Mechanisms of succession and regeneration

Outline:

Mechanisms of succession and vegetation dynamics.

Synthetic concepts and simple models of forest dynamics

Overview of the modern conceptual framework

Mechanisms of Succession and Vegetation Dynamics

A *mechanism* of succession is a process of interaction that contributes to successional change; it is a "proximate cause" of vegetation change.

What is termed a "mechanism" varies according to the level of organization (e.g. landscape/ecosystem, community, and individual plant levels of organization). E.g. stand-level tree mortality caused by drought can be a mechanism at a landscape or ecosystem level, competition is a mechanism of succession at the community level, and physiological processes are mechanisms at the level of individual plants.

A *pathway* of succession is a temporal pattern of ecosystem change (i.e. the sequence of plant communities that develop and change during succession).

A *model* of succession is a conceptual construct to explain a successional pathway by combining various mechanisms and specifying the relationships among the mechanisms and the various phases or stages of a successional pathway.

Models may be verbal, diagrammatic, or quantitative.

Models may be specific to a system or they may be general.

Clements' (1916) mechanisms (also called processes) of successional change:

nudation–   removal of vegetation by disturbance

migration –   arrival of the plants to the available site

ecesis –   establishment of plants (from seed and vegetative reproduction)

competition –   interaction of the plants which may eliminate some species

reaction --   modification of the site by the plants in a way that guides or drives succession

Egler's (1954) model of *initial floristic composition* versus *relay floristics* (see Kimmins Fig. 17-4)

Relay floristics model emphasizes reaction and seral stages resulting from successive waves of plants occupying the site.

Initial floristic composition model stresses the individualistic concept of the plant association of H. Gleason and the importance of differential growth rates and longevities of species. Many of the species that are dominant in later seral stages may be present early in succession but may be less abundant or

grow more slowly.

<u>Connell and Slatyer's (1977) three-way pathway model of succession</u>

They recognize three general pathways and associated mechanisms of successional change (see Fig. 17-3 in Kimmins):

a. *Facilitation*—a limited group of "early successional species" modify the environment so that it is less suitable for new recruitment of early successional species and more suitable for "late successional species (similar to Clements' reaction)

Possible modes of facilitation are:

amelioration of environmental stress

increase in resource availability

enhanced invasion

b. *Tolerance* – plants modify environment so that it becomes less suitable for "early successional species" but this has little or no effect on subsequent recruitment of late successional species

Possible modes of tolerance are:

passive tolerance (differences in life history traits such as growth rate and longevity)

active tolerance (ability to endure low resource levels)

c. *Inhibition* -- early occupants modify the site and inhibit both early and late successional species.

Generalizations about Connell and Slatyer mechanisms:

a. Most successional sequences involve a mixture of mechanisms (Egler 1954). Facilitation at early stages may be replaced by inhibition or tolerance at later stages.

b. More than one mechanism may operate simultaneously in the same stand (i.e. at the same seral stage).

c. The same species may be involved in more than one mechanism at different life history stages.

Advantages of the Connell and Slatyer model:

a. more precise vocabulary for describing plant interactions;

b. focus on demographic and ecophysiological proximate causes rather than vague and controversial causes of succession such as Clements' emphasis on the life history of the super-organism (or, supraorganism).

Some Simple Conceptual Models Useful in Forest Dynamics

The Forest Growth Cycle (T. Whitmore)

This stresses the importance of tree-fall gaps and the adaptations of some tree species to regenerate beneath gaps of different sizes. (This is similar to P. Grubb's concept of the *regeneration niche* discussed under population ecology.)

The forest growth cycle was formalized by T. Whitmore in c. 1976 for tropical rain forests but is based on the ideas of A.S. Watt (1925) about "gap dynamics" in beech woodlands in England.

The forest growth cycle stresses the phasic development of forests:

The gap phase -- focus on the role of gaps in filtering which species establish in the gap; importance of gap traits (size, shape, drainage, presence of tree mounds, logs, etc.); rate of gap closure by lateral encroachment versus height growth of juveniles.

The building phase -- patch of rapidly growing and self-thinning trees in transition from the understory to the main canopy; focus is on height growth rates of different species.

The mature phase -- long period of continued dominance of the site; focus is on maximum longevity, residence time in the canopy, modification of the understory site conditions (e.g. inhibition mechanisms), long-lasting site modifications (e.g. of the soil).

The approach often aims at the identification of specific traits of trees that may make them dependent on gaps (i.e. "gap specialists") or dependent on gaps of particular characteristics (e.g. large vs. small gaps, well-drained vs. poorly drained gaps, etc.)

The "forest growth cycle" conceptually is the basis for computer simulation models known as "gap models" that simulate the growth and succession of tree species in small plots representing the canopy gap created by the death of a large tree (e.g. JABOWA and FORET models; see Kimmins ch. 21). These models initially made the simplifying assumptions (1) that trees established as "saplings" to avoid dealing with the complexities of germination, seedling establishment and seedling survival, and (2) that the saplings grow according to their diameter-age relationship as limited mainly by light competition and modified by soil moisture, soil nitrogen, and temperature. Thus, gap computer models are based on simplifying assumptions of the more complex features of gap dynamics.

Through the forest growth cycle it is possible that *global compositional equilibrium* may be maintained throughout the whole stand, whereas at any point in the stand the species composition may be unstable. This is similar to the "shifting mosaic" idea of A. Aubreville (1938) and the "shifting mosaic steady-state" of Borman and Likens (1979).

Oliver's Model of Whole-Stand Replacement (see p. Kimmins p. 401 and notes on Population Ecology).

In this model the emphasis is on severe, coarse-scale disturbances that initiate even-aged tree populations. Over time, differential tree growth rates and differences in species' abilities to tolerate understory conditions result in the pattern of stand development. In the structurally complex, multi-age stage of old growth the dominant mechanisms of forest change are quite similar to those described by Whitmore's Forest Growth Cycle.

The forest growth cycle has been applied both to fine-scale treefall gap dynamics and to "whole-stand replacement" following coarse scale disturbances that destroy entire stands.

<u>Tree Regeneration Modes</u> (see Veblen 1992)

The concept of regeneration mode is a useful way of describing broad patterns of tree regeneration in relation to both The Forest Growth Cycle and Oliver's Model of Whole-Stand Replacement.   The focus is on characterizing the regeneration mode of a tree population rather than describing a pattern of multi-species stand development.

Regeneration mode describes a species' behavior in relation to disturbances of different spatial scales. It can be inferred from data on tree age structures and spatial patterns.

There is a <u>continuum</u> of regeneration modes described as:

1. *Catastrophic mode* – cohort establishment after coarse-scale disturbance; even-aged structure; fits early stages of Oliver's model of whole stand replacement.

2. *Continuous mode* – highly shade tolerant species that can complete their life cycle beneath a relatively closed forest canopy; in a strict sense this is relatively rare. Implies continuous juvenile recruitment and growth into the main canopy, even though attainment of dominance may be favored by the death of another canopy tree.

3. *Fine-scale gap phase mode* – tree regeneration is dependent on canopy openings created by the death of the former canopy occupants; the scale of the canopy gap needs to be defined but is usual small (e.g. canopy opening diameters of c. 4 m to 40 m). Difference between continuous and gap-phase mode, is that in the latter juveniles remain suppressed or die in the absence of a gap whereas in the continuous mode juveniles survive and slowly grow even in the absence of a gap.

Two sub-modes of fine-scale gap phase regeneration (P. Marks 1974):

a. *new recruitment* from new seed dispersal or from a seed bank;

b. *reorganization response* in which advance regeneration is released (either from seedlings or vegetative shoots). Reorganization response also includes growth of non-tree species and lateral encroachment from surrounding mature trees.

The regeneration mode concept allows description of the behavior of separate tree populations in a mixed-species stand (some may be remnants from the catastrophic mode and others originated from fine-scale gap phase regeneration).

Modern Framework: A Hierarchical Patch Dynamics Paradigm of Vegetation Dynamics

<u>Disturbance and the Patch Dynamics Perspective</u>

Disturbance: "any relatively *discrete* event in time that disrupts ecosystem, community, or population structure and *changes resources*, substrate availability or the physical environment." (Pickett and White 1985).

How does this definition compare with Grime's (1979) definition of disturbance?

Is disturbance the same as *perturbation*?

1. *Patch dynamics perspective*: the patchiness in vegetation is both due to patchiness in the underlying

physical environment and to vegetation responses to disturbances.

2. A *disturbance regime* is a description of the spatial and temporal characteristics of disturbances affecting a particular landscape over a particular time period.

Descriptors (or parameters) of a disturbance regime are for each kind of disturbance (e.g. fire, blowdown, insect outbreaks, etc.):

a. size of area disturbed per event

b. spatial distribution (in relation to environmental gradients and also in terms of large patch size vs. small patch size, etc.)

c. frequency (mean number of events per time period)

d. mean return interval (mean number of years between successive events)

e. predictability (i.e. do events occur regularly or sporadically? High statistical variance of the mean means low predictability. Simply minimum and maximum intervals between disturbance events are useful descriptors of predictability)

f. rotation period (also called turnover time or disturbance cycle; it is the average time required to disturb an area equivalent to the size of the study area once.)

g. magnitude measured as:

> 1. intensity (physical force), or as

> 2. severity (impact on the vegetation; usually measured as amount of plant mortality)

h. disturbance interactions:

> 1. synergism (combined effects are greater than the sum of independently occurring disturbance events; e.g. insect outbreak in combination with a pathogen attack, or an earthquake during a drought)

> 2. timing or sequence of occurrence (e.g. browsing following fire has a different impact than browsing before a fire)

A Broad-Scale Causal Hierarchy of Vegetation Dynamics

> see Pickett et al's "hierarchy of causes of succession" in Table 17-1 (p. 476) in Kimmins.

> Three broad categories that incorporate proximate causes or mechanisms of succession across a range of organizational levels from ecosystems, communities, populations and individual organisms:

> 1. Site availability due to coarse-scale disturbance.

> 2. Differential species availability due to dispersal differences, seed banks, bud bank, etc.

> 3. Variations in species performance (ecophysiology, life history, competition, allelopathy, etc.)

This hierarchy is useful as a checklist of possible causes of succession and vegetation dynamics.

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