Lecture 18:
Plant community ecology

- Plant community ecology
  - Plant ecology statics: concept of the species association
  - The organismal hypothesis versus the individualistic hypothesis
  - Gradient studies as a resolution of the debate

1

Community: collection of species

in a certain area

2

Plant community ecology originally focused on discovering "community types"

- What species regularly occur with each other?
- Do find significant species associations, (e.g., beech-maple forest, oak-hickory forest, bur-oak savannah)
- Mostly descriptive: experimentation is a recent addition

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Early controversy: Conflicting views of causes of associations

- Organismal or holistic hypothesis: certain species found together because they are biologically integrated and depend on each other's presence like tissues of an organism (typological community concept)
- **Predicts** (1) significant relationships among species and (2) that communities are discrete entities that can be distinguished from one another

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"The developmental study of vegetation necessarily rests upon the assumption that the [association] is an organic entity. As an organism the [association] arises, grows, matures, and dies."

Frederick Clements 1916

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Early controversy: Conflicting views of causes of associations

- Individualistic hypothesis: species are distributed independently of each other; important limitations are 1. dispersal and 2. filtering by the physical environment
- **Predicts** (1) no strong relationship between species and (2) communities are species that share similar range of tolerance to local, abiotic factors

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"…every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favorable conditions…

Plant associations…depend solely on the coincidence of environmental selection and migration…"

Henry Gleason 1926

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How can these conflicting hypotheses be tested?

- **Organismal** (1) significant relationships among species and (2) that communities are discrete entities that can be distinguished from one another
- **Individualistic** (1) no strong relationship between species and (2) communities are species that share similar range of tolerance to local, abiotic factors

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How *were* these conflicting hypotheses tested?

- First, by invective – arguing in the literature (Clements won, Gleason left ecology)
- Second, decades later, by actual data (Gleason won in the long run)
- Data used is gradient analysis
- Pioneers of gradient analysis were Robert Whittaker and John Curtis (1950's)

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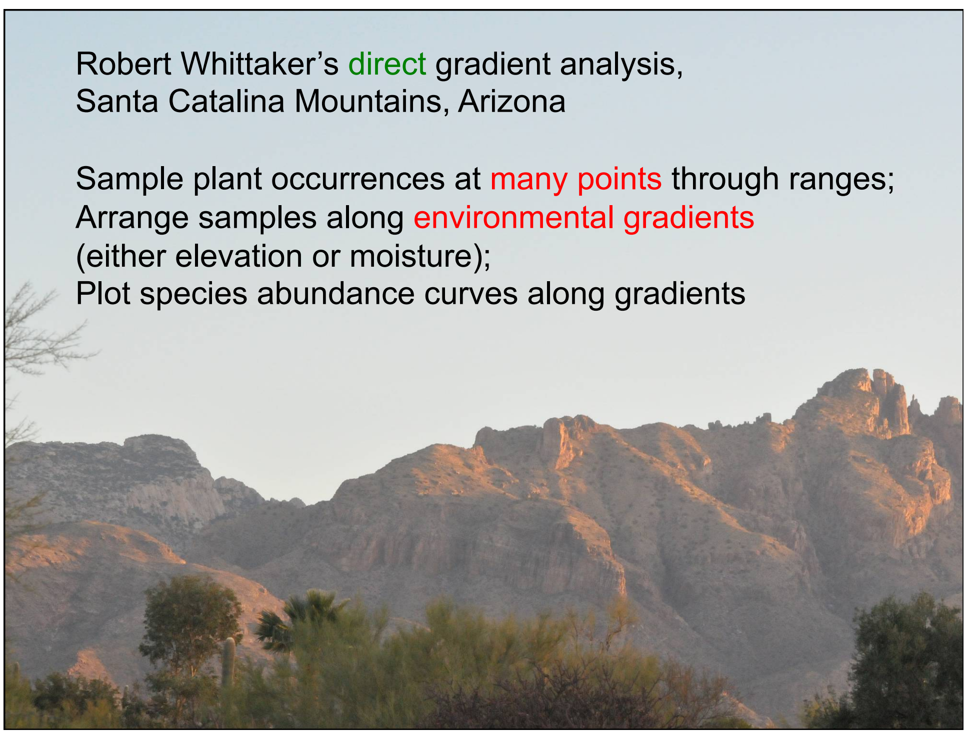

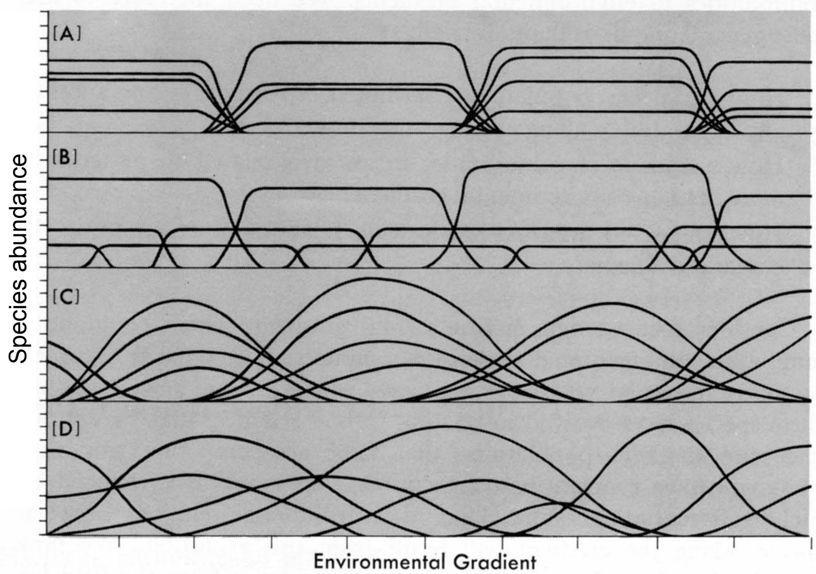

Figure 3·1. Four hypotheses on how species populations might relate to one another along an environmental gradient. Each curve in each part of the figure represents one species population and the way it might be distributed along the environmental gradient.

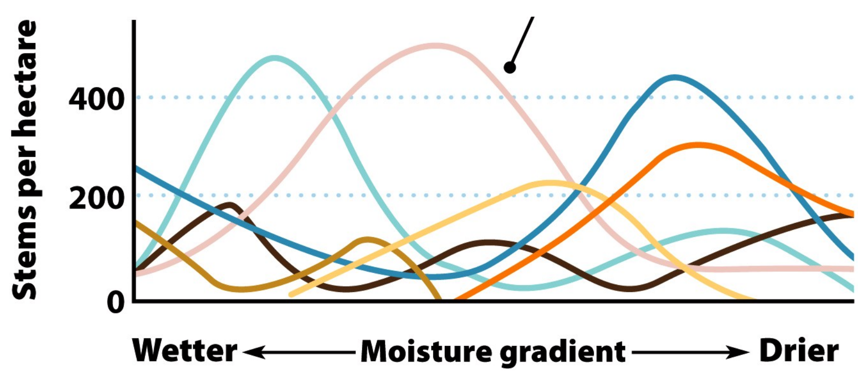

Figure 18.9
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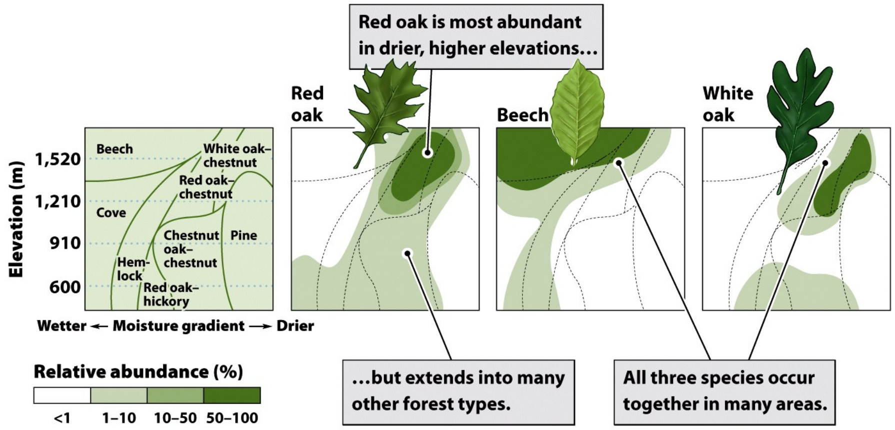

Figure 18.8
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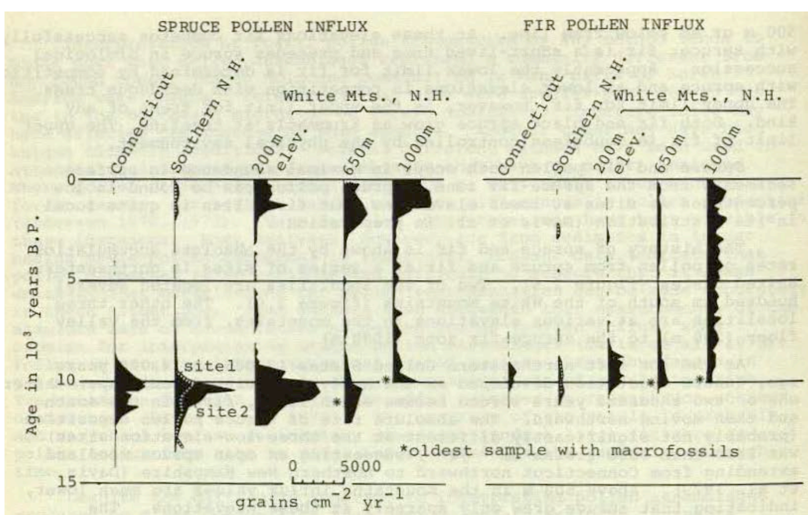

Margaret Davis (1978) looked at pollen from different tree species that was collected in the bottom of bog lakes – could look at occurrence and abundance 1000s of years ago to see if species migrated into area together or individually after glaciers retreated

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Other evidence?

- Curtis's "indirect" gradient analysis reached same conclusion more objectively, using multivariate statistics to assign stands positions along a compositional continuum: did not find strong clustering
- Multiple lines of evidence often needed to topple an old paradigm

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Modern consensus for terrestrial vegetation community structure

- Primarily individualistic: contemporary and paleo data agree that variation is fundamentally continuous, not discrete, and that the strongest environmental filtering is driven by physical factors…
- …but concede that species interactions affect some functions

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Lecture 19: Species interactions: From 2-species population models to community structure

- Lotka-Volterra model of competition: extension of logistic
- Criteria for competitors to coexist
- Empirical testing: Gause's early experiments with protozoa
- L-V model of predation: Predator-prey-cycles?
- One view of community structure: Competition, resource use, and niche overlaps determine who can coexist

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Partial classification of species interactions

- Types of interaction classified (as + or -) by which population suffers and which one benefits
  - Consumer-resource (+/-)
    - Predator-prey (e.g., predators benefit from prey, prey suffer from predators)
    - Plant-herbivore
    - Host-parasite, host-pathogen
  - Competition (-/-) each is hurt by the other
  - Mutualism (+/+) each is helped by the other
- Two main foci of study
  - Population dynamics (ecological effects on *N*'s, can species coexist?, epidemiological models of disease)
  - Evolutionary dynamics (adaptation, coevolution)

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Interspecific competition for resources

- Basic model: Lotka-Volterra equations for two species competing for resources
- Simple outgrowth of logistic equation:
  - Logistic already a has braking term for intraspecific competition within a species
  - Just add a second braking term for interspecific competition between species

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Braking from sp. 1

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

GO!

1. Rewrite logistic with subscripts to indicate Species 1

Braking from sp. 1

Braking from sp. 2

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right)$$

2. Add a term to show effect on Sp.1 by Sp. 2

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right)$$

3. Write matching equation for Species 2

4. α_{ij} = per-capita effect on *i* by *j* = "competition coefficient"

5. These paired differential equations are the *Lotka-Volterra model* for combined intraspecific and interspecific competition

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Possible outcomes of L-V competition

- Expect now to solve for N_1 and N_2 as *f(t), but…*
- Instead, specify 4 possible equilibria:
  - The two species may stably coexist
  - Species 1 may always win ($N_1 = K_1$, $N_2 = 0$)
  - Species 2 may always win ($N_2 = K_2$, $N_1 = 0$)
  - Identity of winner may depend on starting N's
- Outcomes depend on values of K's and α's
- Coexistence requires both species to inhibit their own growth more than they inhibit each other's
- Can expand to consider *n* species

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"Law of Competitive Exclusion"

= 2 species cannot coexist indefinitely when the same resource limits both species

- LV outcomes became widely interpreted as basically unstable
- This is true for the simple math models, but not so true in nature…
- …because various external factors can prevent even unstable competition from going to completion

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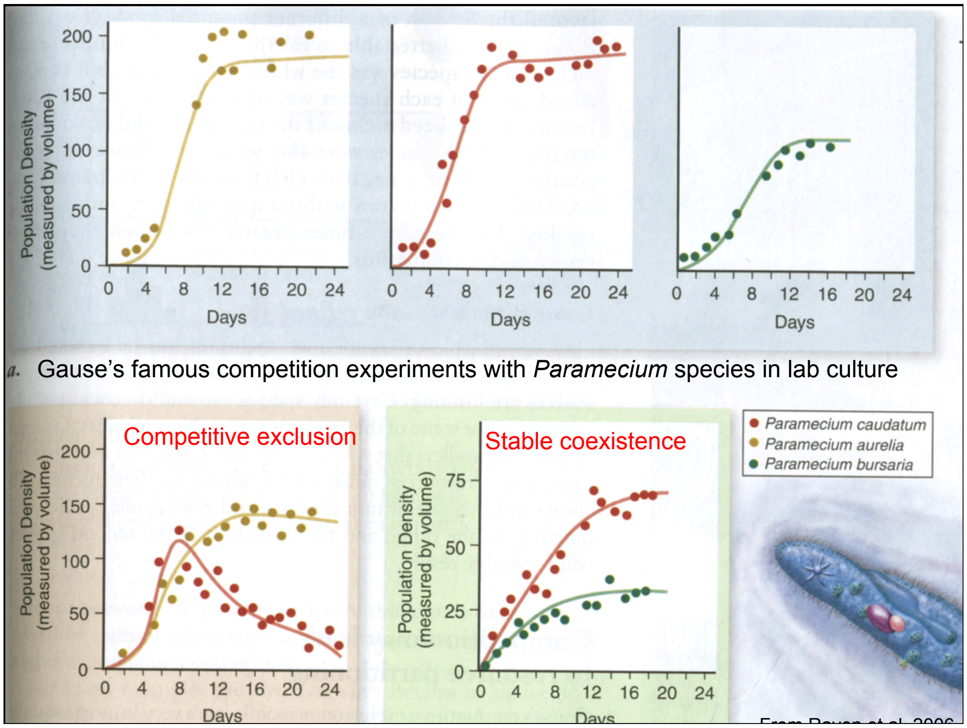
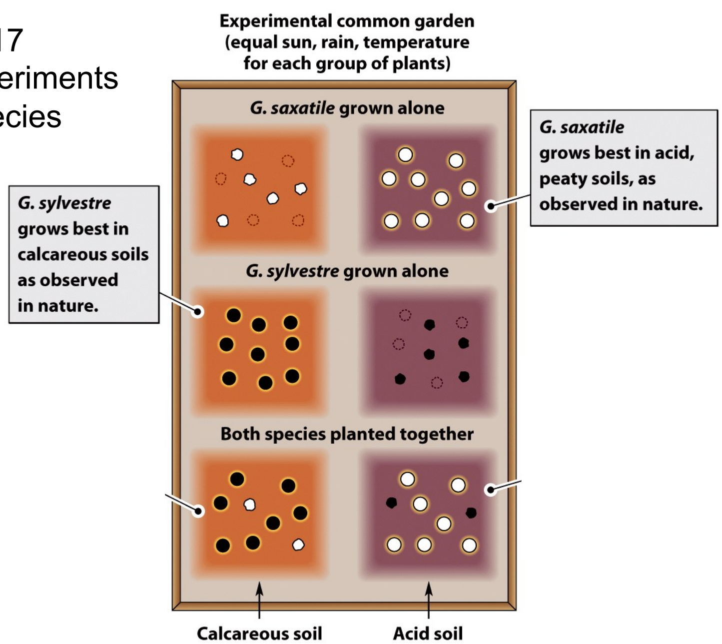


Tansley, 1917
Garden experiments with two species of *Galium:*



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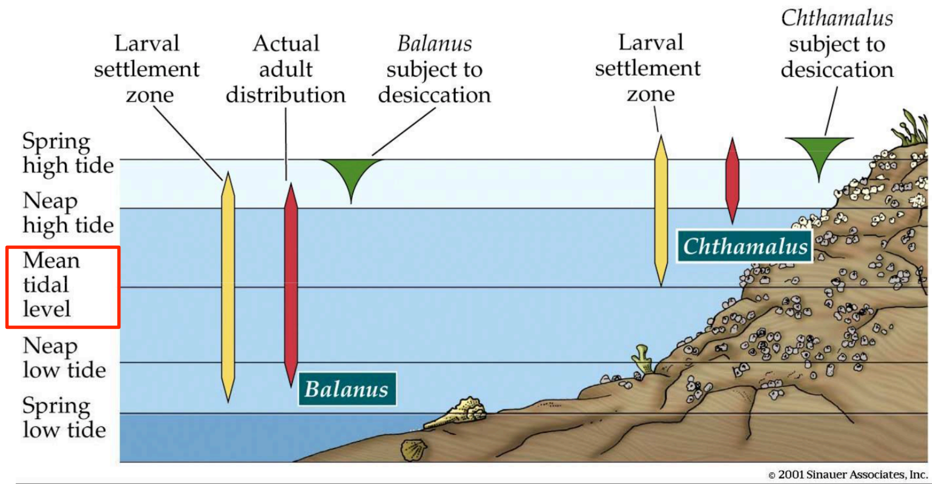
Competition in barnacles



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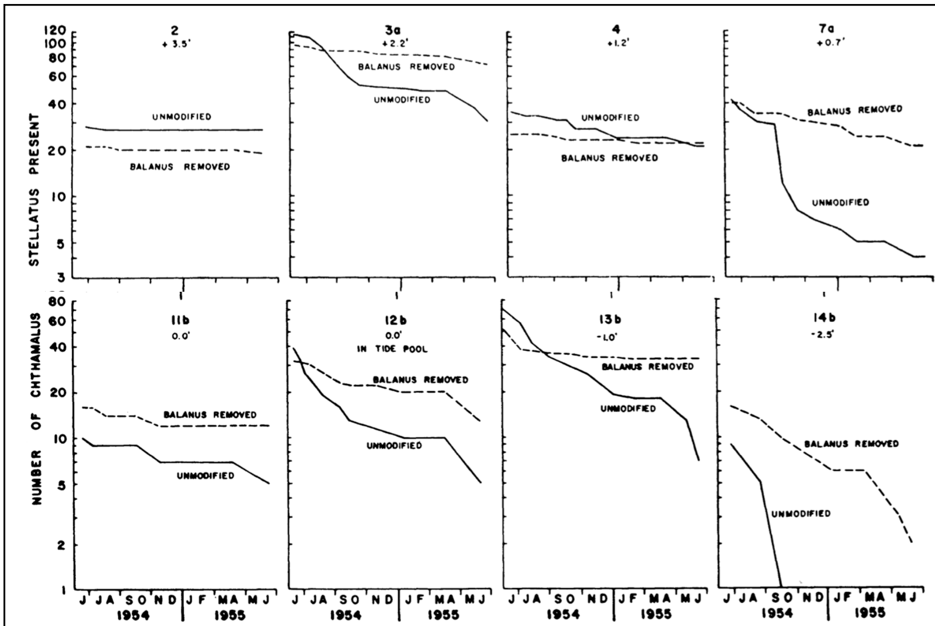

Connell 1961

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Competition in barnacles

- At the majority of sites, *Chthamalus* had higher population size when *Balanus* was removed
- Transplant experiments showed *Chthamalus* could grow at lower levels when *Balanus* removed
- *Balanus* cannot grow at upper levels even when *Chthamalus* is removed

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How are competitive effects manifested in nature, rather than in containers?

- Competitive exclusion is less likely to go to completion…
- …but abundances can be drastically affected…
- …and distributions in space altered.
- Biological effects interact with physical effects: different outcomes in different environments
- Natural selection may select for higher competitive ability or for reducing resource-use overlap

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