Community Change

• Another community property -- change over time
• Species turnover
• Succession
  – Replacement of one type of community by another
  – Nonseasonal directional pattern of colonization & extinction of species

Succession

• An extremely influential idea in the study of terrestrial plants
• Has also been studied in animal communities
  – intertidal invertebrates
  – carrion
• Has also been studied in microbial communities

Two kinds of succession

• Primary Succession
  – Community change on land that has had no previous community present
  – e.g., previously under water or ice for a long time, formed volcanically
• Secondary succession
  – Community change after an extant community has been removed, by man or natural catastrophe
  – e.g., abandoned farm land, after fire
  – soil seed bank remains

Primary succession
Glacial retreat, Glacier Bay, Alaska
Example: Glacial retreat

- Since 1750, glaciers retreated 98 km
- Expose bare crumbled rock & little soil
- Under ice for 100’s or 1000’s of years
- Initially low N, pH ~7.0 - 8.0
- Distance from glacier indicates time since exposure

Successional sequence

1. Mosses & Lichens
   - Fireweed
   - *Dryas* (N fixing)
2. Willow (pH = 7.6)
3. Cottonwood, Spruce (50 yr)
4. Hemlock
5. (WET) *Sphagnum* moss
   - (DRY) Spruce, Hemlock

Primary succession

Lake level decline

- Lake Michigan dunes
- Positions of ancient beaches still visible
- Expose bare sand
- Under water for 1000’s of years
- Initially low N
- Distance from water indicates time since exposure

Successional sequence

1. Marram grass
   - roots stabilize sand, adds organic matter
2. Sand reed grass
   - Little Bluestem
   - Sand Cherry, Willow
3. Cottonwood (1st tree)
4. Jackpine
5. Black oak (~100 - 150 yr.)
   - + associated shade tolerant shrubs
   - 12,000 years … still Black oak
Secondary succession
Abandoned farm

- Old field, NC
- Farm land
- Original forest cleared 100 - 300 yr. ago
- Soil already well developed
- Seeds present in soil

Successional sequence

1. Crabgrass
2. Horseweed, Ragweed (1 yr.)
   - Horseweed self inhibitory
3. Aster, Ragweed (2 yr.)
4. Broom sedge (3 yr.)
5. Pines (5 - 15 yr.)
6. Oaks, Hickories (50 - 100 yr.)

What drives succession?

- Pattern of (apparently) orderly change is obvious
- Hypotheses about causes
  - numerous
  - controversial
  - long history

Clements

- F. Clements, Early 20th century U.S.
- Plant community is an integrated superorganism
  - Different components (species) seem to work toward some end point
  - Primary succession analogous to development
  - Secondary succession analogous to healing
- Climax community -- self-replacing vegetation; the mature superorganism
Superorganism

- Popular concept, widely cited in early ecological literature
- Non-scientific, based on pre-Darwinian philosophy
- H. Gleason (1920s) provided alternative
  - Individual explanation for why/how species replace each other
- Modern hypotheses based on individual mechanisms

Modern hypotheses

- Summarized by Connell & Slatyer in 1977
- Three mechanisms drive species replacement
  - Facilitation
  - Tolerance
  - Inhibition
- Null hypothesis
  - Random colonization & extinction

Facilitation hypothesis

- Succession proceeds because early species make site more suitable for later species
- Early species only are capable of colonizing barren sites
  - specialists on disturbed sites
- Climax species facilitate their own offspring
- Primary process: Site modification (soil)

Tolerance hypothesis

- Succession proceeds because later species outcompete early species
- Adults of any species could grow in a site
- Which species starts succession
  - Chance
  - Dispersal ability
- Early species have no effect on later species
- Later species replace early species by competition
- Climax species are the best competitors
- Primary process: Interspecific competition
Inhibition hypothesis

- Adults of any species could live at a site
- Which species starts succession
  - Chance
  - Dispersal ability
- Early species inhibit (out compete) later species
  - Persist until disturbed
- Later species replace early species after disturbance

Inhibition Hypothesis

- Climax species are most resistant to disturbance
- Primary process: Priority effects

Random colonization hypothesis

- Nothing but chance determines succession
- No competition, no facilitation, no inhibition
- Colonists arrive at random
- Species in the community go extinct at random

Each hypothesis makes testable predictions

- Is there a well-defined set of early species?
- Is the sequence of species predictable?
- What are the characteristics of the climax species?
- What happens if early species are removed?
- What happens if late species are transplanted into an early site?
### Predictions

<table>
<thead>
<tr>
<th></th>
<th>Facilitation</th>
<th>Tolerance</th>
<th>Inhibition</th>
<th>Random</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Early spp.</strong></td>
<td>Well defined set</td>
<td>Unpredict.</td>
<td>Unpredict.</td>
<td></td>
</tr>
<tr>
<td><strong>Successional sequence</strong></td>
<td>Highly predictable</td>
<td>Moderately predictable</td>
<td>Relatively unpredictable</td>
<td>Unpredictable</td>
</tr>
<tr>
<td><strong>Climax spp.</strong></td>
<td>Facilitate offspring</td>
<td>Best competitors</td>
<td>Resist disturbance</td>
<td></td>
</tr>
<tr>
<td><strong>Remove early spp.</strong></td>
<td>Succession stops</td>
<td>Late species unaffected</td>
<td>Late species accelerated</td>
<td></td>
</tr>
<tr>
<td><strong>Transplant late spp. to early site</strong></td>
<td>Cannot survive</td>
<td>Grow &amp; survive with early spp.</td>
<td>Grow &amp; survive if early spp. removed</td>
<td></td>
</tr>
</tbody>
</table>

### Data: Which hypothesis?

- Succession in different places or at different times may proceed via different processes
  - each hypothesis may be accurate somewhere
- Succession in one place may involve >1 process
  - within a sequence, all hypotheses may be accurate for some species

### Generalizations

- **Facilitation**
  - Common in primary succession
  - pioneers stabilize and add to soil
  - e.g. Saguaro cactus
  - late successional, Sonoran desert
  - grow only in shade of “nurse plants”
  - Less common in secondary succession

- **Hypotheses are not mutually exclusive when the whole community is considered**
**Generalizations**

- **Tolerance**
  - common in old field, secondary succession
  - e.g. Northern midwest
    - later grasses better competitors for nutrients, light
    - early species better dispersers
  - e.g. Species removal, secondary succession (Ohio)
    - early -- annuals, biennials
    - late -- perennials

**Removal experiment #1**

- Remove annuals + biennials
- Facilitation: Perennials ↓
- Tolerance: Perennials NC
- Inhibition: Perennials ↓
- Result: Perennials Unaffected

**Removal experiment #2**

- Remove perennials
- Facilitation: Annuals NC
- Tolerance: Annuals ↑
- Inhibition: Annuals NC
- Result: SMALL Increase in annuals

**OVERALL:** Most consistent with TOLERANCE
Clearly inconsistent with INHIBITION

**Generalizations**

- **Inhibition**
  - Algal succession in intertidal
  - Grazing and drying the main disturbances
  - *Ulva* (green) *Gigartina* (red)
  - Remove *Ulva*, growth of *Gigartina* increases
  - *Ulva* holds a site until disturbance kills it
  - *Gigartina* survive beneath *Ulva*
    - *Gigartina* has a persistent & resistant holdfast
### Secondary Succession

- No guarantee that secondary succession leads back to original climax vegetation
- e.g., tropical rainforest
  - nutrients (N, P, K, etc.) held mostly in biomass, not soil
  - cut forest, remove biomass
  - nutrients leach from soil rapidly
  - new soil conditions do not foster forest regeneration

### Dispersal & Colonizing ability

- Some species specialize on exploiting newly opened sites
- Natural disturbances: tree fall gaps, local fires
  - widely spread in space, unpredictable
  - colonizing species need to:
    - be good dispersers
    - grow quickly to exploit newly opened sites

### Early vs. Late successional species

<table>
<thead>
<tr>
<th></th>
<th>Early species</th>
<th>Late species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seeds / biomass</td>
<td>Many</td>
<td>Few</td>
</tr>
<tr>
<td>Seed size</td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>Dispersal</td>
<td>Wind, Birds, Bats</td>
<td>Gravity, Mammals</td>
</tr>
<tr>
<td>Dormancy in soil</td>
<td>Yes</td>
<td>?</td>
</tr>
<tr>
<td>Herbivory</td>
<td>Low resistance</td>
<td>High resistance</td>
</tr>
<tr>
<td>Shade tolerance</td>
<td>No</td>
<td>Tolerant</td>
</tr>
</tbody>
</table>