Agents of Pattern Formation: Biotic Processes
Foundations of the Pattern and Process Paradigm

Watt's (1925, 1947) observations of forest gap dynamics formed the basis for the pattern-process paradigm we use today.
Foundations of the Pattern and Process Paradigm

Watt (1947):
The Unit Pattern

The “unit pattern” is the full representation of the pattern in all its phases.

The phases of the community should be present in relative abundances corresponding to the duration of each phase: translation of temporal dynamics into spatial pattern.
Foundations of the Pattern and Process Paradigm

- Building (15.1%)
- Mature (16.3)
- Degenerate (42.9)
- Hollow (25.7)

Departures from this phasic equilibrium either in space or time could be measured and correlated with the changed factors of the environment.
Foundations of the Pattern and Process Paradigm

- The “climax pattern” (Whittaker 1953) is a steady-state pattern of a variety of community types across a landscape.

- The “shifting mosaic steady-state” (Borman and Likens 1979) is a stationary distribution of successional stages, wherein fine-scale elements undergo gap dynamics while the aggregate forest appears constant.

The steady-state is a statistical construct dependent on the scale of reference!
Foundations of the Pattern and Process Paradigm

Main heuristic points:

- Demographic processes, acting in and of themselves, should generate a pattern with predictable characteristics.
- This expected pattern could serve as a reference standard and departures from this, observed for real systems, could be interpreted as interesting deviations.

Fig. 9. The spatial distribution of stand-development phases in an undisturbed, 1-km-wide, central zone of a Yugoslavian virgin forest. (After Mayer from Remmen 1989)
Demographic Processes as Agents of Pattern

- Establishment
- Growth
- Mortality
- Dispersal
Interactions and Feedbacks: 
*Interactions of biotic processes*

Shugart (1984, 1987)

<table>
<thead>
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<th>Mortality</th>
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<td>Gap</td>
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<td>1</td>
<td>3</td>
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<tr>
<td>No</td>
<td>2</td>
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- Roles 1 and 4 are self-reinforcing
- Role 2 creates conditions that favor other species
- Role 3 depends on other agents for persistence

Environmental conditions lead to characteristic combinations of roles of trees.

- Frequent disturbance?
- Low sun angle at high latitudes?
Interactions and Feedbacks: 
*Interactions of biotic processes with physical template*

Tilman (1982, 1985)

- **Resource-ratio hypothesis:**
  - Species vary in relative growth rates in response to levels of resource abundance.
  - The species best adapted to local resource levels “wins” in competition.
  - Spatial heterogeneity in these resources can generate patterns in species diversity.

Species differences in adaptation to varying resource abundance play out along the physical template (in space and time) to yield characteristic patterns of abundance.
Interactions and Feedbacks:
*Interactions of biotic processes with physical template*

Grime (1977, 1979)

- Life history strategies:
  - *Competitor*: continuously abundant, but depressed under low resource levels (in time or space).
  - *Stress-tolerant*: continuously rare, displaced spatially to resource-poor sites.
  - *Ruderal*: temporarily abundant, displaced in time by more competitive species.

These strategies play out on the physical template (in space and time) to yield characteristic patterns of abundance.
Figure 7.13 Grime’s Triangular Model

- Increasing competition
- Intermediate life history strategies
- Ruderal

Douglas fir

W. hemlock

Red alder
Interactions and Feedbacks:
Interactions of biotic processes with physical template

Smith and Huston (1989)

- Life history strategies entail compromises that dictate competitive abilities under varying resource levels. A plant can be:
  - Competitive for light, but won’t do well in the shade.
  - Tolerant of drought (or low nutrients), but won’t be competitive under high resource availability.
  - Competitive under high light and moisture (nutrients), but not the converse (i.e., shade and drought).

These strategies play out on the physical template (in space and time) to yield characteristic patterns of abundance.
Interactions and Feedbacks: *An Illustration*

METAFORE: Cellular Automaton Model (Urban 1999)

- The physical template
  - Elevation gradient—higher elevations are cooler and wetter

![Diagram showing gradient from Warm to Cool](image)
Interactions and Feedbacks: An Illustration

METAFORE: Cellular Automaton Model (Urban 1999)

- Competitive relationships
  - White fir most competitive
  - Lodgepole pine more cold tolerant
  - Ponderosa pine more drought tolerant
Interactions and Feedbacks: An Illustration

METAFORE: Cellular Automaton Model (Urban 1999)

- Mortality
  - Probability based on cell age and species longevity.

- Seed dispersal/Establishment
  - Probability of a given species establishing in an empty cell is based on the abundance of that species in an 8-cell neighborhood around the empty cell and the environmental response of that species.
Interactions and Feedbacks: An Illustration

METAFORE: simulation results (100x100 cells, 500 years)
Implications: Conservation Practice

- Watt’s unit pattern
  - Landscape at equilibrium with its environment and with its internal biotic processes should exhibit a stationary distribution of patch area in various types. What is the minimum size of ecosystems that could be self-sustaining?

- Smith and Huston’s life history strategies
  - On homogeneous, mesic sites--strategy would be to manage in time, maintaining a variety of stand ages, because succession would lead to less diversity through competitive exclusion.
  - On heterogeneous sites--strategy would be to manage in space, because a variety of physically contrasting sites will support and maintain more diversity.
Implications: Anthropogenic Climate Change

Biotic processes (competition) displace species from their optimal sites (fundamental niche) to sites where they can persist under competitive pressures (realized niche).

THUS...predicting species responses to climate changes by translating species distributions to a shifting environmental template is problematic. Must also consider competitive relationships and their changes in a changing environment.