Definitions

- (meta)population
- (meta)community

Neutral Theory of Ecology (Hubbell 1997)

	Spatial environment	
Species attributes	Homogenous	Heterogeneous
Different niches	1. Patch dynamics (see Chapter 12)	2. Mass effects/source-sink dynamics 3. Species sorting
Demographically equivalent	4. Neutral theory	

COMMUNITY ECOLOGY, Figure 13.1

- Classic approach – species all differ in n-dimensional niche space. Overlapping niches result in competitive exclusion.
- **Neutral Theory**
  - Species are functionally similar.
  - Patterns of distribution and abundance arise from random (colonization and extinction in homogeneous environments) processes.
  - Asymmetric biotic reactions are not allowed
- Null hypothesis to niche theory

Metapopulation → Metacommunity

	Spatial environment	
Species attributes	Homogenous	Heterogeneous
Different niches	1. Patch dynamics (see Chapter 12)	2. Mass effects/source-sink dynamics 3. Species sorting
Demographically equivalent	4. Neutral theory	

COMMUNITY ECOLOGY, Figure 13.1

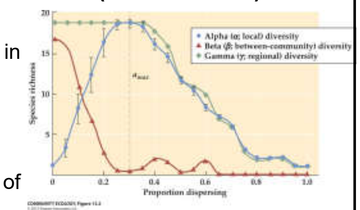
- Metacommunity – group of local communities linked by dispersal
- Four different views of how metacommunities may "work"
  - **Patch dynamics** - Homogeneous environment, simple extension of Levins metapopulation model to multiple species
  - **Mass-effects** – Heterogeneous environment, extension of source-sink model (dispersal plays an important role on diversity at multiple scales)
  - **Species-sorting** – Heterogeneous environment, dispersal has minimal influence as all species disperse equally to viable patches.
  - **Neutral Theory**

Metacommunity model example

- Species A and B are both regional, what determines occupancy locally?
  - **Patch dynamics** – colonization-competition tradeoff, one will outcompete while the other is the first colonist. A and B do not coexist.
  - **Species Sorting** – A and B differ in niche, each excludes the other in some habitats. A and B do not coexist.
  - **Mass effect** – similar to species sorting, but higher dispersal (source-sink model) allows coexistence in some situations.
  - **Neutral** – A and B can coexist, no competitive exclusion or niche differences.

Source-Sink Metacommunities (mass-effects)

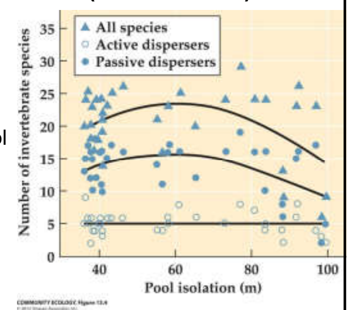
- Environments are heterogeneous (variability in patch quality) and we expect species to differ in patch use (**source-sink dynamics**)
- How does movement rate of species at the patch scale impact metrics of diversity?
- Metapopulation-community model
  - Local species compete for available patches
  - Variable rates of colonization



Low movement: low α, high β and γ
Med movement: high α and γ, low β
High movement: low α, β and γ

Source-Sink Metacommunities (mass-effects)

- Support for this general model.
- Invertebrate species richness is highest at intermediate levels of pool isolation (=intermediate levels of colonization)



Metacommunity Patterns

- Patterns of species distributions among sites
  - **Checkerboard** – pairs of species have mutually exclusive distributions, such pairings across the community are all independent of each other.
  - **Nested subsets** – groups of species tend to occur as formal sets.
  - **Random** – species can coexist at random, no groups of species that occur more often.

Metacommunity Patterns

- On a community scale, how do you test for these?
  - **Coherence** – the degree to which community structure among sites can be collapsed into a single dimension.
  - Quantified as the number of embedder absences (absences when a species is expected to be present.)

Coherence, species turnover, and boundary clumping: elements of meta-community structure

Mathew A. Leibold and Gregory M. Mikkelson

Fig. 1. Coherence as indicated by the occurrence of embedded absences in ordinated matrices. Entries denote the presence (1) or absence (0) of species (rows) at sites (columns). Statistics for each matrix are described in the text.

a) Perfectly Coherent

Sites

	1	1	1	1	1	1	0	0	0	0
S	0	1	1	1	1	1	1	1	1	0
p	0	1	1	1	1	1	1	1	1	0
e	0	0	0	1	1	1	1	1	1	0
c	0	0	0	0	1	1	1	1	1	1
i	0	0	0	0	0	1	1	1	1	1
e	0	0	0	0	0	0	1	1	1	1
s	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	0	1

Embedded Absences:
Actual Number = 0
Expected Number = 20.5
Standard Deviation = 3.1
$p < .025$

b) Moderately Incoherent

Sites

	1	1	0	0	0	0	0	0	0	0
S	1	0	1	0	1	0	1	0	0	0
p	1	1	1	1	1	1	0	1	0	0
e	1	0	1	0	0	1	0	1	0	0
c	1	1	1	1	0	1	0	1	1	0
i	1	0	1	0	0	0	1	0	1	0
e	0	1	1	1	1	1	1	0	1	1
s	0	0	1	0	1	1	1	1	0	1
	0	1	0	0	0	1	1	1	1	1
	0	0	0	0	0	0	0	1	1	0

Embedded Absences:
Actual Number = 22
Expected Number = 20.5
Standard Deviation = 3.1
$p \approx .325$

Metacommunity Patterns

- **Turnover** – one species replacing another along the gradient.

Coherence, species turnover, and boundary clumping: elements of meta-community structure

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a) Highly Nested (Low Turnover)

Sites

	1	1	1	1	1	1	1	1	1	1
S	0	1	1	1	1	1	1	1	1	1
p	0	0	1	1	1	1	1	1	1	1
e	0	0	0	1	1	1	1	1	1	1
c	0	0	0	0	1	1	1	1	1	1
i	0	0	0	0	0	1	1	1	1	1
e	0	0	0	0	0	0	1	1	1	1
s	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	1

Replacements:
Actual Number = 0
Expected Number = 124.4
Standard Deviation = 52.9
p < .025

b) Moderately Non-Nested (Moderate Turnover)

Sites

	1	1	1	1	1	1	1	0	0	0
S	0	1	1	1	1	1	1	1	0	0
p	0	0	1	1	1	1	1	1	1	0
e	0	0	0	1	1	1	1	1	1	1
c	0	0	0	0	1	1	1	1	1	1
i	0	0	0	0	0	1	1	1	1	1
e	0	0	0	0	0	0	1	1	1	1
s	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	1

Replacements:
Actual Number = 191
Expected Number = 149.3
Standard Deviation = 53.8
p ≈ 0.200

c) Anti-Nested (High Turnover)

Sites

	1	0	0	0	0	0	0	0	0	0
	1	1	0	0	0	0	0	0	0	0
	1	1	1	0	0	0	0	0	0	0
S	1	1	1	1	0	0	0	0	0	0
p	1	1	1	1	1	0	0	0	0	0
e	0	1	1	1	1	1	0	0	0	0
c	0	0	1	1	1	1	1	0	0	0
i	0	0	0	1	1	1	1	1	0	0
e	0	0	0	0	1	1	1	1	1	0
s	0	0	0	0	0	1	1	1	1	1
	0	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	1

Replacements:
Actual Number = 575
Expected Number = 411.7
Standard Deviation = 83.2
p < .025

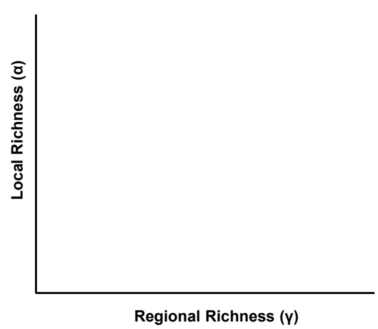
Fig. 2. Species turnover as indicated by the number of times one species replaces another between two sites. Entries denote the presence (1) or absence (0) of species (rows) at sites (columns). Statistics for each matrix are described in the text.

Metacommunity Patterns

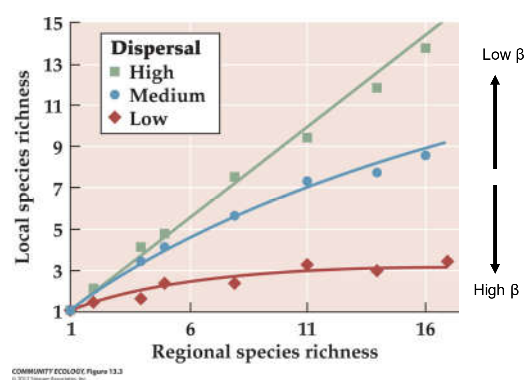
- Patterns of species distributions among sites
  - **Checkerboard** – pairs of species have mutually exclusive distributions, such pairings across the community are all independent of each other.
    - Negative coherence
    - No pattern of turnover
  - **Nested subsets** – groups of species tend to occur as formal sets.
    - Positive coherence
    - Low/zero turnover
  - **Random** – species can coexist at random, no groups of species that occur more often.
    - Random coherence and turnover

Community Saturation and Dispersal

- How does local richness relate to regional richness?
- If local richness plateaus, we describe the local communities as being **saturated**.
- Saturated local communities are resistant to invasion and colonization.



Community Saturation and Dispersal



Local vs. Regional Control of Diversity

- Local control
  - Communities are saturated, resistant to invasion
  - Physically similar sites should have similar diversity, regardless of regional diversity
  - Local diversity independent of regional diversity
- Regional control
  - Communities tend not to be saturated, prone to invasion
  - Physically similar sites have different diversity due to different richness of regional pools
  - Local diversity closely linked to regional diversity

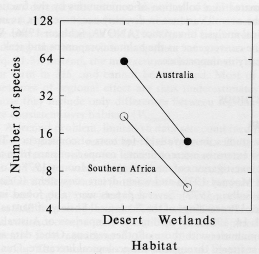
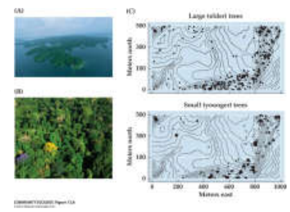


Figure 21.1 The number of lizard species in deserts and tropical wetlands of Australia and southern Africa. Desert data are from Pianka (1986), and combine species from all his study sites. Wetland data are from Simbotwe and Friend (1985), and represent complete lists from a national park on each continent.

Schluter and Ricklefs 1998

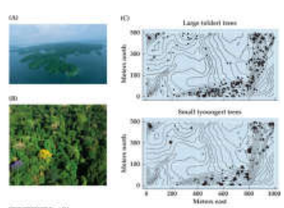
Neutral Theory

- Hubbell mapped trees in tropical rain forest
- Assumptions
  - Number of individuals in the community is fixed
  - Death of one individual is followed by random replacement by another
  - Death rate is fixed
- Models predicts a random walk towards single species dominance.
- Offset by the rate of speciation.



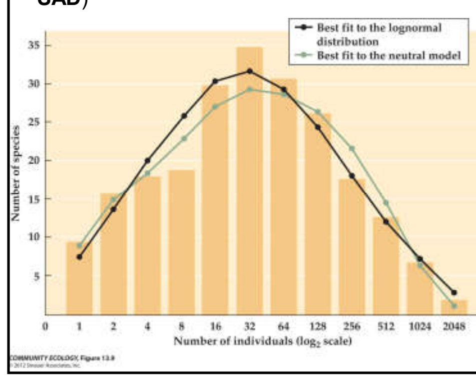
Neutral Theory

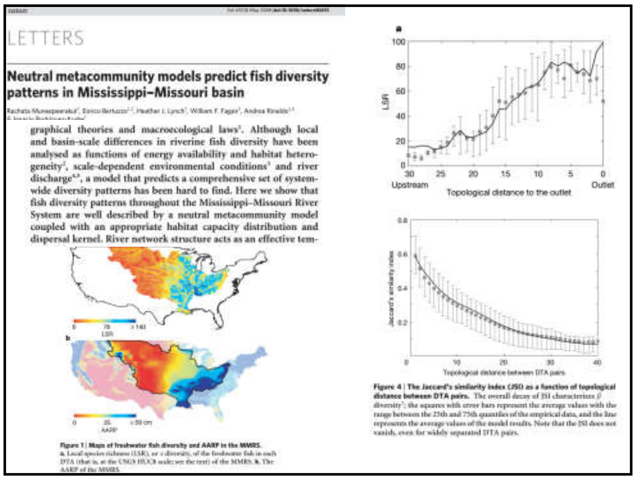
- Expanded to metacommunity…
  - Local community has a fixed number of individuals, open space (due to death) followed by colonization either by local species of colonizers.
  - On the community scale, number of individuals fixed
  - Loss of species (extinction) is counteracted by speciation, also occurring at a predictable rate



Neutral Theory Predictions

- Neutral theory makes specific predictions about patterns of diversity and abundance (**species abundance distributions, SAD**)





LETTERS

Neutral metacommunity models predict fish diversity patterns in Mississippi–Missouri basin

graphical theories and macroecological laws[1]. Although local and basin-scale differences in riverine fish diversity have been analysed as functions of energy availability and habitat heterogeneity[2], scale-dependent environmental conditions[3] and river discharge[4,5], a model that predicts a comprehensive set of system-wide diversity patterns has been hard to find. Here we show that fish diversity patterns throughout the Mississippi–Missouri River System are well described by a neutral metacommunity model coupled with an appropriate habitat capacity distribution and dispersal kernel. River network structure acts as an effective tem-

Figure 1 | Maps of freshwater fish diversity and AARP in the MMRS. **a**, Local species richness (LSR), or α diversity, of the freshwater fish in each DTA (that is, at the USGS HUC8 scale; see the text) of the MMRS. **b**, The AARP of the MMRS.

Figure 4 | The Jaccard's similarity index (JSI) as a function of topological distance between DTA pairs. The overall decay of JSI characterizes β diversity[7]; the squares with error bars represent the average values with the range between the 25th and 75th quantiles of the empirical data, and the line represents the average values of the model results. Note that the JSI does not vanish, even for widely separated DTA pairs.

- Predation, parasitism, competition, commensalism, symbiosis
- Mutualism (evolved via reciprocal exploitation), habitat facilitation, (endo)symbiosis
- Examples and various direct and indirect effects (trophic cascade, apparent competition, keystone predation)
- $\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 + a_{12} N_2}{K_1}\right)$
- Keystone species, ecosystem engineer
- Succession (primary, secondary, autogenic, allogenic, degradative), models and mechanisms of succession (Horn species replacement, Tilman R*, stress gradient hypothesis)
- Detecting community change (qualitative vs. quantitative measures), gradient analysis and ordination
- Predation and community structure
- Food webs structure (connectance, trophic levels, complexity (May 1972 model of stability)), network topology, maximal food chains
- Energy flow vs. functional webs – strengths of interactions (strong vs. weak interactors, metrics and detection)
- Eltonian pyramid and food web energetics (efficiency, reasons for inefficiency)
- Body size ratio as predictor of interaction strength
- Community stability and food web modularity
- Assemblage rules (Drake 1991)

- Abundance at trophic levels – top down vs. bottom up control (HSS), is the world "green"?
- Oksanen et al. (1981) models based on G – mechanisms, predictions and experimental support
- Keystone predation (diamond shaped food web) altering expected food web abundance
- Trophic cascade (examples and critique)
- Food chain length
- Spatial ecology – patch, metapopulation, source, sink, rescue effect
- Movement models (spatially explicit, diffusion, non-spatially explicit)
- Levins metapopulation model, colonization and extinction equilibrium (effects of number of patches, c and m on population persistence). Extinction debt
- SLOSS, corridor function and efficacy, facilitated dispersal
- Metapopulation models (importance of spatial heterogeneity and variability in dispersal),
- Fugitive species, checkerboard distribution, nested subsets
- Metacommunity models (mass-effects, neutral theory, patch dynamics, species sorting), importance of species attributes (niche or dispersal abilities) and spatial heterogeneity in predicting patterns.
- Regional vs. local diversity and saturation