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)

} Herbaceous, Pioneer Stage

- 2. Willow (pH = 7.6)
-   Alder (pH = 5.0 N fixing)

} Shrubs

- 3. Cottonwood, Spruce (50 yr)
- 4. Hemlock
- 5. (WET) *Sphagnum* moss
-   (DRY) Spruce, Hemlock

} Trees

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

} Pioneer Stage

- 2. Sand reed grass
-   Little Bluestem

} Grass & Shrubs

-   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

} Trees

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.)

} Pioneer Stage

} Trees

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
- Nonscientific, based on pre-darwinian philosophy
- H. Gleason (1920's) 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

	Facilitation	Tolerance	Inhibition	Random
Early spp.	Well defined set	Unpredict.	Unpredict.	
Successional sequence	Highly predictable	Moderately predictable	Relatively unpredict.	Unpredictable
Climax spp.	Facilitate offspring	Best competitors	Resist disturbance	
Remove early spp.	Succession stops	Late species unaffected	Late species accelerated	
Transplant late spp. to early site	Cannot survive	Grow & survive with early spp.	Grow & survive if early spp. removed	

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

Data: Which hypothesis?

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

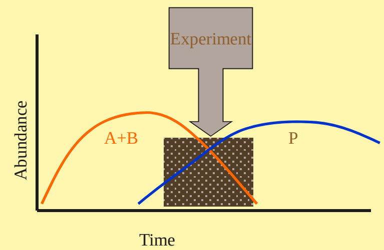
Generalizations

- **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

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

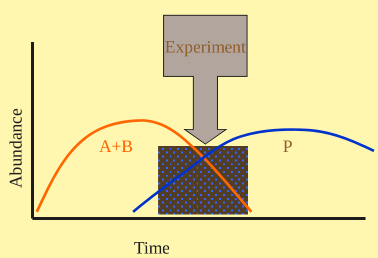


Remove annuals+biennials

Facilitation: Perennials ⇓
Tolerance: Perennials NC
Inhibition: Perennials ⇑

Result: Perennials Unaffected
TOLERANCE

Removal experiment #2



Remove perennials

Facilitation: Annuals NC
Tolerance: Annuals ⇑
Inhibition: Annuals NC

Result: SMALL Increase in annuals
TOLERANCE

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

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