

paper "The Individualistic Concept of the Plant Association" (Gleason 1926). Gleason's writings, as reviewed by McIntosh (1975), have provided a point of departure for the development of population-level theories of succession that consider new insights into evolutionary biology and the importance of consumer as well as producer influences. Reviews by Drury and Nisbet (1973) and Horn (1974, 1975, 1981) explored theories of succession that are based on properties of organisms rather than emergent properties of the ecosystem. The basic premise is that evolutionary strategy (Darwinian selection and competitive exclusion) and characteristics of the life cycle determine the position of species in successional gradients that are constantly changing depending on disturbances and physical gradients. Because Clements' holistic theory can also be viewed as an evolutionary theory of population and ecosystem, ecologists may not be so far apart as a reading of their respective position papers might indicate. This position, in general, is the one taken by Whittaker and Woodwell (1972), Whittaker (1975), and Glasser (1982), who noted that although the early colonization phase is often stochastic (chance establishment of opportunistic organisms), later stages are much more organizational and directional.

Sooner or later, theories get tested in the practical world of applied science—for example, in forest management. Foresters, by and large, find that forest succession is directional and predictable. To assess future timber potential, they often develop models that combine natural successional trends with disturbance and management scenarios that modify natural development. For example, on the Georgia Piedmont, the natural forest succession is from pines to hardwoods. Because pines are now more valuable commercially than hardwoods, efforts are made to arrest this succession, so that the pine stages can be retained and regenerated, especially in areas under commercial timber management. It is predicted that hardwood stages will continue to increase in area coverage, although at a slower rate than would be the case if only natural succession were involved. Urbanization and suppression of fire, both of which favor hardwoods over pines, are important factors in future projections. Because the composition of the Piedmont forest is strongly influenced by human management, projected future composition will follow trends of natural succession. The interface between theory and forest management is discussed in detail by Shugart (1984) and Chapin et al. (2002).

Self-Organization, Synergetics, and Ascendancy

A major key to ecosystem development is the concept of *self-organization*, based on Prigogine's theory of non-equilibrium thermodynamics (Prigogine 1962). **Self-organization** can be defined as the process whereby complex systems consisting of many parts tend to organize to achieve some sort of stable, pulsing state in the absence of external interference. The spontaneous formation of well-organized structure, pattern, and behavior from random or unorganized initial conditions—in other words, going from chaos to order—is widespread in nature. Self-organized ecosystems can only be maintained by a constant flow of energy through them; therefore, they are not in thermodynamic equilibrium. The process of many parts working together to achieve order has been termed **synergetics** by Haken (1977). Ulanowicz (1980, 1997) used the term **ascendancy** for the tendency for self-organizing, dissipative systems to develop complexity of biomass and network flows over time, as is seen in the process of ecological succession. Both Holland (1998) and S. Johnson (2001) spoke of the process as **emergence**.

We see that ecosystem development is more than just a succession of species, and more than just evolutionary interactions, such as competition and mutualism; there is an energetic basis. There is a large volume of literature on self-organization, including papers by Eigen (1971), H. T. Odum (1988), and Müller (1997, 1998, 2000); and books by Kauffman (1993), Bak (1996), and Camazine et al. (2001), in addition to those cited earlier. For a less technical discussion of self-organization, see Li and Spratt (2000). Wesson (1991), in his book *Beyond Natural Selection*, argued that what we call *self-ordering* must be added to natural selection to explain the evolution of complex systems. Smolin (1997) extended the self-organization theory to the origin and evolution of the universe that began with the Big Bang and a mass of random-moving molecules but evolved into the current, highly organized system including Earth.

2 Concept of the Climax

Statement

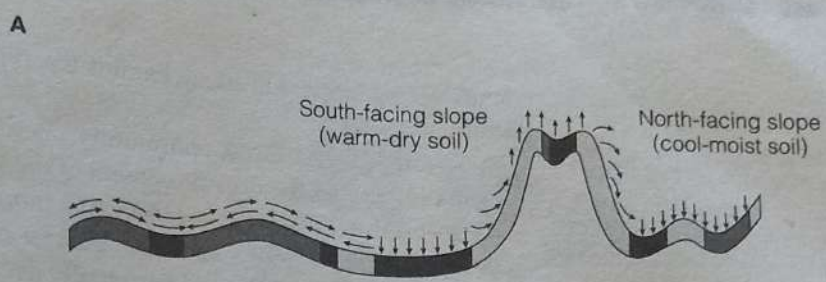
The final $P = R$ community in a developmental series (*sere*) is the **climax community**. In theory, the climax community is self-perpetuating, because it is more or less in equilibrium with itself and with the physical habitat. For a given region, it is convenient, although quite arbitrary, to recognize (1) a **regional or climatic climax**, which is determined by the general climate of the region; and (2) a varying number of **local or edaphic climaxes**, which are determined by topography and local microclimate (see Fig. 8-12), that would not occur in the absence of disturbance. Succession ends in an edaphic climax when topography, soil, water, and regular disturbances such as fire are such that the development of the ecosystem does not proceed to the theoretical end point.

Explanation and Examples

In terms of species composition, the **polyclimax** concept (choice of climatic and edaphic climaxes) is illustrated by mature forest communities associated with various physical situations, such as in the hilly region located in Ontario, Canada, diagrammed in Figure 8-12A. On level or moderately rolling areas where the soil is well drained but moist, a maple-beech community (*Acer saccharum* and *Fagus grandifolia* being the dominant species) is found to be the terminal stage in succession. Because this type of community is found again and again in the region wherever land configuration and drainage are moderate, the maple-beech community can be designated the *climatic climax* of the region. Where the soil remains wetter or drier than normal (despite the action of communities), different species are dominant in the climax community. Still greater deviations from the climatic climax occur on steep south-facing slopes, where the microclimate is warmer, or on north-facing slopes and in deep ravines, where the microclimate is colder (Fig. 8-12B). These steep-slope climaxes often resemble climatic climaxes found farther south and north, respectively. Accordingly, if you live in eastern North America and wish to see what a climax forest would be like farther north, view an undisturbed, north-facing slope or ravine. Similarly, a

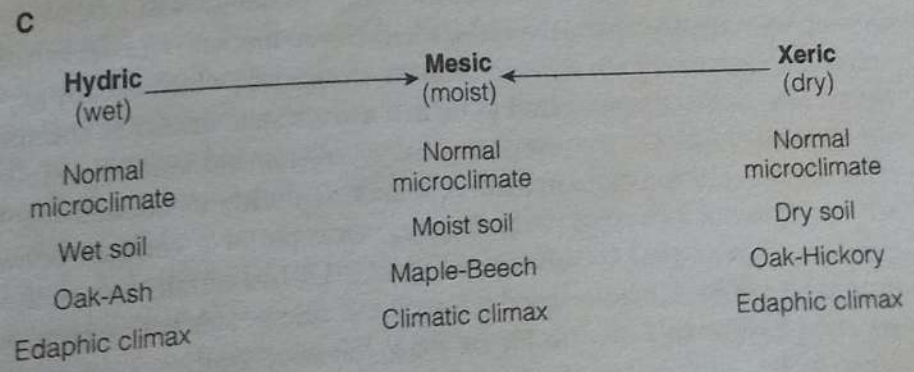
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Figure 8-12. Climatic and edaphic climaxes in southern Ontario, Canada. (A) Distribution of climax communities depending on local conditions. (B) Overview of possible climax communities. The maple-beech community is the climatic climax, occurring whenever conditions are moderate. Changes in microclimate conditions lead to various other (edaphic) climaxes. (C) Theoretical development of edaphic climaxes at extremes of moisture (wet or dry) toward a climatic climax at intermediate moisture conditions (simplified from Hills 1952).



B

	Microclimate (habitat) conditions	Climax community
Soil moisture	Normal microclimate Moist soil	Maple-Beech
	Normal microclimate Wet soil	Oak-Ash
	Normal microclimate Dry soil	Oak-Hickory
	Warm microclimate Moist soil	Tulip-Walnut
	Warm microclimate Wet soil	Sycamore-Tulip
	Warm microclimate Dry soil	Oak-Chestnut
	Cold microclimate Moist soil	Elm-Ash
	Cold microclimate Wet soil	White spruce-Balsam fir
	Cold microclimate Dry soil	Hemlock-Yellow birch



south-facing slope will likely exhibit the type of climax forest to be found farther south.

Theoretically, a forest community on dry soil would, if given indefinite time, gradually increase the organic content of the soil and raise its moisture-holding properties, and thus eventually give way to a more moist forest, such as the maple-beech community (Fig. 8-12C). Likewise, a forest community under wet soil conditions, if given time, theoretically would gradually decrease moisture in the soil as the organic content in the soil is stored as tree biomass (and output as increased plant transpiration), also resulting in a moist maple-beech community. Whether these scenarios would actually occur or not is unknown, as little evidence of such change has been seen, and records of undisturbed areas have not been kept for the many human generations that probably would be required. The question is academic anyway, because long before any autogenic change could occur, some climatic, geological, or anthropogenic force would likely intervene. The alternative to recognizing a series of climaxes and seres associated with physiographic situations in the case of a landscape mosaic like that described in Figure 8-12A would be some form of *gradient analysis*. Ecological succession is essentially a gradient in time that interacts with spatial, topographical, and climatic gradients. As emphasized at the beginning of this chapter, all climaxes would exhibit a pulsing balance between *P* and *R*.

Autogenic ecological succession results from changes in the environment brought about by the organisms themselves. Therefore, the more extreme the physical substrate, the more difficult modification of the environment becomes, and the more likely that community development will stop short of the theoretical regional climax. Regions vary considerably in the proportion of area that can support climatic climax communities. On the deep soils of the Central Plains of the United States, early settlers found a large fraction of the land covered with the same climax grassland. In contrast, on the sandy, geologically young, lower Coastal Plain of the southeastern United States, the theoretical climatic climax (a broad-leaved evergreen forest) was originally as rare as it is today. Most of the Coastal Plain is occupied by edaphic climax pine or wetland communities or their seral stages. Hurricanes frequently have a devastating impact on these coastal ecosystems, causing massive defoliation and blowdowns of timber and altering nutrient cycling. Hurricane Hugo, for example, which swept through the southern United States and Puerto Rico in 1989, destroyed much of the stands of old-growth longleaf pine (*Pinus palustris*)—prime habitat of the red-cockaded woodpecker (*Picoides borealis*).

In contrast, the oceans, which occupy geologically ancient basins, can be considered to be in a mature state insofar as community development is concerned. However, seasonal succession and succession following disturbance do occur, especially in inshore waters, as already mentioned.

A dramatic example of a contrast between regional and edaphic climaxes is shown in Figure 8-13. In a certain area on the coast of northern California, giant redwood forests occur side by side with pygmy forests of tiny, stunted trees. As depicted in Figure 8-13, the same sandstone substrate underlies both forests, but the pygmy forest occurs where an impervious hardpan close to the surface greatly restricts root development and movement of water and nutrients. The vegetation that reaches climax condition in this special situation is almost totally different in species composition and structure from that of adjacent areas that lack the hardpan.

Human beings, of course, greatly affect the progress of succession and the achieve-

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