

food particles to scarcer food concentrated in bigger units and dispersed in a more organized (stratified) environment; and

- In the later stages of succession, total energy transfer may be lower, but its efficiency seems to improve.

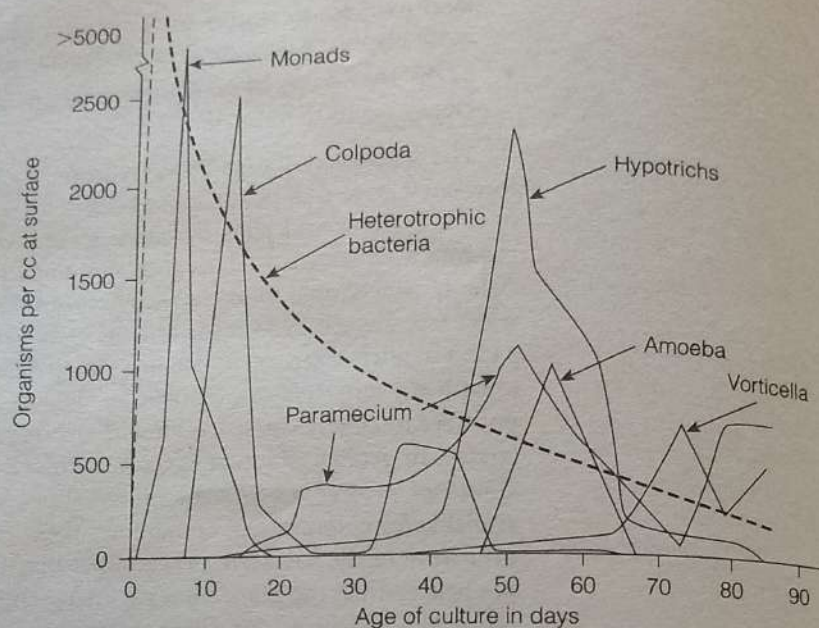
The succession of organisms on artificial substrates in aquatic environments has received a great deal of attention, because of the practical importance of the fouling of ship bottoms and piers by barnacles and other sessile marine organisms. Small replicated substrates, such as glass slides or squares of plastic, wood, or other material, are widely used to assess the effect of pollutants on biota in both fresh and salt water (see Patrick 1954 regarding the early use of this method). Such substrates are a kind of microcosm, on which one would expect ecological succession to occur, but as with any restricted or simplified model, one must be cautious about projecting hypotheses to larger, less space-limited, open systems that possess many kinds of substrates. In general, the first species to colonize these substrates are those that have abundant propagules available in the water when and where the surfaces become available for colonization. Sometimes, these pioneers change the physical or chemical nature of the substrate in ways that may facilitate the invasion of other species, but just as often the pioneers resist encroachment by other species and endure until replaced by a better competitor. As already noted in discussing intertidal communities on rocky coasts (see Chapter 7), negative interaction (competition and predation) plays a greater role than positive interaction (coexistence and mutualism) in determining the replacement of species in confined or space-limited habitats.

Heterotrophic Succession

A laboratory hay-infusion microcosm experiment provides an example of *heterotrophic succession*—and also a laboratory experiment for an ecology class. When a culture medium made by boiling hay is allowed to stand, a thriving culture of bacteria develops. If some pond water (containing seed stock for various protozoa) is then added, a definite succession of protozoan populations with successive dominants occurs, as shown in Figure 8-10. A similar succession of protozoa occurs when un-vegetated soil is first exposed to colonization (Bamforth 1997). In the hay infusion experiment, energy and nutrients are maximal at the beginning and then decline. Unless new medium is added, or an autotrophic regime takes over, the system eventually runs down, and all the organisms die or go into resting stages (spores or cysts)—quite different from autotrophic succession, in which energy flow is maintained indefinitely. The hay-infusion microcosm is a model for the kind of succession that occurs in decaying logs, animal carcasses, fecal pellets, and the secondary stages of sewage treatment. It might also be considered a model for the “downhill” succession that must be associated with a society dependent on fossil fuels that is slow to develop alternative energy sources. In all these examples, there is a series of transient stages in a declining energy gradient, with no possibility of achieving a mature climax state.

Heterotrophic and autotrophic successions can be combined in a laboratory microecosystem model if samples from a derived system are added to media enriched with organic matter. The system first becomes “cloudy” as heterotrophic bacteria bloom; then it turns bright green as nutrients and growth substances (especially the vitamin thiamine) required by algae are released by the activities of the bacteria. This

Figure 8-10. Succession in a hay-infusion culture, with dominance by successive species. This is an example of heterotrophic succession (after Woodruff 1912).



succession, of course, is a model of the *cultural eutrophication* resulting from organic pollution, such as inflow of incompletely treated municipal sewage.

Selection Pressure: Quantity Compared with Quality

Stages of the colonization of islands, as first described by MacArthur and Wilson (1967), provide parallels with stages in ecological succession on continents. In the early, uncrowded stages of island colonization; as in the early stages of succession, *r*-selection predominates, so that species with high rates of reproduction and growth are more likely to colonize. In contrast, selection pressure favors *K*-strategist species, with lower growth potential but better capabilities for competitive survival, under the high density of later stages of both island colonization and succession (Table 8-1).

Genetic changes involving the whole biota may be presumed to accompany the successional change from quantity production to quality production, as indicated by the tendency for the size of the individual organism to increase (Table 8-1). For plants, the change in size appears to be an adaptation to the shift of nutrients from inorganic to organic. In a mineral- and nutrient-rich environment, small size is of selective advantage, especially to autotrophs, because of the higher surface-to-volume ratio. As the ecosystem develops, however, inorganic nutrients tend to become more and more tied up in the biomass (that is, to become intrabiotic), so that the selective advantage shifts to larger organisms (larger individuals of the same species, larger species, or both), which have greater storage capacities and more complex life histories and are thus adapted to exploiting seasonal or periodic releases of nutrients or other resources.

Diversity Trends

Although both components of diversity (richness and apportionment) in Table 8-1 almost always increase in the early stages of ecosystem development, the peak of diversity seems to come somewhere in the middle of the sere in some cases and near

sion. The level of diversity achieved may well depend on energetics, as the maintenance of high diversity has an energy cost and can be destabilizing (the "too much of a good thing" syndrome again).

Although little studied, aspects of biotic diversity other than species variety and relative abundance would logically be expected to show increasing trends during the course of autogenic ecosystem development. Jeffries (1979), for example, reported that as marine communities mature and become more complex, so do the fatty-acid compositions of the plankton and benthos. During plant succession on land, the variety of antiherbivore chemicals required by long-lived trees to survive increases with succession, thereby countering the tendency for insects to become resistant to pesticides, both natural and human-made. These are examples of an increase in *biochemical diversity* during ecosystem development.

Historical Review of Theoretical Considerations

At the beginning of this section, it was stated that ecosystem development resulted from (1) modification of the physical environment by the community acting as a whole, and (2) the interaction of competition and coexistence between component populations. Although one could logically assume that both ecosystem-level and population-level processes contribute to the many-faceted successional progressions described in this section, some ecologists have chosen to argue either for one level or for the other but not both. Connell and Slayter (1977) compared three theories: (1) the *facilitation model*, in which early seral species change the conditions of existence and thereby prepare the way for later invaders; and (2) the *inhibition model*, in which the pioneer species resist invasion and remain until they are replaced because of competition, predation, or disturbance; and (3) the *tolerance model*, in which a species invades a new habitat and becomes established independently of the presence or absence of other species. Connell and Slayter strongly favored the inhibition model, at least for secondary succession. Proponents of population-level theories of causation essentially argue that if observed successional trends can be explained by interactions at the species level, there is no need to invoke higher-level processes. Conversely, other theorists argue that species succession is only a part of the process of self-organizing development, which is a property of whole ecosystems, and hence there is less need to look in detail into the interaction of component populations in order to explain basic trends. We favor the self-organization theory, as explained in the next section.

The idea that ecological succession is a holistic phenomenon goes back to Frederick E. Clements and his 1916 monograph "Plant Succession" (subsequently reprinted in 1928 under the title "Plant Succession and Indicators"). His notions that a community repeats in its development the sequence of stages of development of an individual organism and that all communities in a given climatic area develop toward a single climax (the *monoclimax* concept; see next section) are deemphasized or modified today. Clements' main thesis—that *ecological succession is a developmental process and not just a succession of species each acting alone*—remains one of the most important unifying theories in ecology. Margalef (1963a, 1968) and E. P. Odum (1969) reworked and extended Clements' basic theory to include functional attributes such as community metabolism.

The contrary concept—that ecological succession does not have an organizational strategy but results from the interactions of individuals and species as they struggle to occupy space—goes back to H. A. Gleason's studies, especially the classic

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**.