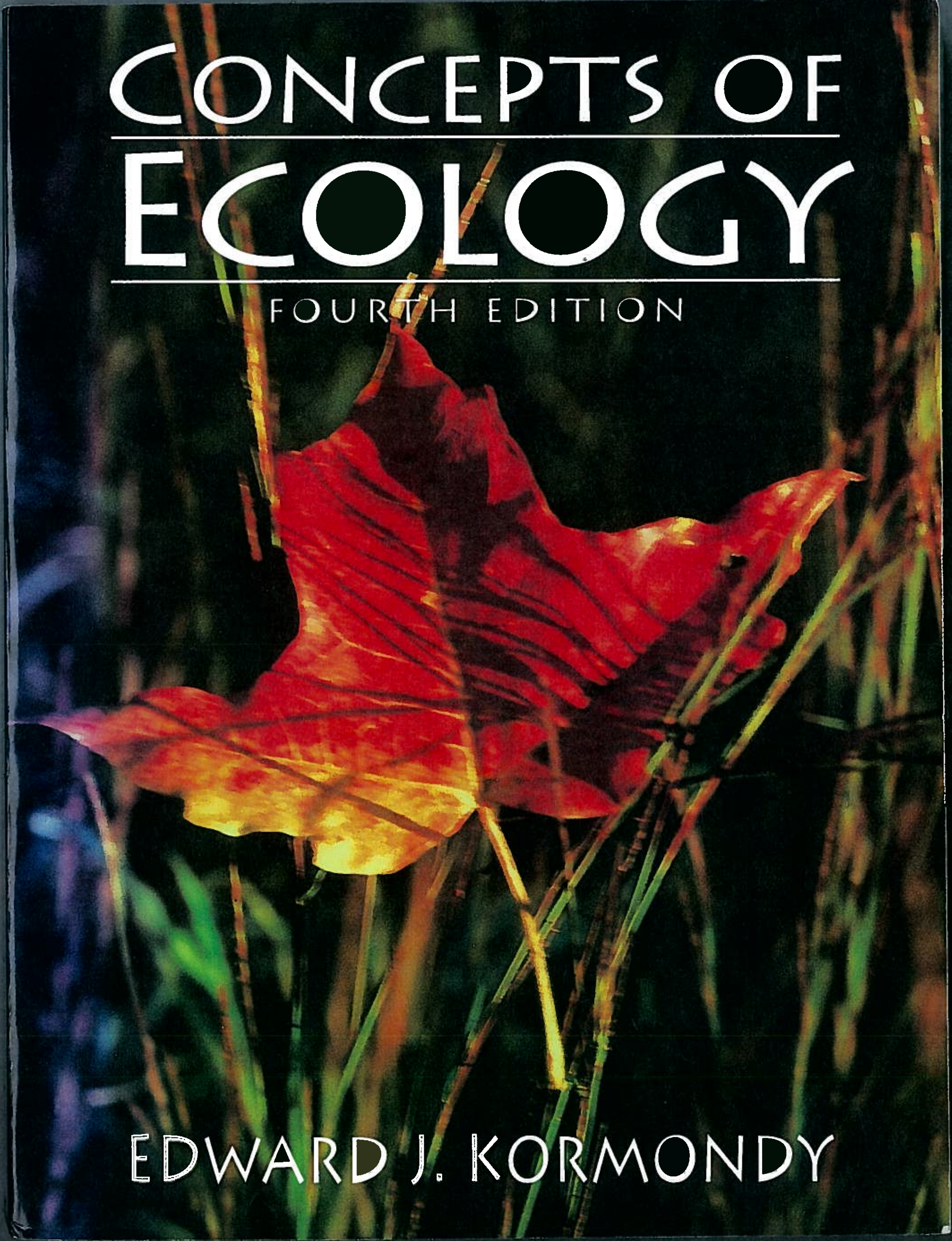
CONCEPTS OF ECOLOGY

FOURTH EDITION



EDWARD J. KORMONDY

Concepts of Ecology

Fourth Edition

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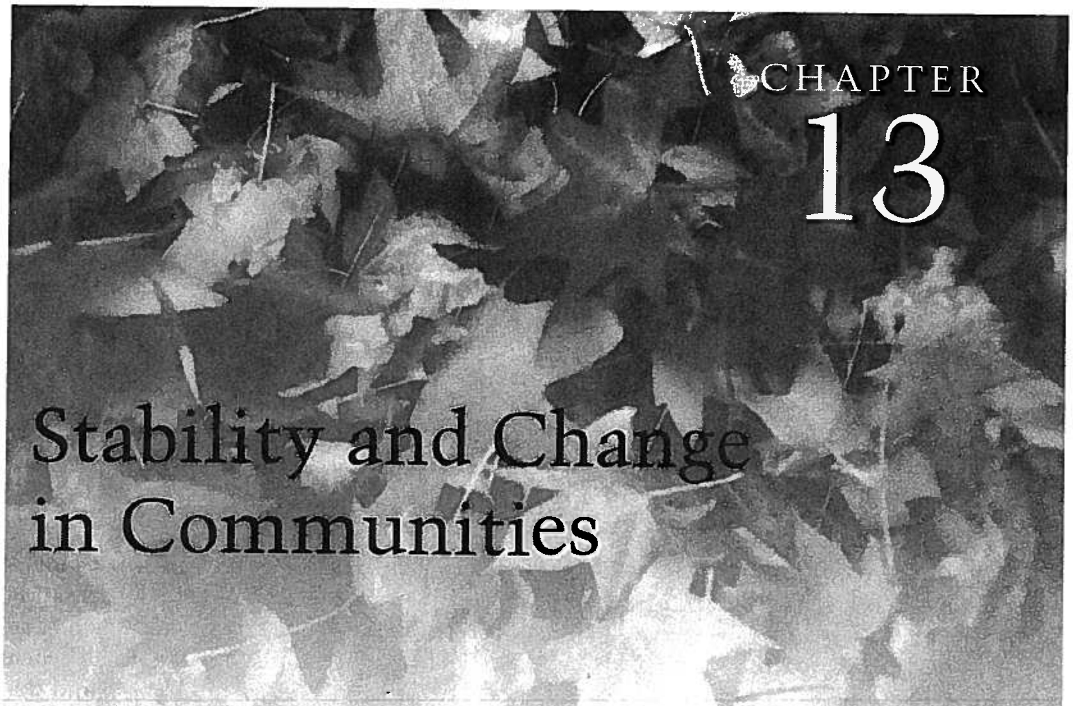
Contents

Part VIII Human Ecology



CHAPTER 13

Stability and Change in Communities

The aphorism "nature abhors a vacuum," expressed by the seventeenth century Dutch exponent of pantheism, Baruch Spinoza, aptly describes a major ecological phenomenon, that of *succession.* Bare ground does not remain that way for long because "Nature" in the form of vegetation moves in with dispatch. The initial colonization is followed by a series of sequential vegetational (as well as animal) replacements, or successional changes, that are often predictable in a given area or site. For example, in a series of studies, among which is a classic one published in 1899, American ecologist Henry C. Cowles showed that the different communities initially present in Indiana in such diverse habitats as flood plains, sand ridges, shallow and deep ponds, and clay banks, all demonstrated a predictable sequential series of structural changes; further, each culminated in a more or less stable community of beech-maple forest. Although the degree of such regularity and predictability was disputed by a number of later ecologists (including Jackson, Futyma, and Wilcox 1988), it is the case that structural and compositional changes in a community over time, both in the present and in the distant past, are recognizable. The factors that regulate such changes, predictable or not, are, as we shall see, complex.

The phenomenon of succession is not accepted without argument; these arguments are not about whether succession occurs, but rather what is occurring. Are the sequential changes occurring within a community or between communities? Are whole clusters of species replaced by other whole clusters of species, or is it a case of a simple species-by-species replacement? Are we observing an organism that is developing from an incipient state through a number of determinate stages to maturity or a sequence of increasingly complex biological communities related to but more or less independent of those that preceded and those that follow? These are among the contending views on succession, not entirely unrelated to the contention about individualistic and organismic views of ecological communities. There are no easy answers, and that is one of the exciting and demanding challenges of contemporary community ecology.

Before exploring the regulation of communities, including their successional characteristics, it will be instructive to gain some understanding of the nature of succession, both structurally and functionally, in a variety of communities and the effect of environmental perturbations on that process.

SUCCESSION IN THE PRESENT

Succession in Beach Ponds

Along the south shore of Lake Erie, at Erie, Pennsylvania, is a peninsula some 4 miles long known as Presque Isle (see Figure 18-1). Owing to a combination of its sandy shore and its exposure to the violent storms and heavy wave action for which Lake Erie is notorious, the peninsula is subject to the frequent establishment of small beach ponds (Figure 13-1a). These ponds are created when an elevated bar of sand develops, thereby isolating a small portion of the lake. The ponds are seldom more than 100 to 200 m long, 10 to 20 m wide, and 1 m deep. Some ponds are wiped out days, months, or even a few years later by subsequent storms that either break down the sand bar or blow in enough sand to fill in the basin. A better-protected pond survives this geological fate only to be immediately subject to its biological fate, ecological succession (Figure 13-1b). Because of the geological history of the peninsula and the persistence of some beach ponds, it was possible to identify ponds of different chronological ages and therefore to study some structural and functional changes that occurred as the ponds progressed from an open water to a vegetated semiterrestrial state (Kormondy 1969).

Structural changes. From a structural standpoint two major changes were observed in successively older ponds: (1) a change in species composition and (2) a change in variety or diversity (Figure 13-2). Some plant species that were present during the initial stages are missing from the more advanced stages. Stonewort alga (*Chara*) and cattail (*Typha*) demonstrate this kind of change. Similarly, some species are not present until fairly late in succession, the yellow water lily (*Nuphar advena*), for example. Yet other species, of which the bulrushes (*Scirpus*) are prime examples, persist as major components of the system for much of its history. These differences are doubtless tied to the tolerance limits characteristic of each species as well as to the subtleties of interspecific competition. Comparable shifts of species composition in phytoplankton and, to a less marked degree, in the animals were also observed.

In addition to these changes in composition, there is a marked increase in the number and kind of both autotrophs and heterotrophs. Sparseness of distribution and limitation of kinds mark the early ponds; increased density and heterogeneity characterize the older ponds. The relative simplicity of structure of the young pond

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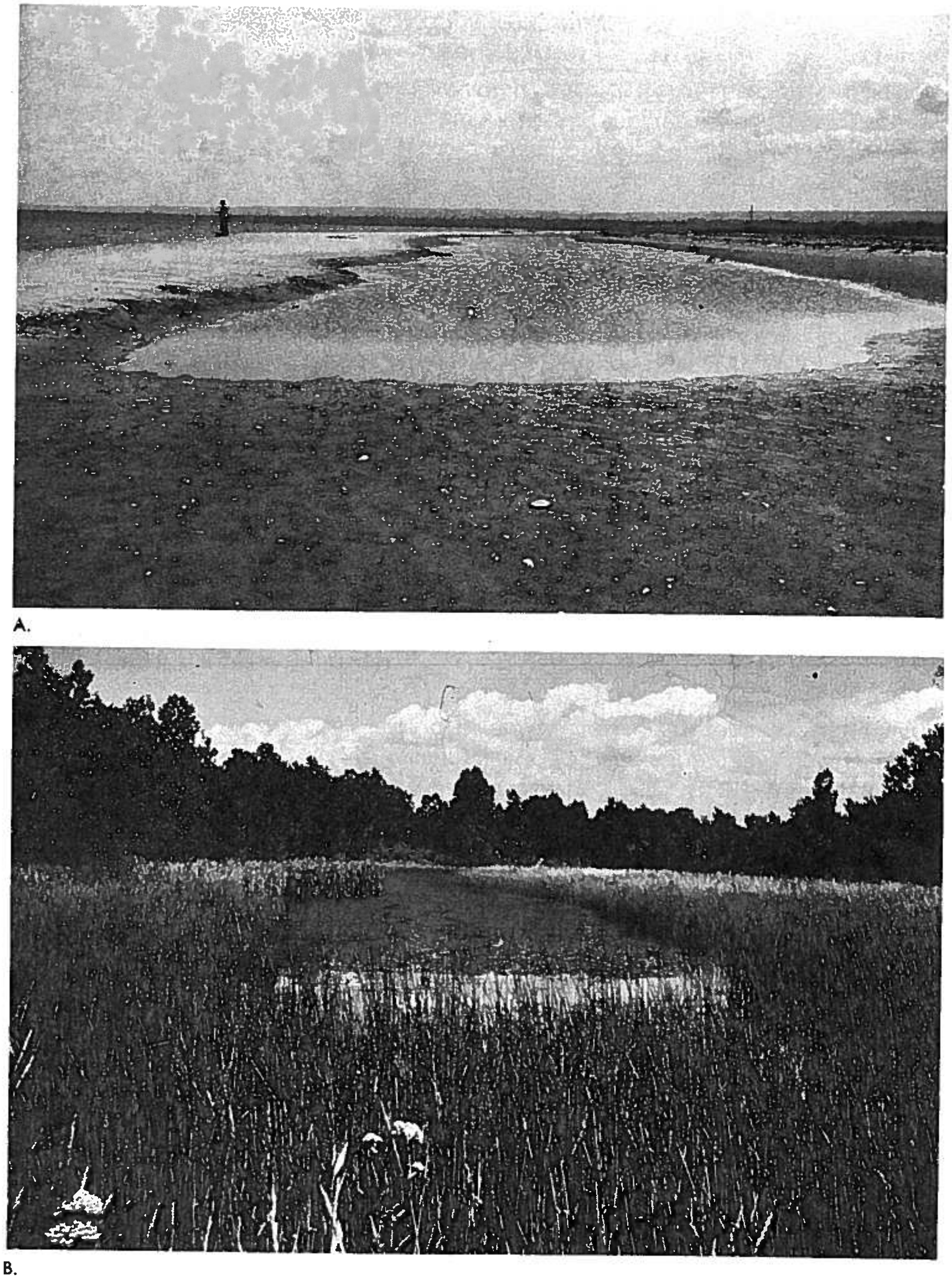


Figure 13-1 Beach ponds on Presque Isle at Erie, Pennsylvania. (a) A newly formed beach pond less than 1 year old; (b) a beach pond about 50 years old. (Photos by author.)

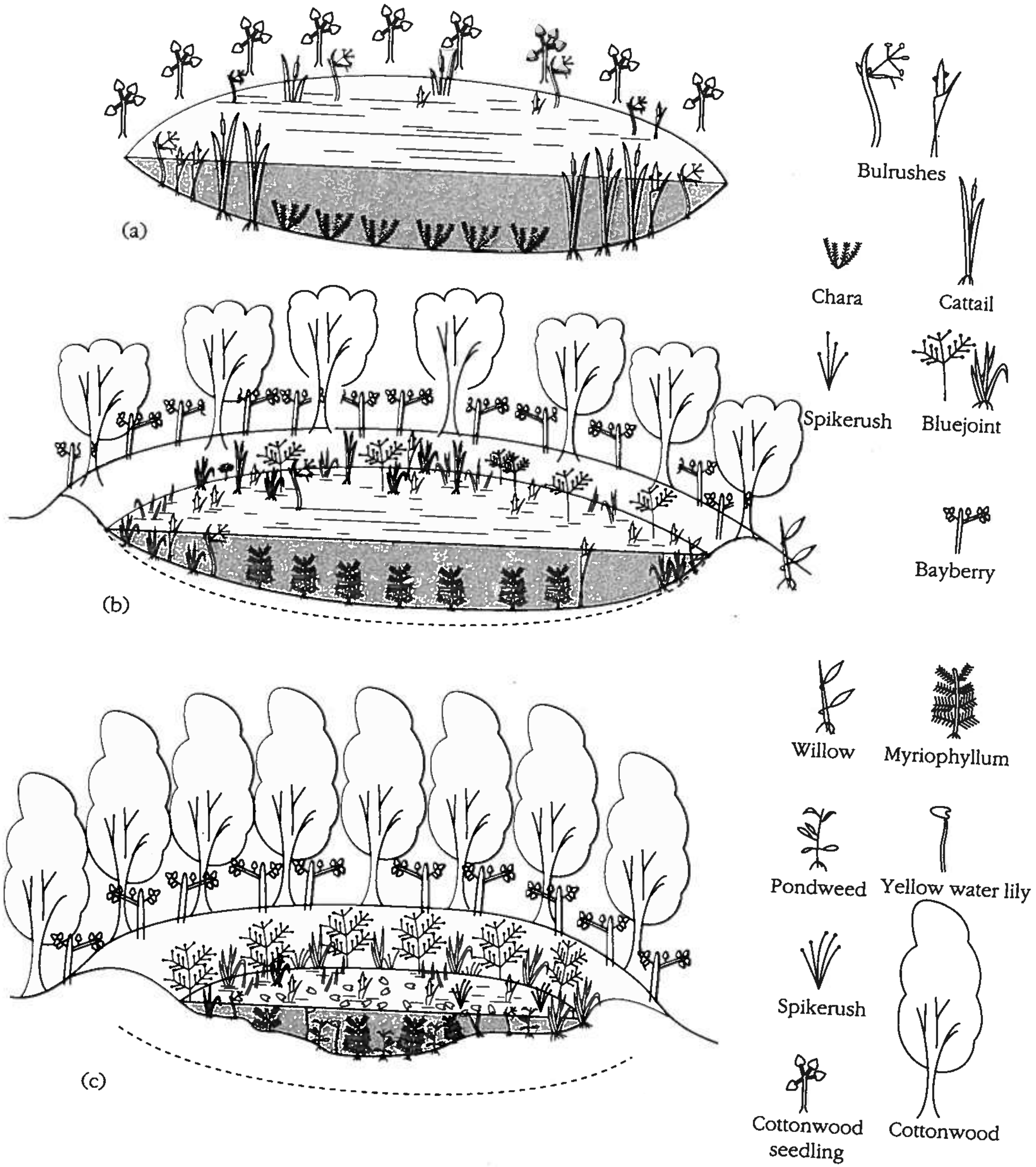


Figure 13-2 Generalized stereo-profiles of beach ponds on Presque Isle at Erie, Pennsylvania, at (a) 4 years, (b) 50 years, and (c) 100 years of age. Note the changes in kind, distribution, and abundance of different species and the accumulation of organic matter filling in the bottom.

is in striking contrast to the relative complexity of the more advanced stages in succession (Figure 13-2).

Functional changes. On the functional side, two major changes can be noted. One is a progressive increase in the amount of both living and dead organic matter. In part, this biomass increase is expected from the already noted increase in numbers; and because the amount of living organic matter shows an increase, there would be an eventual increase in dead organic matter. The accumulation of organic matter on the bottom reaches the point, it may be noted, that the pond is progressively filled in. Measurements of other organic components, such as plant pigments, notably chlorophyll, also show a progressive increase with more advanced stages of succession.

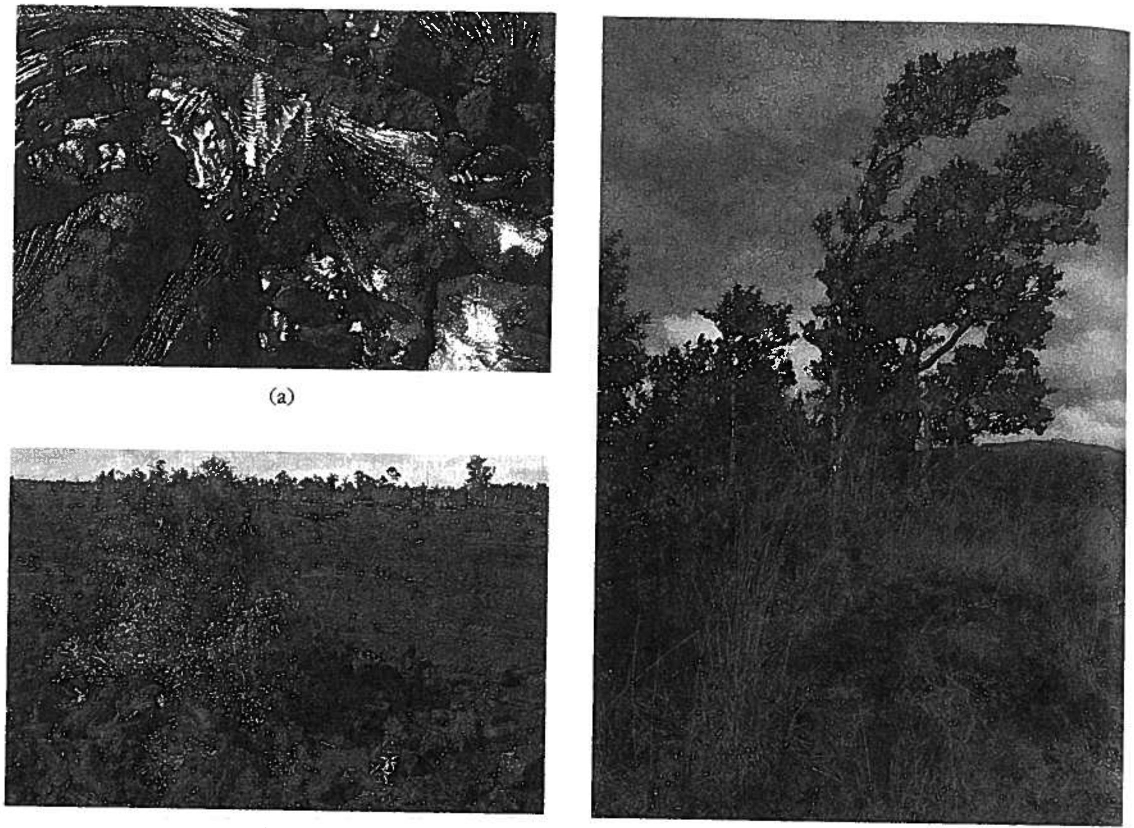
The second major functional change is a shift in community metabolism from young ponds, which are autotrophic ($P/R > 1$), to those that are stabilized ($P/R = 1$), and, finally, heterotrophic ($P/R < 1$). Although the number and kind of primary producers increase and result in increased gross production, at least initially, the increasing respiratory demand of the system results in a progressive decrease in the metabolic ratio. The increasing heterotrophy of these aquatic systems applies to that phase of their succession in which they achieve a terrestrial condition. Although no studies were conducted beyond this transitional stage, evidence elsewhere strongly indicates that such systems would continue to undergo terrestrial succession with an accompanying trend toward stability of their metabolic ratio.

Succession on New Islands

The opportunity to study succession in newly created environments is limited to situations such as beach ponds, recent lava flows (Figure 13-3) and newly emerged islands. An opportunity for the latter was provided between 1882 and 1985 when the water level of Lake Hjalmaren in Sweden was lowered about 130 cm, resulting in the emergence of a large number of new islands. Beginning in 1886 and extending through 1985 a series of plant surveys was conducted on the islands at several time intervals (1886, 1892, 1903–04, 1927–28, and 1984–85) by various investigators; these were analyzed by Rydin and Borgegard (1991), who conducted the last survey. Their report focuses on the 30 islands for which a complete 100-year set of data was obtained.

Successional stages. Of the 112 plant species that occurred on at least 10 islands or were abundant on at least 3 islands in any one of the surveys, six major categories or stages of species composition were recognized based on frequency or abundance:

1. Pioneers (13 species) reached their maximum at the first survey, decreasing drastically after the first or second survey;
2. Pioneer Stayers (6 species) reached many islands by the first survey and remained at similar levels until the fourth or fifth survey;
3. Early Successionals (16 species) showed a distinct increase between surveys one and two, a maximum in the second or third and declined thereafter;



(a)

(b)

(c)

Figure 13-3 Succession on a lava flow in Volcanoes National Park, Island of Hawaii. Pioneers are ferns (a) followed by low shrubs (b) and finally by *Ohia* trees (c). (Photos by author.)

4. Early Successional Stayers (10 species) had a distinct increase between surveys one and two, but no subsequent decline;
5. Mid Successionals (20 species) had a maximum at survey three and/or four and declined after the latter;
6. Mid Successional Stayers and Late Species (47 species) reached their maximum between survey three and/or four but maintained their importance in the fifth survey or increased between survey four and five, reaching a maximum in the latter.

Examples of each of these categories is shown in Figure 13-4.

Structural characteristics. The Pioneers formed a distinct group and had a high proportion (8 of 13 species) of therophytes (annuals) that were autogamous (self-pollinating), along with insect-pollinating species. The 6 species that lacked animal,

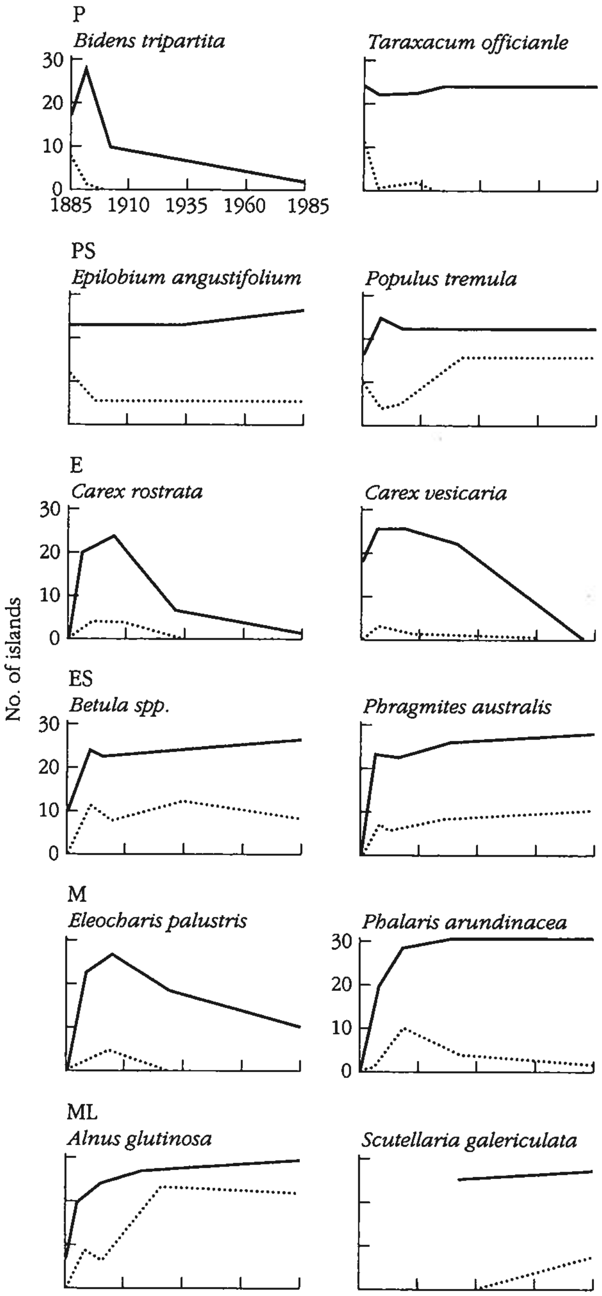


Figure 13-4 Occurrence of species during a century of succession on islands in Lake Hjalmaren, Sweden. Solid line shows the number of islands where the species was found (frequency); dotted line shows the number of islands with larger populations (abundance). The groups, based on abundance, are: P, Pioneers; PS, Pioneer Stayers; E, Early Successionals; ES, Early Successional Stayers; M, Mid Successionals; ML, Mid Successional Stayers and Late Successional Stayers. (Adapted with permission from H. Rydin and S.-O. Borgegard. 1991. *Ecology* 72:1089–1101.)

wind, or water dispersal ability all showed late arrival times on the islands. Pioneer Stayers and Early Successional Stayers were on the average taller than Pioneers, and both groups had higher seed numbers (fecundity) than the others. Pioneers and Early Successionals had higher light requirements than the other groups. Seeds in Pioneers were not smaller than in Early Succesionals or Mid Successionals and did not differ between annuals and perennials, but species with the heaviest seeds arrived late, these being dependent on dispersal by birds. The observations that light requirements, as well as a preference for open habitats, decreased over time suggests that physiological factors may play a more important role than inherent life history patterns in the replacement of species after the Pioneer stage.

Remote Sensing of Succession

A major problem in observing succession is that ecologists don't live long enough! As we have seen in the two foregoing examples, the time-span of succession was in the order of a century. The observations on Lake Hjalmaren were conducted by a number of different ecologists who, fortunately, carefully documented their work so that Rydin and Borgegard could provide a description of succession over 100 years. In the instance of the beach ponds, it was assumed that the differences in structure in ponds of different age were so slight that an inference of successional stages was permissable. Since succession is a long-term process, long-term studies are in order and, to be most accurate, should have continuity of personnel and equipment; this translates to studies over a 20 to 30 year period at best. The newly developing technique of remote sensing, however, offers the possibility not only of reliably determining the course of succession over a period of time but the encompassing of much larger areas than can be studied by an individual or even a team of ecologists. Other applications of remote sensing in ecological studies are discussed by Matson (1991).

Forrest Hall and a group of associates (Hall et al. 1991) studied landscape units of an area of 3600 m^2 using satellite remote sensing over a period from 1973 to 1983. Changes in these large areas were supplemented and corroborated by ground-observed and photo-interpreted plots in 1983. Over the 10-year period it was possible to observe sizeable values of transition rates and changes in structure using the remote-sensing data. Based on these observations, this technique would permit monitoring of forest succession over as much as a 20-year period, an important benchmark for identifying the effects of air pollution and other environmental perturbations. Importantly, it would not be necessary for the same individual to make those observations over those lengthy periods of time.

PERTURBATIONS AND SUCCESSION

The series of changes in communities observed in newly created environments such as beach ponds and new islands are referred to as *primary succession*. *Secondary succession* refers to those sequential changes that occur when an established ecological community is disturbed and subsequently undergoes changes in its structure and function. Whether the secondary sequence follows the pattern of the primary sequence depends on a host of abiotic and biotic factors, both as agents of the disturbance and as components of the redeveloping community. Among the former are fires, ice storms, floods, drought, high winds, landslides, and large waves. Among the latter are such direct interactions as grazing, predation, competition and infection (disease) and the indirect effects of habitat modification caused by activities such as burrow digging by earthworms and rodents or stream damming by beavers, let alone numerous human actions such as bulldozing, construction, and pollution.

The extent of the impact of a disturbance on an established community depends, among other factors, on the severity of the disturbance, the time of its occurrence in the successional process, the multiple interactions that occur among the members of the surviving community, and the proximity to other communities of like or dissimilar nature. The role of disturbance in ecological communities has been an arena of increased ecological interest and has led to the phrase *patch dynamics* (Thompson 1978) used to describe the common focus of such efforts on the conditions created by disturbance (frequency, severity, intensity, and predictabliity) and the responses of organisms to the disturbances. Excellent reviews of the role of disturbance on ecological communities are to be found in Sousa (1984) and Pickett and White (1985). A few examples of perturbations and their effects on succession are in order to give meaning to these comments.

Perturbations in Terrestrial Communities

Fire ants. During the 1940s, the fire ant *Solenopsis invicta* (its name derives from the severe burning sensation its bite creates) invaded the southwestern United States from South America, creating a wave of destruction of naturally occurring communities during this time. At a field station in central Texas, Porter and Savignano (1990) observed that an invasion of fire ants resulted in a 70 percent drop in the number of native ant species and a drop in the total population of native ants of 90 percent. Similarly, the number of species of non-ant arthropods (isopods, mites, and certain scarab beetles) dropped 30 percent and their population numbers 75 percent. The primary causal factor appears to have been competition, another result of which was that there was a 10- to 30-fold increase in the number of ants at the infested sites, more than 99 percent of which were fire ants. The likelihood of this arthropod community reestablishing itself is indeed remote.

Oak wilt. At the time of European settlement in southern Wisconsin, namely about 1840, an area known as Noe Woods was an oak savanna that soon developed into a fairly pure black oak–white oak (*Quercus velutina* and *Q. alba*, respectively) forest of a type common to the region (McCune and Cottam 1985). Between 1956 and 1983, oak wilt disease (caused by *Ceratocystis fagacearum*) caused a 15 to 20 percent rate of death for the black oaks during each of the periods between the 5-year censuses of the forest. White oak increased in basal area but declined in numbers, and the black cherry, boxelder, and American elm that replaced the oaks are, for various reasons, unlikely to fill the latter's self-replacing role in the forest. Here, again, is a community so disturbed that it is unlikely to again have its former characteristic structure.

Depending on their severity, both crown and ground fires can be significant perturbing agents in terrestrial communities (see Chapter 5), as can be parasites, a case in point being that of the sac fungus parasitic on the American chestnut (see Chapter 11).

Perturbations in Freshwater Environments

Flash flooding. We would ordinarily expect that a sudden flash flood, or spate, would likely wipe out an existing community in a stream, as has been observed in a number of cases. However, Boulton et al. (1992) have shown that in a Sonoran Desert stream in central Arizona, a consistent cycle of seasonal changes in the structure of the stream community occurred each year with little alteration by the flooding, the changes being those of relative presence or absence rather than of abundance. For example, seasonal abundance of oligochaetes and mayflies peaked in spring, and a gastropod and caddisflies were dominant in summer. By contrast, there were major changes in the fall community structure influenced, apparently, by drying rather than flooding. The rate of change in species composition declined during succession in all but the spring period, but two summer sequences showed the highest intitial rates of change. Thus unlike the foregoing examples, this community was resilient to the disruptions caused by flooding.

Volcanic intrusion. The once pristine Spirit Lake, lying at the base of Mount St. Helens in the State of Washington and surrounded by steep and densely forested mountain slopes, was drastically perturbed on May 18, 1980, when the volcanic mountain exploded with the force of a 10-megaton nuclear explosion. The resulting pyroclastic lava flow carried immense quantities of debris, old and/or burnt trees, and mineral-containing rock into the lake raising the temperature from about 10°C to 30°C and filling extensive portions of its basin. Extensive and intensive studies have been conducted on Spirit Lake leading to the conclusion that it will never return to its pre-eruption condition (Larson 1993). Significant changes have and are occurring in its flora and fauna and in its chemical composition; its surrounding environs harbor pathogenic bacteria and prolific noxious plants. This is an instance where secondary succession is leading to a markedly different commmunity than existed before an event, as well as being a commentary on nature's power to dramatically alter the landscape.

Given the extensive perturbation caused by the eruption, sites on Mount St. Helens are providing optimum opportunities to study primary succession (del Moral and Bliss 1993), while other, less violently altered sites, allow secondary succession, including recolonization by the fallout of arthropods (Edwards and Sugg 1993).

Perturbations in Marine Environments

Sea grass. Not unlike many introductions of non-native species in marine environments, the sea grass *Zostera japonica* apparently came accidentally to the west coast of North America from Asia in the 1950s by ship, in this case with shipments of oysters used to support the local shellfish industry (Posey 1988). It quickly expanded its range over the coastal area of northwestern United States and continues to spread southward. Using a combination of observations and transplant experiments as the grass expanded to new areas, Posey showed that this foreign or non-native species (technically an "exotic") resulted in changes in the community of bottom-dwelling organisms in midintertidal tideflats with the number of taxa present increasing and the densities of several common organisms changed, some becoming greater, others lesser. Most of the changes are associated not with direct exclusion of resident fauna but rather with modification of the habitat. For example, the blades of the seagrass provide hard surfaces for attachment; the blades also baffle currents, thus increasing filtering ability (and densities) of some suspension feeders.

El Niño. In Spanish, the Christ child is known as *El Niño*, a term that has been applied to a change in the Peruvian and Ecuadorian coastal areas that occurs at Christmastime. Annually during this period, the normally cold water of the north-flowing Peru Current is displaced by a warm, southward current that is considerably less rich in nutrients. On occasion, however, the temperature of the southward current increases, the nutrient content lessens further, and the duration of the displacement lengthens, sometimes as long as a year. Besides the perturbation El Niño creates in the world's weather pattern (Kerr 1988a), a subject of considerable interest but beyond our scope in this text, it can and has had significant detrimental effects on the Peruvian anchovy population and those species that, in turn, are dependent on the anchovies—higher-order fish, guano birds, marine mammals, and even human fishermen (Tegner and Dayton 1987; Glynn 1988). Two of the most severe El Niños of the century (each technically referred to as the El Niño–Southern Oscillation, or ENSO) occurred in 1982-83 and in 1986–87. The impact of the 1982–83 El Niño on a kelp forest community near San Diego, California, was studied by Dayton et al. (1992) who reported significant changes in mortality patterns of the kelp (*Macrocystis pyrifera*) and the first large-scale understory mortality in several decades, obliterating much of the structure of the kelp forest. It also led to outbreaks of understory algae, intraspecific competition, and changes in grazing patterns that resulted in variation in recovery rates of the kelp forest in different areas. All this notwithstanding, there is sufficient survival to allow for prompt recovery to preexisting patterns, except in one southern site where sea urchin grazing had an additional impact and slowed the recovery rate.

SUCCESSION IN THE PAST

Succession in the present represents what occurs over a short period of time and can be studied by direct observation of existing communities, making certain assumptions and inferences in doing so. Succession in the past has occurred over long periods of time, namely thousands of years, and must be inferred from direct observations of relics of the past, such as pollen, seeds, and tree rings. Whereas succession in the present focuses on changes in structure, as well as function in some cases, in more or less circumscribed locations, succession in the past tends to focus on large geographical regions and seeks an identification of particular communities with particular climates. Thus we describe the predominant composition and distribution of the major contemporary biomes (see Chapter 14), tying their characteristics to the major climatic patterns of the region in which they occur. Since there have been major climatic changes during Earth's history, major changes in the boundaries of biomes have also changed. This exciting dimension of ecology is generally referred to as *paleoecology*, which deals with determining major ecological communities from their fossil record and thereby dating the climate in those particular regions. The assumption is that, with minor adjustments, particular kinds of communities observed today in particular climates existed in the past in similar climates.

Postglacial Succession in Eastern North America

As was noted in the discussion of beach pond succession, there is a progressive filling in by organic matter. Among the constituents of this organic matter are pollen grains released both from the community in the pond and the surrounding area. By removing a core of the sediment and tabulating the percentages of each species' pollen grains in successive levels of the deposit, the community composition that prevailed at the time each level was deposited can be deduced. The climate corresponding to each level is then inferred from the particular community composition, on the assumption that the climatic requirements of the species have not significantly changed in the interim.

The principle of determination of the chronology of forest composition and climate by pollen analysis, or *palynology*, had its initial development in Europe about 1915. One of its first applications in the United States was made in the 1920s and 1930s by Paul Sears (1930) (Figure 13-5). The reconstruction of this postglacial forest in northern Ohio enabled Sears to infer the following climatic sequence:

Depth in meters	Climate
4.2-3.6	Cold, wet of northern Labrador
3.3-2.1	Gradual shift from oceanic to continental climate
1.8-1.2	Cool, dry climate of southern Manitoba
0.9-0.6	Period of maximum desiccation
0.6	Abrupt increase in humidity. Cool, moist climate of northern Great Lakes
0.3	Moderation of temperature and continued increase in humidity; present climate of north-central Ohio

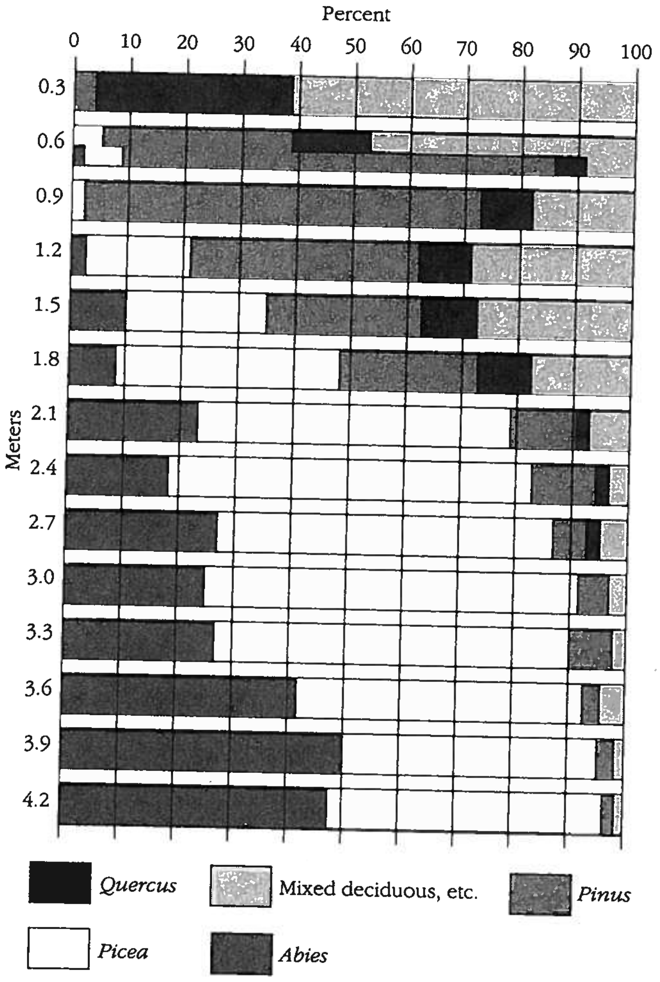


Figure 13-5 Pollen diagram of Bucyrus Bog in northern Ohio showing the proportions of the major genera at each level. According to the investigator, Dr. Paul Sears, "What is labeled *Abies* was probably *Picea canadensis*, illustrating one of the difficulties encountered in early work, namely, the lack of reliable literature for pollen identification." (Redrawn by permission from P. B. Sears. 1930. *Ohio Journal of Science* 30:205–17.)

Additional studies by Sears and by the many students and colleagues he stimulated to engage in this type of investigation have sharpened the picture of postglacial vegetation and climate in North America, in both glaciated and nonglaciated regions. The subsequent application, beginning in the 1950s, of radiocarbon dating of pollen and associated sediments has permitted the assignment of a more precise time scale to the chronology. Based on numerous studies, Sears (1932) advanced the following postglacial sequence for eastern North America:

I. A moist, cool period; maximum of spruce (*Picea*) and fir (*Abies*). Ended about 11,000 years ago.

II. A dry, warmer period; maximum of pine (*Pinus*) with oaks (*Quercus*) almost always an accessory. About 9,000–11,000 years ago.

- **III.** A more humid, warm period; maximum of beech (*Fagus*), with hemlock (*Tsuga*) in some places. About 6,000–9,000 years ago.
- **IV.** A dry, warm period: maximum of oaks and hickory (*Carya*). About 3,500–6,000 years ago.
- **V.** A more moist and cool period; increase of more mesic genera [maples (*Acer*), hemlocks, chestnut (*Castanea*), pine]. The present.

Postglacial Succession in Western North America

Sediment cores from three ponds on the south side of Mount Rainier, Washington, at an elevation of 1,300 to 1,500 m conform to findings east of the Cascade Range in showing little vegetational change during the last 5,000 years (Dunwiddie 1986). Earlier, however, 6,000 to 3,400 B.P. (Before the Present), the dominance of fir (*Abies lasiocarpa* and *A. procera*), Douglas fir (*Pseudotsuga menziesii*) and pines (*Pinus monticola* and *P. contorta*) suggest a warmer and drier climate than we have today, as well as one that favored frequent fires, a condition verified by the presence of charcoal in the sediments.

Postglacial Succession in the Tropics

A number of studies have shown that even the tropics were not immune to the impact of the last glacial advance and subsequent retreat that affected North America's vegetational distributions. For example, analysis of Late Pleistocene (14,350 to 11,050 B.P.) sediments of a lowland tropical lake in Panama indicated a relatively high abundance of montane forest elements such as oak (*Quercus*) and magnolia (*Magnolia*) existing some 900 m below their present range. This suggests a cooling on the order of about 5°C since that time (Bush et al. 1992).

Preglacial Succession in Midwest North America

The ecological communities existing in western Illinois preceding the Pleistocene (about 14,500 B.P.), a period known as the Late Wisconsin and extending back to 28,000 B.P., were determined by an analysis of pollen, vascular plant macrofossils, bryophytes, insects and stratigraphy (Baker et al. 1989). The earlier period, from 27,900 to 26,000 B.P. was dominated by spruce (*Picea*) and jack pine (*Pinus banksiana*); but, during the next period (26,600 to 22,700 B.P.), jack pine had all but disappeared and was replaced by larch (*Larix laricina*), suggesting a climatic cooling as the glaciers began to advance into the Midwest. Further cooling in the next period is suggested by the subsequent decrease in spruce and an increase in sedges (*Cyperaceae*) and spikemoss (*Selaginella*).

Reverse Succession in the Central Yukon

Based on pollen and plant macrofossil evidence, it appears that shrub tundra with groves of balsam poplar (*Populus balsamifera*) occupied the central Yukon between

10,000 and 8,000 B.P. and was gradually replaced beginning about 9,400 B.P. with white spruce (*Picea glabra*) (Cwynar and Spear 1991). About 6,500 B.P., black spruce (*Picea mariana*) and green alder (*Alnus viridis*) increased, characterizing the landscape in open spruce woodlands not unlike today's northern boreal forest. About 5,000 B.P., the forest began to revert to shrub tundra with relict populations of spruce surviving in favorable situations. These changes suggest that Alaska and northwest Canada experienced warmer summers than today from about 10,000 to 6,000 B.P.

40,000 Years of Successional History in Florida

Spanning the geological period of the Middle Wisconsin (40,000 to 29,000 B.P.), the Wisconsin (29,000 to 14,000 B.P.) and the postglacial period (14,000 B.P. to today) is a study on Camel Lake in northwest Florida (Watts et al. 1992). The earliest of these periods was dominated by forests with abundance of pine, oak, and other deciduous tree species including chestnut (*Castanea*), but showed great variation in species composition probably because of climatic variation. The Late Wisconsin period had a species-poor pine forest, and the period from 14,000 to 12,000 B.P., a period that is believed to be the coldest phase at Camel Lake with a suggested climate of −5°C mean January temperature, was marked by spruce and hickory (*Carya*). After 12,000 B.P., oaks and various other deciduous hardwoods were dominant. The present-day turkey oak and long-leaf pine forests began replacing the spruce hickory after about 7,000 to 8,000 B.P.

Interpreting the Fossil Pollen Record

Margaret Davis (1969) has shown that the nature of past (and present) vegetation cannot always be deduced intuitively on a one-to-one correlation from the frequencies of pollen in an assemblage. This is so because of the differences in amount of pollen produced by different species but also because of differences in their dispersal by wind or resistance to decay. Thus it is necessary to determine pollen accumulation rates by relating the pollen concentration in sediments to time intervals and also to take into account the relative pollen production of different species. As a result of such efforts, what was originally thought to have been a forest exclusively made up of pine some 8,000 to 9,500 B.P., because of a pine pollen maximum at that time (see Stage II in Sears's sequence above), was a mixed-deciduous coniferous forest, including pine, such as modern forests of east-central Ohio (see Figure 14-16).

As would be expected from even limited acquaintance with the distribution of contemporary ecosystems, there are differences in the particular sequence of ecosystems in different locations and some disagreement among investigators about given events and interpretation. Anlayses of pollen and macrofossils, as seen in Camel Lake, have shown that the southern limit of spruce in the eastern United States reached what is the present border of Florida and Georgia and that the spruce was replaced by pine about 22,000 B.P. Margaret Davis (1969) argues further that the modern boreal forest biome of Canada does not have an antecedent in the plant communities that existed south of the great ice sheets or that developed as the ice retreated, as would be interpreted from Sears's postglacial sequence (Stage I). Instead this boreal forest appears to be an association established quite recently, an adjustment in a particular environment rather than a product representing continuity in time.

The use of pollen-based methods to reconstruct climates is based on the *dynamic equilibrium hypothesis* (Solomon et al. 1981), which proposes that vegetation changes in response to continuous climatic pressures. This is opposed by the *disequilibrium hypothesis* (Iversen 1960 and Davis 1976, among others) that attributes the different rates and directions of movement of different taxa to the existence of different distribution areas at the time of glacial maximum as well as to different intrinsic rates of spread. In support of the former hypothesis, Prentice et al. (1991) concluded from a study of pollen in eastern North America since 18,000 B.P. measured at intervals of 3,000 years, that the changes in continental-scale vegetation patterns have responded to continuous changes in climate, with lags of about 1,500 years. Their findings do not put other hypotheses to rest but rather add fuel to the debate for current and future ecologists.

Paleoecology Beyond Palynology

Investigations in paleoecology are much broader in scope than might be implied by this discussion of pollen analysis. The principle of the relationship of climatic adaptation and community composition cannot be approached by a study of pollen in a marine stiuation, for example. Here the relative distribution and abundance of key invertebrates, quite often foraminifera and mollusks, serve the same function as pollen in a bog sediment. Dendrochronology, the analysis of growth rings in trees, particularly long-lived species, also provides a key to past climate (Fritts and Swetnam 1989). However, it is not the purpose here to explore these exciting fields in detail but rather to indicate two general points: (1) that the ecology of the past can be studied and offers as many if not more challenges to the investigator than a study of the ecology of the present—and certainly each will make and has already made substantial contributions to the other; and (2) communities are indeed dynamic, ever changing in composition and function in response to both immediate and long-term environmental changes. The seeming stability of present-day communities is indeed deceptive and is likely to give a false sense of security. As a biological unit, they remain stable by not being static.

MATURATION OF COMMUNITIES

The maturation and development of communities have been characterized by Eugene Odum (1969) as a "strategy" of increased control of the physical environment that provides maximum protection from environmental perturbations. The culmination of this dynamic and largely predictable process of community-controlled modification of the environment is a stabilized ecosystem. Odum has identified a number of trends to be expected in the development of ecosystems (Table 13-1), only a few of which have been singled out in the preceding discussion. Of these, the four major structural and functional attributes of ecological succession (increase in species diversity, increase in structural complexity, increase in organic matter, and tendency toward metabolic stability) are, in a sense, both causes and effects of the very processes of change and the eventual stability that generally characterize ecosystems. A newly available environment, like a beach pond, a plowed but unplanted field, a talus after an avalance, or a new island, is fair game for spores and seeds. But not all these spores and seeds can "play the game" in such a rigorous environment, where temperature extremes are intensified, solar exposure is considerable, and moisture is restricted. Those that succeed in becoming established also immediately chemically and physically begin to modify their environment by their metabolic and behavioral activity. They add their waste products and thereby chemically change the nature of the substrate. They may bore into the soil and thereby physically affect drainage. Spinoza, to whom we referred at the start of this section, also noted a basic ecological principle (out of his context, to be sure) in stating that "nothing exists from whose nature some effect does not follow." Thus it is that each species alters its own environment and that of its associates such that it eventually precludes its own and sometimes others' existence; but in so doing, it provides a new set of conditions within the tolerance range of yet other species. Thus organic matter and various metabolites that increase are both results of previous ecological activity and causative agents of subsequent changes.

The Climax Community

If all this is so, then why does an ecosystem eventually achieve a kind of steady state? This is a condition referred to as a *climax community*, one that is self-perpetuating for relatively long periods and one in which the dynamic changes not only occur but are necessary for the maintenance of the community. On Presque Isle the beach ponds ultimately fill in, undergo terrestrial succession, and terminate in a climax community, a beech-maple forest. The climax community results when no other combination of species is successful in replacing it. In part, this situation can be explained by the tolerance limits and optimum requirements inherent in each species.

But stability of the climax is not so simply explained. Nor is there agreement among ecologists that an organismic entity, the climax, exists. As representative of the organismic school, of which he was an early exponent, Clements (1916) contended that there was only one true climax in a given climatic region. This concept is usually referred to as the *monoclimax theory* in which the end stage of succession is reached after an orderly progression to a predictable end point, the *climatic climax*. According to this theory, biotic effects are believed to be the major force in structuring the community, the pattern of which is the result of interspecific interactions.

TABLE 13-1 TRENDS TO BE EXPECTED IN THE DEVELOPMENT OF COMMUNITIES

Ecosystem attributes	Developmental stages	Mature stages
	Community energetics	
1. Gross production/community respiration (*P/R* ratio)	Greater or less than 1	Approaches 1
2. Gross production/standing crop biomass (*P/B* ratio)	High	Low
3. Biomass supported/unit energy flow (*B/E* ratio)	Low	High
4. Net community production (yield)	High	Low
5. Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
	Community structure	
6. Total organic matter	Small	Large
7. Inorganic nutrients	Extrabiotic	Intrabiotic
8. Species diversity—variety component	Low	High
9. Species diversity—equitability component	Low	High
10. Biochemical diversity	Low	High
11. Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well-organized
	Life history	
12. Niche specialization	Broad	Narrow
13. Size of organism	Small	Large
14. Life cycles	Short, simple	Long, complex
	Nutrient cycling	
15. Mineral cycles	Open	Closed
16. Nutrient exchange rate, between organisms and environment	Rapid	Slow
17. Role of detritus in nutrient regeneration	Unimportant	Important
	Selection pressure	
18. Growth form	For rapid growth	For feedback control
19. Production	Quantity	Quality
	Overall homeostasis	
20. Internal symbiosis	Undeveloped	Developed
21. Nutrient conservation	Poor	Good
22. Stability (resistance to external perturbations)	Poor	Good
23. Entropy	High	Low
24. Information	Low	High

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As noted earlier, the organismic view has been challenged by numerous ecologists of the individualistic school of thought, most prominently Britain's Arthur Tansley (1939), and America's Henry Gleason (1926) and Robert Whittaker (1953), among others. In this view, communities are the result of species-specific responses to particular environmental factors, the resulting species assemblages being largely the happenstance of innate life histories that happened to be in the same place at the same time. As a result, a given climatic area can contain a number of climax types forming a mosaic governed by the interaction of climate, soil, and topography, as well as by biotic factors (See Figure 14-18). This concept is usually referred to as the *polyclimax theory*, which conveys a continuity of climax communities varying with the prevailing environmental gradients. Although there are contemporary adherents to the monoclimax view, most ecologists today hold to the polyclimax theory or some modification of it.

REGULATION OF COMMUNITIES

Whether the monoclimax or polyclimax theory is espoused, it is acknowledged that communities do undergo succession, and mature communities do exhibit a degree of stability for varying periods of time. Whether this stability is a property of the individual species composing the community or of the community itself is, as noted at the beginning of the chapter, debatable.

Connell and Slayter (1977) outlined three different models regulating succession: the facilitation model, inhibition model, and tolerance model (Figure 13-6). The *facilitation model* characterizes the monoclimax or climatic climax view, each species making the environment more suitable for the next species or group of species. The *inhibition model* applies to situations in which initial colonists prevent subsequent species from colonizing, a model in which succession depends on who arrives first and in which the successional pattern is not orderly. In the *tolerance model*, which is intermediate between the other two models, any species can start the process of succession but a somewhat orderly process ensues, leading to the eventual climax community.

An examination of some of the factors regulating community development and structure will indicate the complexity of this exciting arena of contemporary ecology. In some large measure the various factors to be considered can be regarded as the relative contributions of "bottom-up" forces (e.g., resources, climate, and other abiotic factors) and "top-down" forces (e.g., biotic interactions) (Matson 1992).

Role of Species Diversity

One mechanism of community regulation that has held considerable persuasion—and generated considerable debate—is species diversity. G. Evelyn Hutchinson (1959), in an essay with the intriguing title, "Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals?", posed the question well. He also suggested an answer, as did Robert MacArthur (1965), who formalized the hypothesis

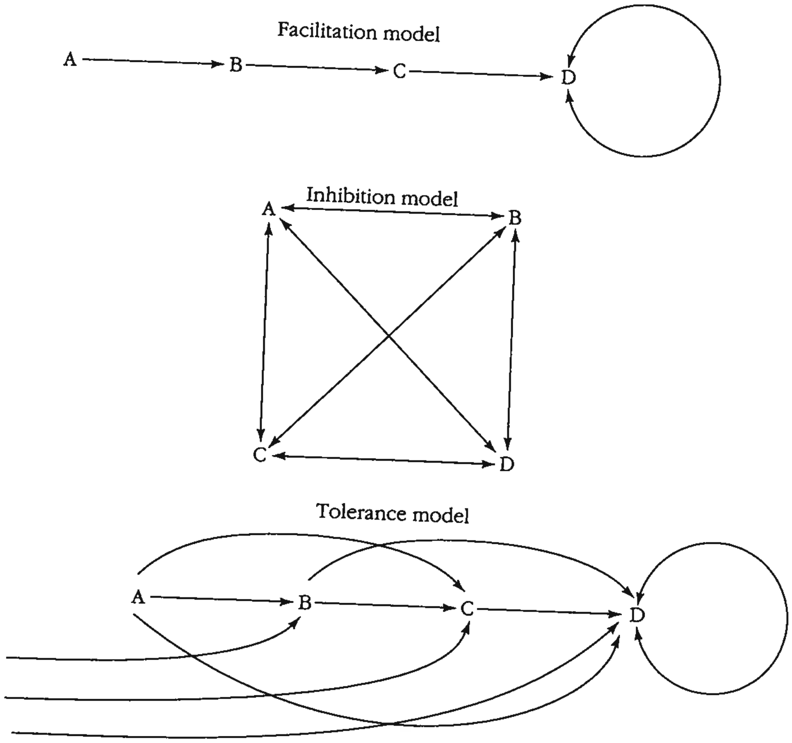

Figure 13-6 Three models of succession proposed by Connell and Slayter. Four species are represented by A, B, C, and D. An arrow indicates "is replaced by." The facilitation model is the classic model of succession. In the inhibition model, all replacements are possible, and much depends on who gets there first. The tolerance model is represented by a competitive hierarchy in which later species can outcompete earlier species but can also invade in their absence. (Reproduced with permission from P. Stilling. © 1992. p. 344. *Introductory Ecology.* Prentice Hall Inc. Upper Saddle River, New Jersey.)

mathematically with particular reference to the number of trophic pathways in an ecosystem.

The species diversity argument. The argument for species diversity as the regulator of community development and stability runs like this: the more advanced the system, the more complex its function by virtue of the increased number and availability of different ecological niches; the more niches, the more diversified the flora and fauna; the more diversified the biota, the less likelihood that a shift in one component would adversely affect the system as a whole. Thus if there are many kinds of producers, each overlapping to various degrees in their respective ability to use various wavelengths and intensities of light, a shift in spectral quality or quantity would tend to affect some but not all producers. The ecosystem would therefore be able to continue with little if any detectable disruption. The persistence of a major change would probably result, however, in new equilibrium levels and new combinations of associations of the "survivors."

Copeland's (1965) study of the shift of the dominant producers from turtle grass to blue-green algae with a shift in light intensity is a case in point in the opposite direction (see Chapter 12). The absence of immediately available alternate routing of production resulted in a dramatic drop in output; recovery eventually came but at the expense of some period of time. Highly integrated and complexly interrelated communities, like those of the climax, possess considerable stability and are therefore capable of responding quite readily to various kinds of short-term environmental insults that are not too severe.

Accordingly, the stability of the climax community is related to its species diversity and, moreover, the aging phenomenon or succession is best described as development toward high diversity—a large number of ecological niches and its counterpart of a large number of species. The latter follows from the Gausian competitive-exclusion principle (see Chapter 11) that only one distinct species population can occupy one distinct niche at any one time. The number of ecological niches in a given ecosystem is a function of the history and development of the system and of the multiplicity of energy flow routes through the system. Evidence presented earlier (see Figures 6-4, 6-5, and 14-19) shows the tendency of productivity to increase from the poles to the tropics. This factor is partly related to differences in abiotic characteristics, such as incident radiation (Figure 4-3), but it may eventually also prove to be related to the higher diversity of species in the tropics (Table 13-2). It should follow, then, that a climax tropical forest should, by virtue of its higher species diversity, be relatively more stable than a climax deciduous forest and the latter more stable than a tundra climax.

Critique of the species diversity argument. Although the hypothesis of a positive relationship between the stability of an ecosystem and its species diversity has a ring of intuitive plausibility to it, empirical verification is largely wanting (May 1984, Goodman 1975). In addition to raising a legitimate criticism that discussions of stability-diversity carry an imprecision of definition of key terms, Nelson Hairston and associates (1968) noted from their laboratory study involving bacteria and grazing and predatory protozoa that stability on a higher trophic level was increased by increased diversity on a lower trophic level (a finding supportive of the Hutchinson-MacArthur hypothesis) but also that stability is not predictable from consideration of only the number of energy pathways in the system.

Luckinbill (1979) has shown that in the interaction of the predator *Didinium nasutum* and its prey *Colpidium campylum* an increase in species diversity caused by adding alternative prey destabilized the association, thus causing extinction of the community. By experimental manipulation using a predatory fish, Zaret (1982) demonstrated that the predator destabilized the community in a lake in Panama by

TABLE 13-2 THE NUMBER OF SPECIES IN DIFFERENT GEOGRAPHIC REGIONS SHOWING A GENERAL INCREASE IN DIVERSITY WITH DECREASING LATITUDE

Insects	Beetles[b]		Ants[a]		Dragonflies[c]	
	Labrador	169	Alaska	7	Nearctic	59
	Massachusetts	2,000	Iowa	73	Neotropical	135
	Florida	4,000	Trinidad	134		
Mollusks	Nudibranchs[a]		Land snails[b]		Lamellibranchs[b]	
	Arctic latitudes	10	Labrador	25	Newfoundland	30
	Temperate latitudes	90	Massachusetts	100	Cape Hatteras	150
	Tropical latitudes	130	Florida	250	South Florida	200
Vertebrates	Coastal marine fish[b]		Snakes[a]		Nesting birds[a]	
	Labrador	75	Canada	22	Greenland	56
	Massachusetts	225	U.S.A.	126	New York	195
	Florida	650	Mexico	293	Colombia	1,395
Plants	Flowering plants[b]		Ferns and clubmosses[b]		Endemic genera of flowering plants[d]	
	Labrador	390	Baffin Land	11	North temperate zone	127
	Massachusetts	1,650	Labrador	31	Tropical zones	465
	Florida	2,500	Massachusetts	70	South temperate zone	55

Data adapted from:

[a] A. G. Fisher. 1960. *Evolution* 14:64–81.

[b] G. L. Clarke. 1954. *Elements of Ecology*. New York: John Wiley & Sons.

[c] C. B. Williams. 1964. *Patterns in the Balance of Nature*. New York: Academic Press.

[d] R. Good. 1953. *The Geography of Flowering Plants*, 2nd ed. London: Longmans, Green and Company, Ltd.

exterminating 13 of 17 native fish, whereas no extermination resulted from the introduction in the adjacent and relatively less environmentally stable river system.

Work by Robert May (1973), among others, on diversity-stability modeling have not supported the idea; and in his studies on forest insect pest species Kenneth Watt (1965) failed to find a positive relationship between stability and diversity. Watt concluded that the factors leading to stability of a pest species included the proportion of the total environment containing food for the pest, an increase in the presence of other species competing for the same host, and a smaller number of enemies.

If species diversity is not the factor or major factor in stabilizing community patterns and processes, then what does govern? Predators, as suggested by the experiments of Luckinbill and Zaret cited above? Competitors, as suggested by Watt? Food webs as suggested by Pimm et al. (1991)? (Also see the discussion of food webs in Chapters 7 and 12.) Abiotic factors such as fire or the availability of nutrients? A brief consideration of alternatives to species diversity will indicate the complexity of this issue.

Role of Predators

A number of field experiments have shown that changes in the densities of predatory (and other) species affect the structure of their ecological communities. Stream-inhabiting midge larvae that weave filamentous algae into tufts that serve as retreats are preyed upon by invertebrate predators such as dragonfly larvae. If the latter are preyed upon by fish, the pressure on the midges is lessened, and they graze down the algae (Power et al. 1992). By experimentally adding, separately and in combination, mantids (*Tenordera sinensis*) and a wolf spider (*Lycosa rabida*), both predators, into a terrestrial old-field community, Hurd and Eisenberg (1990) demonstrated differential effects on the native arthropod community. The mantids depressed not only the total numbers of resident arthropods by 10 to 15 percent but also reduced their biomass by 50 percent, an effect that was confined to the largest-size categories of arthropods. By contrast the wolf spiders had no measurable effect.

Aquatic communities. Diehl (1992) conducted an experimental study of the effect of an introduced omnivorous predator, perch (*Perca fluviatilis*), on a freshwater macroinvertebrate community in the littoral zone (that section containing rooted vegetation and in which light penetrates to the bottom). The results showed that perch consumed predatory and nonpredatory macroinvertebrates almost exclusively, but, in the absence of vegetation, the consumption of the nonpredatory microcrustaceans was increased. An increased density of perch caused a decrease in biomass of predatory invertebrates and the abundance of the dominant predatory invertebrate, a megalopteran, but had no effect on the biomass of nonmolluscan herbivores and detritivores. He showed further that relatively large predatory invertebrates can coexist with fish in the littoral zone and play an important role in the structure of that community. Comparably, Hixon and Beets (1993) found that predation, along with competition, the rate of colonization, availability of naturally occurring refuges (e.g., holes), and other factors, plays a significant role in the structure of coral-reef fish communities.

The Role of Competition

Barnacles. Connell's study of aggressive competition between two species of barnacles (see Chapter 11 and Figure 11-12) was pursued from a successional perspective by Farrell (1991). This experimental study showed that the first colonizer on a cleared plot, *Chthamalus dalli*, was replaced by *Balanus glandula* according to the tolerance model of succession described earlier, in this instance by competition for space. By contrast, the several species of macroalgae that came next in the successional sequence did so only after *Balanus* was established, an instance of the facilitative model of succession. However, the study also demonstrated that a significant role in the rate of succession was played by consumers, namely limpets, which delayed the establishment of *Balanus* and of the macroalgae.

Seedling growth. In a study of primary succession on an Alaskan floodplain, Walker and Chapin (1986) showed that competitive interactions played a significant role in controlling seedling growth. In a greenhouse, alder (*Alnus tenuifolia*), through its associated nitrogen-fixing bacteria, facilitated the growth of seedlings of willow (*Salix alaxensis*) and poplar (*Populus balsamifera*). However, under natural conditions of alder stands in which nitrogen levels were high, seedlings of naturally occurring spruce (*Picea glauca*) and transplanted seedlings of alder and poplar did not grow as well. Experiments employing clearcutting and trenching showed that the alder stands inhibit the growth of seedlings of other alders, as well as spruce and poplar, by root competition and shading.

The Role of Nutrients

The availability of nitrogen cited in the case of alder inhibition of seedling growth suggests, as does the discussion of nutrients in Chapters 5 and 8, that nutrients play a role in succession and in community regulation. A few examples will confirm that position.

McLendon and Redente (1991) studied the effects of five annual applications of nitrogen and phosphorus to a sagebrush community in northwestern Colorado that had been disturbed, for experimental purposes, in 1984. Nitrogen, but not phosphorus, significantly affected the secondary succession for all years except the first by allowing annuals to remain as dominants through the fifth year of the study.

In an old-field community in Ohio, Carson and Barrett (1988) showed that fertilizer enrichment (nitrogen, phosphorus, and potassium) led to dominance by summer annuals during a 3-year study of succession in a 1-year-old experimental plot. Species richness was greater in the enriched plots for only the first year and was significantly lower than the control plots. In a 4-year-old fertilized plot, two summer annuals and a biennial replaced the dominant perennial grasses.

Additions of nitrogen and phosphorus in two freshwater lakes in Michigan resulted in increases in bacterial abundance and chlorophyll levels in phytoplankton (Pace and Funke 1991), altering the structure of the community. But foraging by introduced *Daphnia* on protozoa, which were not affected by the nutrient enrichment, also played an important role in altering community dynamics.

An enriched atmosphere of CO_2 interacting with nutrients and low light resulted in the greatest stimulation of seedling growth of six species of deciduous trees in a Massachusetts forest (Bazzaz and Miao 1993). The early successional species (gray birch, ash, and red maple) showed increased seedling growth with elevated CO_2 only in the presence of high nutrients; by contrast, the later successional species (red oak, yellow birch, and striped maple) showed the greatest increase in seedling growth with low light. Nutrients play a more critical role in the earlier stages of succession, whereas light intensity becomes more significant subsequently.

In these experimental studies, it is clear that nutrients play an important role in community dynamics (see also Vitousek and Reiners 1975); thus, the processes of decomposition and mineralization under natural conditions warrant due attention in understanding community regulation.

Other Factors

Fire. Among other factors involved in regulating communities is fire, a significant nutrient resource-releasing agent and, in some instances, a requisite to forest regeneration by releasing seeds from fire-dependent cones. Because the role of fire as an abiotic factor was described in some detail in Chapter 5, no further discussion is given here.

Alien species. Introduced species of plants and animals, generally referred to as *alien species*, generally alter ecological communities (Vitousek 1992). At the highly disruptive end of the spectrum of mild to strong alteration, communities may become so transformed by alien species as to be scarcely recognizable (Loope 1992). By the same token, Merlin and Juvik (1992) have shown that some island plant species competitively resist alien invaders in the absence of ungulates like wild pigs. In a study of benthic community changes resulting from the invasion of the seagrass *Zostera japonica*, Posey (1988) showed that the alien species changed the physical habitat as well as the richness and densities of the resident fauna. Thus, alien introductions can lead to increased stabilization of an existing community or a change in community composition that, in turn, leads to a new level of stabilization.

Spatial factors. The role of spatial location and spatial differences in community dynamics is another factor receiving increased attention (Karelra 1994). For example, Kratz and DeWitt (1986) demonstrated the importance of spatial dynamics in the development of peatlands, in particular in a peatland lake system in northern Wisconsin. Near the lake edge organic matter accumulates vertically, thickening the floating mat. In the next zone organic matter also accumulates vertically compacting the underlying peat. In the zone farthest from the shore the peat reaches its maximum density and none accumulates. In a study in subalpine habitats on Mount St. Helens in the sixth year following the 1980 eruption, Wood and del Moral (1987) concluded that the characteristics of early succession depended on the spatial position and dispersal abilities of species in the seed pool and not on environmental gradients such as moisture, temperature, and nutrients. And, Lively et al. (1993) found that most of the variation in the percentage of barnacles and brown encrusting algae covering a rocky intertidal community in the northern Gulf of California was due to microspatial effects caused by the foraging patterns of a common predatory snail.

Historical antecedents. Yet another factor to be considered in understanding the diversity of species in given communities and the regulatory factors that govern community structure and function is geological and evolutionary history (Signor 1990). As Brown and Maurer (1987) note, variation on large spatial and long temporal scales determines the biogeographic and evolutionary processes that shape the composition of the pool of species that historically have had access to a geographical region. But also, variation of small spatial scales and short time scales influences the dynamics of local populations of interacting species and determines the combination of species that constitute local communities. These two processes are not independent inasmuch as species cannot occur in local communities unless historical events have given them access to the region, and species cannot remain in the pool unless they are able to maintain populations within local communities.

Concluding Comment

At the outset of this discussion of community regulation the role of species diversity, so intuitively attractive, was found to be wanting. Further exploration indicated that a variety of factors, biotic and abiotic, may be involved at different stages of the successional process including that of the so-called climax. Wilson and Agnew (1992) review the myriad ways in which vegetation in a community provides positive-feedback switches, processes that modify the environment, making it more suitable for that community. Simultaneously or sequentially, predation, competition, herbivory, food webs, pathogens, and other biotic interactions have their regulatory impact (Putman 1994). Succession itself is a complex process driven by many processes acting simultaneously in any given situation (Walker and Chapin 1986). To seek for a single, simple answer to the governance of communities is akin to searching for the Holy Grail. As philosopher Alfred North Whitehead is reported to have noted, "Seek simplicity, and distrust it."

AN EPILOGUE ON BIODIVERSITY AND EVOLUTION

Woven throughout the text have been two topics that warrant further attention: *biodiversity*, the number and abundance of species, and the interaction of ecology and evolution. Each is sufficient for extended treatment, but given the purpose of this book, only a brief introductory discussion can be undertaken.

Biodiversity

It is a paradox of contemporary science that we know how many stars there are in the Milky Way, namely some 10^{11}, the mass of an electron, namely 9.1×10^{28}, and the diameter of the Earth, namely 12,752 km or 7,926 miles, but do not know how many species, let alone organisms, there are. Different projections have been made by a number of ecologists, taxonomists, and evolutionists based on different assumptions and yielding disparate numbers. Among those who have given the matter critical attention are Princeton ecologist Robert May (1988, 1992, among others) and Harvard ecologist E. O. Wilson (1988, 1992, among others). But once having answered that conundrum, why is such information of value? A brief exploration of both questions is in order.

The number of species. Estimates of the total number of species range from 3 to 70 million, meaning that the presently known 1.4 million species constitute only about 2 percent of the total (Raven and Wilson 1992, Groombridge 1992, among others)! Among the many problems encountered in ascertaining the number of species is that different groups of animals have held preeminence among naturalists. Birds and mammals are so well studied that the likelihood of discovering new species is remote. However, 11 of 80 known living species of whales and porpoises were discovered in this century, the most recent in 1991 (Raven and Wilson 1992). In 1992 a new genus of a large land mammal (now named Vu Quang ox) was found in the rugged region dividing Vietnam and Laos, the fourth new genus found in this century; this is a region that subsequently yielded two new species of deerlike animals and a new species of fish resembling carp (Linden 1994).

As well studied as butterflies and beetles have been, only a portion of their actual numbers are probably known; terrestrial vascular plants are pretty well catalogued but not so for their marine counterparts—however, botanists recently discovered three new families of flowering plants in Central America and southern Mexico (Raven and Wilson 1992). When we turn to bacteria, fungi, and even protozoa the unknown far outnumbers the recorded. Likewise, some environments are well studied (e.g., temperate forests and grasslands) and the component species are well cataloged; however, organisms of the polar regions, the ocean benthos, coral reefs, and soils are not.

Without delving into the various methodologies that have been employed to arrive at estimates, an exploration that would take us too far afield for the immediate purposes (but which are described in the articles by May and Wilson cited above), a conservative comparison of the estimated number of species will be instructive.

Among the many phenomena in biological diversity are two worthy of note: the relative contributions different groups of organisms contribute to diversity (Table 13-3) and the relative abundance of species in different geographical regions (Table 13-2). Of the some 1.4 million recorded species, groups like mammals, amphibians, bacteria, and echinoderms represent only a small proportion of the whole. The 4,000 species of mammals, for example, constitute only 0.25 percent of the total. Algae, protozoa, fungi, and mollusks have considerably more species described than the preceding group, but less than noninsect arthropods and trees; insect species are the most numerous, constituting more than half of all known species. But, again, these numbers are deceptive in that a number of species at least equal to or even twice or many times more than those identified have not yet been discovered, described, or recorded; this is especially so among those groups that have been given the least attention.

Patterns in diversity. Beyond the comprehensive viewpoint of global diversity, that is the total number of species on Earth, ecologists are interested in the configurations or patterns in which diverse groups of organisms exist. The most common perspective is that of *point* or *α-diversity*, that is the number of species in a given area and the geographical distribution patterns that result. As we shall see momentarily, point diversity is relatively well documented for a wide variety of organisms and has led to such generalizations as an increase in diversity with decreasing latitude. Much less is known about the other kind of diversity, known as *β-diversity* (Pimm and Gittleman 1992), which is the turnover of species across space, including the dimensions of a species' range. As Pimm and Gittleman note,

TABLE 13-3 NUMBERS OF DESCRIBED SPECIES OF LIVING ORGANISMS

Kingdom and major subdivision	Common name	No. of described species	Totals
Virus			
	Viruses	1,000 (order of magnitude only)	1,000
Monera			
Bacteria	Bacteria	3,000	
Myxoplasma	Bacteria	60	
Cyanophycota	Blue-green algae	1,700	4,760
Fungi			
Zygomycota	Zygomycete fungi	665	
Ascomycota (including 18,000 lichen fungi)	Cup fungi	28,650	
Basidomycota	Basidomycete fungi	16,000	
Oomycota	Water molds	580	
Chytridomycota	Chytrids	575	
Acrasiomycota	Cellular slime molds	13	
Myxomycota	Plasmodial slime molds	500	46,983
Algae			
Chlorophyta	Green algae	7,000	
Phaeophyta	Brown algae	1,500	
Rhodophyta	Red algae	4,000	
Chrysophyta	Chrysophyte algae	12,500	
Pyrrophtya	Dinoflagellates	1,100	
Euglenophyta	Euglenoids	800	26,900
Plantae			
Bryophyta	Mosses, liverworts, hornworts	16,600	
Psilophyta	Psilopsids	9	
Lycopodiophyta	Lycophytes	1,275	
Equisetophyta	Horsetails	15	
Filicophyta	Ferns	10,000	
Gymnosperma	Gymnosperms	529	
Dicotolydonae	Dicots	170,000	
Monocotolydonae	Monocots	50,000	248,428
Protozoa			
	Protozoans: Sarcomastigophorans, ciliates, and smaller groups	30,800	30,800
Animalia			
Porifera	Sponges	5,000	
Cnidaria, Ctenophora	Jellyfish, corals, comb jellies	9,000	

TABLE 13-3 (CONTINUED).

Kingdom and major subdivision	Common name	No. of described species	Totals
Animalia			
Platyhelminthes	Flatworms	12,200	
Nematoda	Nematodes (roundworms)	12,000	
Annelida	Annelids (earthworms and relatives)	12,000	
Mollusca	Mollusks	50,000	
Echinodermata	Echinoderms (starfish and relatives)	6,100	
Arthropoda	Arthropods		
Insecta	Insects	751,000	
Other arthropods		123,161	
Minor invertebrate phyla		9,300	989,761
Chordata			
Tunicata	Tunicates	1,250	
Cephalochordata	Acorn worms	23	
Vertebrata	Vertebrates		
Agnatha	Lampreys and other jawless fishes	63	
Chrondrichthyes	Sharks and other cartilaginous fishes	843	
Osteichthyes	Bony fishes	18,150	
Amphibia	Amphibians	4,184	
Reptilia	Reptiles	6,300	
Aves	Birds	9,040	
Mammalia	Mammals	4,000	43,853
TOTAL, all organisms			1,392,485

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if the range of a species is large, then α-diversity is almost independent of the area sampled; contrarily, total diversity may be high while α-diversity is low, with species' ranges being small and adjoining rather than overlapping.

Geographical distribution of biodiversity. As just noted, the geographic distribution of diversity is of the α-diversity type, the number of species in a given area. In part this has already been pointed out earlier in this chapter (see Table 13-2), with the discussion of the trend to increasing diversity with decreasing latitude, that is from the Arctic/Antarctic through the temperate to the tropical. Among the few statements to which all ecologists appear to agree is that **although tropical rainforests occupy only about 7 percent of the land surface, they contain more than half the species of the entire biota of the world.**

Wilson (1988), for example, notes that he recovered 43 species of ants belonging to 26 genera from one leguminous tree in a tropical rain forest in Peru, a number equal to the entire ant fauna of the British Isles, and that Peter Ashton of Harvard's Arnold Arboretum found 700 species of trees in ten 1-hectare plots in Borneo forests, the same number as in all of North America! As Wilson further notes, it is not unusual for a square kilometer of forest in Central or South America to contain several hundred species of birds and many thousands of species of butterflies, beetles, and other insects.

By contrast, drylands have been found to be the richest of South America's six major macrohabitats, including rainforests, in the number of mammals and to be more biologically diverse (Mares 1992). Conservation efforts that address only tropical rainforests, the major focus today, will result in short-shrift to the diversity of fur-bearers.

Using 94 data sets from around the globe, Scheiner and Rey-Benayas (1994) found that: (1) more plant species are found in well-lit, well-watered places, that is, sites of high levels of photosynthesis (perhaps not a surprising finding); (2) more species are found in places where the temperature between summer and winter varies widely than in those with relatively even seasons, a finding somewhat contrary to what some ecologists have held, namely that equitable climates make it easier for new species to evolve and persist; and (3) not only do warm locations with large seasonal temperature fluctuations have more species, they also are more likely to have different varieties at different sampling sites.

Supporting part of the foregoing findings Reice (1994) has suggested that perturbations and heterogeneity, rather than equilibrium, generate biodiversity. He notes that ecological communities are always recovering from the last disturbance, the biota adapting to predictable disturbances, such as annual snowfalls and snowmelts, but losing out when the disturbance is erratic.

The fragility of biodiversity. Although, as we have seen, naturally occurring phenomena such as fire, volcanic action, and floods can adversely affect community structure and thereby diversity, it is without question that human activity, especially on fragile environments, has far greater impact on the maintenance of biodiversity, primarily through habitat destruction.

Tropical rain forests, presumably the richest source of biodiversity, are also among the most fragile and hence vulnerable habitats for several reasons. First, the predominant soils are oxisols (see Table 5-1), typically acidic, nutrient poor, and rich in iron oxides. These soils tend to harden, forming lateritic boundaries, from which vital elements such as calcium and potassium are leached and in which phosphorus forms insoluble compounds with iron and alumninum, thus reducing its availability. Secondly, the high rates of decomposition and primary production mean most of the carbon and nutrients are bound up in the biomass, thus precluding rapid regeneration in the case of clearcutting. Finally, because seeds of most rain forest species germinate within a few days or weeks, most sprout and die in the hot, nutrient poor oxisols (Gomez-Pompa et al. 1972); thus, along with the foregoing factors, the regeneration of a mature rain forest takes centuries, and natural restoration may never occur.

Given this fragility, it is significant to note that tropical deforestation is reducing species by one-half of a percent per year; likewise, coral reefs, the marine counterpart to tropical rain forests, are also being subjected to degradation, largely through human activity. Although the topic of deforestation is explored more fully later, here it is pertinent to note that about 1 percent of the total tropical forests of the world are being permanently cleared or converted to slash-burn agriculture each year. If continued at this rate all tropical rainforests will be gone by the year 2135. And, of course, with that devastation would come the total destruction of the largest pool of biodiversity in the world.

The values of biodiversity. As described in more detail later, tropical rain forests are the reservoirs of many resources of great utilitarian value. These include oils, gums, rubber, fibers, dyes, tannin, resins, and turpentine, along with a wide variety of fruits, root crops (most of which have not been exploited to meet human food needs), and ornamental plants, as well as a number of modern medicines (Cox and Balick 1994). Geographic varieties have provided the materials for agricultural manipulation of more productive and disease-resistant strains. Deforestation reduces the uptake of carbon dioxide in photosynthesis, thereby increasing the presence of this global-warming, Greenhouse gas (see Chapter 20) but also decreasing the amount of oxygen contributed to the atmosphere.

As Ehrenfeld (1988) points out, these utilitarian values placed on biodiversity justify it in economic terms, and a cost/benefit analysis might well support full exploitation of tropical rain forests for maximum economic gain. Further, he notes that although a great many chemical compounds of potential benefit to human health may probably be obtained from tropical rain forests, pharmaceutical researchers believe they can get new drugs faster and cheaper by computer modeling of the molecular structures found promising on theoretical grounds. If these utilitarian and economic values are not sufficient, what remains then is the inherent and intrinsic value of diversity as its own warrant for survival—that is, biodiversity has value in and of itself, and it is inherently wrong to destroy it. Precisely what is to be preserved and how is the subject of considerable debate (Ehrlich and Wilson 1991, Levin 1993, Solbrig 1992, among many others). We shall explore further the valuing of the environment toward the end of the book.

Ecology and Evolution

Throughout the foregoing chapters there has been an underlying and sometimes explicit theme of adaptation—predators to prey, parasites to hosts, physiology to climatic and edaphic factors, behavior to both abiotic and biotic factors, communities to habitats, and so on. Although the study of the interrelationships of ecology and evolution is a highly active one resulting in an abundance of literature, a full exploration would require considerably more time and space than is intended for this introductory text. However, some brief comments are in order.

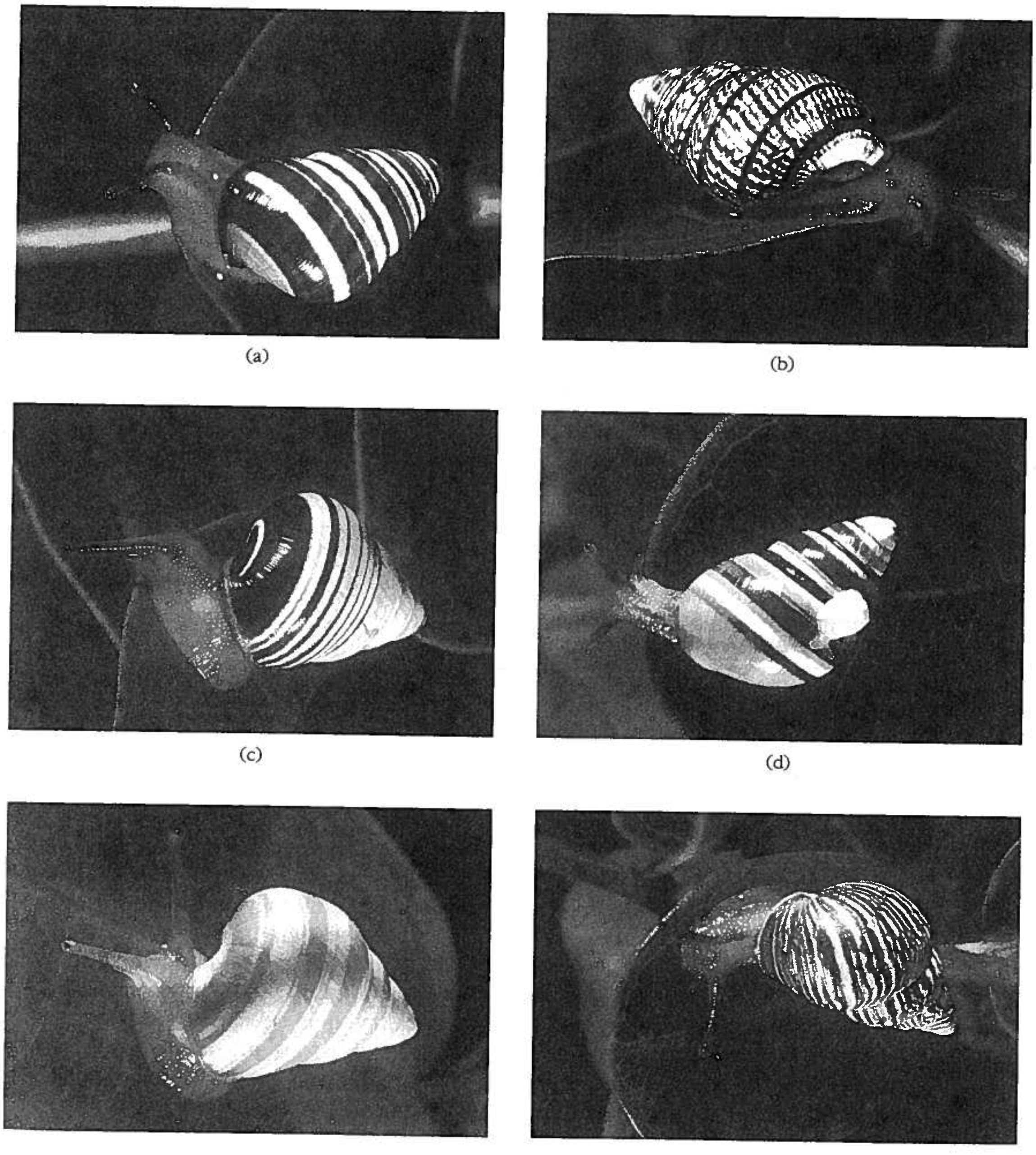
Darwinian evolution. As we all know, the founder of modern evolutionary theory was Charles Darwin, whose famous voyage on the ship *The Beagle*, which began in 1831 and lasted for 5 years (see Moorehead 1969 for an excellent account of this journey), made him aware of the tremendous variety of both living and fossil organisms. This coupled with his subsequent reading of Malthus's treatise on human population growth led to the basic tenets of the theory of evolution by natural selection, or "survival of the fittest." He finally published the *Origin of Species* in 1859, some 20 years after its formulation, prompted, in part, by the development of virtually identical ideas by Alfred Russel Wallace. In brief, the formulation of natural selection can be reduced to three basic steps: (1) more organisms are born than can survive given the limitations or carrying capacity of the environment, (2) organisms vary in a variety of structural and functional ways, and (3) organisms with variations that are favorable in given environment survive and reproduce; others die off.

The major development in evolutionary theory subsequent to Darwin's formulation was its marriage to genetics (a field that was initiated some 40 years after Darwin's major publication), and particularly with population genetics. Genetics provided the explanation of the origin of variation and population genetics the basis of isolating mechanisms that lead to speciation. The most widely accepted of such mechanisms today is referred to as *allopatric speciation* (literally "other country"), which involves the separation of populations by a geographic barrier. The converse, or *sympatric speciation* (literally "same country"), applies to populations that are not geographically isolated, a mechanism whose models include self-fertilization and polyploidy and which is debatable.

Given the tremendous literature on natural selection, speciation, and the interrelationships of ecology and evolution, selecting a topic to discuss here is difficult. However, the islands of Hawaii, a part of the world largely unknown to most of the world, serve as a unique natural laboratory for evolutionary studies and provide some equally unique insights into this fascinating, fundamental field of contemporary biology.

Evolution in Hawaii

Gulick and *Achatinella*. It has often been said that had Darwin visited the Hawaiian Islands, then known as the Sandwich Islands after the Earl of Sandwich, he might well have observed the effects of geographical isolation on speciation and considerably advanced his hypothesis of natural selection. Actually it was the second edition of Darwin's published observations during the 1845 voyage of *The Beagle* that stimulated the first true student of evolution in Hawaii, John T. Gulick (1832–1923). Gulick, born into a missionary family in Hawaii, came to advocate the importance of isolation in the evolution of new species, a position that was in the minority in the 1880s (Amundson 1994). Darwin himself, by the time of the publication of the *Origin of Species*, had come to doubt the importance of isolation as a condition for natural selection to operate and held instead to the view of environmentally controlled speciation (Amundson 1994). The basis of Gulick's tenet was his observations and collections of arboreal snails, mostly of the genus *Achatinella* (Figure 13-7). Based on his mammoth collection of these snails, whose finely graded variations were found



(a) (b) (c) (d) (e) (f)

Figure 13-7 *Achatinella* and *Partulina* tree snails in Hawaii showing some of the variation between species: (a) *Achatinella pulcherrima*; (b) *A. mustelina*; (c) *A. leucorraphe*; (d) *Partulina mighelsiana bella*; (e) *P. semicarinata*; (f) *P. proxima*. (Photos by William P. Mull.)

across the ridges and valleys of Oahu, Gulick is reported to have noted, "... all these *Achatinellae* never came from Noah's Ark." Gulick maintained that natural selection was inadequate to explain the geographical observations he had observed in tree snails, or, in other words, that biological variations overshot environmental differences.

Hawaii's unique flora and fauna. In the more than the century since Gulick's work, substantial efforts have yielded a considerable body of information about Hawaiian evolutionary biology, excellent summaries of which appeared in volumes of *Trends in Ecology & Evolution* in July 1987 and *Natural History* in December 1982. In an introductory essay, Simon (1987) encapsulates some of the salient aspects of the uniqueness Hawaii offers for the study of the interrelationships of ecology and evolution as well as the major contributions to understanding that have resulted from such studies.

Even though it is the most isolated oceanic island group in the world, the Hawaiian Archipelago, volcanic in origin and dated with considerable accuracy (hence contributing to determining rates of speciation), has a spectacular array of species and unique ecosystems that have evolved with a level of *endemism* (i.e., found nowhere else) higher than any other region in the world: some 1,000 species of flowering plants, 2,000 lower plants, 7,000 to 8,000 insects, 1,000 land snails, 1,500 marine mollusks, more than 100 birds, 680 fish, 3 sea turtles, 1 bat, and 1 seal. There are no native amphibians nor terrestrial reptiles in Hawaii.

These endemic species are largely related to Indo-Pacific fauna and flora and arrived over hundreds of thousands of years by various means of overseas dispersal. The large numbers of potential habitats created by varied topography and by steep gradients in rainfall, climate, and altitude, provided unfilled ecological niches that are among the major contributing factors to speciation, making Hawaii the world's premier showcase for examples of adaptive radiation (Tangley 1988; Kaneshiro 1988). The best known of these radiations include *Drosphila*, tree snails, honeycreepers, and several groups of plants.

There are more than 700 species of endemic Drosophilidae in Hawaii, constituting about one-fourth of the world's known Drosophilidae described. The differences among species involve internal and external morphology and some astonishing patterns of mating behavior (Kaneshiro and Boake 1987). Among land snails, the arboreal *Partulina* has 42 species and *Achatinella* 41 species, all of which show variation with respect to shape, sculpture, and size (Figure 13-7). Darwin's finch advocates to the contrary, Hawaiian honeycreepers, with 43 species, are a better example of radiation than the 14 Galapagos finches due to numbers of species, bill morphology (Figure 13-8), plumage coloration, and behavior, as well as interspecific flocking, male coloration relative to females, and nest morphology and position (Freed, Conant, and Fleischer 1987).

Fragility of Hawaii's biota. As Simon (1987) and others have underscored, the extraordinary characteristics of island biotas such as those of Hawaii, which are of great interest, are also the characteristics that create their fragility: specialization, limited ranges, loss of dispersal ability, flightlessness, and lack of defenses (e.g., tox-

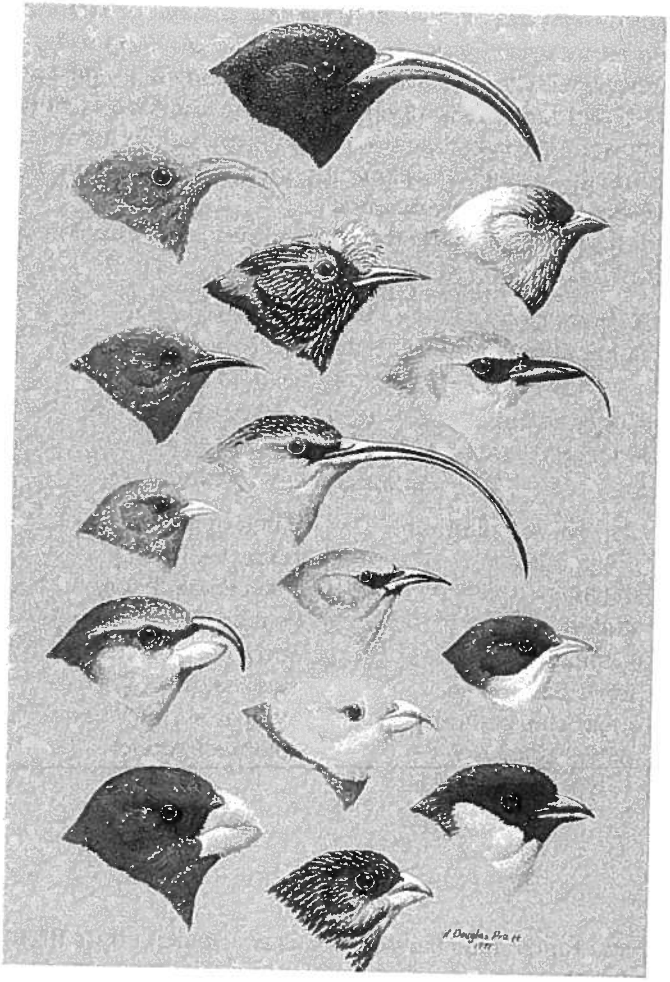


Figure 13-8 Variation in bill morphology and color patterns of selected Hawaiian honeycreepers: (a) mamo (*Drepanis pacifica*); (b) iiwi (*Vestiaria coccinea*); (c) crested honeycreeper (*Palmeria dolei*); (d) ula-ai-hawane (*Ciridops anna*); (e) apapane (*Himatione s. sanguinea*); (f) akiapolaau (*Hemignathus monroi*); (g) Kauai akialoa (*Hemignathus procerus*); (h) Hawaii akepa (male, *Loxops c. coccinea*); (i) Hawaii amakihi (*Hemignathus v. virens*); (j) Kauai creeper (*Oreomystis bairdi*); (k) Maui parrotbill (*Pseudonestor xanthophrys*); (l) ou (male, *Psittirostra psittacea*); (m) grosbeak finch (*Chloridops kona*); (n) Nihoa finch (female, *Telespyza ultima*); (o) poouli (*Melamprosops phaeosoma*). Painting by and courtesy of H. Douglas Pratt, Jr.

ins and thorns are largely absent!). Native snails, for example, are being decimated by introduced predators, and it is estimated that nearly 70 percent of the original avian land fauna is extinct; nearly one-third of the native species of flowering plants are endangered. The causes are basically twofold: conversion of habitats (e.g., shoreline modifications for beaches and harbors, housing developments, agriculture, forestry) and the introduction of alien predators, competitors, and disease. We can also consider such environmental perturbations as volcanic eruptions on the largest island of the archipelago, Hawaii, and the devastating hurricanes such as those that beset the islands in 1982 (Iwa) and 1992 (Iniki).

From the first Polynesian settlements in the third or fourth century A.D. to Captain Cook's arrival in 1778, dogs, pigs, rats, chickens, and about 30 kinds of plants for cultivation (e.g., taro, breadfruit) were introduced. Since 1778, Stone and Scott (1985) estimate that more than 2,000 arthropods, 50 land birds, 18 mammals, and

600 plants have been introduced to Hawaii. Those doing the most damage include feral pigs, feral goats, cattle, and mongooses among mammals (in addition to humans themselves, of course), along with the western yellowjacket, strawberry guava, and certain grasses (Vitousek, Loope, and Stone 1987). The mongoose introduction is one of the most inept: mongoose were introduced to control rats, but rats are nocturnal, and mongooses are diurnal. Instead of preying on rats, which continue to thrive, mongooses have devastated ground-nesting birds.

These largely human interferences with natural ecological systems are explored in greater detail in the next and final section of this book.

SUMMARY

VOCABULARY

- alien species
- allopatric speciation
- β-diversity
- biodiversity
- climatic climax
- climax community
- disequilibrium hypothesis
- dynamic equilibrium hypothesis
- el Niño
- endemism
- facilitation model
- inhibition model
- monoclimax theory
- paleoecology
- palynology
- patch dynamics
- point/α-diversity
- polyclimax theory
- primary succession
- secondary succession
- succession
- sympatric speciation
- tolerance model

KEY POINTS

- The series of structural and functional changes in succession that ensue in an ecological community are either primary, that is initiating on or in a newly created environment, or secondary, reinitiating in a previously established ecosystem that has been disturbed, usually by abiotic forces such as fire, flood, and volcanic eruptions.
- Major ecological communities existing in the past can be determined from their fossil record; pollen analysis has been one of the major vehicles for such studies, all of which are based on the assumption that the climatic requirements of species populations have not changed significantly in the intervening period.
- Four major structural and functional attributes of succession (increase in species diversity, structural complexity, and organic matter, and tendency toward metabolic stability) can be regarded as both causes and effects in leading to a more or less steady community state known as the climax community.

- "Bottom-up" (e.g., resources, climate) and "top-down" (biotic interactions) factors are involved in the regulation of communities. Species diversity, a seemingly attractive agent in stabilization, is nonetheless suspect because of the lack of empirical verification.
- Predators, competitors, fire, nutrients, spatial factors, and food webs all appear to play some role in the regulation of some communities or the members of same.
- The number and abundance of species in the world, biodiversity, are only best estimates. Diversity tends to increase with decreasing latitude. Tropical rainforests, the most fragile of ecosystems, are the most diverse, containing half the known species of the world's entire biota and serving as reservoirs of resources of great utilitarian value.
- Hawaii's relative isolation and its topography have enabled the evolution of a unique flora and fauna that is fragile in the face of both natural processes and human intervention.