Four perspectives for multiple species

- **Patch dynamics** – principles of metapopulation models (patchy pops, Levins)
- **Mass effects** – principles of source-sink and rescue effects
- **Species-sorting** – species differences in patch use in heterogeneous environment
- **Neutral** – functionally identical species, random dispersal
Models can be organized by spatial environment and species specialization.

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<thead>
<tr>
<th>Species Attributes</th>
<th>Spatial environment</th>
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<tbody>
<tr>
<td>Homogenous</td>
<td>Heterogeneous</td>
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<tr>
<td>Different niches</td>
<td>1. Patch dynamics</td>
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**Metacommunities**

Spatial Ecology of Communities

- Heterogeneous environment means species performance varies among patches; homogeneous means performance does not vary

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- 1. Patch dynamics
- 2. Mass effects or source-sink dynamics
- 3. Species sorting
- 4. Neutral theory
Metacommunities
Spatial Ecology of Communities

- Species attributes differentiates communities where species vary in tolerance of different niche types and where they don’t vary.

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Metacommunities
Spatial Ecology of Communities

• A different depiction of relationship of four primary metacommunity models

• Should consider dispersal, food web topology; trophic and mutualistic interactions, energy and matter flow in meta-ecosystem and evolutionary dynamics

Logue et al. 2011. TREE 26:482-491
• Trade-offs, such as competition and dispersal, mean not all species are the same.
  – Root/shoot trade-off = species good at competition for light weak at competing for soil nutrients
  – Activity level/mortality risk = species good at avoiding predators may be weak at finding mates or resources

• Trade-offs contribute to co-existence; mass effects and species-sorting expand this coexistence in spatially heterogeneous landscape

• Neutral species assumes no species differences; can be treated as a null model to evaluate power of data
Metacommunities
Mass Effects

• Mass effects = dispersal from high quality patches (net positive pop growth) to low quality ones (net negative pop growth)

• Mouquet and Loreau (2003) model: dispersal among local patches affects alpha (within-community), beta (among community), and gamma (regional) diversity

Figure 13.2 Simulation results from Mouquet and Loreau’s model of source-sink metacommunities shows how species richness at different spatial scales (alpha, beta and gamma diversity) should vary as a function of the proportion the local reproductive output that disperses between communities. Local species diversity is maximized at $\alpha_{\text{max}}$. (After Mouquet and Loreau 2003.)
Metacommunities
Mass Effects

• Each local community contains S species, compete for a limited proportion of vacant patches
• N local communities differ in env conditions. Species vary adaptations, higher r in environmentally matched communities
• Regional scale, constant proportion a of each local pop disperses (prop of local reproductive output exported); assumed equal for all spp
• Simulated 20 spp in 20 local communities, ran to equilibrium
Metacommunities
Mass Effects

- A zero dispersal, each local community is dominated by best local competitors; low alpha diversity and high beta and gamma diversity
- Prop dispersing increases, alpha increases because of rescue effect, beta diversity decreases.
- Prop dispersing passes alpha max, alpha drops because superior competitor at each scale dominates
- Ultimately, one large regional community with regional best competitors

• Model also predicted that variation in proportion of individuals dispersing from local communities affects relationship of region and local species richness.

Metacommunities
Mass Effects

• Empirical studies provide some support for model
• Diversity of macroinvertebrates in rock pools in So Africa
• Local species richness (alpha diversity) peaks intermediate levels of pool isolation, mostly because of passive dispersing spp

Vanschoenwinkel et al. 2007. Oikos 116:1255-1266
Metacommunities

species sorting and mass Effects

• Protozoans in pitcher plants, species richness highest at intermediate dispersal (weekly mixing – low; bi-weekly mixing – high)
• Effect lost when predaceous mosquito larvae present

Figure 13.5  (A) The highly modified leaves of Sarracenia purpurea contain a characteristic community of invertebrates (e.g., protozoans, rotifers, insect larvae), many of which are obligate pitcher plant dwellers. (B) In the absence of predatory mosquito larvae in the community, mean species richness within a given pitcher plant ("mean local richness") peaked when dispersal was intermediate (the "low dispersal" treatment). When predators were present, however, the frequency of dispersal had no effect on local species richness. Error bars are ±1 SE. (A courtesy of David McIntyre; B after Kneitel and Miller 2003.)
Metacommunities
species sorting and mass Effects

• Difference between mass effects and species sorting perspectives is in rate of dispersal
• Species sorting assumes dispersal at low rate such as no direct effect on species abundance or outcome of interactions (no ‘mass effect’)
• Migration just high enough for each spp to reach the habitat where it is best adapted
Metacommunities ecosystem function

- Species sorting: a low rate of species input by dispersal may permit communities to track environmental change as a ‘complex adaptive system’
- Addition of species with all competitive abilities and differing mortality risks dampens trophic-level effects of increasing basal resources and leads to increased biomass across all trophic levels through spp compositional shifts
- Example: FW communities established from local spp pools show different function than those from regional pool; regionally source community tracks resource gradient better

Naeslund and Norberg. 2006. Oikos 115:504-512
Metacommunities measuring dispersal

- Dispersal is hard to study and we have relatively little information on actual rates of movement between communities
- Obs by rate of colonization of new habitats
- Examine genetic dissimilarity to determine ‘isolation by distance’
- Similarly, compare spp composition in community samples as a function of distance; expect clumping of poor dispersers (greater spatial autocorrelation)
Metacommunities
species sorting and mass effects

Can also examine community dissimilarity and environmental gradients to separate species sorting versus dispersal limitation. Ex. Everglades fish and macroinvertebrates

M-H: densities for differences in dominance of common taxa

J: pres/abs data for differences in composition

principal coordinates of neighbor matrices=pcnm
Used to assess spatial effects by correlation of community to site distance matrix
34 connected lakes in Belgium

3,600 zooplankton per hour dispersed through rivulets, turn-over time of 13 days

Fig. 1. Location of the nature reserve “De Maten,” Genk, Belgium, and the spatial configuration of the different ponds and the connecting elements (overflows and rivulets). There are two different input sources (I1 and I2 come from the Stienenbeek, and I3 from the Heiweyerbeek), and two output sources (O1 and O2).

• Despite high turnover, zoop composition predictably related to local lake environments, particularly presence/absence of fish and macrophytes (consistent with species-sorting model)

• Dispersal increased spp richness of cladoceran zoops by average of 3 spp (a mass effect) facilitated predictability of local community response to env change

• Both spp sorting and mass effects present and contribute

Steve Hubbells’ Unified Neuthral Theory of Biodiversity and Biogeography (2001)

- Niches absent, all spp functionally equivalent
- Demographically identical: vital rates of birth, death, and dispersal
- Can spp diversity be maintained if all are functionally equivalent?
- Hubbell’s theory is analogous to neutral theory of population genetics: How maintain high levels of allelic diversity in mutations that are neutral in effects?
Metacommunities
Neutral Model

• Model for tropical forests: 300 spp on 50 ha plot on Barro Colorado Island; 250,000 individuals over 1 cm stem diam.

• Assumptions:
  – Space is limiting and all occupied, number of individuals constant. Yields a zero-sum game, increase of spp1 must come from loss of spp2
  – Probability of colonization to replace a death is equal among spp; colonizers drawn at random from spp present so probability = relative abundance
  – Death occurs at constant fixed rate
Long-term (equilibrium) community composition is a random walk to dominance by a single spp. However, spp are long-lived so this takes a long time… Hubbell and Foster (1986) argued long enough for new spp to arise.
Metacommunities
Neutral Model

- Hubbell (2001) extends model to local community in a metacommunity
- Local community has J total individuals whose offspring compete for sites opened by a death
- Every individual has equal chance of colonizing open space (neutrality) and each death is replaced (zero-sum)
- local recruits compete with those from elsewhere in the metacommunity
Among predictions from Hubbell’s model are species abundance distributions (SAD).

For a local community receiving species from a metacommunity at a migration rate $m$, the neutral model predictions converge on the lognormal distribution.

Hubbell and Foster’s Barro Colorado data match these predictions well.

Note: Lognormal SAD was first described by Preston (1948) building on work by Fisher (1943). MacArthur (1960’s) broken stick model failed in attempt to explain this pattern.
Figure 2.17  (A) An example of Fisher’s log series distribution fit to data on species abundances in moths collected at light traps over a 4-year period at Rothamsted, England. (B) A hypothetical example of Preston’s lognormal distribution, showing how the distribution of species abundances can be normalized when log-transformed, in this case by using an x axis where each successive abundance class represents a doubling in species abundance (log$_2$ scale). (A after Hubbell 2001.)
Neutral model makes specific predictions about SADs over space or time that can be compared to data.

Several studies have found species turnover over short distances was greater than predicted. For example, Wootton (2005. Nature 433:309-312) found good fit to neutral theory predictions of SAD, but made poor predictions of species turnover over 7-year study of sessile marine invertebrates.

Neutral theory and niche differentiation models equally successful in predicting SADs

Species turnover in space and time are not well predicted by neutral theory, though sometimes well predicted by niche differentiation models

Neutral theory provides a null model for spatial ecology and community assembly; focusses attention on dispersal limitation as “null condition” for community assembly (essentially a random walk model)

Real communities may be composed of mix of spp with a continuum of neutral and niche-based interactions