Passive and adaptive dispersal in metacommunities

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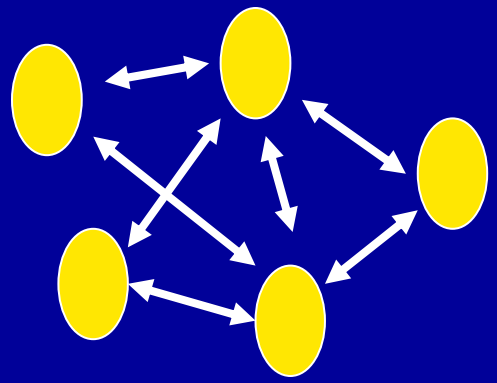
What is a metacommunity?

- A set of local communities interconnected by dispersal of at least some species.
- Local communities can consist of patches
- Patches can differ in local conditions
- Patches differ in community composition



A real metacommunity

http://jtintle.wordpress.com/2005/11/22/

-Patches differ in size, isolation, location relative to other patches
-Patches have different populations
-Patches probably differ in local abiotic conditions
-Patches are subject to changes through time
-Species differ in responses to abiotic condition
-Species differ in how they interact with each other
-Species differ in how they disperse
    -Some disperse passively.
    -Some disperse adaptively, they probably differ in the rules they follow.
    -They have different costs of dispersal.
    -They differ in the number of dispersing propagules.

Three important roles for dispersal in community assembly

- Provide colonists that ‘fuel’ community assembly
- Support maladapted sink populations in communities where they would go extinct
- Gene flow that alters evolution

What is the current state of metacommunity thinking?

- Theoretical frameworks
- Approach to dispersal
- Overall empirical evaluation
- Topics addressed

- Four modeling frameworks for metacommunities
  (Leibold et al. 2004)

  - Neutral: stochastic demography and dispersal combined with ecological equivalence means there is no deterministic component to assembly
  - Mass effects: source-sink relations among patches
  - Species sorting: all local communities go to assembly endpoints
  - Patch dynamics: In addition to deterministic component, there are also stochastic extinctions (either due to stochastic demography or to environment disturbance/change)

Species sorting in metacommunities

- There are many heterogenous patches
- Each patch is at its deterministic endstate
- There is correspondence between species composition and environment
- If endstates are stable communities, there is no spatial structure in the metacommunity
- If endstates are cycles or alternate states, there could be some spatial structure (i.e. nearby patches are similar in composition even if they differ in environment)

Space and environment in metacommunities

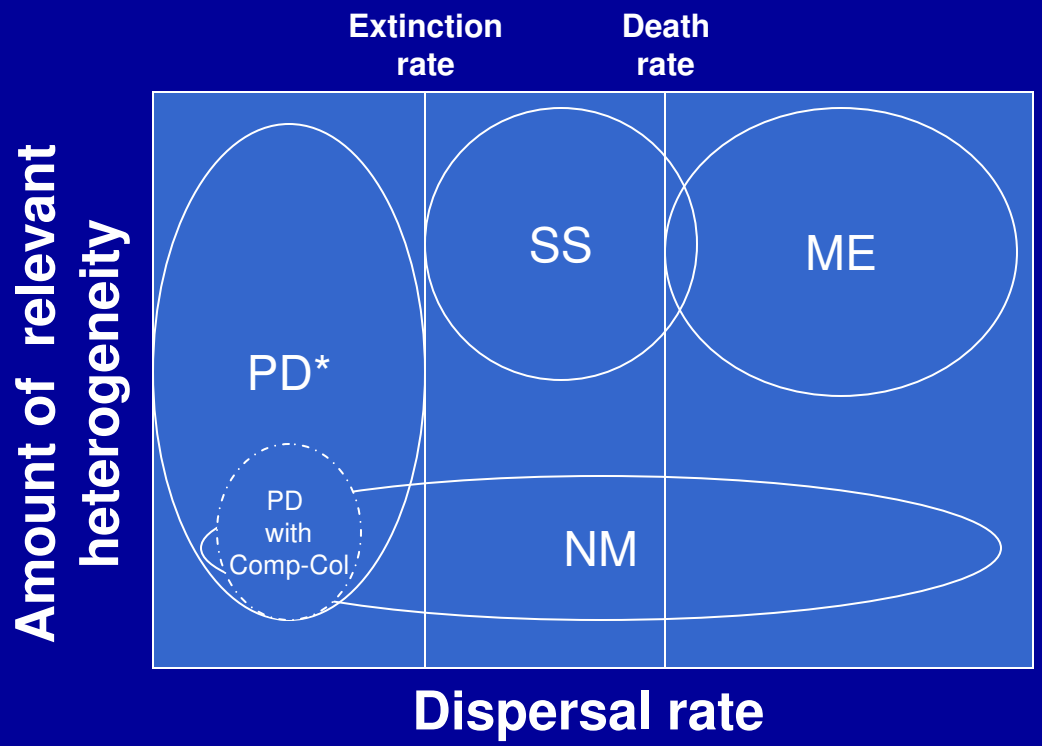
- Species sorting: if you know the environment you can predict the composition of local communities
- Proximity effects due to dispersal are not likely to be important unless there are alternate stable states or endpoint cycles

Other views of metacommunities

- Neutral models: there is strong spatial signal but no environmental effects because all species respond symmetrically to environment
- Mass effects: source sink relations are stronger between nearby patches so there are both spatial and environmental effects
- Patch dynamics: in many models all patches are identical – only spatial effects
  - But this is not necessary, there can be patch dynamics models with patch heterogeneity
  - If so, there should be spatial effects and environmental ones
- Also possible: Mix of species sorting and neutral effects (Leibold and McPeek 2006): Both spatial and environmental effects likely. Mixtures of all four views.

Regulation of metacommunities by dispersal and environmental heterogeneity

(Leibold 2009)



* Patch dynamics is most often implemented in absence of heterogeneity where they mostly involve Competition-Colonization Trade-offs, but this is not necessary, see Shurin et al. 2004.

- There is a continuum of possibilities
- Different organisms can be in different parts of the continuum
- Dynamics involving one group of organisms will probably influence other groups (but we don't know how this works yet)

dispersal

- To date almost all work in metacommunity ecology has assumed dispersal is:
  - Passive
  - Relatively uniform among species
  - Relatively uniform among patches
  - Undirected
- In some spatial models this is not so but these often don’t address as broad a scope of issues
- In this workshop:
  - Adaptive dispersal
  - Different rules for different species
  - Different types of patches

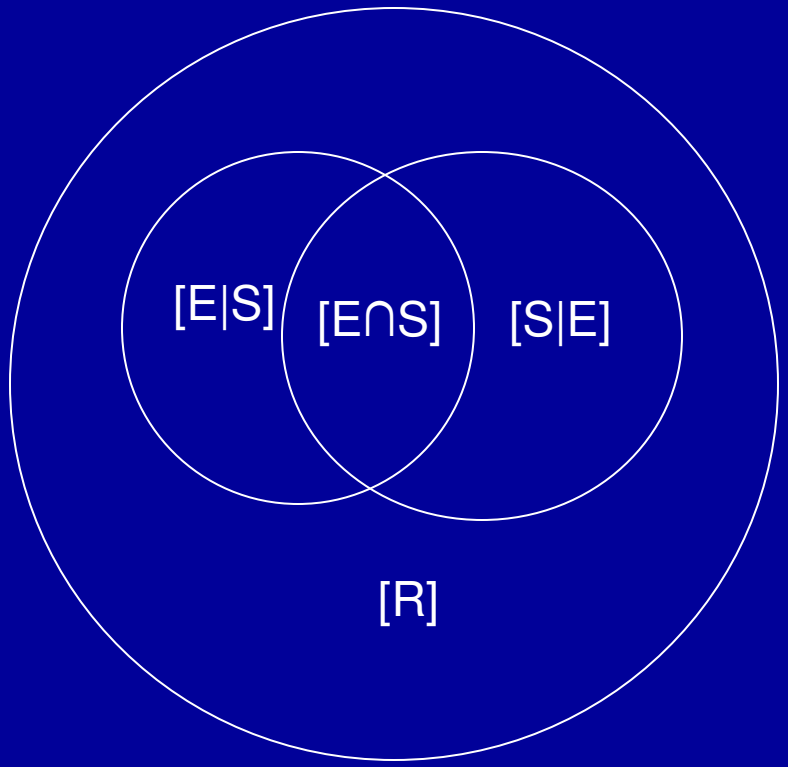
A general empirical evaluation

- How is local community composition regulated by environmental vs spatial factors?
- Cottenie 2005

Cottenie (2005) Variation decomposition of space and environment as test for metacommunity regulation

Community composition = Pure Environment + Pure Spatial + Colinearity + Residual

$[C] = [E|S] + [S|E] + [E \cap S] + [R]$



Is [S|E] really a measure of the effects of dispersal?

- Space can vary with unmeasured environmental variables, thus [S|E] can be an overestimate of pure spatial effects
- Environment is not just abiotic but also depends on biotic assembly itself
- [S|E] is likely an overestimate of spatial effects

Is [E|S] a pure indicator of species sorting?

- Unmeasured environmental variables likely contribute to [S|E], [E∩S], and [R], would be in [E|S] instead if we knew what to measure.
- Dispersal and successful colonization more likely if source environment more similar to target
- Mass effects between sites stronger if environmental similarities greater
- [E|S] likely an underestimate of environmental effects

Analysis of natural patterns for metacommunity regulation

Model	Patch Dynamic	Species Sorting	Mass Effects	Neutral Theory
Environmental Structure	Maybe	Strong	Strong	None
Spatial Structure	Yes	Weak	Yes	Yes

Empirical patterns in metacommunity structure:
Which perspectives are more likely?

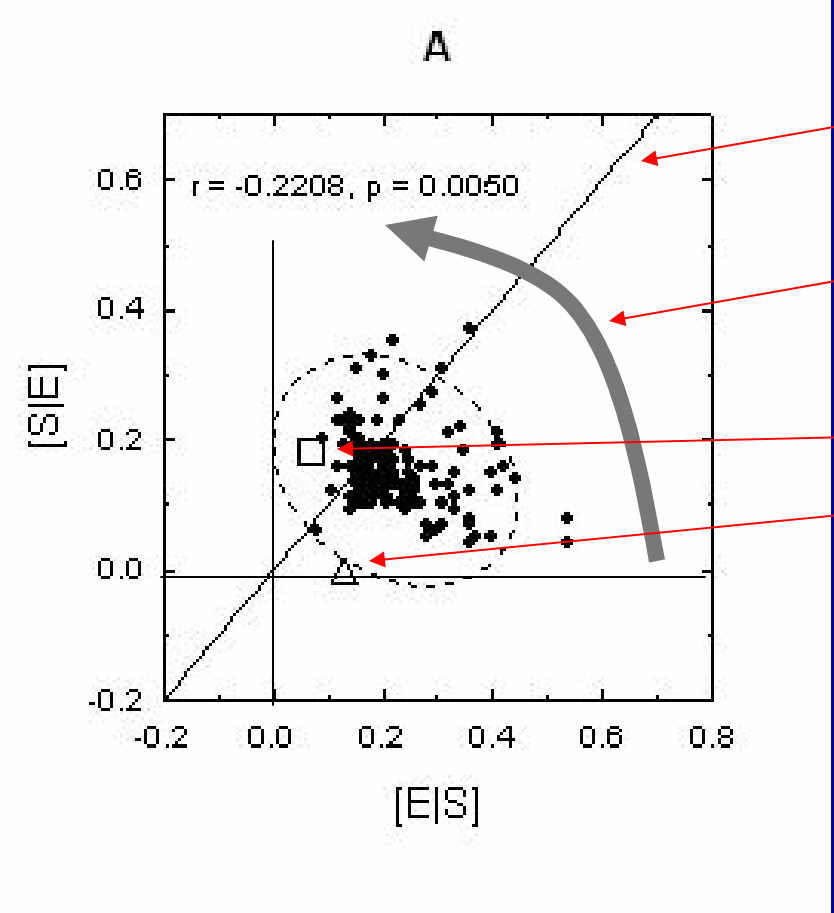
Variance decomposition (modified from Cottenie 2005). Test by partitioning variance in community pairwise similarity into spatial, environmental and colinear components. Calculate pure spatial [S|E] and pure environmental [E|S] effects. Diagnose which type the metacommunity is.

* Modified from Cottenie 2005

	[S|E]	[E|S]	#	%
Species Sorting	0	X	69	44%
Mass effects, patch dynamics in heterogenous patches, mix of species sorting and others	X	X	46	29%
Neutral or patch dynamics in homogenous patches	X	0	13	8%
None	0	0	30	19%

But really there is a continuum:

- **Some metacommunities show strong environmental regulation**
- **Fewer show strong spatial structure**
- **Probably most show a mix or intermediate patterns**



[E|S] = [S|E]

Likely bias

- Hubbell's BCI data
- Leibold's pond data

Summary

- Species sorting is important. Much can be understood by starting with this view
- Spatial effects are also common within a framework of environmental drivers
  - Multiple causes possible
    - Patch dynamics
    - Mass effects
    - Neutral dynamics
    - Others
    - Combinations

Adaptive dispersal?

- Re-enforces species sorting
- Reduced costs of dispersal, lowered importance of regional control on the metacommunity
- Novel sets of interactions among organisms with different dispersal methods
- What are the consequences to metacommunity ecology?

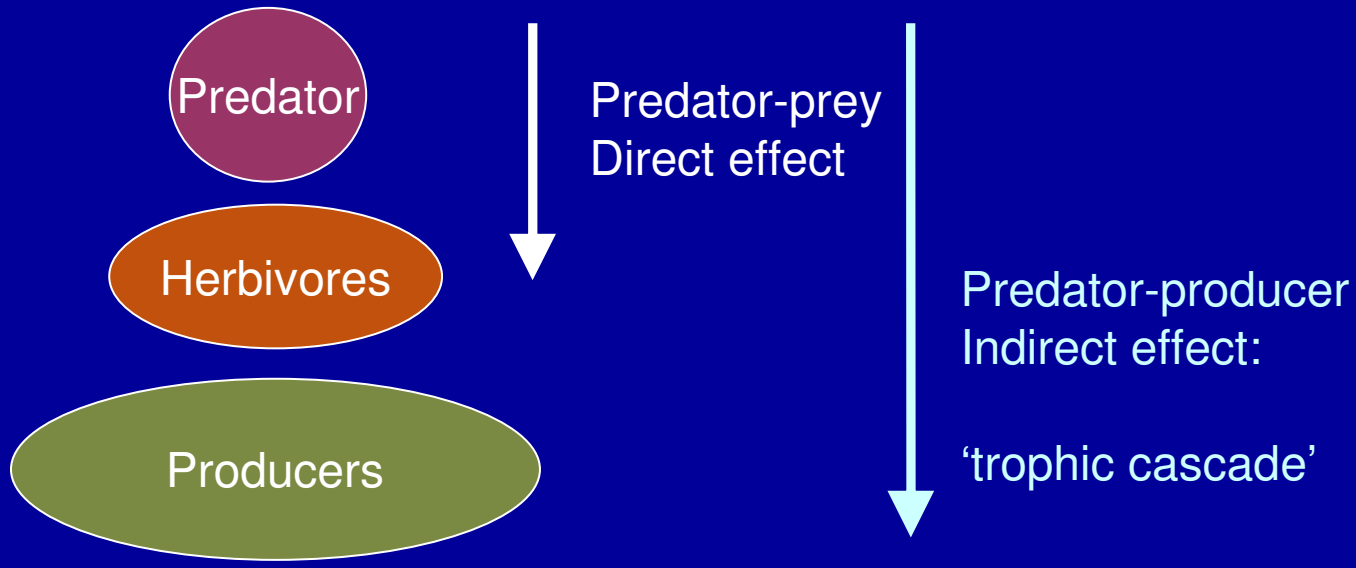
Some topics in metacommunity ecology

- Co-existence and similarity
- **Trophic cascades**
- Trophic structure and eutrophication
- Biodiversity and eutrophication
- Food web complexity
- Biodiversity and stability

Trophic cascades in metacommunities

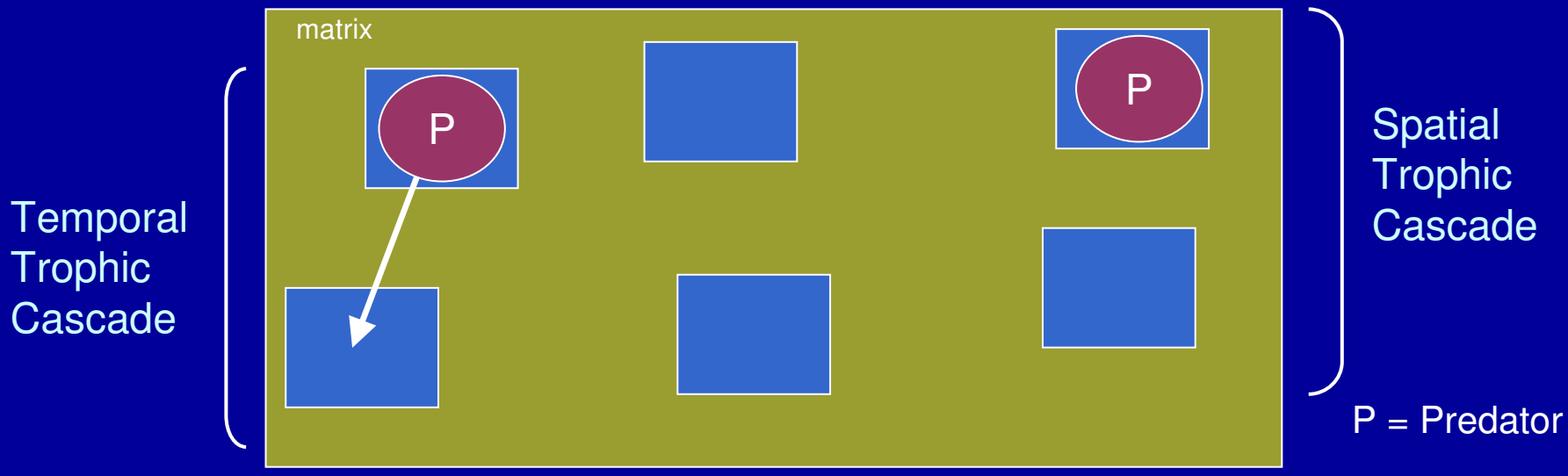
(Howeth and Leibold 2008)

- Unexplained variation in the strength of trophic cascades (e.g. Brett & Goldman 1996, Leibold *et al.* 1997, Shurin *et al.* 2002)
- Classic trophic cascade theory (Hairston *et al.* 1960) assumes communities are closed to migration and are only structured by local interactions.

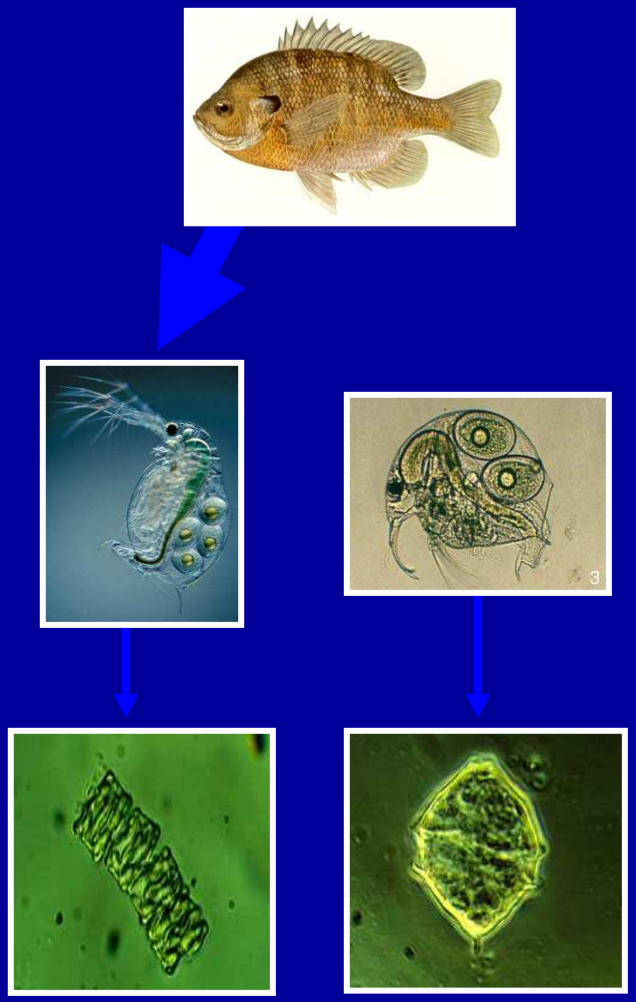


Effects of dispersal on trophic cascades

- Two types of trophic cascades in metacommunities
  - Spatial: comparing two sites that have long differed in predation
  - Temporal: within a site, what happens when predators invade or go extinct
- In both cases, dispersal occurs in lower trophic levels
  - Allows compositional change
  - Can general source sink relations between patches



Dispersal may alter the strength of spatial and temporal trophic cascades



Closed / Hairston *et al.*

Open

Biomass

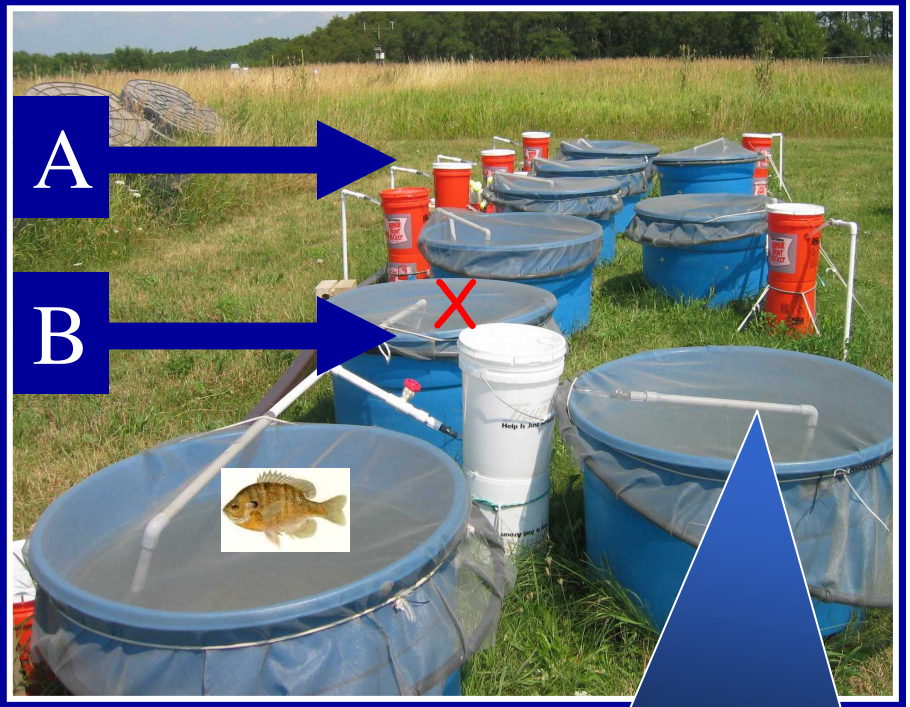
Biomass

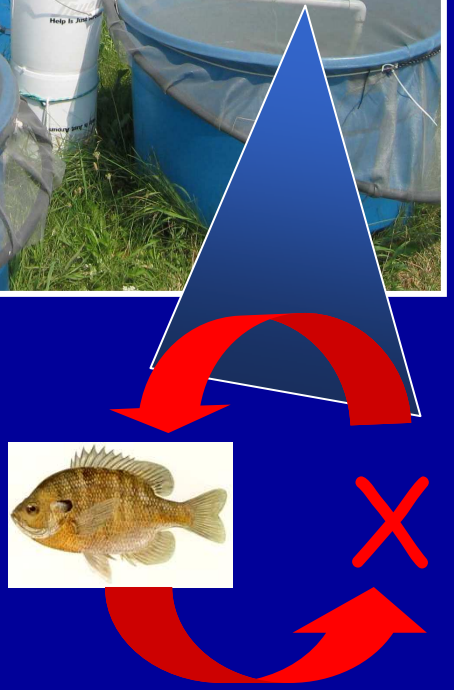
Biomass

TIME

TIME

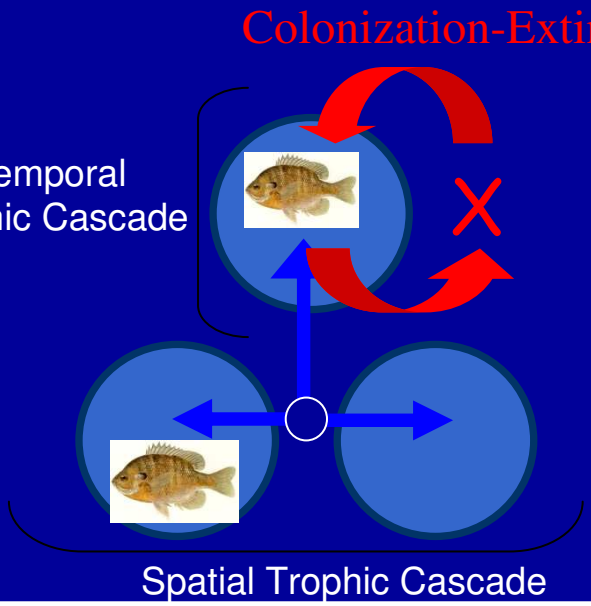
A metacommunity perspective: spatial and temporal trophic cascades



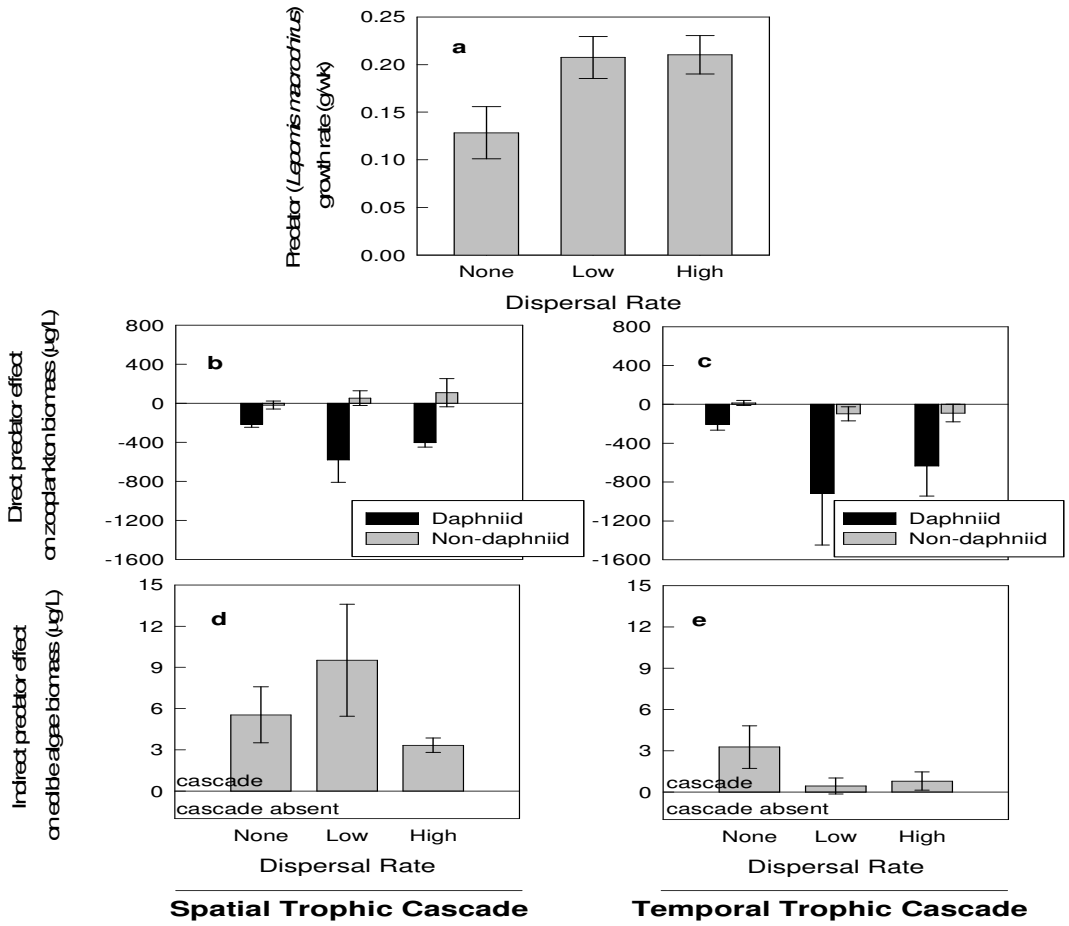


Three dispersal treatments:

- no dispersal (control) (0% / week)…….. A
- low dispersal (5% / week)…….. A
- high dispersal (140% / week)…….. B



Contrasting trophic cascade strength in spatial vs temporal cases



Conclusions:

- Spatial trophic cascades were strong in all dispersal treatments. No apparent homogenization even at high dispersal
- Temporal trophic cascades were strongly dampened in open communities
- Dispersal can cause variability in the strength of [temporal] trophic cascades, and may explain some of the variability found in previous meta-analyses.

What would adaptive dispersal do?

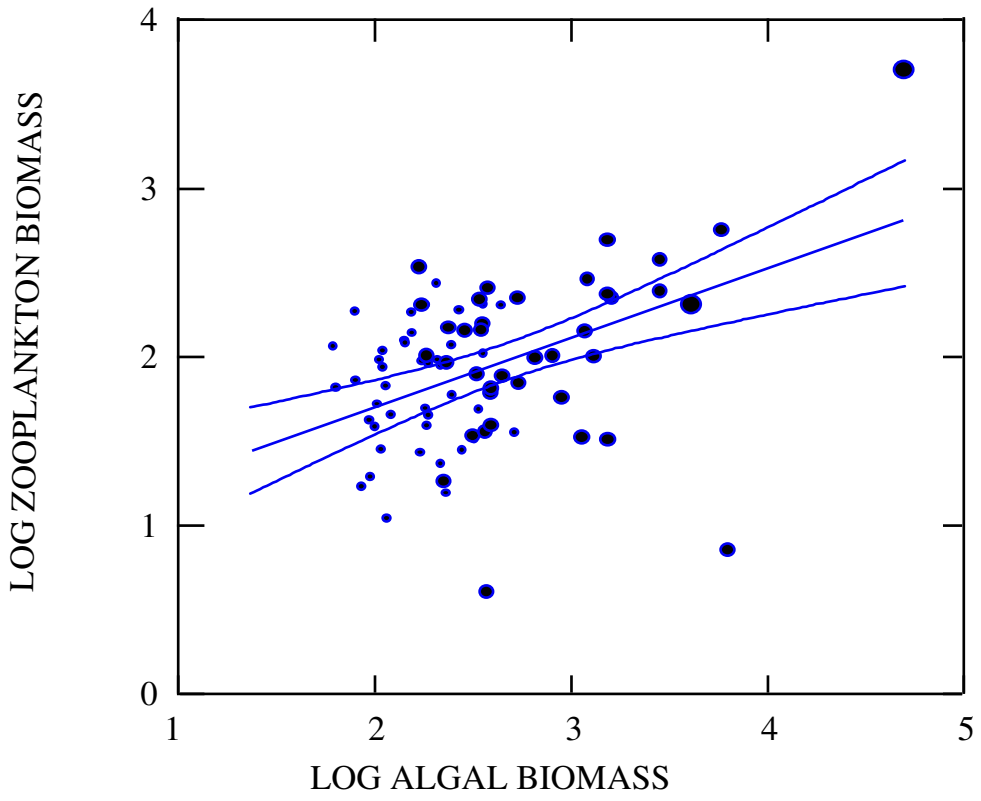
- If organisms disperse at different scales, this can affect stability of trophic cascades (McCann et al. 2005)
- Trophic cascade strength is probably altered depending on dispersal rules used by different species in different trophic levels
  - E.g. plants disperse passively whereas higher trophic levels (which ones?) disperse adaptively

Some examples of metacommunity ecology

- Co-existence and similarity
- Trophic cascades
- **Trophic structure and eutrophication**
- Biodiversity and eutrophication
- Food web complexity
- Biodiversity and stability

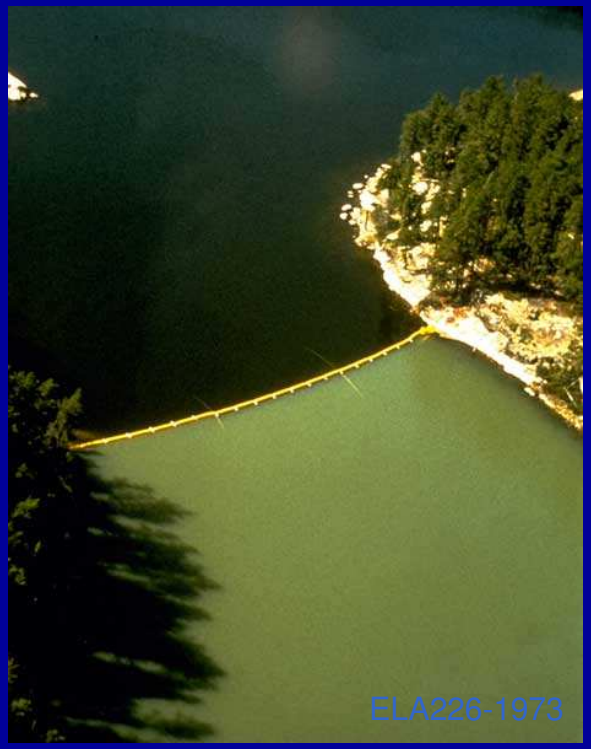
Trophic Structure in Lakes

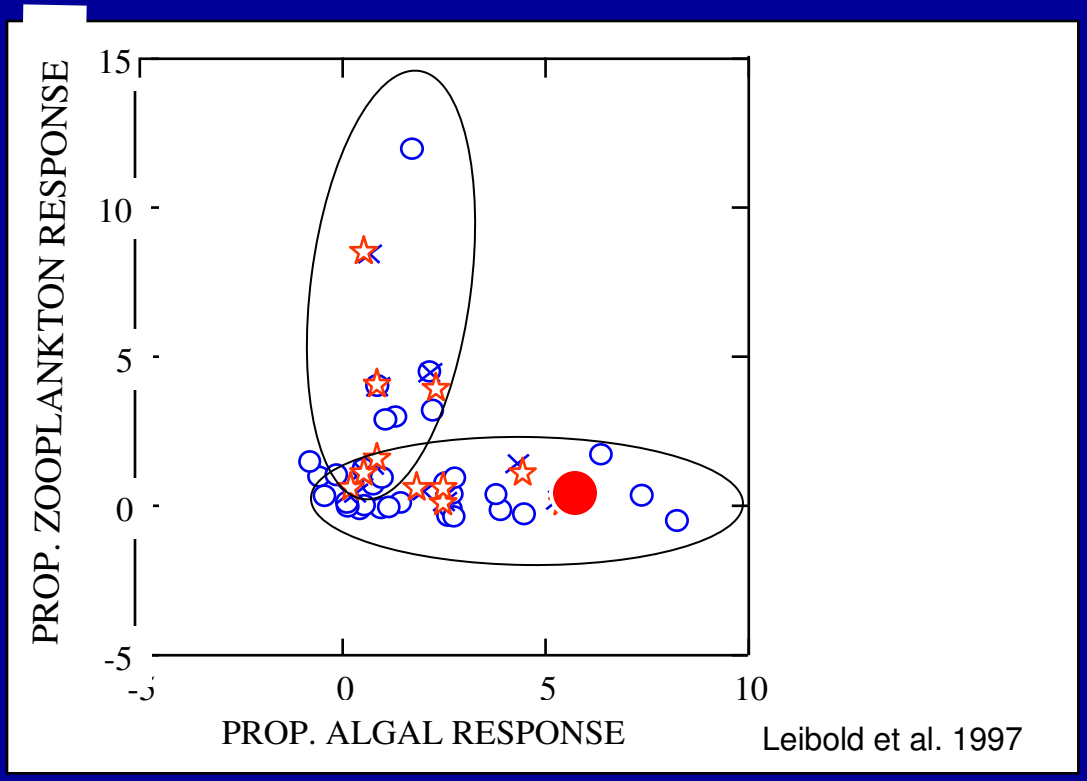
(Leibold et al. 1997, see also Gliwicz 1975. McCauley & Kalff 1981, Hanson and Peters 1984, Yan 1986)



- Joint correlations between plant and herbivore biomass
- Both also correlate with nutrient levels
- Not predicted by many models of food webs that have local populations
- Eutrophication experiments should show the same pattern

Eutrophication experiments show a different pattern





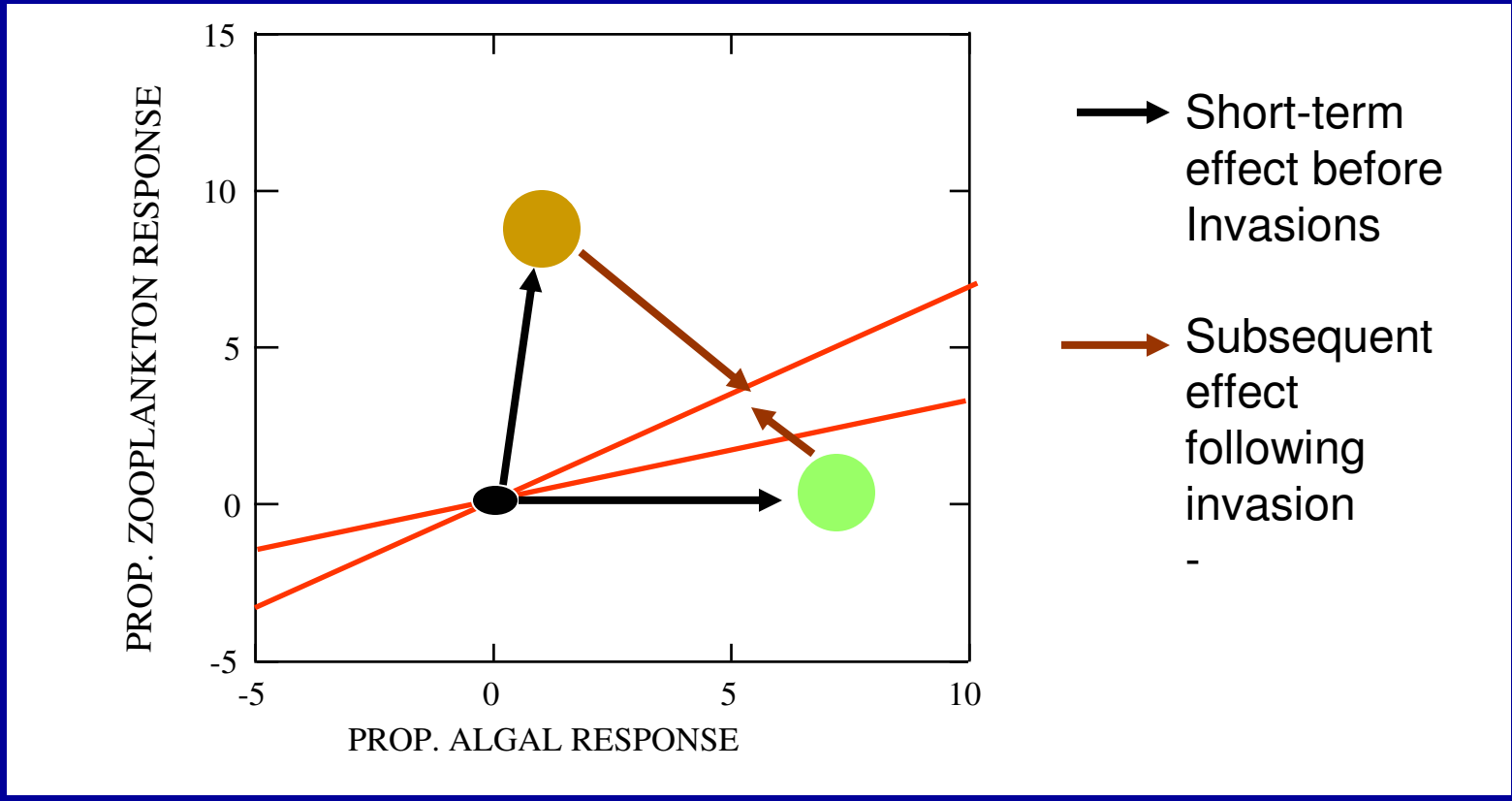
What would happen if we allowed (or increased) dispersal among lakes with different levels of productivity?

Metacommunity thinking: 'Species sorting' in food webs

The 'edibility hypothesis'

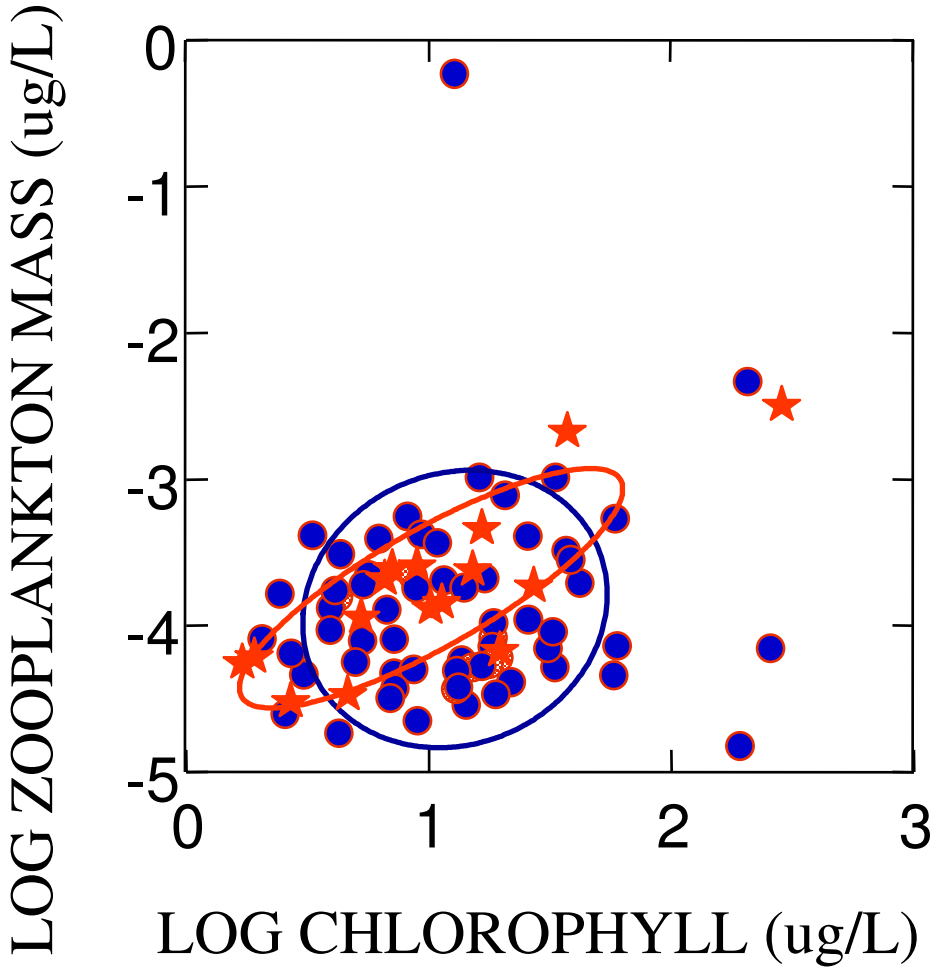
(Leibold 1989, 1996, see also Holt et al 1994, Grover 1995)

Colonizations will alter how trophic structure responds to eutrophication



Effects of Species Pool on Trophic Structure Response to Nutrients

(Leibold and Smith, ms)



Species Pool

★ In a metacommunity

● Isolated communities from single ponds

Trophic Structure in productivity gradients

- Colonizations (and extinctions) from nearby areas allows for species sorting
- Species sorting prevents strongly skewed biomass responses
- Regional biodiversity has an influence on properties of local ecosystems
- Very different outcomes occur in closed local communities

What would adaptive dispersal do?

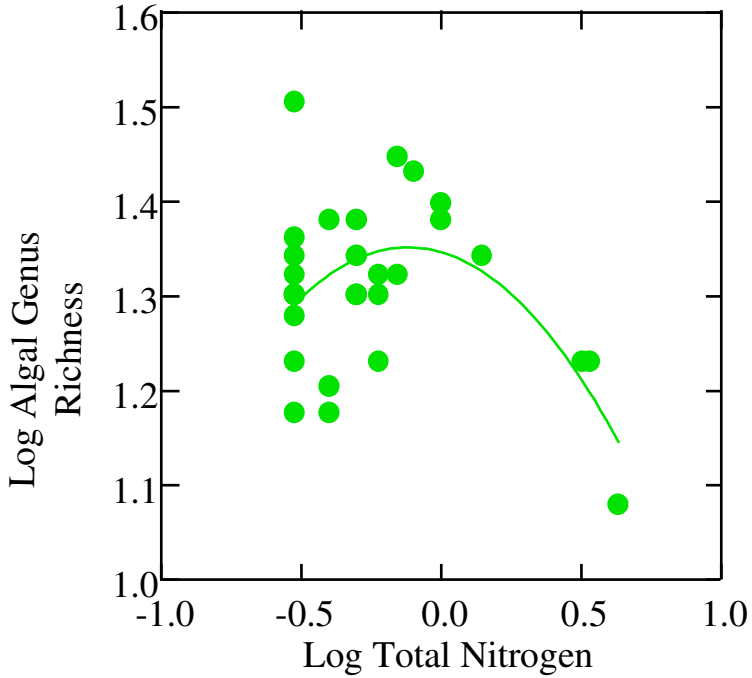
- Using ‘adaptive dynamics’, Loeuille and Loreau showed that different levels of ‘adaptive change’ in plants vs herbivores could alter trophic structure
  - If plants have greater ‘adaptability’ then results congruent with passive dispersal
  - If herbivores have greater ‘adaptability’ then patterns look different (similar to models by Oksanen et al. 1981
  - If both have comparable levels, then outcomes can vary greatly and are parameter dependent

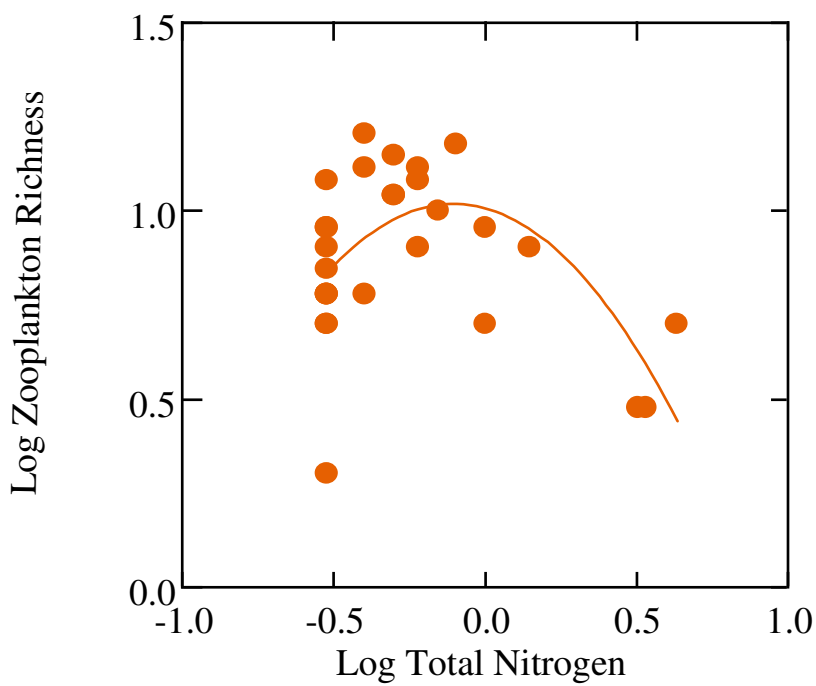
Some examples of metacommunity ecology

- Co-existence and similarity
- Trophic cascades
- Trophic structure and eutrophication
- **Biodiversity and eutrophication**
- Food web complexity
- Biodiversity and stability

Effects of eutrophication on biodiversity

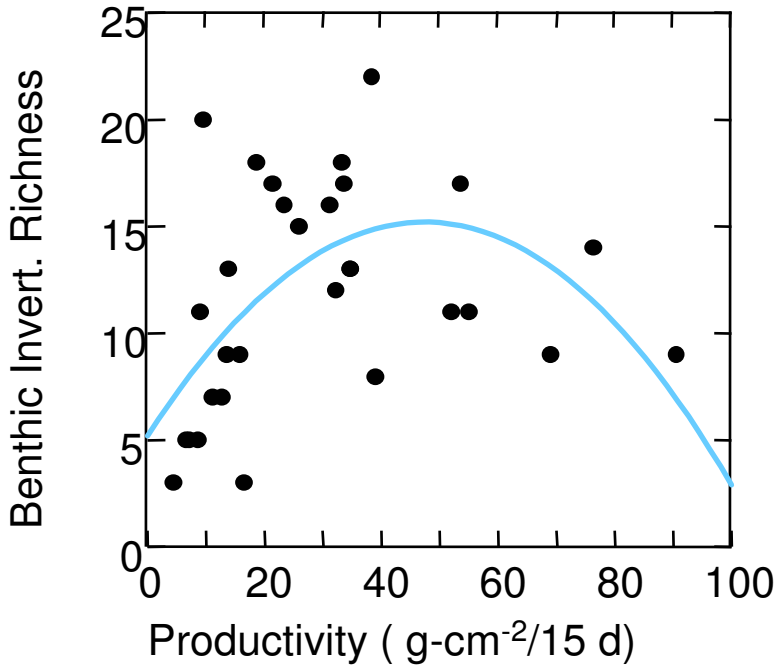
(Leibold 1999, see also: Ogawa and Ichimura 1984, Agusti *et al.* 1991, Dodson 1992, Dodson et al. 2000, Irigoien et al. 2004)



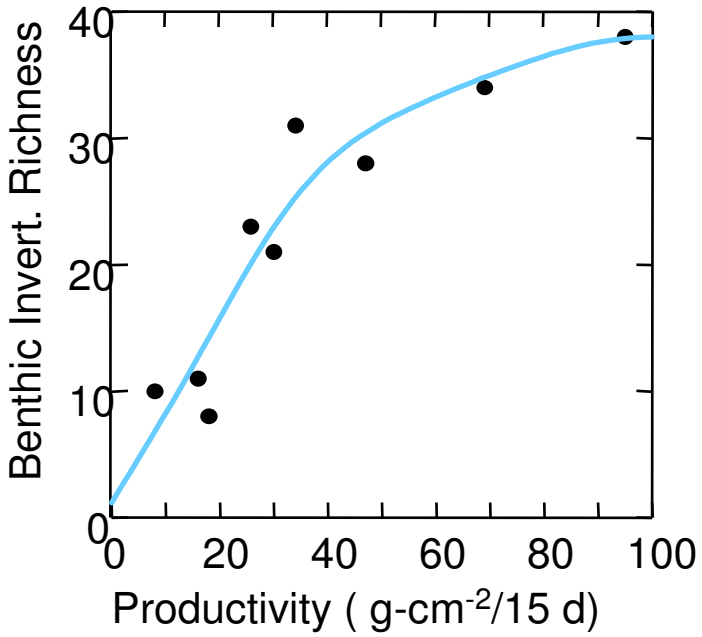


The pattern is dependent on spatial scale: Is this a metacommunity process?

Unimodal local

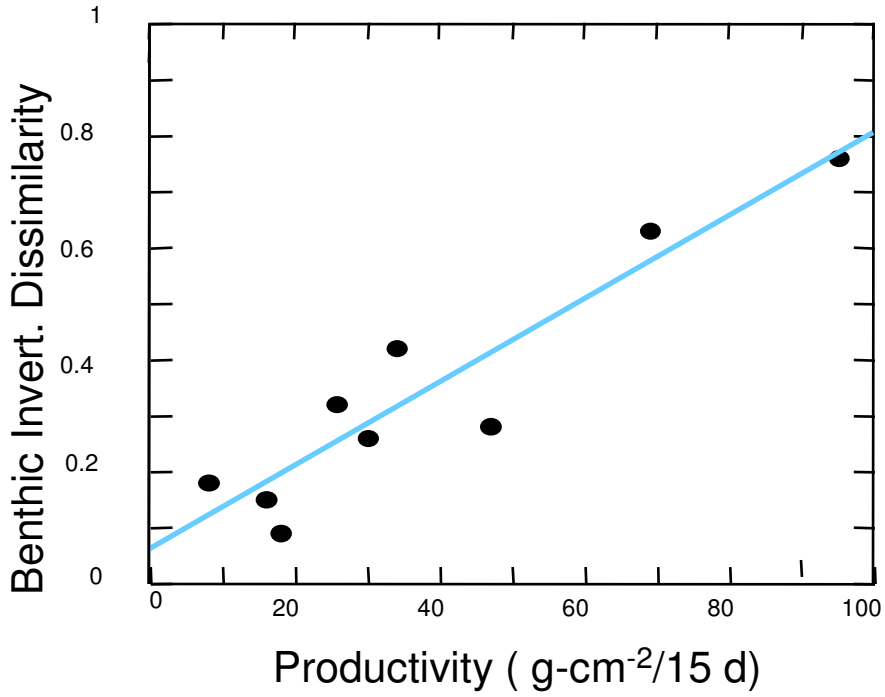


Monotonic regional



Chase and Leibold 2002

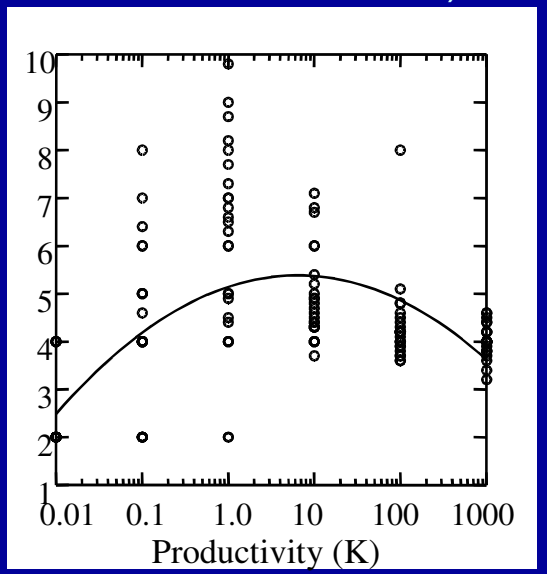
This occurs because there is greater spatial turnover (compositional differentiation) at high productivity

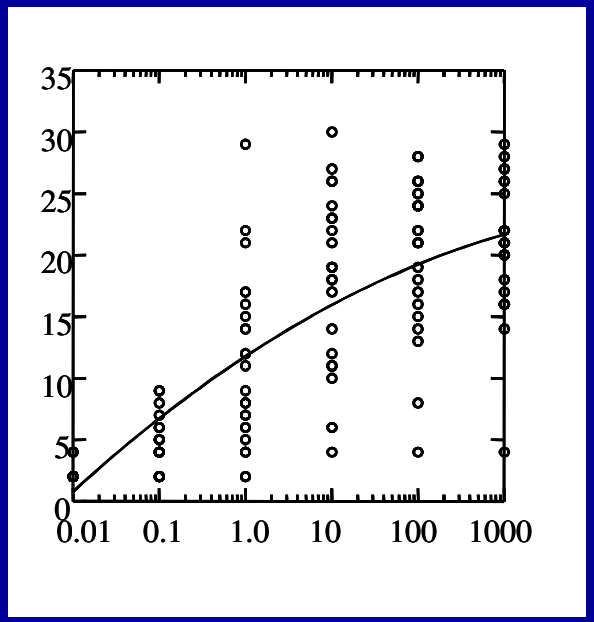


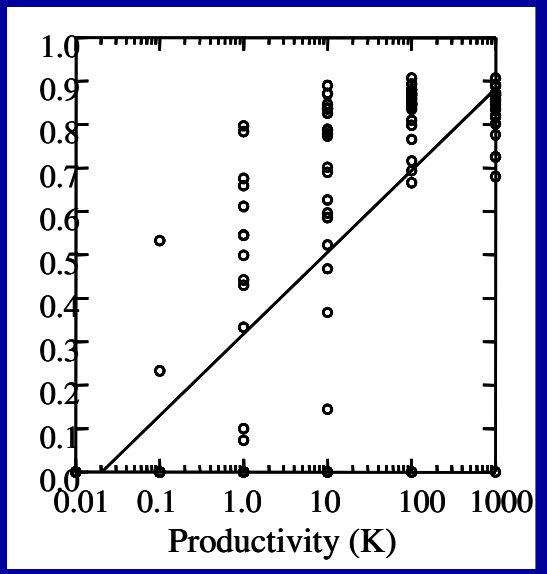
Chase and Leibold 2002

A food web assembly with dispersal (Steiner and Leibold 2003)

- Unimodal local effects only when there are multiple trophic levels
- Regional diversity increases with productivity
- Spatial turnover increases even more
- Only occurs in food webs

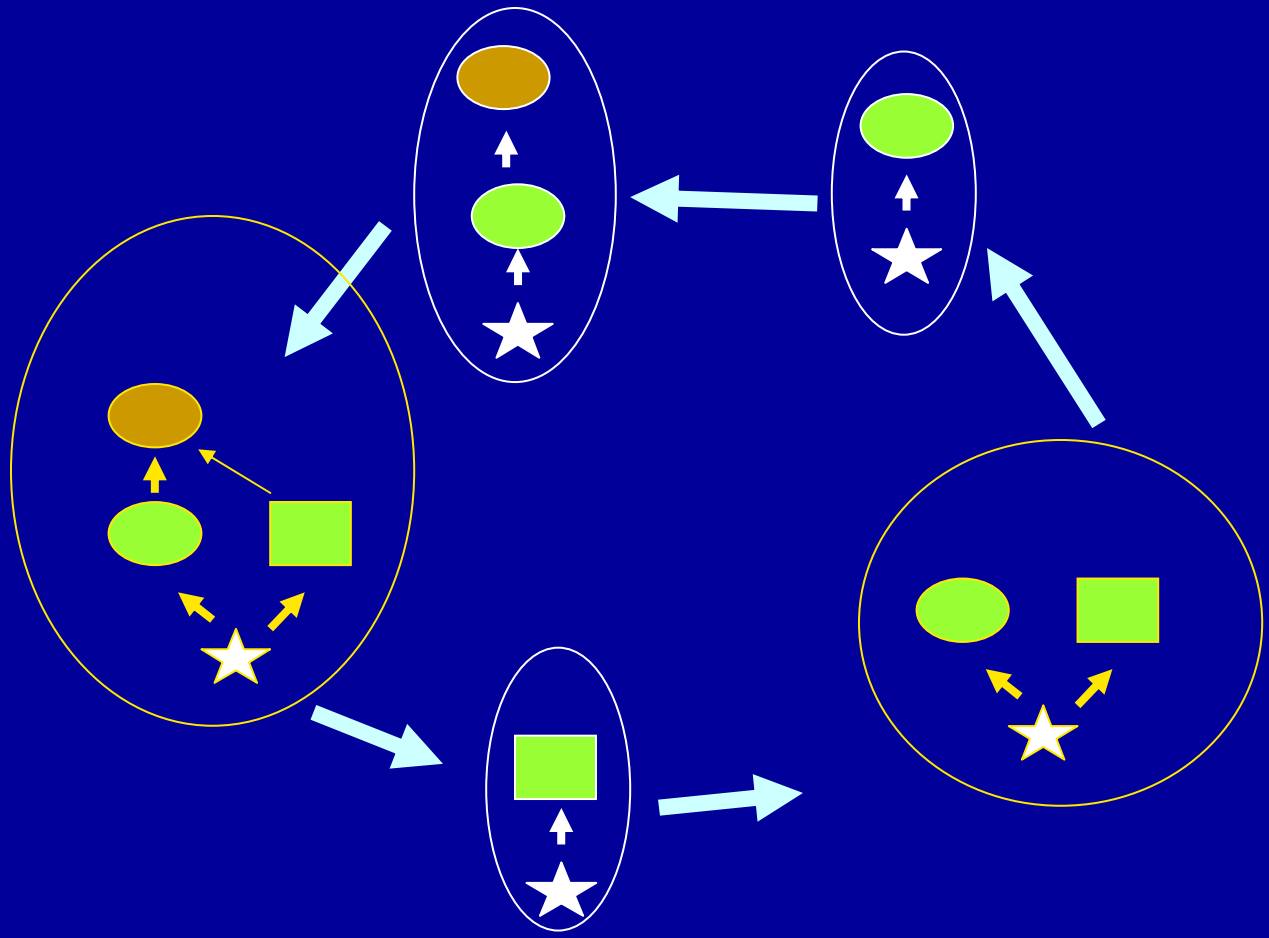






Spatial turnover occurs because there is temporal turnover in food web assembly

- Different local communities are at different points in the cycle
- There is more of this going on at high productivity



Is there higher temporal turnover at higher productivity?

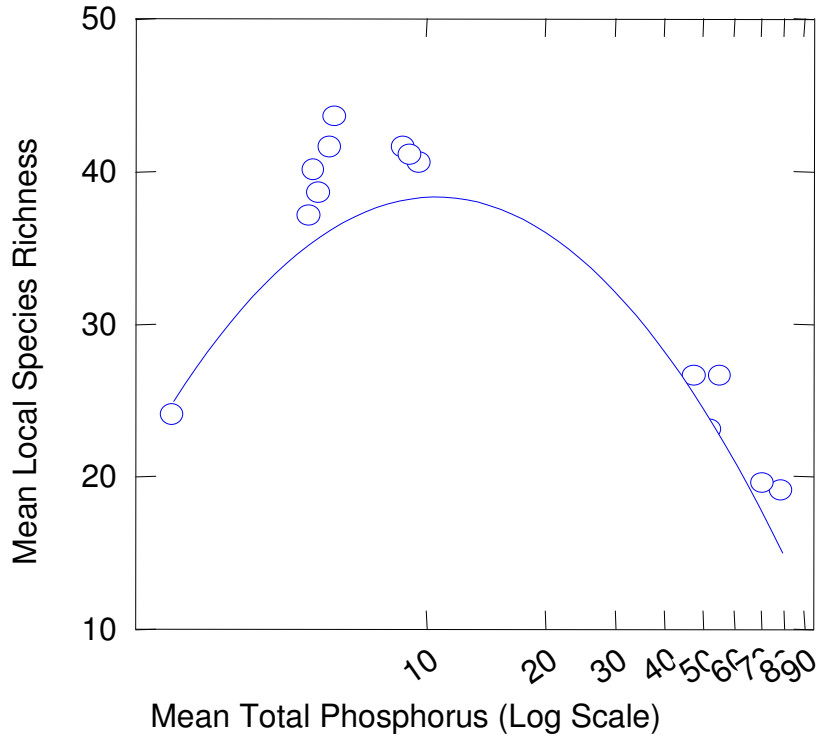
(Pinel-Alloul and Methot, unpub data

- Three geographic areas with different natural levels of productivity (nutrient loading)
- Common methods and taxonomy over 2-8 years/lake
- Pristine lakes in relatively uninhabited areas
- Cumulative species list by year to account for possible seasonal effects.

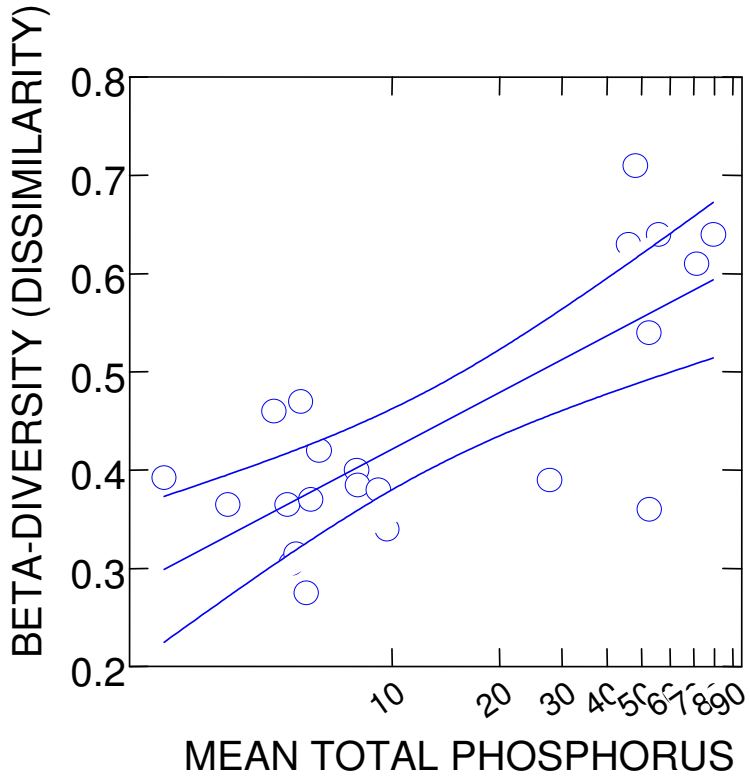
There is higher temporal turnover at higher productivity

- Annual turnover is just a bit smaller than within year spatial turnover (not shown)

Local annual diversity



Mean turnover between years



Effects of eutrophication on biodiversity are also a metacommunity process

- Colonization causes turnover in food webs
  - Species sorting with cyclical assembly trajectories
  - Need more data to evaluate if this is what is going on here or elsewhere

What would adaptive dispersal do?

- Good question!

Some examples of metacommunity ecology

- Co-existence and similarity
- Trophic cascades
- Trophic structure and eutrophication
- Biodiversity and eutrophication
- **Food web complexity (McCann)**
- Biodiversity and stability

Some examples of metacommunity ecology

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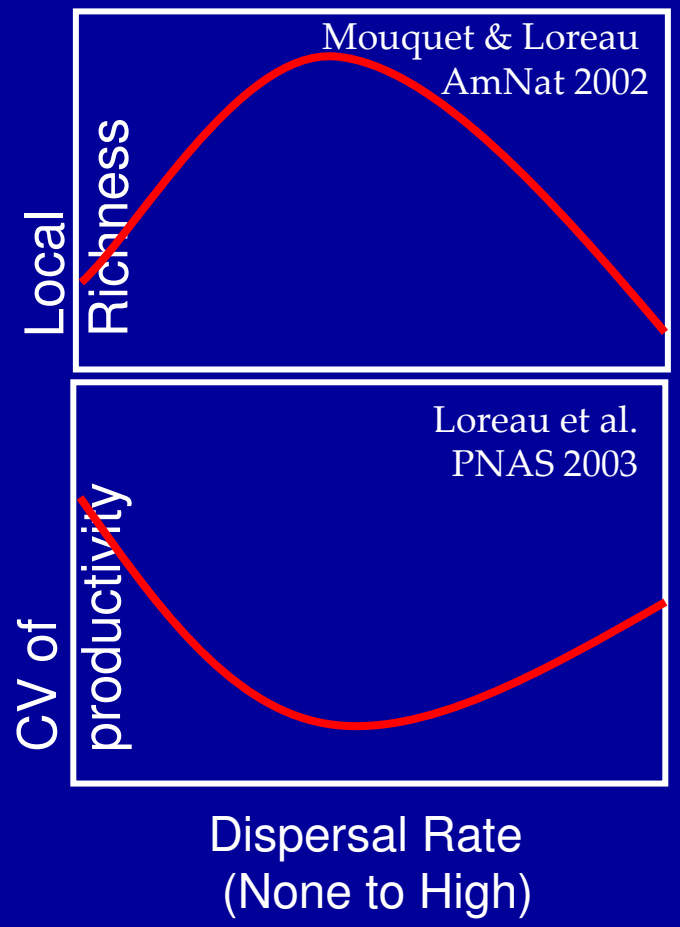
- **Biodiversity and stability**

Dispersal-diversity-stability relationships (Howeth and Leibold accepted pending revisions)

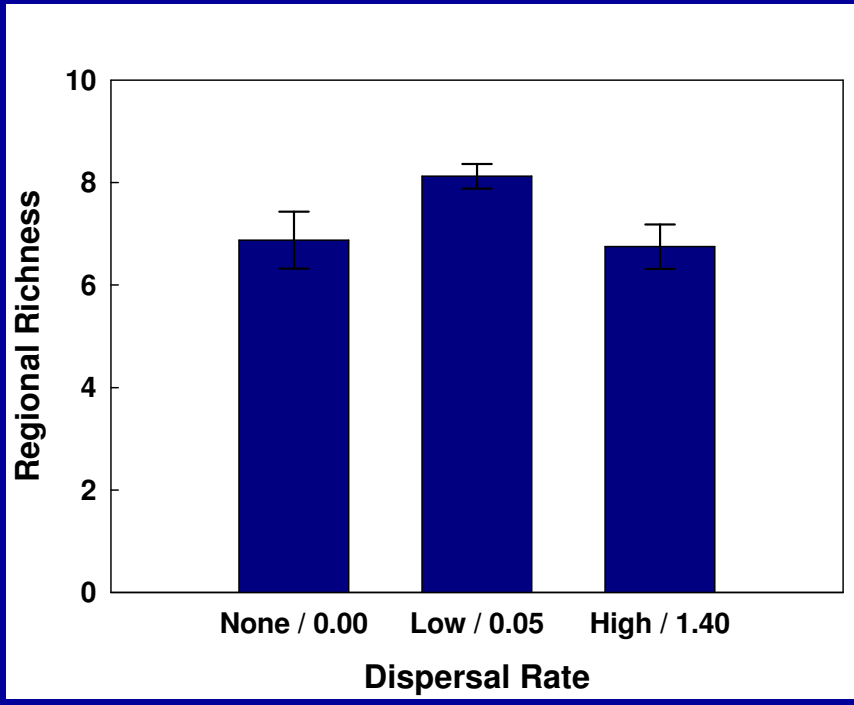


- positive correlation between local species richness and ecosystem stability
- stability is a direct result of an increase in functional compensation due to an increase in richness at intermediate dispersal
- consequences of perturbations to dispersal-diversity-stability relationships?

Zooplankton species richness

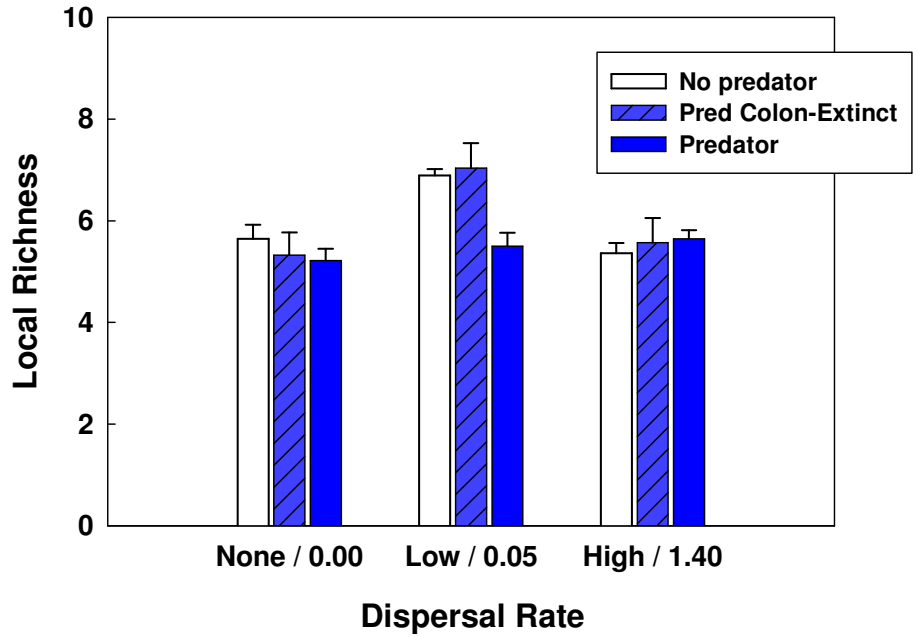
Regional / Metacommunity

rmANOVA, $P = 0.05$



Local

rmANOVA, Disp $P = 0.003$
Pred $P = 0.026$
Disp * Pred $P = 0.045$



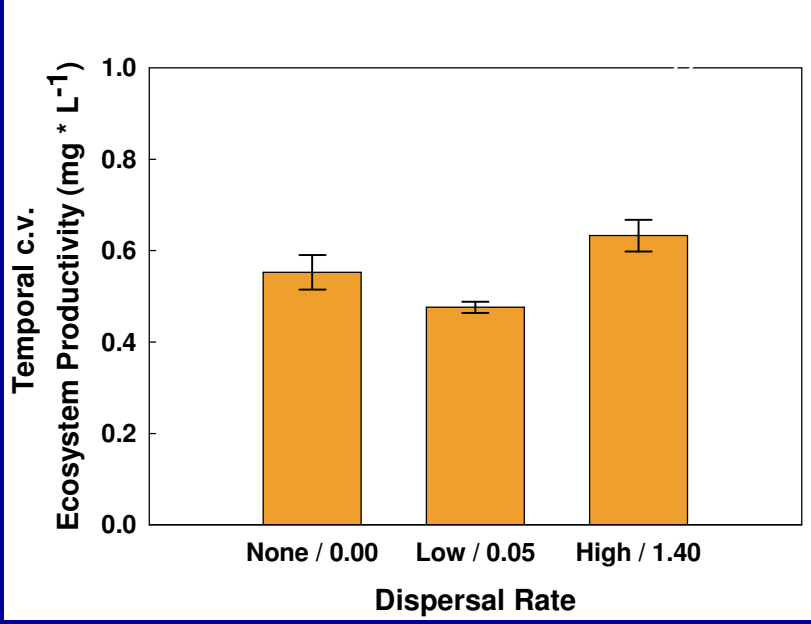
Ecosystem stability

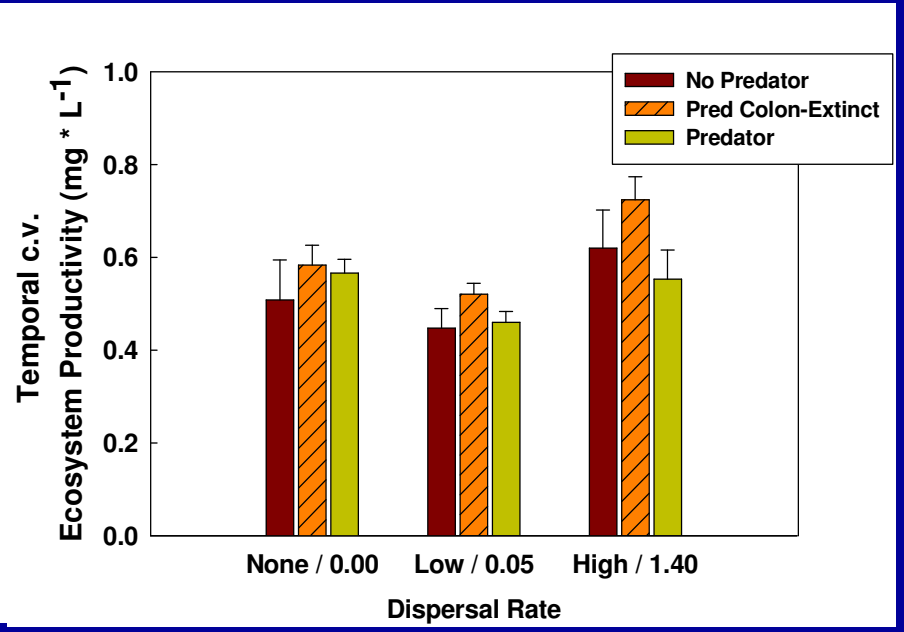
Regional / Metacommunity

Local

Disp, $P = 0.006$
Pred, P = NS
Disp * Pred, P = NS

$P = 0.01$





Dispersal-diversity and ecosystem stability

- Dispersal enhanced diversity unimodally
- Some of this involved source sink relations between different communities
- Some involved additional species in regional community at low dispersal but not high
- Dispersal enhanced stability, especially in cases with fluctuating fish predation: here dispersal is in organisms at lower trophic levels rather than higher ones… does the effect of dispersal not depend on trophic level?
- Even very high dispersal did not significantly homogenize the metacommunity
- Overall Dispersal → Diversity → Stability as in the models by Loreau et al.

What would adaptive dispersal do?

- Increase likelihood that stabilizing effect would also occur at high connectivity? (McCann et al. 2005)

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- Trophic cascades
- Trophic structure and eutrophication
- Biodiversity and eutrophication
- Food web complexity
- Biodiversity and stability

Some topics in metacommunity ecology

- Co-existence and similarity (will discuss later)
- Trophic cascades
- Trophic structure and eutrophication
- Biodiversity and eutrophication
- Food web complexity
- Biodiversity and stability

Metacommunity dynamics of various types alter how we might think of many (most?, all?) aspects of community ecology

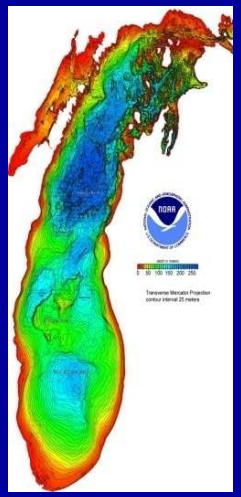
What appears to be species sorting in metacommunities with heterogeneous patches is common.

Spatial effects that may be unrelated to species sorting also seem to occur

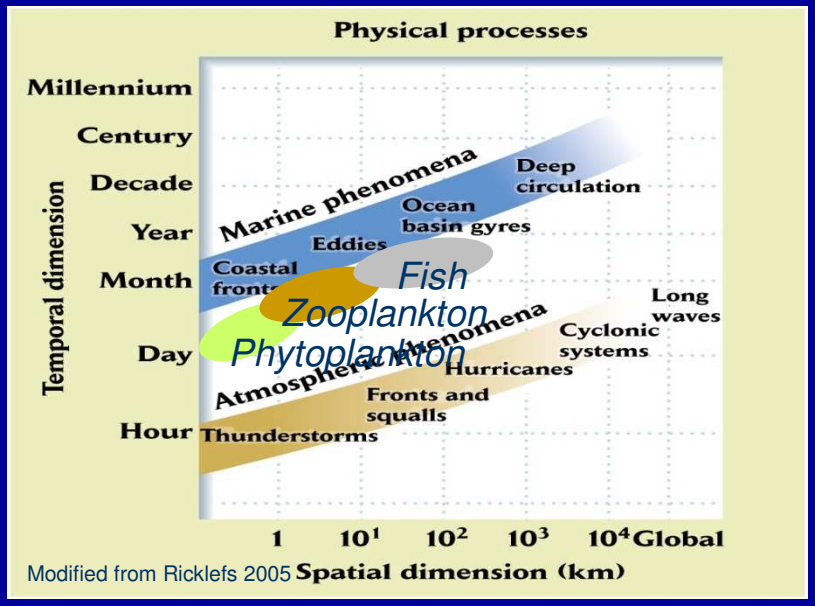
How does adpative dispersal affect these consequence and can we figure that out?

Three important roles for dispersal in community assembly

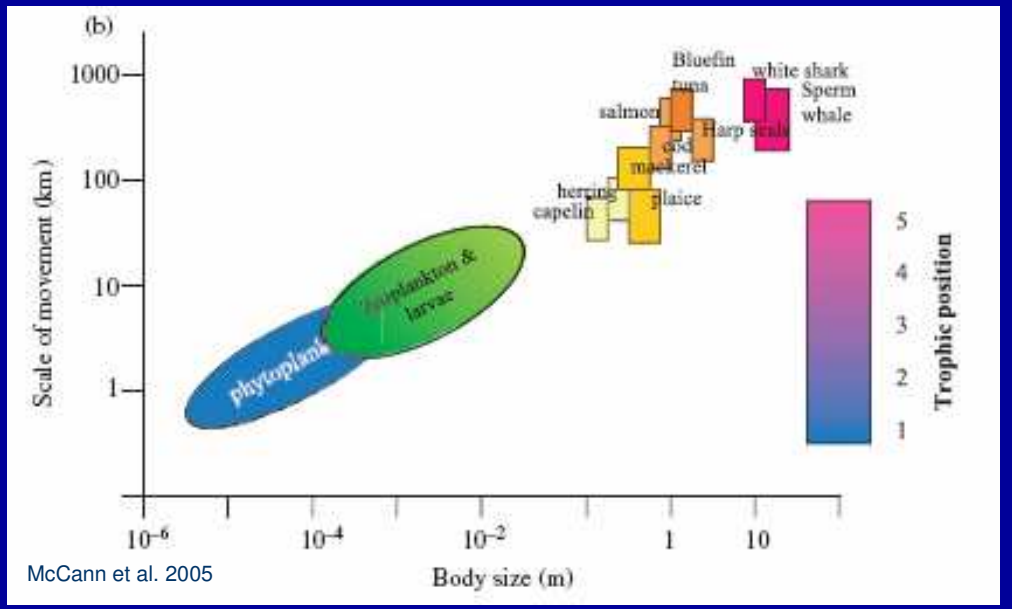
- Provide colonists that ‘fuel’ community assembly
  - How does adaptive dispersal alter such occasional colonization events?
- Support maladapted sink populations in communities where they would go extinct
  - How do such maladapted sinks occur when there is adaptive dispersal?
- Gene flow that alters evolution
  - How does such gene flow in the presence of adaptive dispersal change evolutionary dynamics?



Patches or continuous habitat?



Modified from Ricklefs 2005



McCann et al. 2005