VII. Pre-settlement / settlement effects on maintenance of species diversity

A) Review of Hypotheses for maintenance of diversity (summarized and reviewed by Connell ‘78)

Recall, Ho’s can be categorized into one of two general categories:

1) Equilibrium hypotheses
2) Non-equilibrium hypotheses

Test the possible importance of each hypothesis in a particular community by testing:

a) assumptions necessary for each hypothesis
b) predicted dynamics and structure of assemblage in response to a perturbation
c) test both observationally and/or experimentally

I. Equilibrium Hypotheses

- involve settlement and post-settlement processes
- stress biotic interactions
- mostly competition based - competitive exclusion principle
- community structure and dynamics are predictable
- predictable return to pre-perturbation state!

Niche Diversification Hypothesis

Assumptions:

a) competition based (assumes resources are limiting)
b) resource partitioning (each species is a superior competitor for particular resources or within particular niche)
c) for test, assume perturbation does not alter resource availability, only diminishes species abundances

Predictions:

a) total number of individuals and total number of species limited by resources, \( \Rightarrow \) assemblage-wide carrying capacity (K)
b) relative abundance of spp. determined by relative niche availability \( \Rightarrow \) specific carrying capacity for each species
c) predictable composition and relative abundance

Niche Diversification Hypothesis

- Total abundance
- Species A
- Species B
- Species C

Time
**Niche Diversification Hypothesis**

- **Assumptions:**
  - Total abundance
  - Species A
  - Species B
  - Species C

- **Predictions:**
  - Proportional abundance

**Compensatory Mortality**

- **Assumptions:**
  - a) competition based (assumes resources are limiting)
  - b) disturbance or generalist predator removes most abundant species, thereby freeing resources for competitively inferior, rarer species
  - c) for test, assume perturbation does not alter resource availability, only diminishes species abundances

- **Predictions:**
  - a) inverse relationships in species abundances
  - b) most abundant species at any time suffers disproportionate mortality
Predation Hypotheses (equilibrial-based)

Different equilibrial-based mechanisms:
- **Compensatory mortality** (predators feed on most abundant species)
- Predators “switch” to feed on most abundant species, disproportionately reducing that species
- **Keystone predation** where predator prefers competitive dominant, freeing up resources for subordinate competitors
- Induces competition for refuge from predation (i.e. overall K for assemblage)
- **Regulate** populations of prey species separately (density dependence)

Assumptions:
- a) predator causes disproportionately higher mortality in most abundant prey species (competitive dominant)
- b) Induces competition or otherwise regulates prey populations
- c) allows persistence of rare species or inferior competitors

Predictions:
- a) inverse relationships in species abundances
- b) most abundant species at any time suffers disproportionate mortality

Note similarity of predicted pattern with compensatory mortality
**Predation Hypotheses (equilibrial-based)**

Predictions for recruitment patterns:
- **Compensatory mortality, switching** - differences in recruitment diminish over time as numbers converge
- **Induced competition for refuge** - pattern similar to niche diversification
- **Regulate** populations of prey species separately (density dependence) - leads to predictable relative abundance of recruits

**Recruitment pulse**

- Various processes can be involved: competition, predation, disturbance, limited recruitment
- Relative and total abundance fluctuates unpredictably
- Species composition is unpredictable
- Species composition and abundance does NOT return to pre-perturbation state

**Intermediate Disturbance**

- discussed at length previously
- competition based — mediated by physical or biological disturbance
- involves mostly post-settlement interactions but also attributes of pre-settlement stages (recall both r vs K species characters and Sousa’s work)
- not discussed further here

**Lottery Hypothesis**

*Connell’s “Equal Chance” Hypothesis*

Peter Sale 1977

**Assumptions:**
- competition based (resource limitation)
- larval pool saturates resource (space)
- no resource partitioning (all species equal competitors)
- likelihood of creating and acquiring resource (space) due to random chance (deaths and larval settlement unpredictable)
- equal likelihood of settlement from larval pool
  - **but** requires some mechanism in plankton to maintain similar relative abundance of species in larval pool! Assumes species compositions on different reefs out of synch!
Lottery Hypothesis
(Connell’s “Equal Chance” Hypothesis)
Peter Sale 1977

Predictions:
• unpredictable as to what species will recruit to any location or at any time
• maximum total abundance across species ($K$)
• relative abundance of species fluctuates unpredictably
• including after perturbation

Lottery Hypothesis

Lottery Model – Storage Effect
(Hutchinson’s “Gradual Change” Hypothesis)
Bob Warner and Peter Chesson 1985

Assumptions:
• competition based (resource limitation)
• same assumptions as lottery hypothesis, but
• relative recruitment success of species changes through time (akin to “gradual change” hypothesis)
• variable success due to variation in larval production, planktonic conditions, settlement conditions
• species persist through bad recruitment periods and “store” recruitment events in extended lifetime (age classes) of adults

Predictions:
• same as Lottery Hypothesis but different mechanism
**Recruitment Limitation Hypothesis**  
Peter Doherty 1983, Ben Victor 1986

**Assumptions:**
- Assumes high mortality of pelagic larvae limits number of recruits to benthic populations
- Larval supply limits recruitment below that which is required to saturate resources
- No competition so mortality is density-independent

**Predictions:**
- Total numbers and relative abundance fluctuates with variable larval supply

**NOTE:** pattern and response similar to Lottery Hypothesis, but mechanism cannot be distinguished!
“Pluralistic” Approach

Assumptions:
• probably a combination of several of the above
• varying in importance over scales of space and time
• because several of these competing hypotheses create similar patterns of variability in relative and combined numbers, helps to distinguish them experimentally
• involves orthogonal manipulations of competition, predation and disturbance

Predictions:
• relative importance of post-recruitment competition
• extent to which recruitment is modified by post-recruitment processes

Post-recruitment (PR) Competition

<table>
<thead>
<tr>
<th>PR Competition</th>
<th>Intense</th>
<th>Weak</th>
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<tbody>
<tr>
<td>Recruitment modified by (PR) processes</td>
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<tr>
<td>Recruitment NOT modified by (PR) processes</td>
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<tr>
<td>Competition Model (Niche Diversification)</td>
<td>Predation Disturbance Models</td>
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<tr>
<td>Lottery Hypothesis (Model)</td>
<td>Recruitment Limitation</td>
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