 regions in Europe, North America, and Australia). (B) Percentage of collapsed (circles) and extinct (triangles) fisheries in relation to regional fish species richness. Significant linear regression lines are depicted ($P < 0.01$).



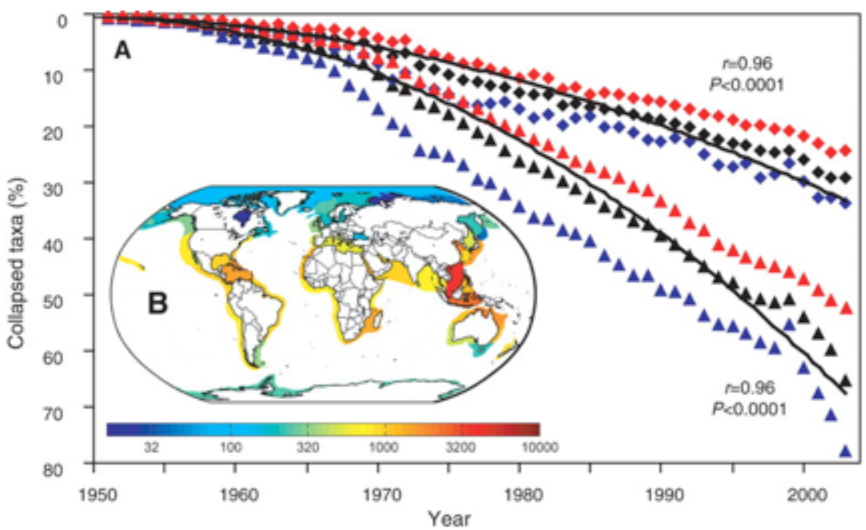


Worm et al 2006 *Science*

Consequences of diversity (loss)

- At a global scale, fishery collapses occurred at a higher rate in species – poor ecosystem

Species poor large marine ecosystems
Species rich large marine ecosystems
All systems



▲ cumulative

◆ each year

Worm et al 2006 *Science*

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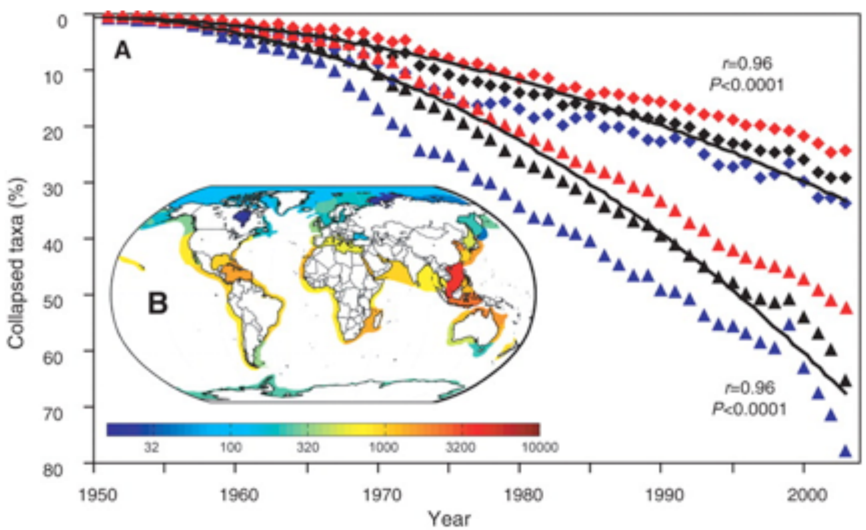

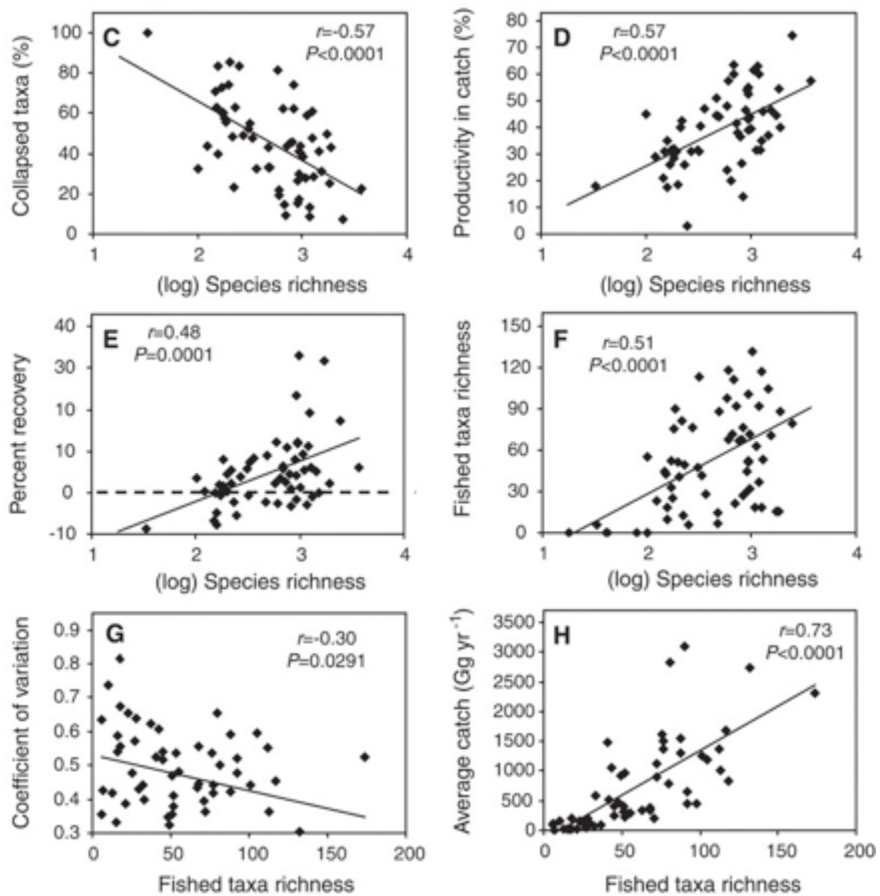

▲ cumulative

◆ each year

Worm et al 2006 *Science*

Consequences of diversity (loss)

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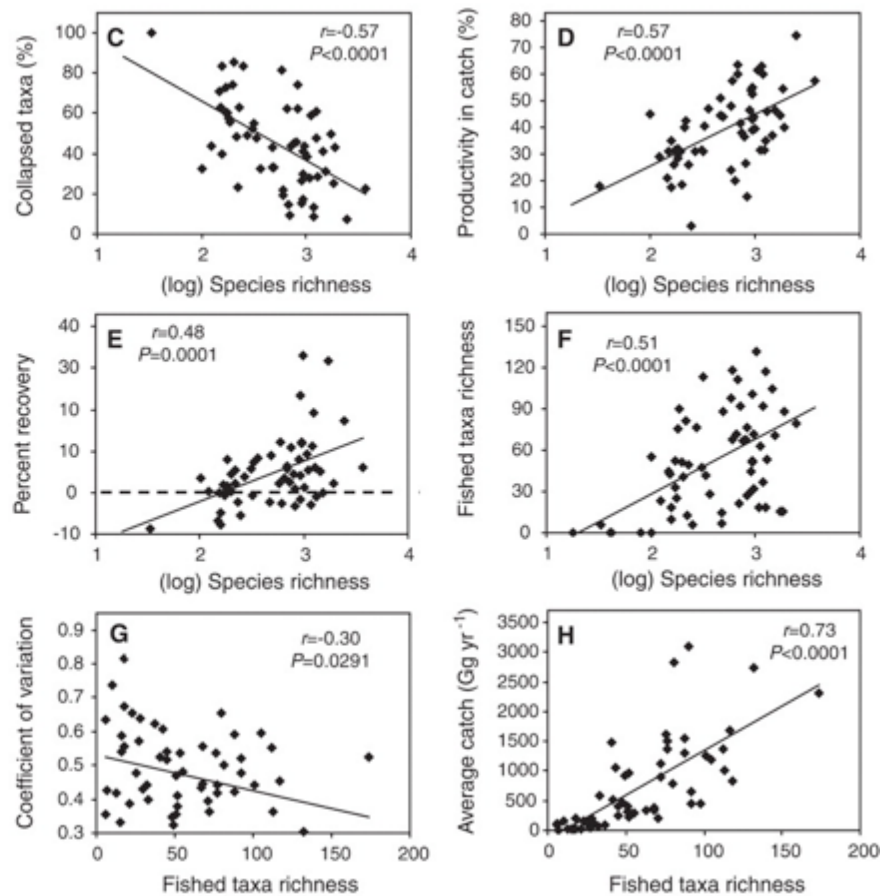
(C) Proportion of collapsed fish and invertebrate taxa, (D) average productivity of noncollapsed taxa (in percent of maximum catch), and (E) average recovery of catches (in percent of maximum catch) 15 years after a collapse in relation to LME total fish species richness. (F) Number of fished taxa as a function of total species richness. (G) Coefficient of variation in total catch and (H) total catch per year as a function of the number of fished taxa per LME.



What is stability?

Table 1 Definitions of stability

Term	Definition
Definitions of dynamic stability	
Equilibrium stability	A discrete measure that considers a system stable if it returns to its equilibrium after a small perturbation away from the equilibrium. A stable system, therefore, has no variability in the absence of perturbations.
General stability	A measure which assumes that stability increases as the lower limit of population density moves further away from zero. Under non-equilibrium dynamics, such limits to population dynamics generally imply a decrease in population variance (see variability definition below).
Variability	The variance in population densities over time, usually measured as the coefficient in variation. Common in experimental tests of stability.
Definitions of resilience and resistance stability	
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Resistance	A measure of the degree to which a variable changes after a perturbation. Frequently used as a discrete measure that assesses a community's ability to resist invasion (that is, if an invader fails, the community resists invasion).

From the following article:
The diversity–stability debate
Kevin Shear McCann
Nature **405**, 228-233(11 May 2000)
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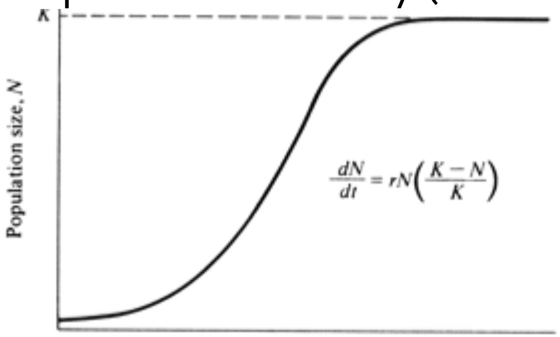
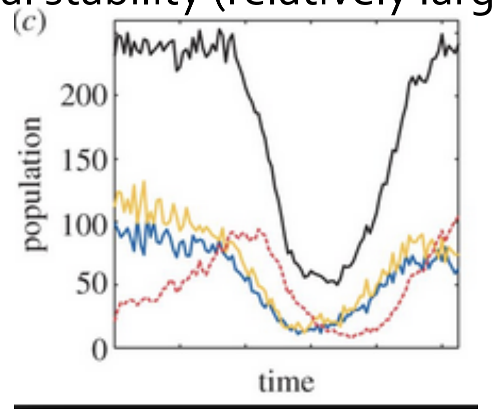
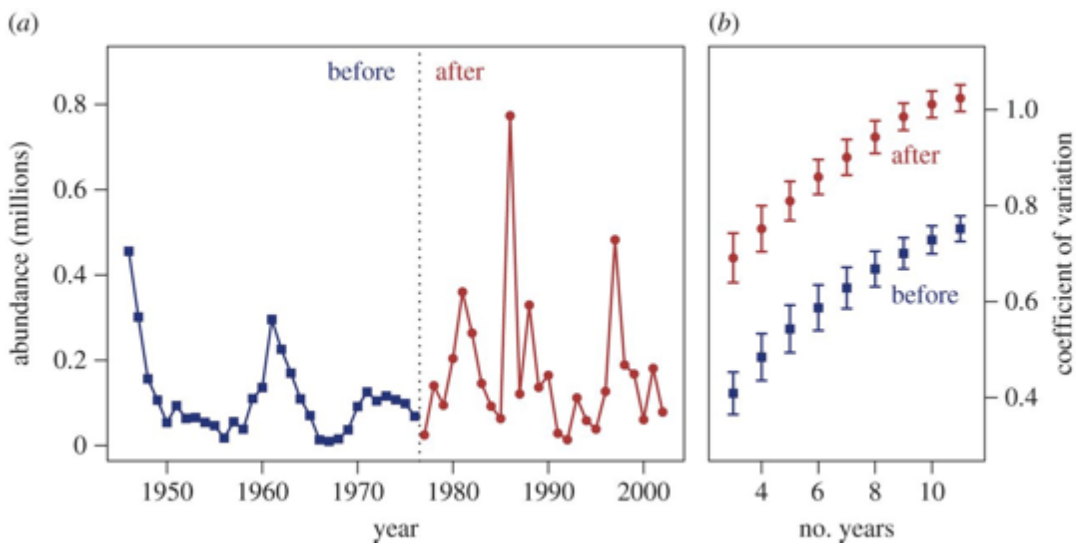
What is stability?

Equilibrium stability (no variance)



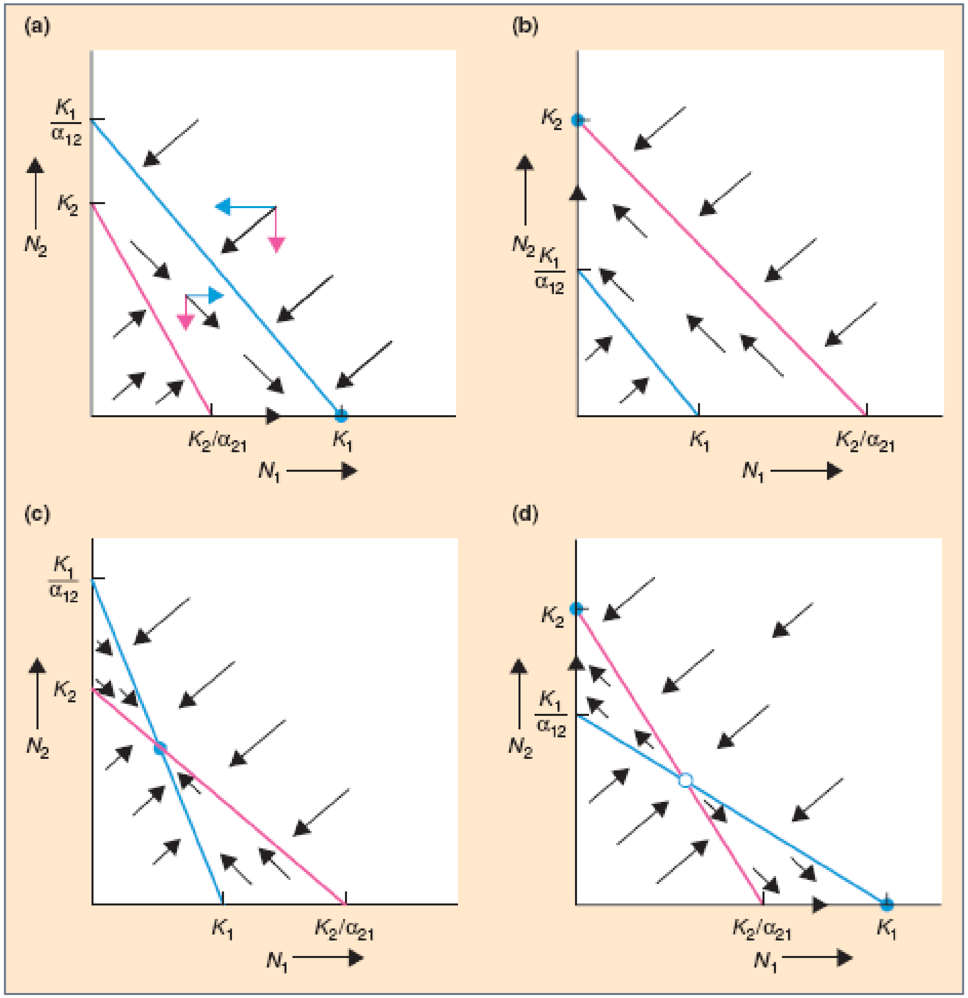
General stability (relatively large minimum)



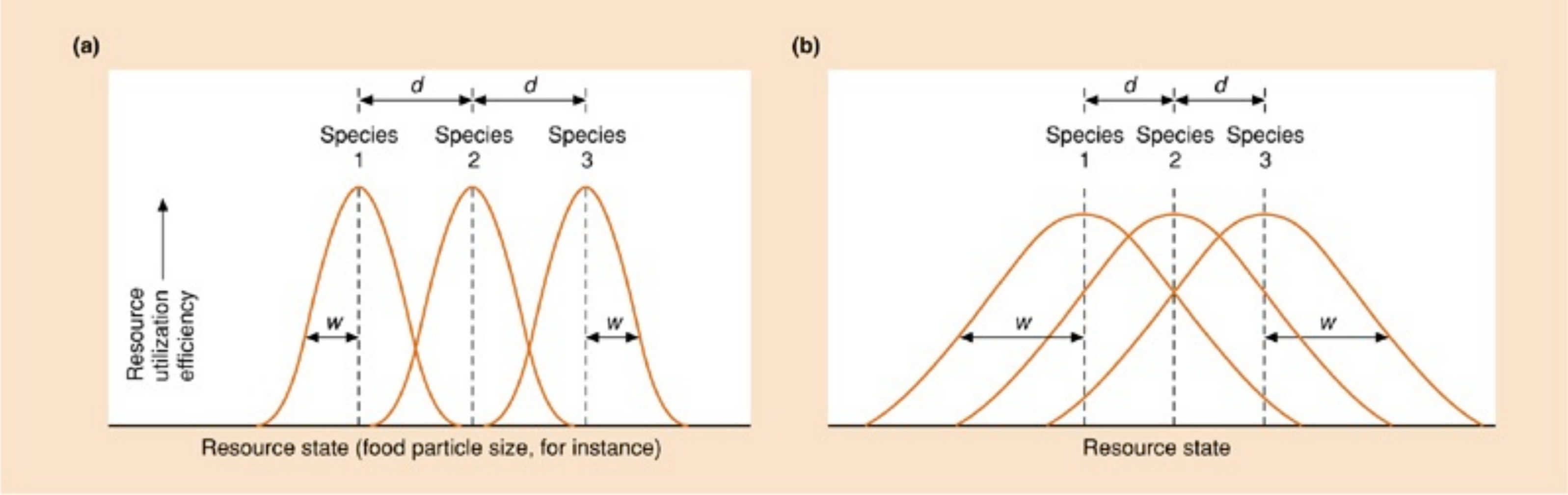


Variability (low variance or coefficient of variation)

Competition & stability (recap)



Resource Utilization Functions



Narrow niches with little overlap (d>w)

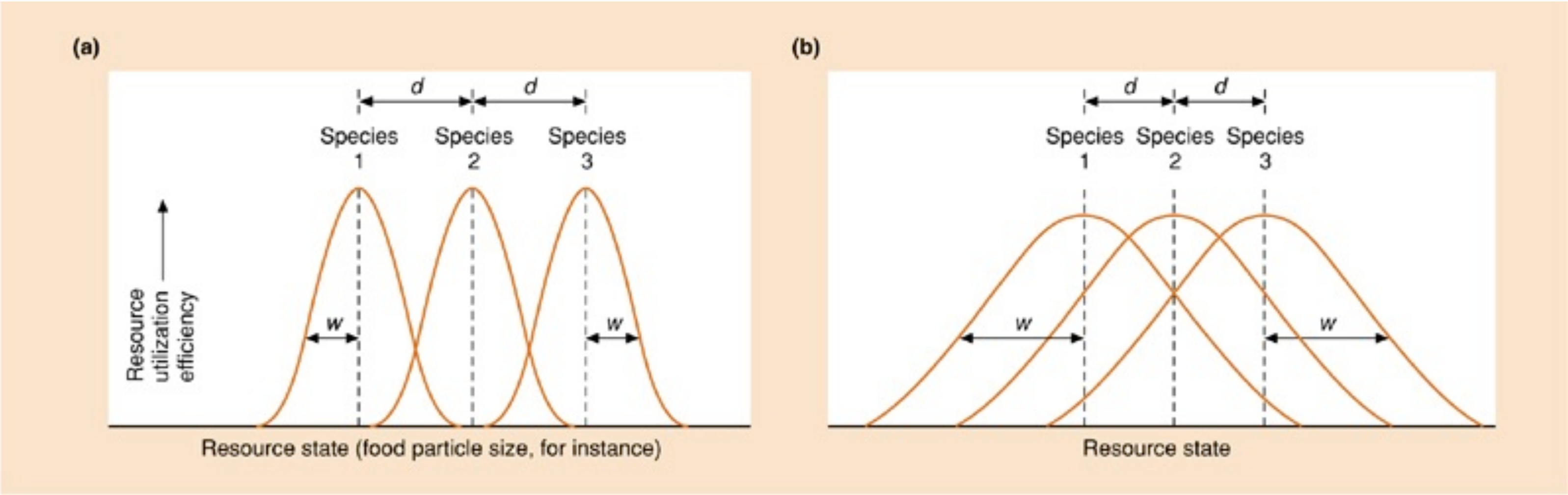
Broad niches with greater overlap (d<w)

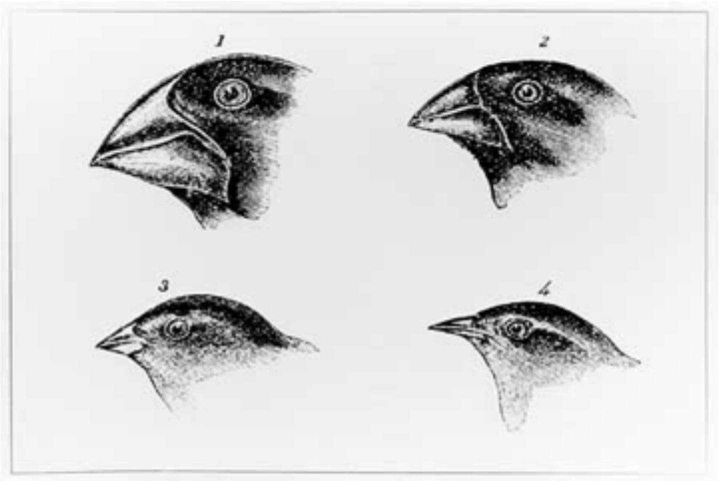
One species

$$r(x) = r_0\left(1 - \left[\frac{x - x_0}{w}\right]^2\right)$$

$$\frac{dN}{dt} = r(x)N$$

Resource Utilization Functions





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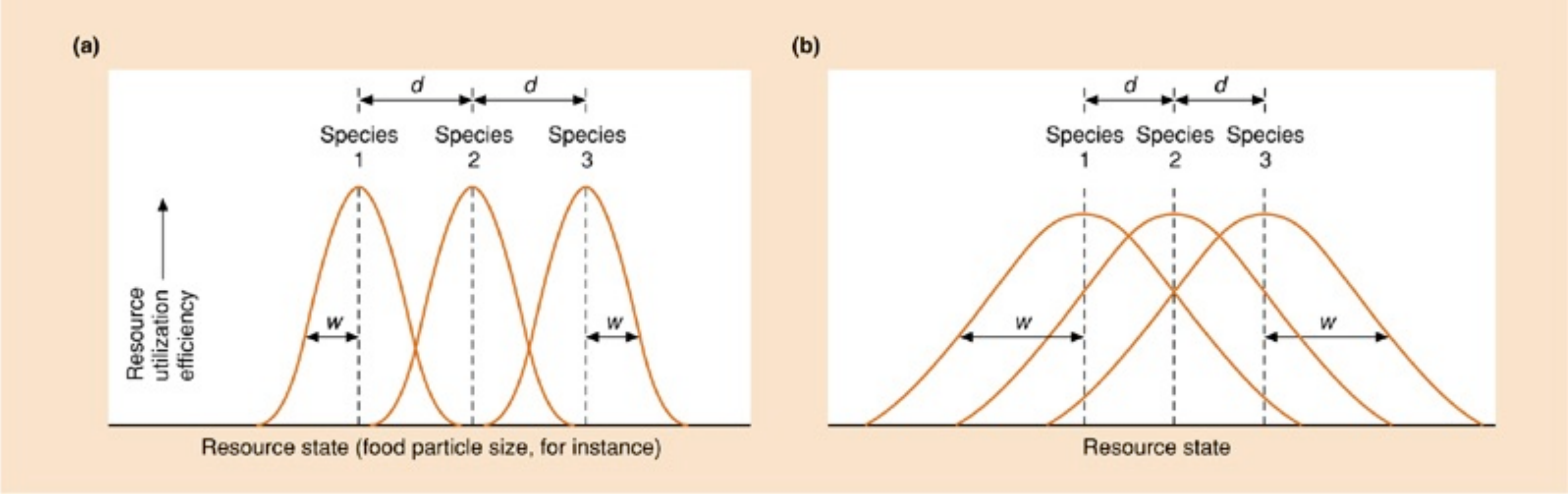
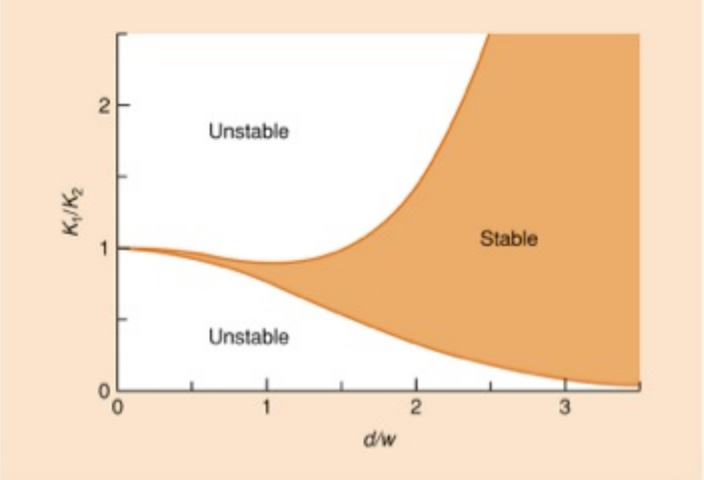


Several species

$$\alpha = e^{-c\frac{d^2}{w^2}}$$

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - N_i - \sum_j \alpha_{ij} N_j}{K_i} \right)$$



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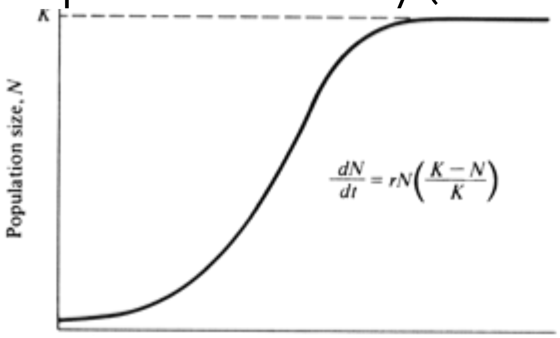
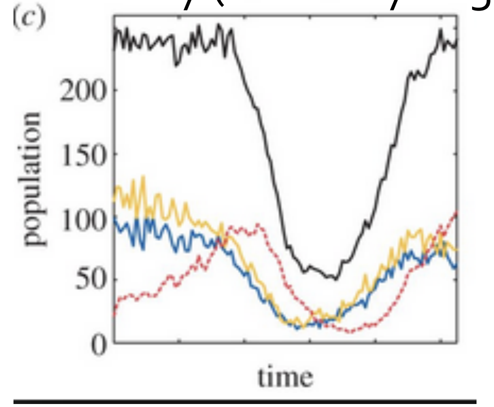
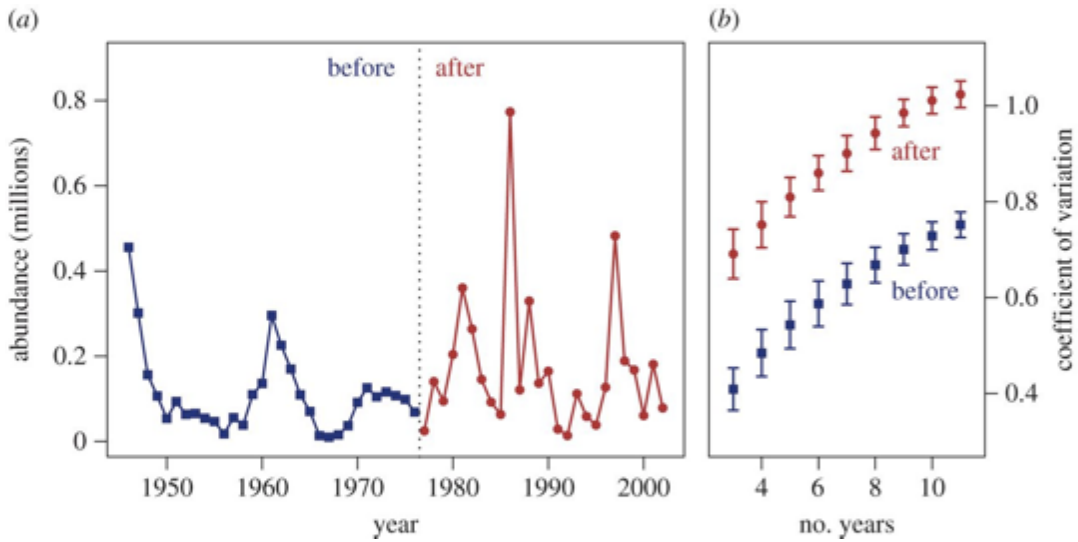
Equilibrium stability (no variance)



General stability (relatively large minimum)





Variability (low variance or coefficient of variation)

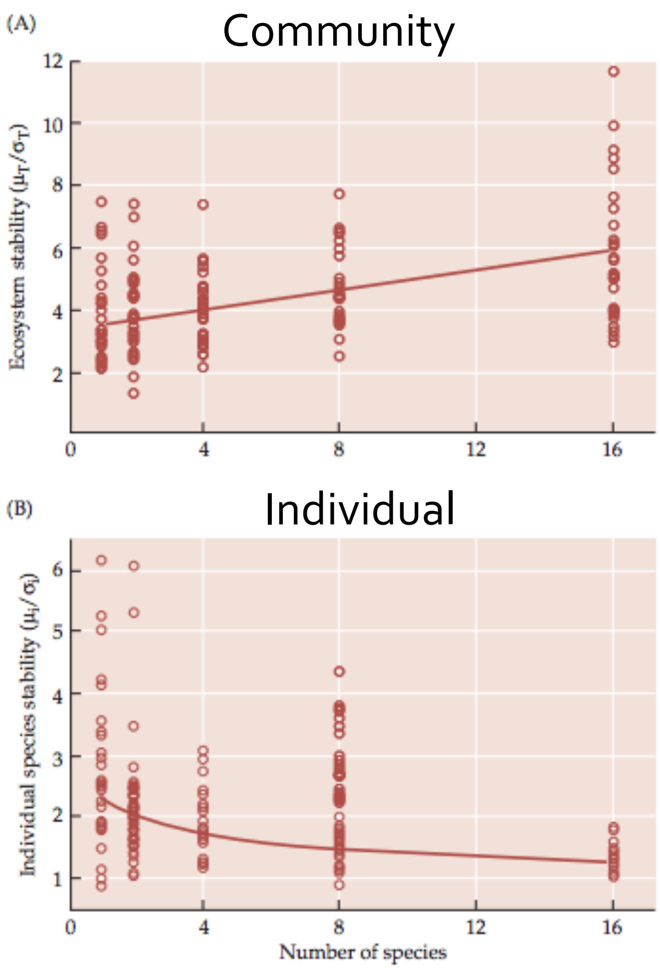
Diversity & ecosystem stability

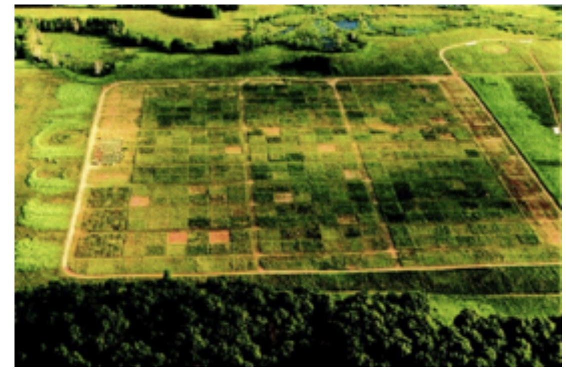
Gold

Blue

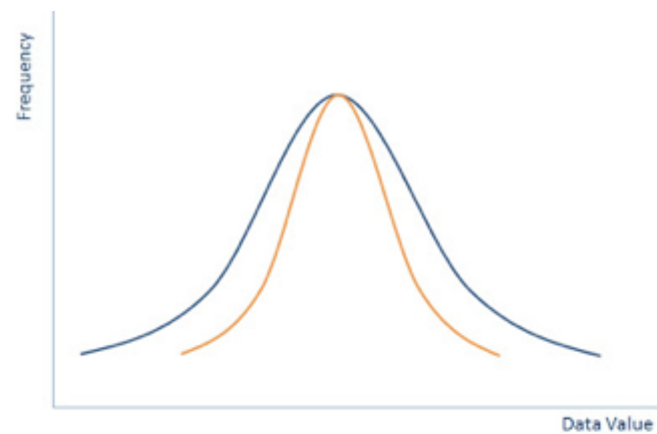
Gold

Blue





Cedar Creek, MN



Community stability increases with S.R.

Individual stability decreases with S.R.

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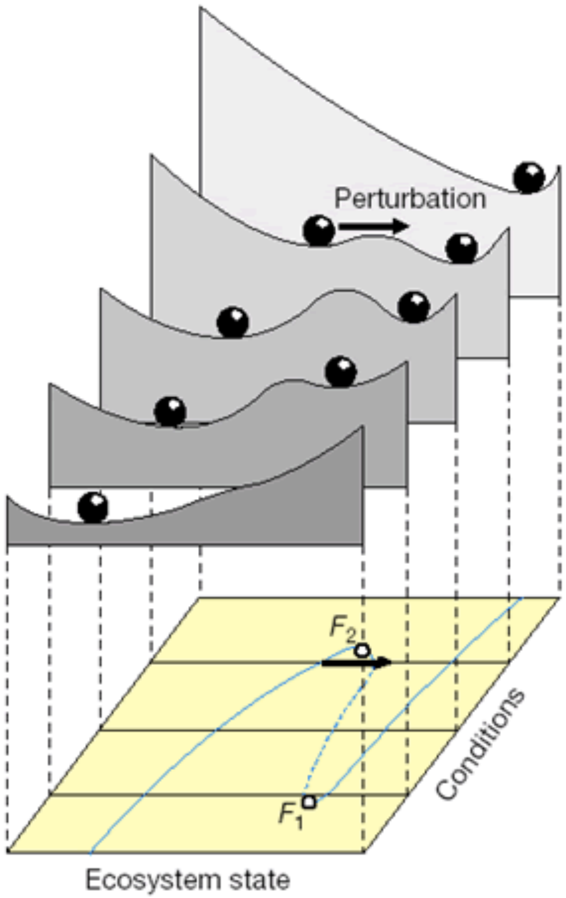
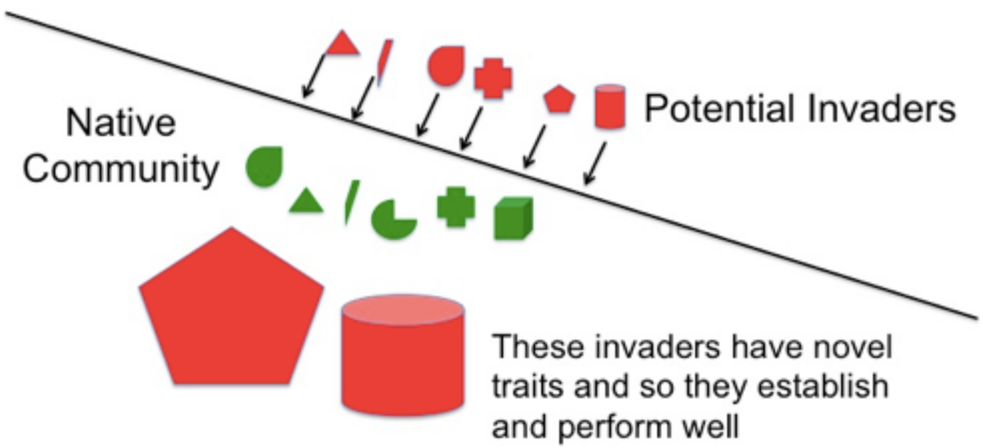




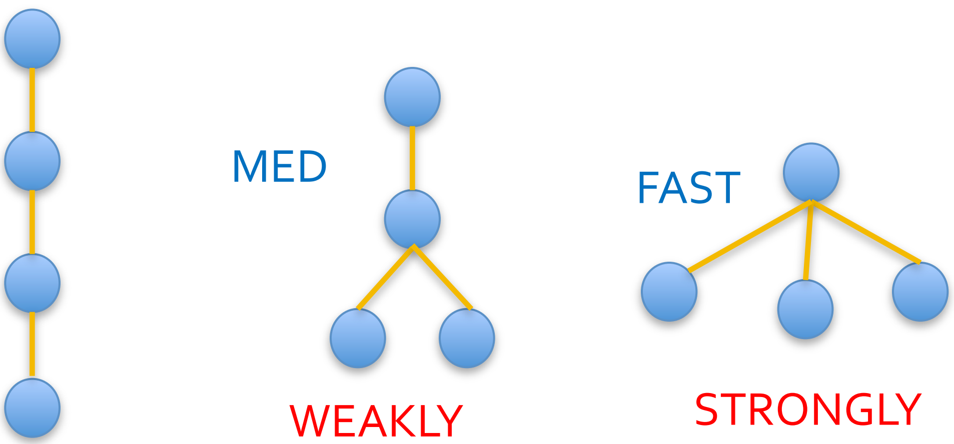
Dynamic food webs (extension of LV model)

$$\frac{dX_i}{dt} = X_i\left(b_i + \sum a_{i,j} X_j\right)$$

Change in species i

Depends on species i

And interaction with other species



Connectance: proportion of all possible links actually realized

Pimm & Lawton (1977, 1978)

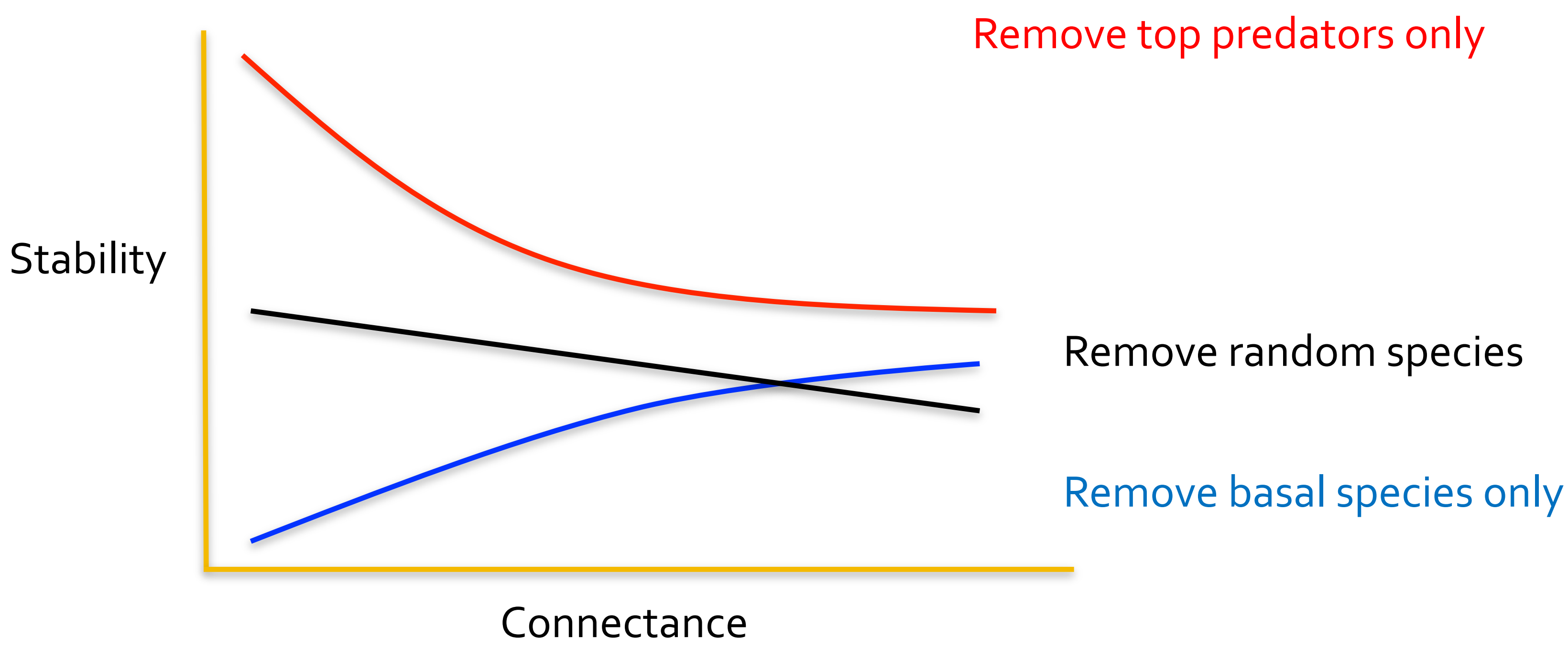
Dynamic food webs (extension of LV model)

- May (1972,1973) 1st to construct random food webs **with *s* species**
- All species had intra-specific density-dependent regulation
- Interactions between species could be + or – (drawn from normal distribution, **variance *i***) or 0
- Prob. that interaction is non-zero **gives connectance, *c***
- May found that webs were **generally stable if $i(sc)^{1/2}<1$**

Community is more stable if *s* (species richness) is small!

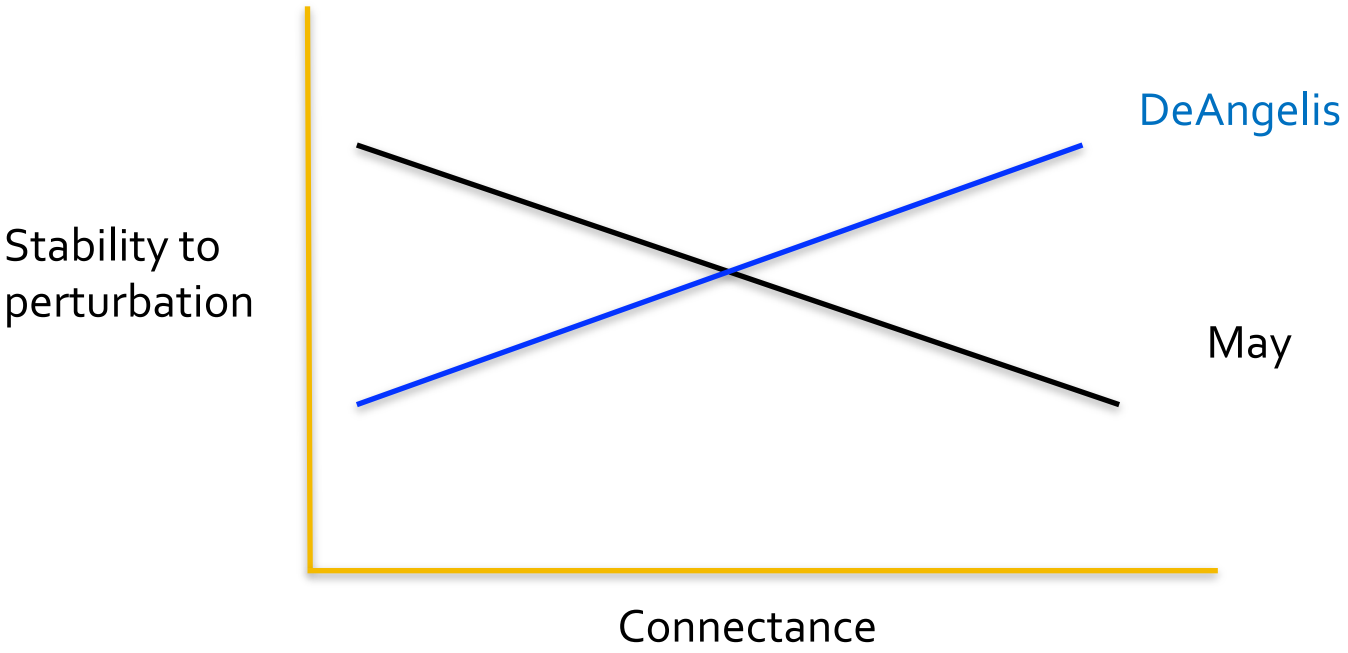
First, Pimm's work…

In models like May's, he removed a species and determined the probability that no other species went extinct (different from May's perturbation)

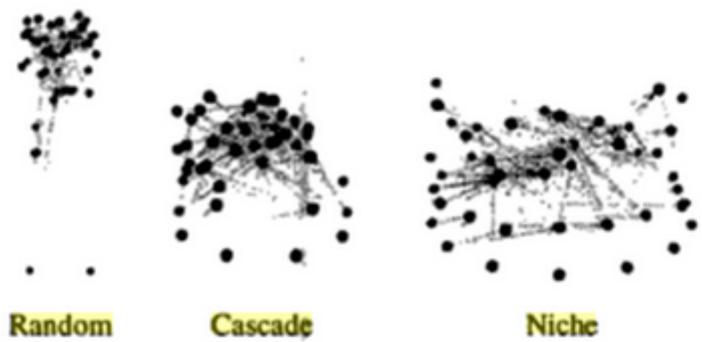


Next, DeAngelis…

Used the same perturbation stability as May, but considered situations where the basal resources were not limiting



Realistic foodwebs



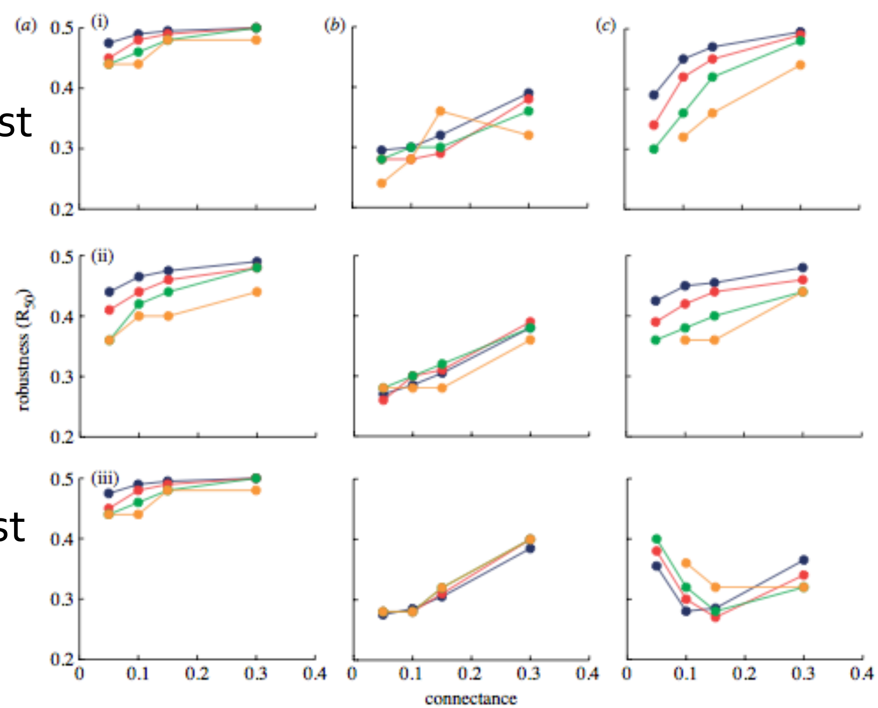
Generally

- Network structure matters
- Diversity (s) increases stability
- Complexity (connectance) increases stability

Remove most connected

Remove random

Remove least connected



Species richness

s=25

s=50

s=100

s=200

Dunne & Williams, 2009

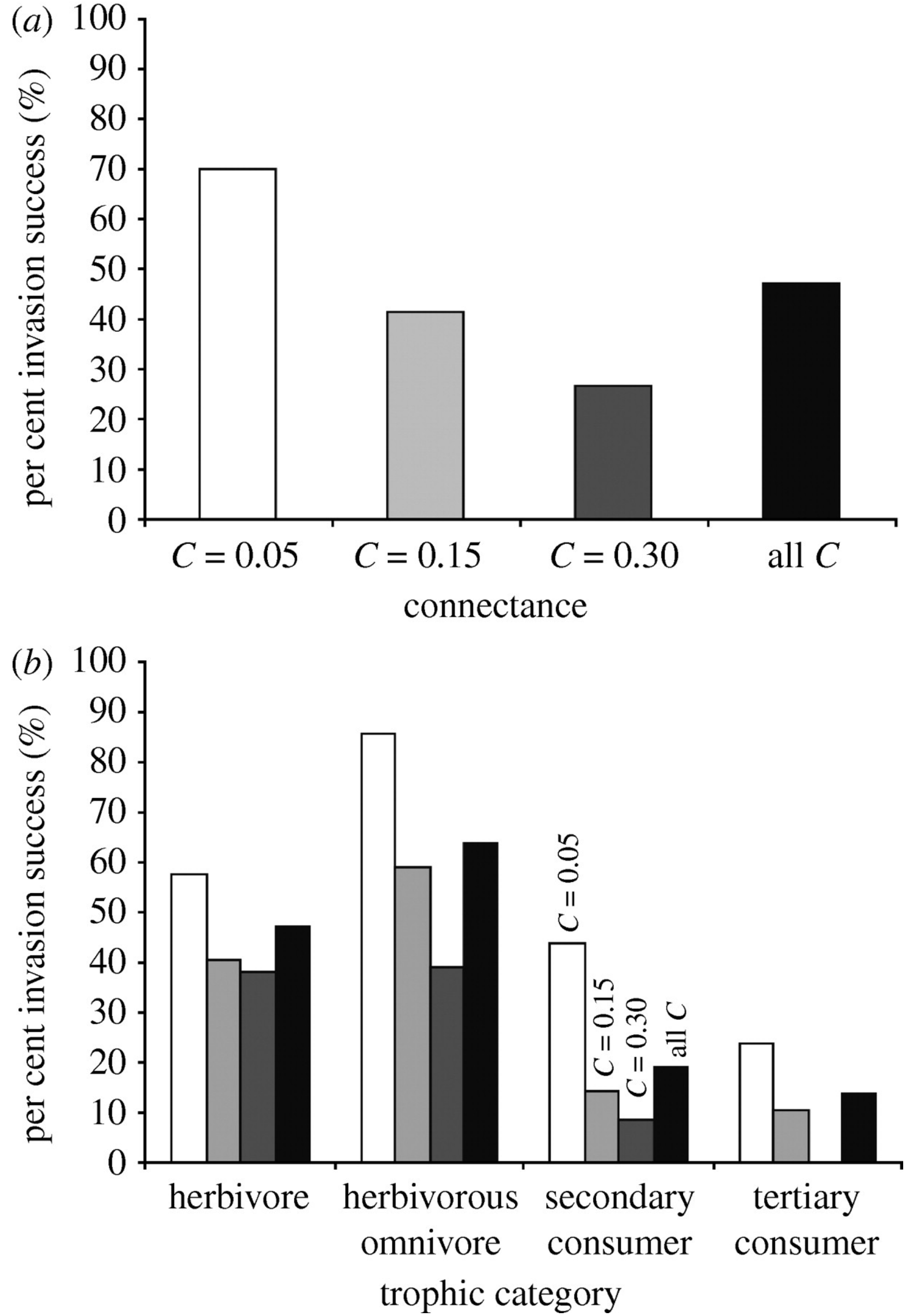
Predicting the next invasion?

Food webs & Invasion success

(computer simulation)

Easier to invade low connectance food webs

Better to occupy a low trophic level (and be omnivorous)



Romanuk T N et al. Phil. Trans. R. Soc. B 2009;364:1743-1754

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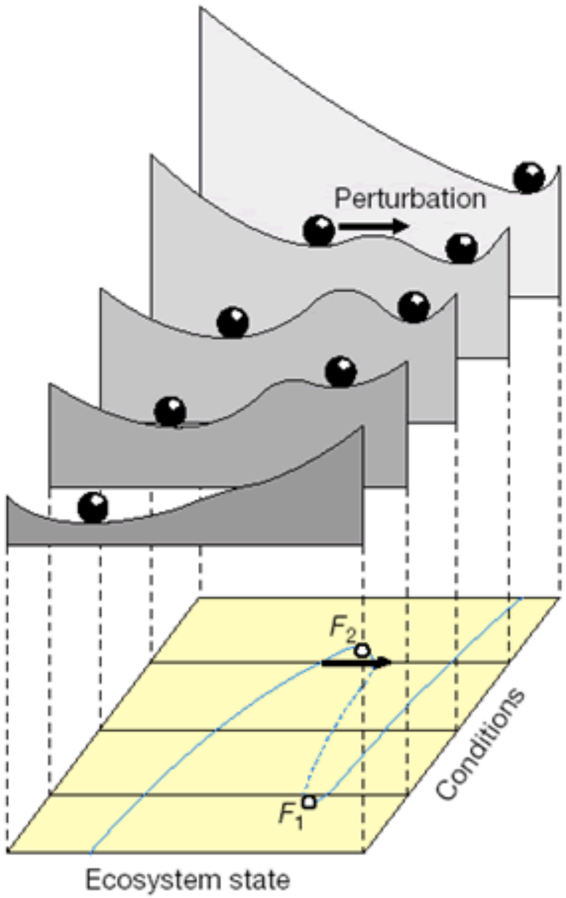
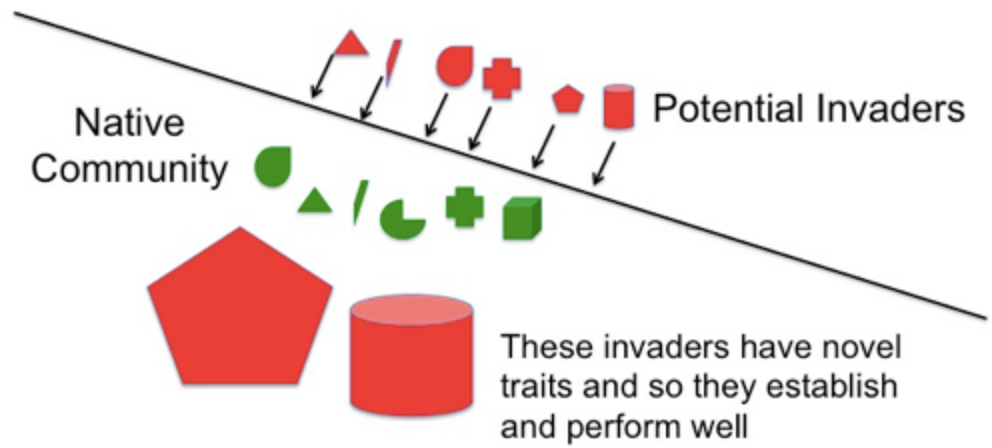
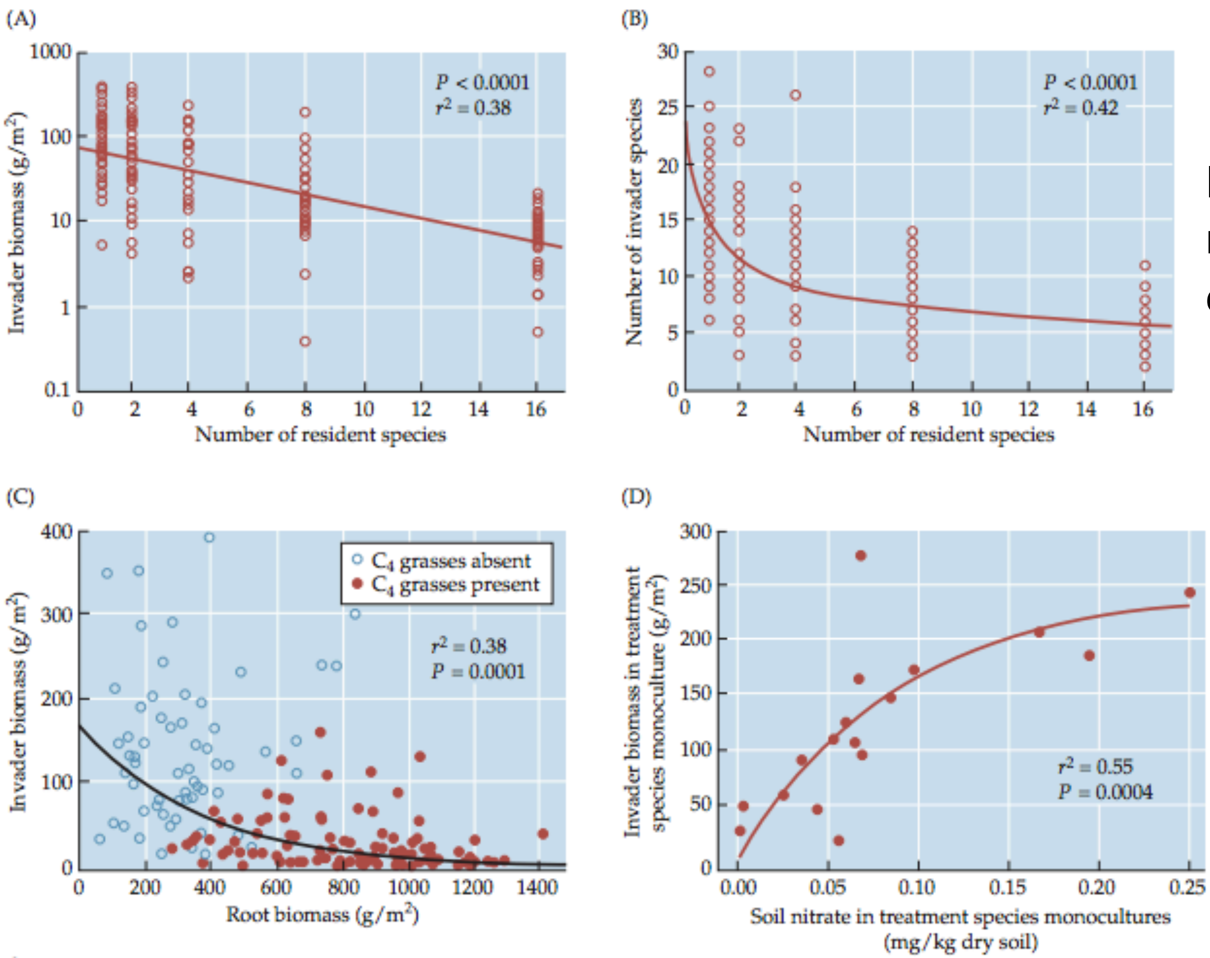




Diversity and invasibility

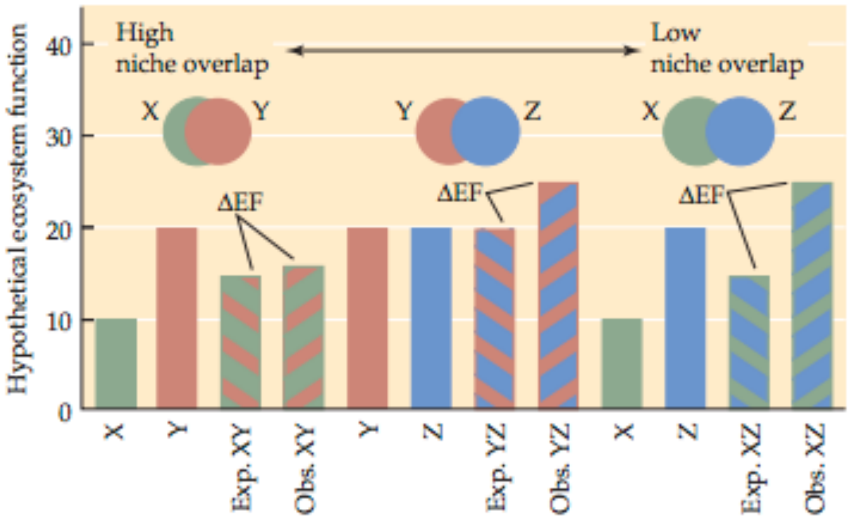


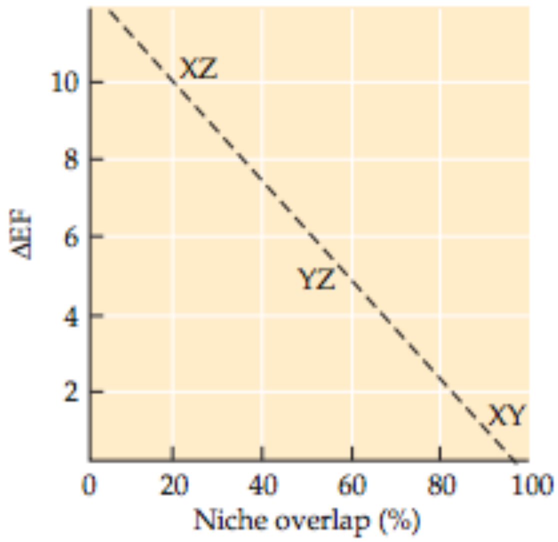
Both invader biomass and number of invaders decrease with resident S.R.

Explanations include resident root biomass and available soil nitrate

Niche complementarity

If species use different resources, then we might expect elevated ecosystem functioning

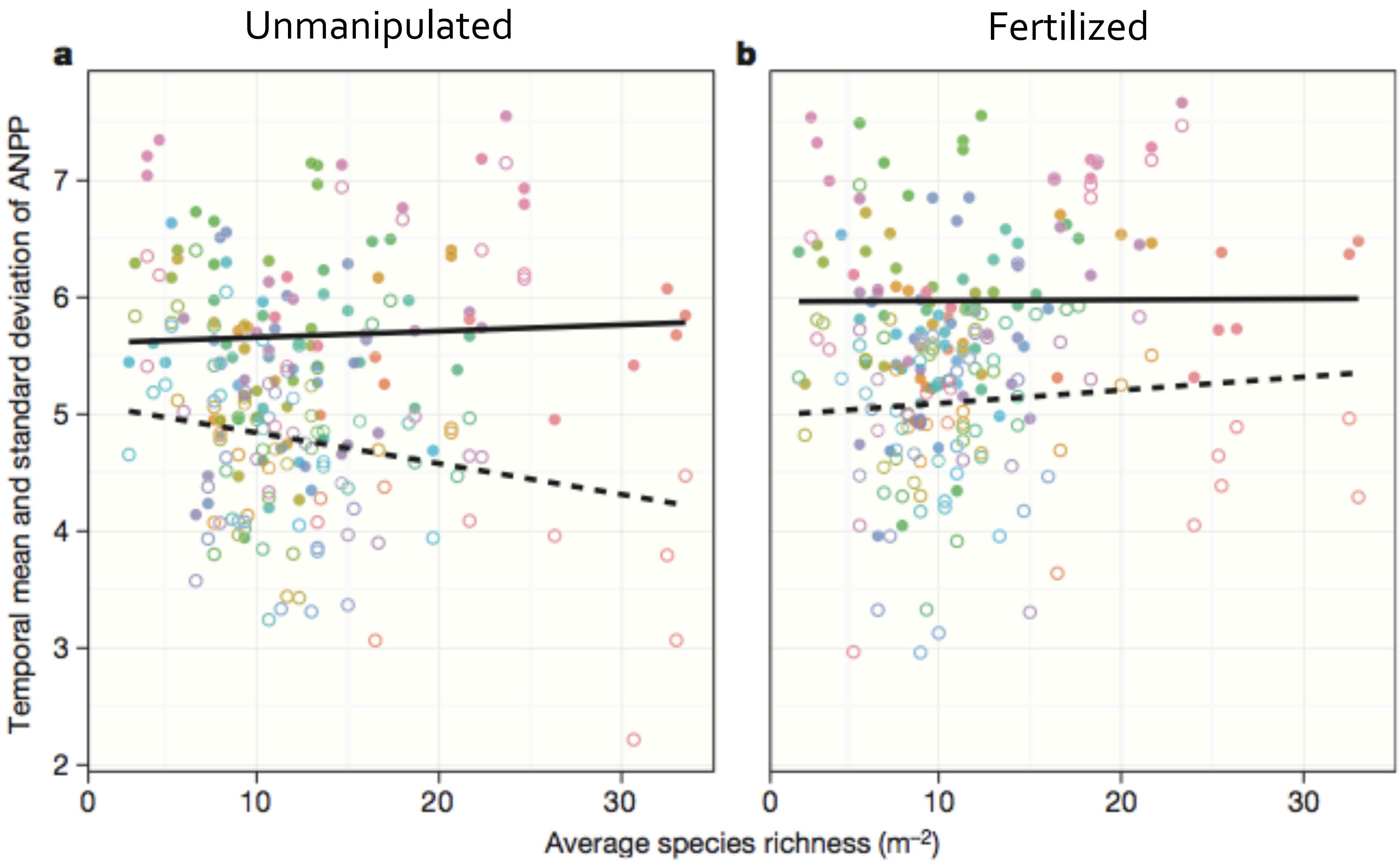




Flip side: Removal of certain species can alter ecosystem function with downstream effects on remaining species – So high **niche overlap (more common in species rich communities) provides an insurance hypothesis**

Anthropogenic effects (beyond species loss)

Fertilization reduces positive effects of plant diversity on stability



ANPP: aboveground net primary productivity
Solid line=mean, dashed line=standard deviation

Hautier et al. 2014, Nature

Conclusions

- Loss of single species can lead to further losses (keystone species, trophic cascades)
- Multiple ways to measure stability (depends on question/practical constraints)
- Generally diversity promotes stability
- May’s theory suggests opposite
- Adding more reality generally leads to ‘diversity promotes stability’ conclusions
- Diversity helps communities resist invasions and maintain ecosystem function (insurance hypothesis)
- Eutrophication may lead to instability even if no species lost