V) Maintenance of species diversity

1. Ecological succession

A) Definition: the sequential, predictable change in species composition over time following a disturbance

- **Primary succession** - succession starts from a completely empty community (i.e. bare substratum) such as that following glaciations or a volcanic eruption
- **Secondary succession** - when the majority of individuals are removed by a disturbance of lesser intensity, often leaving propagules (seeds, spores, larvae) only (e.g., flooding, forest fire)

- Change in community will, given sufficient time, result in a climax community, in which the competitive dominants will prevail

B) Why is there succession?

i) Species differ in life history characteristics

ii) Species cannot optimize all characters, so there appears to be trade-offs among characters that influence how a species responds to a disturbance

---

1. Ecological succession

C) Comparison of early and late successional species:

<table>
<thead>
<tr>
<th>Character</th>
<th>Early Successional (&quot;r-selected&quot;)</th>
<th>Late Successional (&quot;K-selected&quot;)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproduction</td>
<td>semelparous (once)</td>
<td>iteroparous (multiple)</td>
</tr>
<tr>
<td>Fecundity</td>
<td>high</td>
<td>low</td>
</tr>
<tr>
<td>Dispersal ability</td>
<td>good-long</td>
<td>poor-short</td>
</tr>
<tr>
<td>Growth rate</td>
<td>fast</td>
<td>slow</td>
</tr>
<tr>
<td>Life span</td>
<td>short</td>
<td>long</td>
</tr>
<tr>
<td>Generation time</td>
<td>short</td>
<td>long</td>
</tr>
<tr>
<td>Competitive ability</td>
<td>POOR</td>
<td>GOOD</td>
</tr>
</tbody>
</table>

- not all species fit these categories but it is a useful general scheme
- **Early species** - good at dispersing to and colonizing newly disturbed sites, grow rapidly, reproduce and are out-competed
- **Late species** - poor at dispersing to and colonizing newly disturbed sites, grow slowly and out-compete earlier species.

---

D) Models of succession: (Connell and Slatyer 19XX American Naturalist)

i) Facilitation: early species modify the environment...

- make it more suitable for later species
- later species can’t colonize until environment modified
- modified environment sometimes not so good for early species

ii) Inhibition: early species inhibit later species from colonizing...

- later species colonize as early species die
- as they colonize, later species out-compete earlier species

iii) Tolerance: no interactions (positive or negative) between earlier and later species...

- earlier species are quick to colonize (arrive earlier)
- later species are slow to colonize (arrive later)
- later species “tolerate” earlier species and lower resource availability
Upward Shifts

Endocladia 1992

Barnacles 2000

Silvetia 1992

Silvetia 2000 (+0.3 meters)

Endocladia 2000 (+0.3 meters)

Spring 1992

Spring 1993

Spring 1995

Fall 1999

More upward shifts

Endocladia 1992

Barnacles 2000 (+0.5 meters)

Endocladia 2000 (+0.6 meters)
V) Maintenance of species diversity

2. Losses of diversity

A) Interspecific competition
- Examples of competitive exclusion
  i) Connell showed how *Semibalanus* out-competed and excluded *Chthamalus* from the mid-intertidal
  ii) Menge showed how mussels out-competed and excluded barnacles and algae in the mid-intertidal at exposed sites
- Thus, to maintain diversity, consider how species are...

B) Release from interspecific competition
  i) Resources are unlimited (unlikely, but we’ll discuss “recruitment limitation”!!)
  ii) Reduction in populations through other interactions (e.g., predation, intraspecific competition) to levels where resources are not limiting
  iii) Disturbance interrupts succession sequence

V) Maintenance of species diversity

3. Some specific mechanisms: Connell 1978 Science

A) If intraspecific competition > interspecific competition
  i) If $K_A$ (carrying capacity for species $A$) is lower than population size of species $A$ that would exclude species $B$ and vice versa, both species will coexist
  ii) Examples...
    - allelopaths that kill conspecifics, not other species
    - behavioral interactions: territorial indiv.s less tolerant to (more aggressive toward) conspecifics than other species

B) Circular networks (largely hypothetical)
  i) Competitive hierarchy: $A > B > C > A$
  ii) Only example is intraspecific (Sinervo’s lizards)

V) Maintenance of species diversity

3. Some specific mechanisms: Connell 1978 Science

C) Compensatory mortality
  i) Mortality is disproportionately greater in competitive dominant simply because it is more abundant
  ii) “frequency dependent”
  iii) Sources of mortality include predation, disturbance

D) Gradual change
  i) Competitive rank varies with changing environmental conditions: Abundance
    - $A > B > C > D$
  ii) Hutchinson’s “paradox of the plankton”
  iii) Species must not decline to extinction before environment changes to favor it again

V) Maintenance of species diversity

4. Predation
  i) Keeps population level of dominant competitor below that which would cause competitive exclusion
  ii) Can create patchiness in the environment

A) Proportional predation
  i) Generalist predator eats prey as they are encountered (like a disturbance!)
  ii) Most abundant species (competitive dominant) encountered most often... eaten most often
  iii) No species can exclude another

B) “Switching” predator (e.g., Murdoch 1969, Ecology)
  i) Predator preference (behavior) switches with relative abundance of prey species
  ii) Common species eaten disproportionately more than uncommon ones
V) Maintenance of species diversity

4. Predation

B) “Switching” predator (e.g., Murdoch 1969, Ecology)
   iii) Rare species can therefore become more abundant
   iv) Once rarer species becomes more abundant, predator switches to feeding on it

C) Keystone predation (e.g., Paine 1974, American Naturalist)
   i) Predator prefers (behavioral) competitive dominant species
   ii) Predator is a specialist on competitive dominant

D) Contrasting predicted patterns of predation mechanisms

Result: Coexistence and Stability

E) Examples (switching and keystone)

1.) Switching (Raimondi et al. 20XX, Ecology)
   i) System: rocky intertidal in northern Gulf of California
      - Chthamalus - barnacle
      - Brachiodontes - mussel
      - Acanthina - predatory snail (w/ spine)
      - Morula - predatory snail
   ii) Pattern: barnacle and mussel coexist

   Percent cover
   TIME
   barnacle
   mussel

   Percent species A in diet
   Percent species A in field
   1:1
   Proportional
   Switching
   Keystone

   Time
   Abundance

   A
   B

1.) Switching (Raimondi et al. 20XX, Ecology)
   i) General hypothesis: Acanthina or Morula are switching predators
      H₀: proportion of prey in diet will be disproportionate to prey abundance
      H₁: proportion of prey in diet will NOT be disproportionate to prey abundance
   iv) Design:
      a) Manipulate frequency of barnacles and mussels in cages with each species of predator
      b) Count number of prey killed of each species
V) Maintenance of species diversity

v) Results:

<table>
<thead>
<tr>
<th></th>
<th>Morula</th>
<th>Acanthina</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent barnacles in diet</td>
<td><img src="image1.png" alt="Graph" /></td>
<td><img src="image2.png" alt="Graph" /></td>
</tr>
<tr>
<td>Percent mussels in diet</td>
<td><img src="image3.png" alt="Graph" /></td>
<td><img src="image4.png" alt="Graph" /></td>
</tr>
</tbody>
</table>

- a) Morula switches but prefers mussels
- b) Acanthina switches but prefers barnacles

vi) Conclusions:

i) Switching predation may be (in part) responsible for maintaining coexistence

ii) Other factors may also be important:
- mussels require barnacles to settle on
- mussels out-compete barnacles, but
- barnacles settle 10X the rate of mussels

V) Maintenance of species diversity

2) Keystone predation (Paine 1966 American Naturalist)

a) Pattern:

i) Presence of competitively dominant mussels leads to exclusion of other primary space holders → lower diversity

ii) *Pisaster* is a mussel specialist

b) Working hypothesis:

*Pisaster* keeps mussels from excluding all other species in mid- to lower intertidal.
V) Maintenance of species diversity

2) Keystone predation (Paine 1966 American Naturalist)
   c) Specific hypothesis:
      Ha: In areas where Pisaster is removed, species diversity will decrease compared to unmanipulated controls.
   d) Test: removed Pisaster (you know the story…)
   e) Results:
      i) diversity in control areas unchanged
      ii) diversity in removal areas declined from 25 to 1 species

V) Maintenance of species diversity

5. Disturbance
   A) Marine examples:
      1) Waves
      2) Rolling boulders
      3) Logs
      4) Freshwater (low salinity)
      5) Freezes (thermal)
      6) Exfoliation (removal of rock surface)
      7) Sedimentation
      8) Sand burial / scour
      9) Eutrophication-anoxia
      10) Desiccation
      11) UV radiation

V) Maintenance of species diversity

5. Disturbance
   B) Consequences to populations and communities
      i) generally, considered a source of density-independent mortality
e.g., a log lands on half a rock surface and kills half the barnacles regardless of how many are there
      Relationships:
      \[
      \begin{align*}
      \text{Mortality rate} & \quad \text{Constant proportion are killed regardless of density} \\
      \text{density} & \quad \text{Percent lost} \\
      \end{align*}
      \]
      \[
      \text{Percent cover} \quad \text{linear = constant rate}
      \]
      As the number of individuals outside refuge increases, the proportion killed increases!

V) Maintenance of species diversity

5. Disturbance
   B) Consequences to populations and communities
      ii) Alternatively, can be a source of density-dependent mortality if constant amount of refuge from mortality exists (leads to changing proportion of mortality)
e.g.,
V) Maintenance of species diversity
5. Disturbance
B) Consequences to populations and communities
   ii) Alternatively, can be a source of density-dependent mortality if constant amount of refuge from mortality exists (leads to changing proportion of mortality)

Say, refuge holds 50 individuals...

### Survival rate

<table>
<thead>
<tr>
<th>Density (in and out of refuge)</th>
<th>100%</th>
<th>50%</th>
<th>25%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Refuge</td>
<td>50/50</td>
<td>50/100</td>
<td>50/200</td>
</tr>
</tbody>
</table>

D-d mortality can regulate upper bounds of population size

### D-d mortality can regulate upper bounds of population size

![Graph showing survival rate vs. density](image)

V) Maintenance of species diversity
5. Disturbance
C) Example of Disturbance (Dayton 1971 Ecological Monographs)
   i) System: rocky intertidal of Washington state; looked at competition, predation, & disturbance in determining the size and structure of barnacle (Balanus cariosus) pop.s.
   ii) Examined effect of disturbance by waves & logs pounding on the intertidal
   iii) Example of how disturbance leads to a renewal of resources (space)!

![Graph showing nail survival](image)

v) Results:

<table>
<thead>
<tr>
<th>percent nails surviving</th>
<th>100</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>low</td>
<td>high</td>
<td>high w/ logs</td>
</tr>
<tr>
<td>high</td>
<td>low</td>
<td>high w/ logs</td>
</tr>
</tbody>
</table>

For population structure...

Compare % cover of large mature barnacles
5. Disturbance  
D) Intermediate disturbance hypothesis  
iii) Logic  
\begin{itemize}  
\item[a)] Disturbance interrupts successional sequence by creating patches of different ages \rightarrow different states of succession  
\item[b)] In absence of disturbance, succession leads to climax community characterized by monospecific stand of competitive dominant (or a few) \rightarrow low diversity  
\item[c)] but, at extremely high levels of disturbance, nothing or only a few species of rapid colonizers (or disturbance tolerant species) would persist \rightarrow low diversity  
\item[d)] Recall that competitively superior species typically have poor colonizing capabilities.  
\end{itemize}
5. Disturbance  
D) Intermediate disturbance hypothesis  
iii) Very cool example: Wayne Sousa 1979, Ecology  
   a) System: macroalgae in intertidal boulder field at Ellwood, CA  
   b) Pattern: (succession)  
   successional sere: early $\rightarrow$ mid $\rightarrow$ late  
   species: *Ulva* $\rightarrow$ *Gelidium* $\rightarrow$ *Chondracanthus*  
   *Mastocarpus*  
   *Gigartina*  

5. Disturbance  
D) Intermediate disturbance hypothesis  
iii) Very cool example: Wayne Sousa 1979, Ecology  
   b) Pattern cont’d:  
   physical disturbance - boulders of different sizes roll at different frequencies:  
   
   ![Graph showing disturbance frequency vs. boulder size](image)  

5. Disturbance  
D) Intermediate disturbance hypothesis  
iii) Very cool example: Wayne Sousa 1979, Ecology  
   c) General hypothesis:  
   Species diversity of macroalgae is maintained by intermediate frequencies of disturbance  
   
   d) Specific hypothesis: (observational based)  
   Boulders of intermediate size roll at intermediate frequencies and will have highest species diversity  

5. Disturbance  
D) Intermediate disturbance hypothesis  
iii) Very cool example: Wayne Sousa 1979, Ecology  
   e) Results:  
   ![Graph showing species diversity vs. boulder size and disturbance frequency](image)  

   f) Conclusions:  
   Pattern consistent with intermediate disturbance hypothesis
5. Disturbance
D) Intermediate disturbance hypothesis
   iii) Very cool example: Wayne Sousa 1979, Ecology
       Alternative approach...

   g) Specific hypothesis: (experimental based)
      boulders of similar sizes manipulated to alter their frequency of disturbance will exhibit patterns of species diversity predicted by IDH.

   h) Test:
      i) Collected and sterilized 32 small boulders
      ii) Glued 16 to the bottom to prevent rolling
      iii) Monitored succession of algae

   ii) Glued 16 to the bottom to prevent rolling

   iii) Monitored succession of algae

   i) Results:
      After 1 year, small boulders glued down developed algae communities similar to larger boulders that rolled infrequently