Ecological succession

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Publication year: 2020

A directional change in an ecological community. Populations of animals and plants are in a dynamic state. Through the continual turnover of individuals, a population may expand or decline depending on the success of its members in survival and reproduction. As a consequence, the species composition of communities typically does not remain static with time. Apart from the regular fluctuations in species abundance related to seasonal changes, a community may develop progressively with time through a recognizable sequence known as the sere. Pioneer populations are replaced by successive colonists along a more or less predictable path toward a relatively stable community. This process of succession results from interactions between different species, and between species and their environment, which govern the sequence and the rate with which species replace each other. The rate at which succession proceeds depends on the time scale of species' life histories as well as on the effects species may have on each other and on the environment which supports them. *See also:* ECOLOGICAL COMMUNITIES; POPULATION ECOLOGY.

The course of ecological succession depends on initial environmental conditions. Primary succession occurs on novel areas such as volcanic ash, glacial deposits, or bare rock, areas which have not previously supported a community. In such harsh, unstable environments, pioneer colonizing organisms must have wide ranges of ecological tolerance to survive. In contrast, secondary succession is initiated by disturbance such as fire, which removes a previous community from an area. Pioneer species are here constrained not by the physical environment but by their ability to enter and exploit the vacant area rapidly.

As succession proceeds, many environmental factors may change through the influence of the community. Especially in primary succession, this leads to more stable, less severe environments. At the same time interactions between species of plant tend to intensify competition for basic resources such as water, light, space, and nutrients. Successional change results from the normal complex interactions between organism and environment which lead to changes in overall species composition. Whether succession is promoted by changing environmental factors or competitive interactions, species composition alters in response to availability of niches. Populations occurring in the community at a point in succession are those able to provide propagules (such as seeds) to invade the area, being sufficiently tolerant of current environmental conditions, and able to withstand competition from members of other populations present at the same stage. Species lacking these qualities either become locally extinct or are unable to enter and survive in the community.

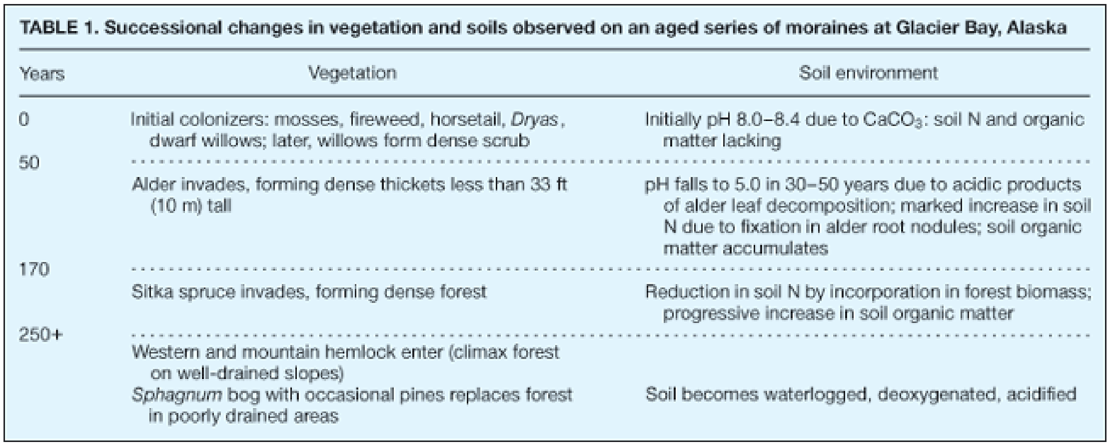


TABLE 1. Successional changes in vegetation and soils observed on an aged series of moraines at Glacier Bay, Alaska

Years	Vegetation	Soil environment
0	Initial colonizers: mosses, fireweed, horsetail, *Dryas*, dwarf willows; later, willows form dense scrub	Initially pH 8.0–8.4 due to $CaCO_3$: soil N and organic matter lacking
50	Alder invades, forming dense thickets less than 33 ft (10 m) tall	pH falls to 5.0 in 30–50 years due to acidic products of alder leaf decomposition; marked increase in soil N due to fixation in alder root nodules; soil organic matter accumulates
170	Sitka spruce invades, forming dense forest	Reduction in soil N by incorporation in forest biomass; progressive increase in soil organic matter
250+	Western and mountain hemlock enter (climax forest on well-drained slopes)	
	Sphagnum bog with occasional pines replaces forest in poorly drained areas	Soil becomes waterlogged, deoxygenated, acidified

Primary succession

In some cases, seres may take hundreds of years to complete, and direct observation at a given site is not possible. Adjacent sites may be identified as successively older stages of the same sere, if it is assumed that conditions were similar when each seral stage was initiated.

Glacier Bay. In the Glacier Bay region of Alaska glaciers have retreated, in phases, some 61 mi (98 km) since 1750, leaving a series of moraines of known ages supporting a range of seral vegetational types. Soil factors become modified by vegetation, enabling new species to become established (**Table 1**). Acidic decomposition products of alder leaves sharply reduce soil pH, whereas virtually no change occurs on bare glacial till or under other vegetation. Pioneer species must tolerate low nitrogen levels, but alder is able to fix atmospheric nitrogen (N) by the presence of microbial symbionts in root nodules and is correlated with a rapid increase in soil nitrogen by way of leaf fall. After invasion by spruce, levels of accumulated nitrogen fall as nitrogen becomes incorporated in forest biomass, and the annual additions from alder are reduced. Soil organic matter increases progressively, and influences the structural development of the soil. The mature forest remains only on well-drained slopes. In areas of poorer drainage, invasion by *Sphagnum* moss leads to replacement of trees by wet acidic bog or muskeg.

Lake Michigan. Another example of primary succession has been recorded on a sequence of dune ridges bordering Lake Michigan, ranging in age to 12,000 years. Succession is initiated on a bare sand surface either following a fall in lake level, as occurred in phases since the last glaciation, or due to wind erosion of an existing dune redepositing sand (**Table 2**). Marram grass impedes the transport of sand across bare dune surfaces and so promotes accretion of sand. At the same time, it grows and branches vigorously, thus maintaining cover on the expanding dune (**Fig. 1**).

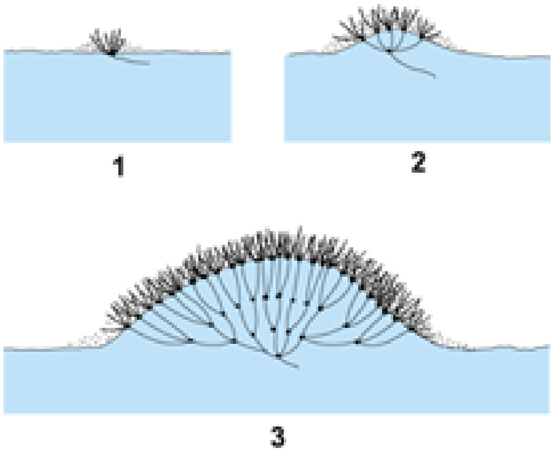


Fig. 1 **Dune formation by the gradual deposition of wind-carried sand particles around aerial shoots of *Ammophila arenaria*. 1, 2, and 3 indicate successive periods of time. (*After K. A. Kershaw, Quantitative and Dynamic Ecology, 2d ed., Arnold, 1973*)**

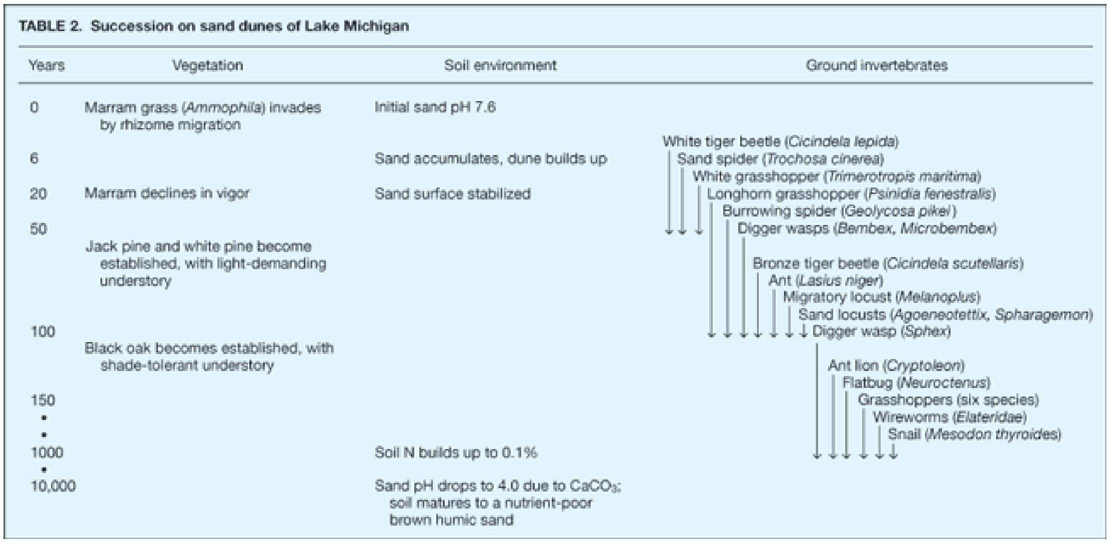


TABLE 2. Succession on sand dunes of Lake Michigan

Years	Vegetation	Soil environment	Ground invertebrates
0	Marram grass (*Ammophila*) invades by rhizome migration	Initial sand pH 7.6	
			White tiger beetle (*Cicindela lepida*)
6		Sand accumulates, dune builds up	Sand spider (*Trochosa cinerea*) White grasshopper (*Trimerotropis maritima*)
20	Marram declines in vigor	Sand surface stabilized	Longhorn grasshopper (*Psinidia fenestralis*) Burrowing spider (*Geolycosa pikei*)
50	Jack pine and white pine become established, with light-demanding understory		Digger wasps (*Bembex, Microbembex*) Bronze tiger beetle (*Cicindela scutellaris*) Ant (*Lasius niger*) Migratory locust (*Melanoplus*) Sand locusts (*Agoeneotettix, Spharagemon*) Digger wasp (*Sphex*)
100	Black oak becomes established, with shade-tolerant understory		Ant lion (*Cryptoleon*) Flatbug (*Neuroctenus*)
150			Grasshoppers (six species) Wireworms (*Elateridae*) Snail (*Mesodon thyroides*)
• •			
1000		Soil N builds up to 0.1%	
•			
10,000		Sand pH drops to 4.0 due to $CaCO_3$; soil matures to a nutrient-poor brown humic sand	

Succession on Lake Michigan dunes demonstrates that local factors may modify the typical pattern (**Fig. 2**). In damp depressions with impeded drainage, a grassland community develops. Sheltered pockets on lee slopes have a moister microclimate and tend to accumulate leaf litter from more exposed parts of the dunes, as well as receiving protection from frequent fires. As a result, a more nutrient-rich soil can develop, and succession proceeds via basswood to more nutrient-demanding oak-hickory and finally maple-beech woodland, typical of normal soils of the region. The black oak association appears to be stable on dune soils, since it is tolerant of low

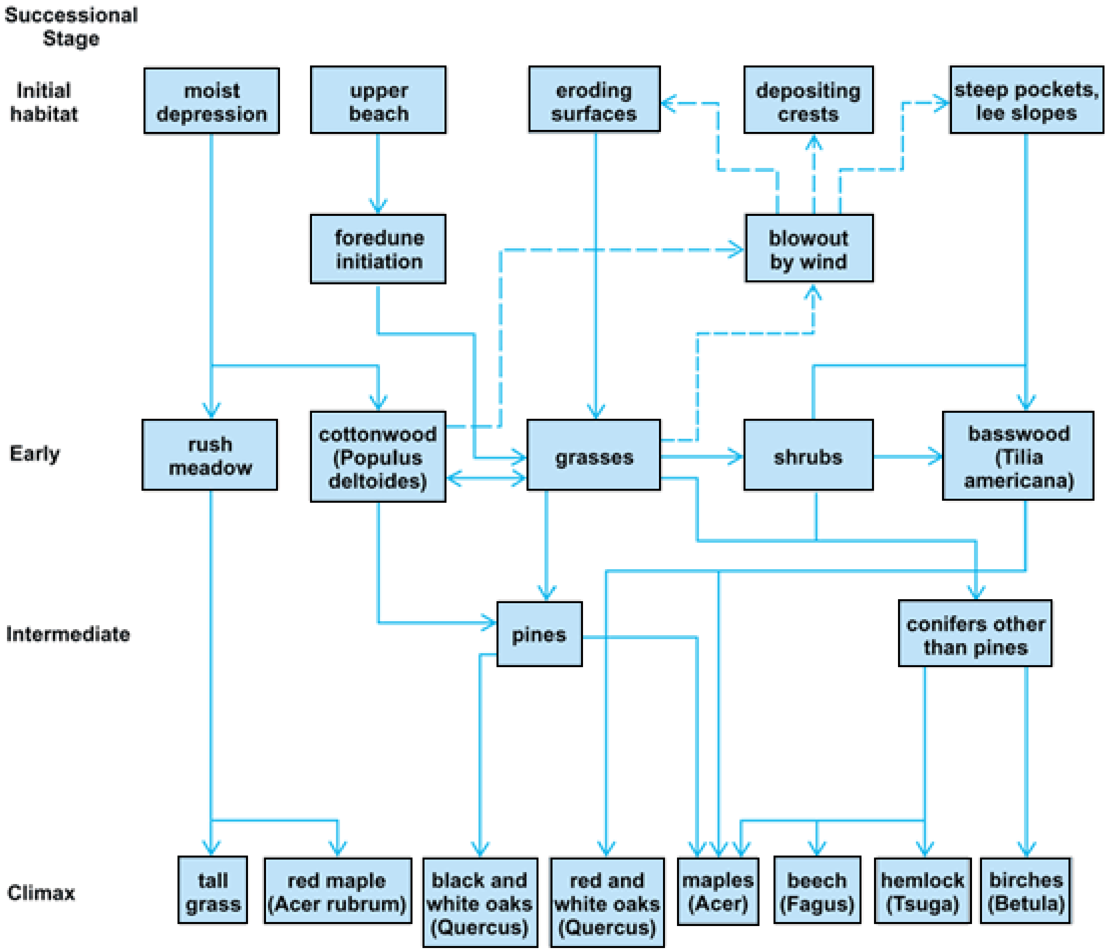


Fig. 2 **Alternative patterns of primary plant succession on Lake Michigan dunes, depending on initial conditions, extrinsic variables, and colonization-invasion patterns. (*After S. J. McNaughton and L. L. Wolf, General Ecology, 2d ed., Holt, Reinhart, and Winston, 1979*)**

nutrients and water limitation, and tends to maintain these conditions by returning few nutrients in the leaf litter.

Climax community

Early stages of succession tend to be relatively rapid, whereas the rates of species turnover and soil changes become slower as the community matures. Eventually an approximation to the steady state is established with a relatively stable community, the nature of which has aroused considerable debate. Earlier, the so-called climax vegetation was believed to be determined ultimately by regional climate and, given sufficient time, any community in a region would attain this universal condition. This unified concept of succession, the monoclimax hypothesis, implies the ability of organisms progressively to modify their environment until it can support the climatic climax community. Although plants and animals do sometimes ameliorate environmental conditions, evidence suggests overwhelmingly that succession has a variety of stable end points. This hypothesis, known as the polyclimax hypothesis, suggests that the end point of a succession depends on a complex of environmental factors that characterize the site, such as parent material, topography, local climate, and human influences.

In the Lake Michigan sand dunes, the course of succession and its climax appear to be determined by physiographic conditions at the start (**Fig. 2**). Similarly, the transformation of glacial moraine forest to muskeg depends on local drainage. In the tropical rainforest of Moraballi Creek, Guyana, five apparently stable vegetation types have been distinguished on different soil types under the same climate. A mixed forest is present on red loam, whereas the Wallaba forest occurs on bleached sand, with the Mora forest type in areas liable to flooding.

Autogenic vs. allogenic factors

In the examples of succession discussed above, the chief agent in modifying the environment is the community itself: thus marram stabilizes the sand dune surface, and alder increases the soil nutrient status of moraine soil. These actions of the community on the environment, termed autogenic, provide an important driving force promoting successional change, and are typical of primary succession where initial environments are inhospitable. Alternatively, changes in species composition of a community may result from influences external to the community called allogenic. For example, in aquatic ecosystems (the hydrosere) the community commonly develops from open water with submerged and floating aquatic plant species toward a swamp community in which rooted emergent plants dominate in shallower water, until finally the marsh is colonized by land plants from the surrounding area as sediment deposition continues and the soil dries out. Reduction in water depth, enabling colonization by marsh species and finally terrestrial species, occurs with input of waterborne and airborne sediments—thus the aquatic phase of the hydrosere is controlled by input of materials from outside the system. Similarly, lakes are typically subject to enrichment of nutrients from surrounding areas, resulting in increased productivity. Extremely high production occurs in culturally eutrophic lakes, which receive nutrient inputs from human activities. In aquatic systems where the influence of allogenic factors such as siltation are apparently minimal, vegetation tends to develop via a series of productive intermediate steps toward an oligotrophic community, that is, one with low productivity, dominated by *Sphagnum* moss (**Fig. 3**). *See also:* EUTROPHICATION.

Whereas intrinsic factors often result in progressive successional changes, that is, changes leading from simple to more complex communities, external (allogenic) forces may induce retrogressive succession, that is, toward a less mature community. For example, if a grassland is severely overgrazed by cattle, the most palatable species will disappear. As grazing continues, the grass cover is reduced, and in the open areas weeds characteristic of initial stages of succession may become established.

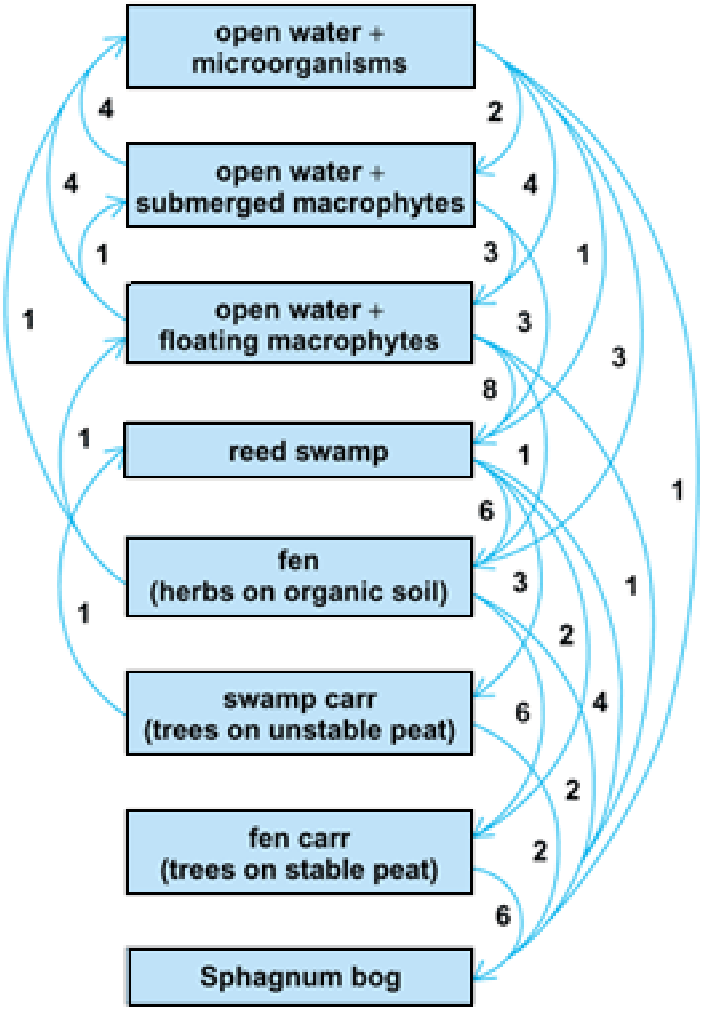


Fig. 3 Transitions between vegetation "stages" free from obvious allogenic influences derived from 20 pollen diagrams for lake sediments and peat. Figures show numbers of observed transitions.

Heterotrophic succession

In the preceding examples of succession, the food web was based on photosynthetic organisms and there was a slow accumulation of organic matter, both living and dead. This is termed autotrophic succession. In some instances, however, addition of organic matter to an ecosystem initiates a succession of decomposer organisms which invade and degrade it. Such a succession is called heterotrophic. In an Illinois pasture, cow dung is degraded by a seral community of some 40 to 60 invertebrate species over a period of 30 days. The newly deposited cow pat is immediately visited by the horn fly (*Haematobia irritans*), which quickly lays eggs and returns to the cow. It is followed by several other dung flies whose larvae are eaten by beetles such as *Sphaeridium scaraboides* which burrow through the dung and lay their eggs. A parasitic wasp (*Xyalophora quinquelinata*) deposits eggs inside maggots of *Sarcophaga* flies. As the dung ages and dries out, it is inhabited by a wider variety of species. Little is known in detail of the importance of the various saprovores in degrading the dung and in modifying the microhabitat, or of their dependence on the activities of saprophytic fungi.

Discharge of organic effluent into a river is detectable downstream by a progression in chemical factors and in the biota. Succession in time is here equivalent to the change in species composition resulting from the decline in organic effluent that corresponds to the distance from the discharge. Marked reduction in dissolved oxygen directly below an outfall results from respiration of microorganisms as they degrade organic matter. Detritivores tolerant of low oxygen concentrations, such as *Tubificidae* and *Chironomidae*, attain high population densities in the bottom sediments. Subsequently, a bloom of algae is typical, utilizing released nitrate and phosphate. As the river flows downstream, the aquatic food web progressively changes from a heterotrophic to an autotrophic basis and productivity declines to its normal level as the "clean water" community returns. *See also:* BIOLOGICALS; PRODUCTIVITY; FOOD WEB.

Secondary succession

Following the partial or complete destruction of an established community by disturbing events such as fire or clearfelling, and similarly on the cessation of grazing or tillage, a sequence of species invasion and replacement ensues. Compared to the slow initial progress of primary succession in which amelioration of the environment plays an important part, secondary succession is characterized initially by rapid turnover of typically opportunist species which invade relatively congenial habitats.

Piedmont. Abandoned fields in Piedmont area of North Carolina show a rapid sequence of replacement of herbaceous species, apparently related to the life histories of the plants (**Table 3**). Horseweed produces seeds in late summer which germinate immediately so that the plant overwinters as a juvenile, grows rapidly the following year, and dies after seeding in the summer. Aster seeds do not germinate until the following spring, and seedlings grow slowly due to shading by established horseweed plants. In addition, decaying horseweed roots inhibit its own growth and, to a greater extent, that of aster. Horseweed attains dominance in the first year by efficient seed dispersal and rapid establishment. Being a perennial, aster is able to outcompete horseweed in the second year despite the inhibitory effect of the latter. Seedlings of aster are present in abundance in third-year fields but are less drought-resistant than those of broomsedge, which outcompetes aster except in fields with more available water, where aster survives the competition longer. *See also:* ALLELOPATHY.

Broomsedge seeds are not available to colonize initially because seeds are not produced until the end of the plant's second year and require a period of cold dormancy before germination. Seedling growth is apparently enhanced by decomposition products of the previous colonists. The late establishment of broomsedge in the succession is dependent not on changes brought about by earlier colonists but on the life history of the plant.

After broomsedge, shortleaf pine invades the herb community. Pine seeds require mineral soil and minimal root competition to become established, and the seedlings are not shade-tolerant. Hence after about 20 years, under a

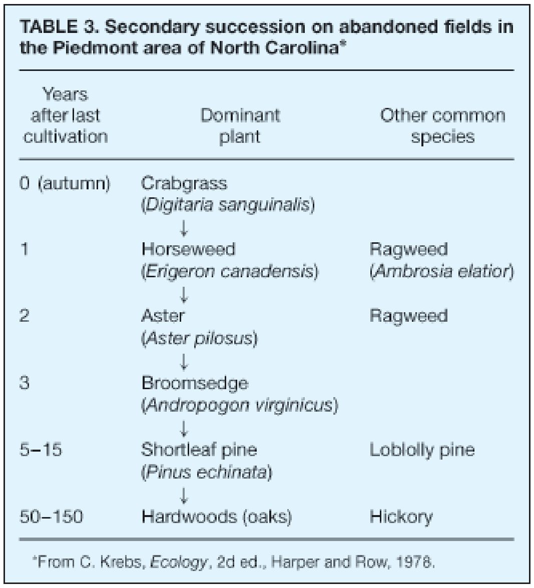


TABLE 3. Secondary succession on abandoned fields in the Piedmont area of North Carolina*

Years after last cultivation	Dominant plant	Other common species
0 (autumn)	Crabgrass (*Digitaria sanguinalis*)	
	↓	
1	Horseweed (*Erigeron canadensis*)	Ragweed (*Ambrosia elatior*)
	↓	
2	Aster (*Aster pilosus*)	Ragweed
	↓	
3	Broomsedge (*Andropogon virginicus*)	
	↓	
5–15	Shortleaf pine (*Pinus echinata*)	Loblolly pine
	↓	
50–150	Hardwoods (oaks)	Hickory

*From C. Krebs, *Ecology*, 2d ed., Harper and Row, 1978.

dense pine canopy, reproduction of pines is almost lacking. Accumulation of litter and shade under pines causes the old-field herbs to die out.

Oak seedlings become established after about 20 years, when the depth of litter is adequate to prevent desiccation of acorns. Organic matter in the soil surface layer also increases, improving its water-holding capacity. After about 50 years, several oak species become established and gradually assume dominance as the pines fail to reproduce. Unlike pine, which is capable of germinating on bare soil, oaks and other hardwoods require changes in the soil resulting from pine litter before their seedlings can establish successfully.

While plant species are the main indicators of succession, it is important to note that animal species are also changing over time. In the Piedmont, the changes in bird species as succession proceeds have been well documented. Just a few species, such as meadowlarks and grasshopper sparrows, are found in the initial stages, while more complicated assemblages of species are common in the latter forest stages.

Nova Scotia forest. Following clearfelling in a Nova Scotia forest, the course of secondary succession involves invasion by shrubs (raspberry) followed by understory trees (pincherry, aspen), followed by shade-intolerant species (red maple, paper birch), and finally a shade-tolerant community (hard maple, yellow birch, white ash). Perhaps shade-tolerant species such as red maple, which are of low commercial value, could be inhibited if strip felling were practiced by the forestry industry as an alternative to clearfelling in large blocks. Commercially desirable shade-tolerant species such as white ash would be favored where there was greater local shading of the regenerating community.

Mechanisms of species replacement

Observed changes in the structure and function of seral communities result from natural selection of individuals within their current environment. Three mechanisms by which species may replace each other have been proposed; the relative importance of each apparently depends on the nature of the sere and stage of development.

1. The facilitation hypothesis states that invasion of later species depends on conditions created by earlier colonists. Earlier species modify the environment so as to increase the competitive ability of species which are then able to displace them. Succession thus proceeds because of the effects of species on their environment.

2. The tolerance hypothesis suggests that later successional species tolerate lower levels of resources than earlier occupants and can invade and replace them by reducing resource levels below those tolerated by earlier occupants. Succession proceeds despite the resistance of earlier colonists.

3. The inhibition hypothesis is that all species resist invasion of competitors and are displaced only by death or by damage from factors other than competition. Succession proceeds toward dominance by longer-lived species.

None of these models of succession is solely applicable in all instances; indeed most examples of succession appear to show elements of all three replacement mechanisms. In secondary succession on North Carolina croplands, stimulation of broomsedge growth by decomposition products of previous colonists, and the requirement of oak seedlings for a deep litter layer in which to germinate, exemplify facilitation. The ability of broomsedge to displace aster in competition for water suggest the tolerance mechanism, whereas the inhibition hypothesis is supported by the greater tolerance of horseweed seedlings than aster seedlings to horseweed decomposition products.

Deterministic vs. stochastic succession

Succession has traditionally been regarded as following an orderly progression of changes toward a predictable end point, the climax community, in equilibrium with the prevailing environment. This essentially deterministic view implies that succession will always follow the same course from a given starting point and will pass through a recognizable series of intermediate states (such as in Fig. 2). In contrast, a more recent view of succession is based on adaptations of independent species. It is argued that succession is disorderly and unpredictable, resulting from probabilistic processes such as invasion of propagules and survival of individuals which make up the community. Such a stochastic view reflects the inherent variability observed in nature and the uncertainty of environmental conditions. In particular, it allows for succession to take alternative pathways and end points dependent on the chance outcome of interactions among species and between species and their environment.

Consideration of community properties such as energy flow supports the view of succession as an orderly process. Early in autotrophic succession gross primary productivity (P_g) increases rapidly with community

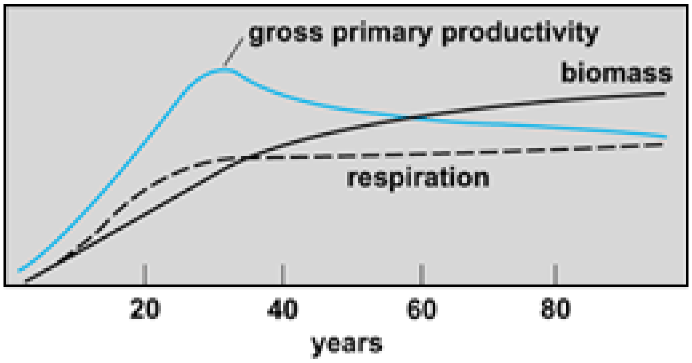


Fig. 4 The energetics of ecosystem development in a forest. The difference between gross primary productivity and respiration is the net primary productivity. (*After E. P. Odum, Ecology, 2d ed., Holt, Reinhart, and Winston, 1975*)

biomass (B), whereas community respiration (R) increases more slowly (**Fig. 4**). As a result, net primary productivity (P_n, where $P_n = P_g - R$) builds up early in succession, and the ratio $\frac{P_g}{B}$ is at its highest in the initial stages. As the community increases in biomass and complexity over time, more complete overall utilization of basic resources such as light limits further increase in primary productivity, whereas R continues to increase because of the increase in tissue to support. Hence zero and the biomass of a mature forest community no longer accumulates. The rate of gross primary productivity typically becomes limited also by the availability of nutrients, now incorporated within the community biomass, and declines to a level sustainable by release from decomposer organisms. Species diversity tends to rise rapidly at first as successive invasions occur, but declines again with the elimination of the pioneer species by the climax community.

Trends in community function, niche specialization, and life history strategy are summarized in **Table 4**. As the community acquires increasing maturity, P_n declines to zero, nutrients become incorporated in biotic pools, broad-niched species are replaced by those with more specific requirements, and the structural organization of the community increases.

Regeneration of an area of subtropical rainforest in Queensland was observed after the vegetation and surface litter were removed with a bulldozer. Because of small environmental differences in the 10 quadrats observed, succession took four directions after the demise of the first ubiquitous colonizing species, resulting in four apparently stable plant associations. This divergence may result merely from small-scale variation in topography within the 65 × 130 ft (20 × 40 m) experimental site and from differing efficiencies of removal of surface litter between the quadrats. Hence the different plant associations detected could be interpreted as divergent products of succession or as phases within a larger-scale vegetation unit.

Stochastic aspects of succession can be represented in the form of models which allow for transitions between a series of different "states." Such models, termed Markovian models, can apply at various levels: plant-by-plant replacement, changes in tree size categories, or transitions between whole communities. A matrix of

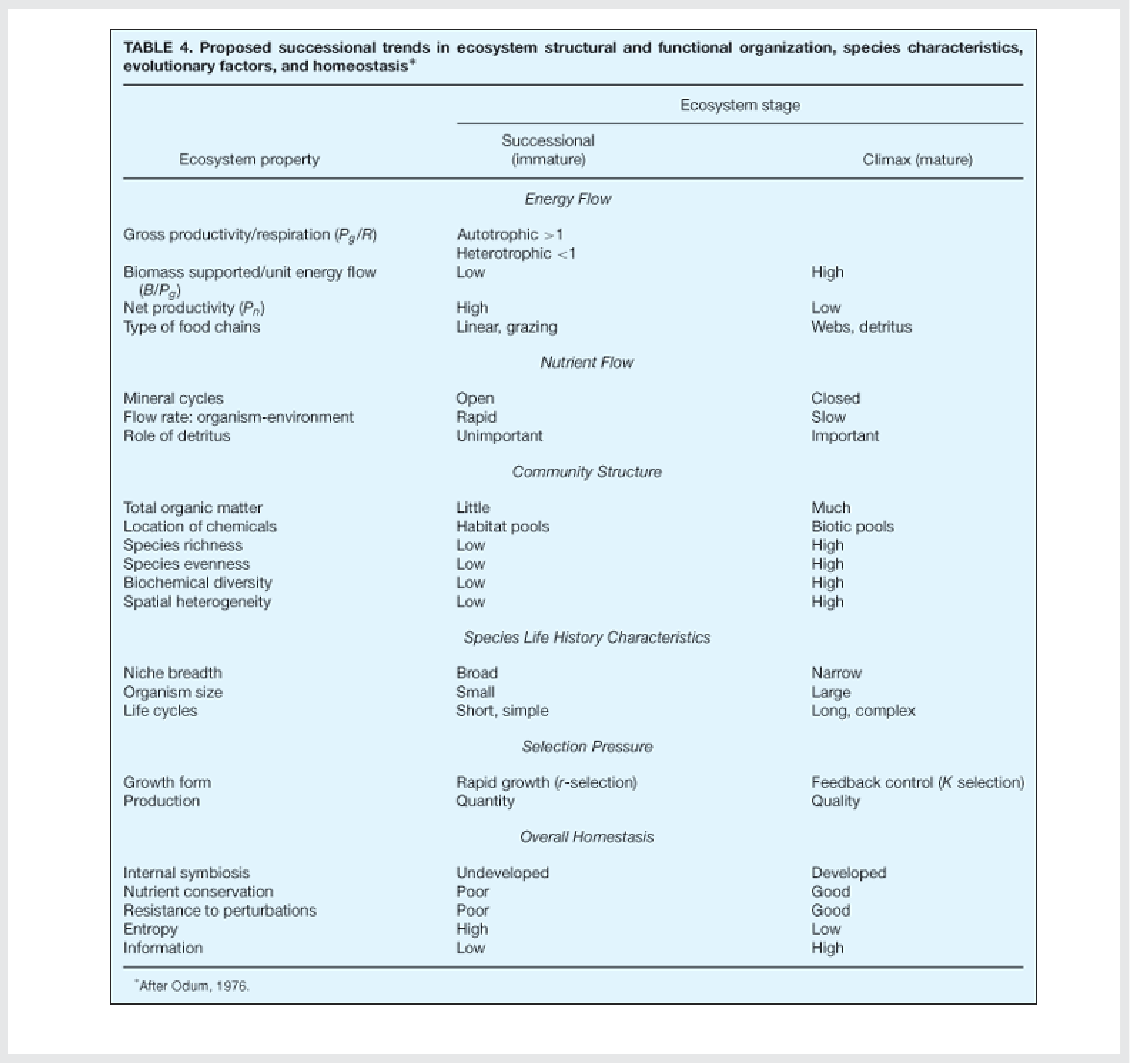
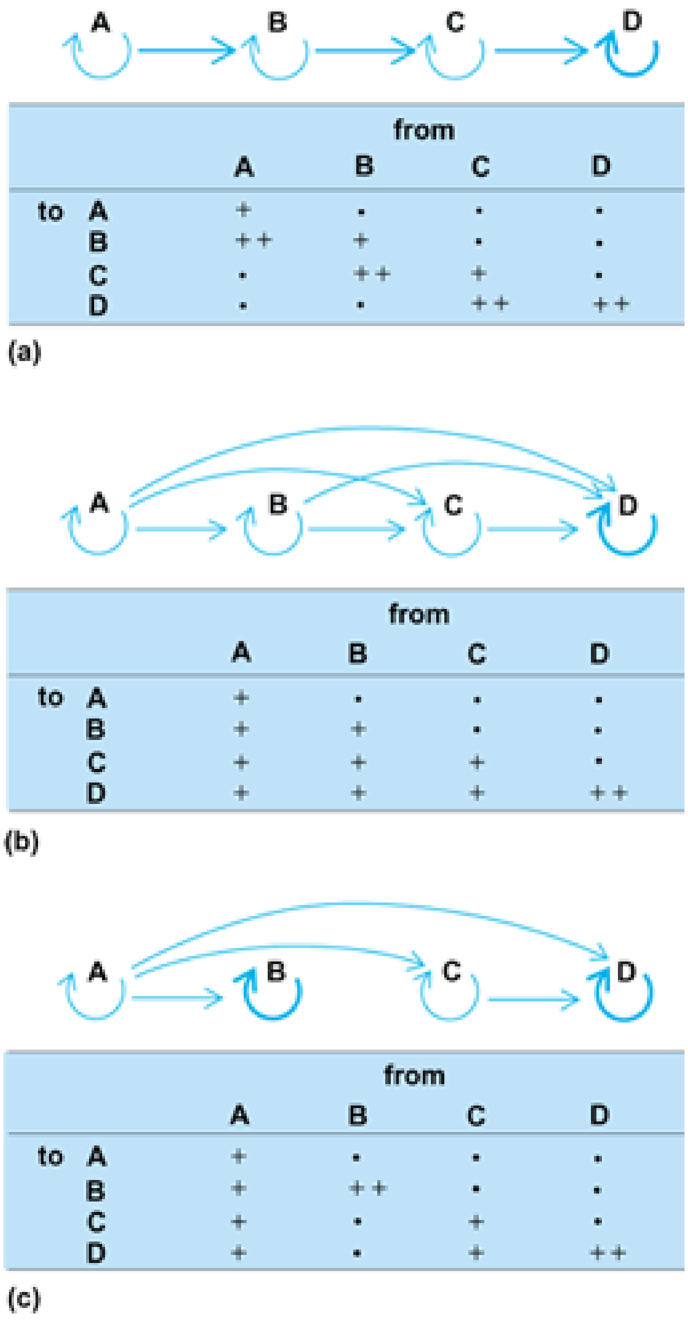


TABLE 4. Proposed successional trends in ecosystem structural and functional organization, species characteristics, evolutionary factors, and homeostasis*

	Ecosystem stage	
Ecosystem property	Successional (immature)	Climax (mature)
	Energy Flow	
Gross productivity/respiration (P_g/R)	Autotrophic >1 Heterotrophic <1	
Biomass supported/unit energy flow (B/P_g)	Low	High
Net productivity (P_n)	High	Low
Type of food chains	Linear, grazing	Webs, detritus
	Nutrient Flow	
Mineral cycles	Open	Closed
Flow rate: organism-environment	Rapid	Slow
Role of detritus	Unimportant	Important
	Community Structure	
Total organic matter	Little	Much
Location of chemicals	Habitat pools	Biotic pools
Species richness	Low	High
Species evenness	Low	High
Biochemical diversity	Low	High
Spatial heterogeneity	Low	High
	Species Life History Characteristics	
Niche breadth	Broad	Narrow
Organism size	Small	Large
Life cycles	Short, simple	Long, complex
	Selection Pressure	
Growth form	Rapid growth (r-selection)	Feedback control (K selection)
Production	Quantity	Quality
	Overall Homestasis	
Internal symbiosis	Undeveloped	Developed
Nutrient conservation	Poor	Good
Resistance to perturbations	Poor	Good
Entropy	High	Low
Information	Low	High

*After Odum, 1976.

replacement probabilities defines the direction, pathway, and likelihood of change, and the model can be used to predict the future composition of the community from its initial state. With alternative transition matrices, this simple model could represent a linear progression toward a stable end state, or a cyclical, recursive sequence of communities. The three postulated mechanisms for species replacement discussed above can be illustrated by the topology of alternative Markovian models (**Fig. 5**). The facilitation model of succession is represented as a linear sequence with greater probabilities of progression toward the final state (D) than maintenance of intermediate states. In the tolerance model, later stages may develop from earlier stages depending on the availability of propagules of subsequent stages and their competitive ability. Again, only state D has a high



		from			
		A	B	C	D
to	A	+	•	•	•
	B	++	+	•	•
	C	•	++	+	•
	D	•	•	++	++

(a)

		from			
		A	B	C	D
to	A	+	•	•	•
	B	+	+	•	•
	C	+	+	+	•
	D	+	+	+	++

(b)

		from			
		A	B	C	D
to	A	+	•	•	•
	B	+	++	•	•
	C	+	•	+	•
	D	+	•	+	++

(c)

Fig. 5 **Schematic representation of three postulated mechanisms for species replacement in succession: (*a*) facilitation, (*b*) tolerance, and (*c*) inhibition. Arrows indicate the direction in which the systems tend to move between different states, A–D. Relative probabilities of movement are indicated by thickness of arrows and by symbols in the accompanying transition matrix, where • = close to zero, + = moderate, and ++ = high.**

probability of self-replacement. In the inhibition model, there is a high probability that an intermediate state (in this case, B) will persist by strong self-replacement, thereby truncating the normal succession toward state D. A very low probability that B will change to C or D is assumed. Hence, a high degree of realism can be achieved with a simple model system, and alternative predictions of successional changes can be compared with observed data. *See also:* ECOLOGY; STOCHASTIC PROCESS.

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