Week 14: Roles of competition, predation & disturbance in community structure.

Lecture summary:

(A) Competition:
- Pattern vs process.
- Simberloff & Strong criticism.
- Neutral models & null hypotheses.

(B) Predation, herbivory, parasitism & disease:

(C) Disturbance:
- Chapters 16, 19, 21 (4th ed.)
2. (A) Role of competition in community structure:

- Prevalent view among ecologists in 1970s:
  - Competition was of overriding importance in, (1) shaping community structure and (2) how many species can coexist.
    - Especially **competitive exclusion**:
      - Existence of a single species when two or more compete for the same limiting resource = limit to similarity of competing species.

- More recently this view has given way to:
  - More prominence for **non-equilibrial & stochastic** factors, such as physical disturbance and condition variability.
  - But under certain circumstances competition can be important, so:
    - “to what extent and in which cases in practice is interspecific competition an active force?”
3. Evidence for competition:

- Intraspecific competition was only detectable in 20% of published studies on phytophagous insects and interspecific competition was found in 41% of them.
- Possibly because many available niches on plants remain unoccupied (Fig. 19.2 4th ed.).
- Herbivores also show less competition than plants, carnivores or detritivores:
  - Perhaps because their food resources are abundant and less likely to be limiting.

(a) England (b) Papua New Guinea (c) New Mexico & Arizona
4. Evidence for competition:

- Evidence of current competition in action includes:
  - Experimental removal of species to determine:
    - Whether remaining species fill the available niche space, or,
    - Resource patchiness may lead to coexistence (Fig. 20.2, 3rd ed.).
  - Connell’s “ghost of competition past” may also have been important in niche differentiation.

![Graph showing coexistence and competitive exclusion](image)

**Heterogeneous environment** (closed symbols) generates **coexistence** and not niche differentiation. **Homogeneous environment** (open symbols) leads to **competitive exclusion**.
5. Evidence from community patterns:

• 2 basic steps:
  
  (1) Predict community structure given the existence of interspecific competition:
  
  • (i) Coexisting competitors should show niche differentiation.
  
  • (ii) Niche differentiation often appears as morphological differentiation.

  • (iii) Negative spatial associations expected among similar species with little niche differentiation.

  (2) Examine real communities to see if they conform to this structure (Fig. 20.3).
  
  • Most likely to detect current competition within feeding guilds:
    
    • “groups of species that exploit the same class of environmental resource in a similar way” (after Root, 1967).
6. Niche differentiation in bumblebees:

- Fig. 20.3
- 3rd ed.
7. **Niche differentiation in weasels (Fig. 20.4, 3rd):**

- Morphological niche differentiation by upper canine size and resource partitioning in weasels (Fig. 20.4).
8. **Temporal niche differentiation in flowering periods:**

- Fig. 20.5 (3rd ed.) shows temporal separation of nectar resources in 10 Costa Rican rainforest plants to reduce competition for hummingbird pollinators.
9. Spatial niche differentiation in birds of the Bismarck Archipelago near New Guinea:

Fig. 19.11: “Checkerboard” distribution of 2 cuckoo dove species (4th ed.).

Fig. 21.19: Incidence functions ($J$) against number of species ($S$) on islands for: (a) “supertramps”, (b) good colonizer/competitor, (c) good competitors on larger islands (4th ed.).
10. The criticisms of Simberloff and Strong:

- Dan Simberloff and Don Strong criticized the tendency to interpret “mere differences” as evidence for interspecific competition.
- They also pointed out the weaknesses inherent in observing patterns rather than experimenting to detect processes such as competition.
11. Simberloff and Strong’s solution:

- Competition theory predicts that niches will be arranged regularly in niche space rather than randomly and similar niches should differ more than would be expected by chance alone.

- Thus they established the criterion of:
  - testing experimentally,
  - whether community patterns differ significantly from random assembly,
  - in the absence of any interactions among the species,
  - before competition can be invoked as a structuring mechanism.
12. Neutral models and null hypotheses:

- These are randomly reassembled mixes of species based on real communities, excluding the consequences of biological interactions.
- Constructed in order to establish a null hypothesis of what a community would look like in the absence of biological interactions.
- If the community under investigation differs significantly (statistically) from this neutral model then the null hypothesis can be rejected, and an alternative hypothesis that invokes a mechanism (such as competition) can be inferred.
  - This is the Popperian method of science in which statistical power is reinforced by hypothesis rejection or falsification as deductive rather than inductive.
  - We cannot test statistically whether things are significantly similar - only whether they are significantly different (hypothesis falsification).
13. Randomly reassembled lizard communities compared to actual community resource use overlaps (Fig. 19.7, 4th):

- RA1
- RA2
- RA3
- RA4

Number of species in the community

Mean overlap in resource use, $\alpha$
14. The role of competition - Conclusions:

• After highly acrimonious argument in the early 1980s about the role of competition and the development of neutral models and null hypotheses, most people now agree that the neutral model approach is appropriate.

• Both critics and supporters of the approach have developed the method and applied it to interactions within guilds where competition is suspected.
15. Problems still remain:

- But neutral models can fail to detect competition even when it is included deliberately because current communities are the product of both current competition and the ghost of competition past which may have eliminated species most vulnerable to competitive exclusion:
  - e.g. Colwell & Winkler, 1984 - “A null model for null models in biogeography” - “God” and “Wallace” models.
  - But this approach still only compares patterns and cannot and should not replace manipulative experiments and detailed understanding of field ecology.
16. (B) Role of predation in community structure

- Effects of grazing herbivores:
  - Herbivory, predation, disease and parasitism, competition, earthquakes, fire, rain, wind, temperature etc. can all disturb communities.
- Disturbance is:
  - “any relatively discrete event in time that removes organisms or otherwise disrupts the community by influencing the availability of space or food resources, or by changing the physical environment. A general consequence is likely to be the opening up of space, or freeing up of resources, that can be taken over by new individuals.”
  - For example, a predator, or herbivore, or lawn mower, or a strong wave, or a strong wind can all open gaps in communities.
17. Effects of grazing disturbance on community richness:

- Grazing by rabbits can strongly influence the structure of plant communities, especially at intermediate grazing intensities (Fig. 21.1, 3rd).
18. Intermediate grazing promotes most diversity through its influence on competition - “exploiter-mediated coexistence” (Fig. 21.2, 3rd ed.):
19. The effects of predators:

- Removal of predatory starfish by Paine (1966) led to reduction in community species number from 15 to 8 because space made available by the predator helped competitively subordinate species and increased species diversity.

- Fig. 7.8 (Begon, Mortimer & Thompson, 1996).

- Exploiter-mediated coexistence.
20. Effect of switching predatory behavior:

- Frequency-dependent effects can also influence community structure:
  - For example, switching in roach according to density of planktonic or benthic waterflea prey (Fig. 21.3, 3rd ed.).
21. The effects of parasites and disease:

- These exploiters can also affect other interactions and facilitate coexistence of species as in Fig. 21.4 (3rd ed.).

![Graph showing the effects of disease on plant growth](image)
22. Impact of invasion into susceptible communities:

- Strongly negative effects on communities can also occur for highly pathogenic invading diseases such as malaria and bird pox in Hawaii which may have exterminated 50% of the endemic bird species.
- Also the destruction of chestnut and elm forests in North America by introduced pathogens.
- These effects are also likely to be frequency dependent:
  - Influenced by the frequency of encounter in high density populations.
23. (C) Role of disturbance in community structure

- Community structure and temporal variation in conditions:
  - Conditions constantly change in space and time and they have a marked impact on ecological processes and hence on species composition of communities (Fig. 21.5, 3rd ed.).
24. Effects of density-independent factors:

- Periodic, density independent reductions in population size may be expected to promote coexistence of competing species (Fig. 21.6, 3rd ed.).
25. Effects of density-independent factors:

- Frequency of disturbance also impacts diversity, as does growth rate (rate of increase) of species:
  - Fig. 21.7, 3rd ed. (Huston, 1979).
26. Effects of both disturbance frequency and species growth rate on community diversity (Fig. 21.8, 3rd).
27. Disturbances and patch dynamics:

• Includes the effects of movement among patches of resource available for colonization:
  • Dynamics within patches are like Lotka-Volterra interactions, but extinctions can be reversed or created by immigration and emigration:
    • Like metapopulations.
28. Dominance-controlled communities:

Some species are competitively superior:

- Gaps lead to succession-like changes in species composition and disturbance knocks the community back to an earlier stage (Fig. 16.16 & Table 21.1) from pioneer species \((p)\) to mid-succession species \((m)\) to climax competitor species \((c)\).
  - Diversity is also greatest at intermediate levels of disturbance (Figs. 16.17 & 16.18) = Connell’s intermediate disturbance hypothesis.
  - Fig. 7.9 (Begon, Mortimer & Thompson, 1996).
Figure 16.16 (4th ed.):
Table 21.1 Some species characteristic of pioneer, mid-successional and climax stages after disturbances in four contrasting communities. The sequence may take hundreds of years after glacial retreat or abandonment of an old field (Crocker & Major, 1955; Tilman, 1988, respectively—see Chapter 17, Section 17.4.3), but only a few years in the case of boulders overturned on a stormswept beach (Sousa, 1979a—see Chapter 17, Section 17.4.3), or a few days in stream pools scour out by a flash flood (Power & Stewart, 1987).

<table>
<thead>
<tr>
<th>Disturbance</th>
<th>Pioneer species, ( p_1 )</th>
<th>Mid-successional species, ( m_1 )</th>
<th>Climax species, ( c_1 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glacial advance and retreat</td>
<td>Mosses, <em>Dryas</em>, prostrate and shrubby willows</td>
<td>Alder, cottonwood, sitka spruce</td>
<td>Western and mountain hemlock</td>
</tr>
<tr>
<td>Old field abandonment</td>
<td>Summer and winter annuals</td>
<td>Herbaceous perennials, red cedar</td>
<td>Sugar maple, American beech</td>
</tr>
<tr>
<td>Overturned boulder</td>
<td><em>Ulva</em></td>
<td><em>Gelidium</em>, <em>Rhodoglossum</em>, <em>Gigartina lectorhynchos</em></td>
<td><em>Gigartina canaliculata</em></td>
</tr>
<tr>
<td>Stream flood</td>
<td>Diatoms and blue-greens</td>
<td><em>Rhizoclonium</em></td>
<td><em>Spirogyra</em></td>
</tr>
</tbody>
</table>
Figure 16.17 (4th ed.):
Figure 16.18:

- 4th ed.
Figure 7.9:

- Connell’s “intermediate disturbance hypothesis”
  - A - opportunistic spp.
  - B - secondarily colonizing spp.
  - C - climax spp.
    - Begon, Mortimer & Thompson (1996)

Heron Island, Queensland, coral reef

△ - damaged
○ - undamaged
34. Founder-controlled communities:

- All species are competitively similar:
  - Succession is not expected.
  - There is no competitive exclusion.
  - Presence in the community becomes a lottery (Fig. 16.21):
    - Some tropical reef fish communities may be like this and diversity may remain high.
    - Species may be competing for living space “in which larvae are the tickets, and the first arrival at the vacant space wins the site, matures quickly and holds the space for its lifetime.”
Figure 16.21 (4th ed.):