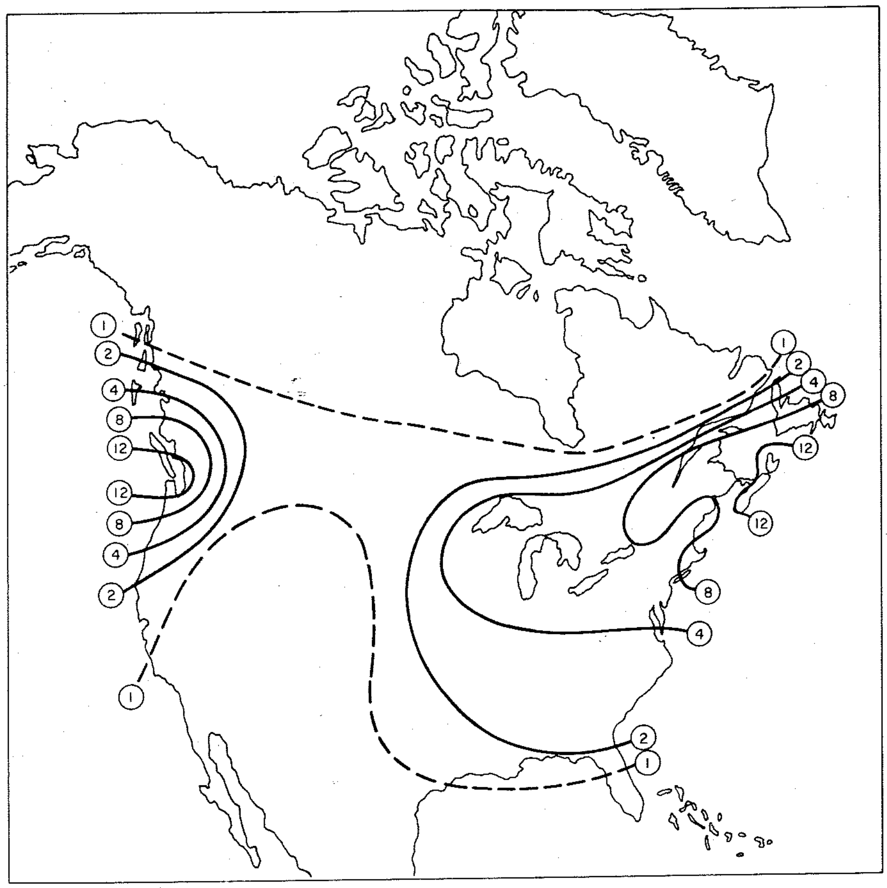

Figure 2.10 The distribution of European carabid beetles in North America. Each line shows the limit to which the number of species indicated at its ends have extended. Note the centers of origin in Nova Scotia and Quebec in the east and Washington and British Columbia in the west. Newfoundland has the highest number of European species (not shown), with 16 species on the Avalon Peninsula. (From Lindroth (1957).)

notable thing about their distribution in North America is that there seems to have been diffusion from small centers of origin on the coasts of Nova Scotia and Quebec in the east, and British Columbia and Washington in the west, toward the center of the continent. We can only conclude that introductions were very local, on a massive scale, and fairly recent.

The basis for this distribution is to be found in the practices of sailing vessels, which visited ports in the locations mentioned above from the early 1600s to about 1850. Ships visited these ports to load various products, but since the human populations at these sites were too low to constitute a lucrative market, there was essentially a one-way traffic of goods from North America to Europe. On the outward-bound trip the ships carried a load of ballast to maintain stability. The ballast, consisting of soil and rocks dug up at ports in Europe, containing many insects and plant seeds, was dumped in the New World and no doubt accounts for the many ground beetles common to both continents.

The sort of pattern seen in Fig. 2.10 is typical of the dispersal of pest species with time. We frequently find that a pest radiated out from a port of entry, or some other point where the initial insects were released; for example, the Japanese beetle; the Argentine ant, *Iridomyrmex humilis* (Mayr); the felted beech scale, *Cryptococcus fagi* Baerensprung; the European elm bark beetle, *Scolytus multistriatus* (Marsham); the gypsy moth in North America (Elton, 1958); and the Colorado potato beetle in Europe (Johnson, 1969). It is unfortunate for the scientist who wishes to learn more about colonizing species, but not so unfortunate for those concerned with the protection of crops and trees, that these introductions do not occur more frequently. We have not yet made sufficient use of these unique events to learn more of the community interactions involved in establishment.

Humans have an impact on the distribution of insects not only by transporting exotic species, but also by introducing new food plants that insects may exploit. Both the Colorado potato beetle and the cotton boll weevil were able to expand their ranges enormously when vast areas in which potato and cotton were planted became contiguous with the original ranges of these insects.

V. COMMUNITY SUCCESSION IN COLONIZATION

We have already seen that as the age of the community inceases, conditions tend to change from severe to equable, and that we are likely to see a trend for the establishment of *K*-selected species rather than *r*-selected species. This trend constitutes only one of the many we see in the succession of communities through time, some of which are summarized in Table 2.1 and Fig. 2.11 (see Odum, 1969). The main driving forces for this succession are the following:

1. Plant species that colonize an area actually change that area and thus make it more suitable for other colonists.
2. Different species of colonists arrive at different times.

The first factor can be broken down into four main influences that plants have on the development of the succeeding community: (1) They create more shade and thus ameliorate the microclimate, making it possible for shade-tolerant species to colonize; (2) they contribute organic matter, which changes soil texture and nutrient status; (3) they produce chemicals (secondary metabolic compounds) that may be toxic to other members of their own species or to other plant species; and (4) they attract animals, including insects, that change factors in the environment by burrowing in soil, leaving

Table 2.1 Comparison Between Early Stages of Succession (Agricultural Situation) and Mature (Climax) Stages of Succession

Characteristics Compared	Early (Agriculture)	Late (Climax)
Community Energetics		
Gross production, standing crop biomass	High	Low
Biomass supported, unit energy flow	Low	High
Net community production (yield)	High	Low
Food chains	Linear (simple)	Weblike (complex)
Community Structure		
Total organic matter	Small	Large
Species diversity	Low	High
Structural diversity	Low	High (stratification)
Biochemical diversity	Low	High
Life histories		
Niche specialization	Broad	Narrow
Size of organism	Small	Large
Life cycles	Short, simple	Long, complex
Nutrient Cycling		
Mineral cycles	Open (wasteful)	Closed (conservative)
Nutrient exchange rate between organisms and environment	Rapid (annual plants)	Slow (long-lived plants)
Overall Homeostasis		
Internal symbiosis	Undeveloped	Developed
Nutrient conservation	Poor	Good
Stability (resistance to change)	Poor	Good
Complexity of organization	Low	High
Selection Pressure		
Strategy for reproduction	*r* selected	*K* selected
Numbers and size of progeny	Many small progeny	Few large competitive progeny
Progeny production	Quantity	Quality

Source: Adapted from E. P. Odum (1969). See Fig. 2.11 for explanations. Reproduced by permission. Copyright 1969 by the American Association for the Advancement of Science.

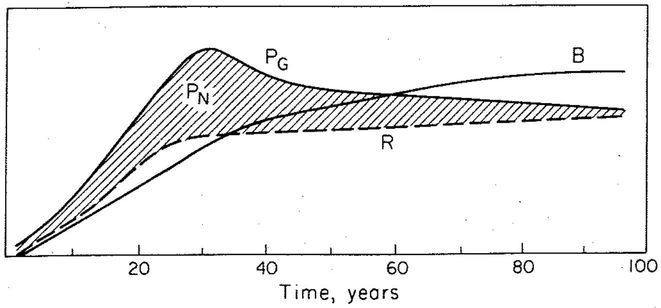

Figure 2.11 A comparison of the energetics of communities leading to a climax forest community. Total biomass B increases rapidly and then reaches a steady state. Total respiration R follows a similar trend, although it reaches the plateau stage earlier. Gross production P_G is the amount of energy fixed by the green plants, which reaches a peak in the early stages of succession and then declines. Since net production P_N is what remains of gross production after some has been used in respiration, that is shown by the shaded area between the lines for P_G and R. (Reproduced by permission from E. P. Odum (1969). Copyright 1969 by the American Association for the Advancement of Science.)

excrement, trampling ground, selectively eating plants, dispersing seeds, pollinating flowers, and attracting their own predators and parasites.

With regard to the second factor it is obvious that plant species with tiny, wind-dispersed seeds arrive very early, for example, dandelions. Eventually enough large seeds arrive to outcompete the resident species, and succession results. Similar trends may be seen in the insect species that colonize an area, although insect size does not correlate so well with competitive ability.

Thus, in time we see changes in the species composition and the complexity of the community. As the microclimate is ameliorated, conditions become more favorable, and more and more species are able to tolerate them. *r*-Selected species are replaced by *K*-selected species, good competitors that tend to become permanent members of the community. As succession progresses, the community acquires an increasing proportion of permanent members. The latter species tend to be more long-lived than those present earlier in the succession. Eventually changes in species composition occur so seldom that there is little noticeable change. We consider this a mature community, also called a climax community. Other trends are summarized in Table 2.1 and Fig. 2.11.

Thus, we see that community succession leads to an increase in the diversity of plants and animals with time. The concept of diversity and its measurement are important in ecology and are explained in the appendix. When there are many kinds of plants and animals in a community, it is clear that there are many sources of food for animals to exploit; in simple communities there are few. Thus, a diverse community contains more buffers against environmental change. Should one food source become scarce, another may be exploited. A change in the status of one species is less likely to have a severe impact on another species; thus, the system is likely to be more stable. Simple systems, with few or only one food source for each animal, are correspondingly less stable.

We can estimate the stability of a community by counting the number of possible routes along which energy can travel through its food web. In Figs. 2.12*a* and *b* we see two possible arrangements of feeding relationships, each with four routes along which energy can pass. Each route is assumed to carry one-quarter of the total energy. Applying the formula for diversity, MacArthur (1955) calculated the stability of these systems, 1.38 in each instance. Adding another predator to the system doubles the number of routes along which energy may pass and increases the stability to 2.08 (Figs. 2.12*c* and *d*). A notable feature of this system of estimating stability is that it generates the same index of stability if four highly specialized predators each feed on a single species of prey (Fig. 2.12*e*) or when one general predator feeds on four species of prey (Fig. 2.12*a*). In this context plants may be considered prey species.

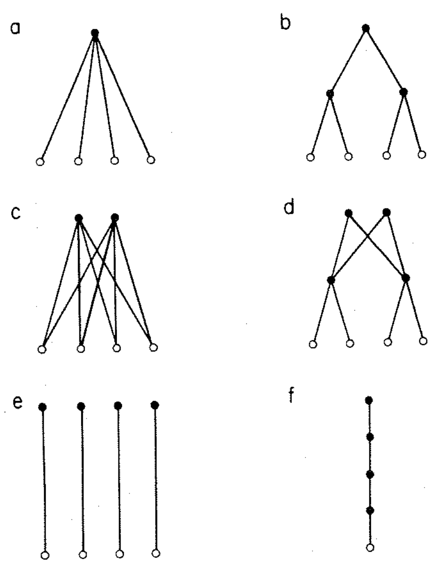

Figure 2.12 The paths along which energy travels determine the stability of the system (*a* and *b*). In (*a*) the lower level represents four herbivores (○), and the upper level represents one predator (●). In (*b*) an additional predator level is added. By adding another predator to the system the number of feeding links is doubled (*c* and *d*). The same stability may be achieved by a generalized predator feeding on four prey species (*a*) or four specialized predators each feeding on a single prey species (*e*). Maximum stability can be achieved by having one consumer on each trophic level, each of which feeds on all lower trophic levels (*f*). Minimum stability for the same number of species exists when one predator feeds on four prey species (*a*). In this context plants may also be considered prey species.

Several properties in relation to stability are worth remembering (from MacArthur, 1955). First, *stability increases as the number of links increases*. Thus:

1. If the number of prey species for each predator remains constant, an increase in numbers of species in the community will increase the stability.
2. A given stability can be achieved either by a large number of species, each with a fairly restricted diet, or by a smaller number of species, each eating a wide variety of other species.
3. Stability is at the maximum for N species if there are N trophic levels with one species on each, each species eating all the species on lower levels. Thus, if $N = 5$, there are eight paths up which energy can travel (Fig. 2.12*f*). Similarly, stability is at the minimum for N species if one carnivore feeds on $N - 1$ herbivores. Thus, if $N = 5$, there are four paths up which energy can travel (Fig. 2.12*a*).

It is clear that restricted diets lower stability, but dietary specialization makes for the efficient exploitation of food. Efficiency and stability are essential for survival. Efficiency enables species to outcompete others, but stability allows individual communities to outsurvive less stable ones. So there must be one of two evolutionary compromises between efficiency and stability:

1. When there are few species, stability can be achieved only if these species eat a wide variety of foods on many trophic levels. We see this pattern in northern latitudes.
2. When there is a large number of species, for example, in the tropics, stability can be achieved even if diets are fairly restricted. Thus, species can specialize in their feeding habits and may feed on only one or at most two trophic levels. These generalizations are, of course, relevant to the strategy of biological control and to an understanding of the impact of insecticide application at different latitudes. Southwood and Way (1970) have considered other aspects of diversity and stability, and the analysis of food webs has been a rapidly developing field (e.g. Pimm, 1982; Schoenly and Cohen, 1991; Schoenly et al., 1991).

Experimental support for the relationship between diversity and stability was provided by Pimentel (1961). He planted some collards in a pure stand, representing a very simple plant community, and others mixed in with natural old-field vegetation, representing a much more diverse environment. At frequent intervals he sampled the arthropods on the collards. In the pure stand several species reached outbreak proportions and did a great deal of damage to the crop; they included aphids, flea beetles, and caterpillars [imported cabbage worm, *Pieris rapae* (L.), and cabbage looper, *Trichoplusia ni* (Hübner)]. The collards in the diverse community suffered no such pest outbreaks.

We must also consider diversity in terms of the environment insects must exploit. This involves understanding the homogeneity or heterogeneity of sites, particularly in relation to the feeding habits (and perhaps oviposition habits) and the size of individual species. One species, for example, a carabid beetle, may feed on many food items and select them more or less in the proportion in which they occur in the habitat. Each food item may be viewed as a small grain of food in a multitude of grains, and we can call this a fine-grained food resource for a carabid. However, a monophagous herbivore in the same habitat can utilize only one plant species of the many that are present, and we may visualize individual plants as relatively large grains of food and the food resource as coarse-grained (see MacArthur and Levins, 1964; MacArthur and Wilson, 1967). With this approach it becomes obvious that increasing diversity has little impact on a species utilizing fine-grained resources, but makes food finding much more difficult for a species exploiting a coarse-grained resource, because its food becomes relatively less frequent in the community. Conversely, simplifying the community is more favorable to a species requiring a coarse-grained resource, as the grains become relatively dense. The extreme case is in agricultural crops with one plant species predominating. Species requiring a coarse-grained resource, often pests, are favored far more than those needing a fine-grained resource, often their predators.

In a similar vein we must consider diversity in terms of the distance insects are capable of traveling. For highly mobile insects diversity must be viewed on an extensive areal basis. Other insects are much more confined in their movements. If cultural methods are used for increasing diversity with a view to reducing pest problems, the distinction becomes important. For example, during the spring colonization of crops the mobility of insects depends very much on the stage in development they have reached. The European corn borer emerges as an adult in the spring and flies considerable distances in order to lay eggs on new corn. Thus, it is difficult to create an agricultural ecosystem diverse enough to seriously lessen the chance that this insect will discover a host plant. In contrast, the northern corn root-worm overwinters in the egg stage, and it is the first-instar larva that must discover food; in this instance we can measure diversity in terms of the few centimeters the larva is able to travel in the soil before starvation ends its search for food. For the farmer, of course, it is easiest to increase diversity in time, by crop rotation, which works admirably for the northern corn rootworm but not for the European corn borer.

Diversity is also influenced by grazing animals, but in different ways according to the intensity of grazing. Lightly grazed pastures frequently increase in diversity, particularly if the preferred food of the grazer is the dominant plant in the pasture community (Harper, 1969). This is because grazing pressure prevents the dominant plant from outcompeting other species. As stated earlier, herbivores also increase the number of sites available to colonizers by leaving excrement and changing the compaction of the soil and microtopography. Heavy grazing tends to reduce plant species diversity by strong selection for a few species with resistance to grazing pressure. Not only is species diversity reduced, but so is structural diversity, because many species never produce flowering stems under grazing pressure (see Fig. 2.1). For further discussion of the influences on plant species diversity in managed systems, see Duffey and Watt (1971). Naturally, as plant species diversity and structural diversity decline, there is a similar decline in the insect species that can be supported (e.g., Morris, 1967, 1971a,b). Dempster (1971) concluded that either overgrazing or undergrazing may cause local extinction of the cinnabar moth, *Tyria jacobaeae* L.

Finally, as we have seen earlier, the diversity of the matrix in which a crop is grown has an enormous effect on the diversity of plant and animal life in the crop. The reader should refer to Section IV, where this is discussed in detail.

The concepts of ecological succession, habitat stability, *r*- and *K*-selected insects, and population dynamics have been nicely integrated into a synoptic model by Southwood (1975) and Southwood and Comins (1976). Further discussion is provided by Southwood (1977) (Fig. 2.13). The synoptic model presents the theoretical population growth of an insect species in relation to its density, from *r*-selected species in unstable environments in a continuum

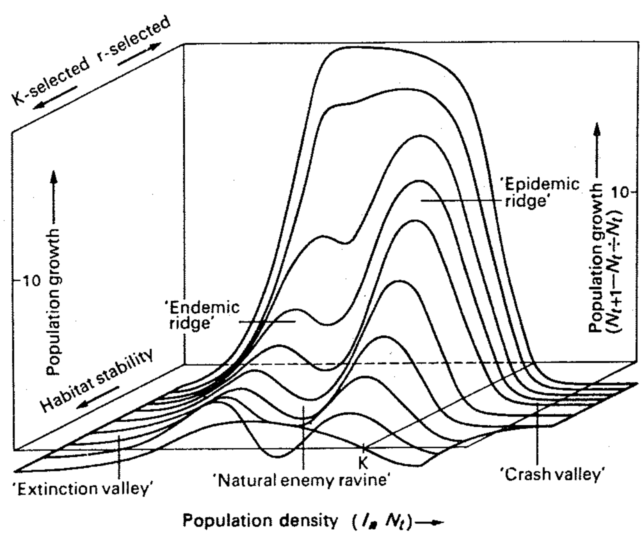

Figure 2.13 The synoptic model of population growth. (From Southwood and Comins (1976) and Southwood (1977). Reprinted with permission from the *Journal of Animal Ecology* **45**:949–965. Copyright © 1976 by Blackwell Scientific Publications Limited.)

to *K*-selected species in stable environments. The shapes of the curves in this continuum depend to a large extent on the rate of growth of the population relative to the capacity of natural enemies to counteract this growth. Strongly *r*-selected species colonizing new habitats have population growth rates so high that enemies seldom prevent the development of epidemic populations. At the other extreme, strongly *K*-selected species in very stable habitats where resident enemies are likely to be numerous invest much energy in defense, making enemies less effective. Between these extremes, however, enemies can be important agents in stabilizing populations at an endemic level (see the endemic ridge in Fig. 2.13), because at higher population densities enemies, acting in a density-dependent manner, take a higher proportion of the prey available. This leads to a depression in the growth rate (the natural enemy ravine in Fig. 2.13). This brief and simplified explanation of the synoptic model should be enlarged upon by a study of the original papers.

The synoptic model was developed from a review of many insect species from a variety of vegetation types (see Southwood, 1975) and its validity remains to be tested. However, it reinforces the view that the *r*-selected species that frequently appear as pests in agricultural systems have the capacity to escape severe enemy impact through the interaction of an excellent colonizing ability, a high population growth (both discussed in Section III), and the destabilizing effects of simple systems (discussed in Section V).

VI. STRATEGIES OF THE FARMER IN RELATION TO ECOLOGICAL CONCEPTS

The farmer's major activities, expressed in ecological terms, are to start the successional process by planting seed, to keep succession in a very early state by cultural activities, and to truncate succession by harvesting and plowing. Thus, the farmer maintains an agricultural ecosystem typified by the set of characteristics given in Table 2.1 for early successional stages. Nevertheless, the more desirable characteristics listed in Table 2.1 are usually properties of mature communities. Thus, any pest-management approach should try to develop an ecosystem that emulates later stages of succession as much as possible, for this is how stability can be achieved.

The farmer actually uses a great deal of energy performing jobs that would normally be done naturally and thus requires large subsidies in terms of fossil fuel and services from the city, also supported by a fossil fuel economy. The work that supports the farmer and that the farmer does may be divided into six main activities (H. T. Odum, 1971; see also Pimentel et al., 1973):

1. Mechanized and commercial preparation of seeds and planting to replace the natural dispersal system

2. Fertilizer application that augments and largely replaces the natural system of mineral cycling
3. Chemical and power weeding that largely replace the natural system of competition and extinction
4. Soil preparation and treatment to augment natural soil-building processes
5. Application of insecticides, which replaces the system of plant diversity, and carnivores in preventing epidemic grazing and disease
6. Development of varieties capable of passing on the savings in work to net food storages. New varieties are developed as disease and insect pests appear, thus providing the genetic selection formerly provided by natural selection.

The farmer creates a relatively simple ecosystem by tile-draining to provide uniform soil moisture, by removing rocks, stones, trees, and shrubs, by channeling streams and rivers, and by growing only a few crops. And yet stability can be most easily achieved in a complex eocsystem. As E. P. Odum (1963) states, "The only way man can have both a productive and a stable environment is to insure that a good mixture of early and mature successional stages are maintained, with interchanges of energy and materials. Excess food produced in young communities helps feed older stages that in return supply regenerated nutrients and help buffer the extremes of weather."

Even though the farmer operates in a simple ecosystem, he still has a good deal of control: He can decide when to start succession and when to terminate it, and this must be decided in terms of damage by weather and pests. Late planting of winter wheat to avoid attack by the Hessian fly, *Mayetiola destructor* (Say), is a good example; another is the delay of plowing until spring to avoid soil erosion over winter. The timing of harvesting may be influenced by the possible migration of insects from one crop to another, or changed to prevent the further buildup of a pest population, in alfalfa, for example. Thus, the farmer has already exercised considerable control over the start and termination of the successional process, although the potential for its further development is great.

The profound effect that agricultural practices may have on insect populations is well illustrated by the European corn borer. This species overwinters only as a larva in the stalk or, occasionally, in the cob or shank of the ear. Although European corn borers are not host-specific, in the Midwest they are practically confined to corn. It should therefore be possible to control them by clean-plowing cornfields before the adults emerge in spring. However, clean-plowing will probably fail to give good control as long as corn is harvested on the ear and stored in cribs. Many larvae survive the winter in cribs, and in southern Minnesota at least 26% of the moths in the field in spring come from this source (Chiang, 1964). The more recent use of the picker–sheller harvester should avoid this problem, since with this method of harvest only the kernels are removed and the rest of the ear is discarded in the field, where it can be plowed down.

Another major influence the farmer may exert on the agricultural ecosystem is the control of diversity. We should remember that small crop islands are likely to have higher extinction rates, and distant stands to have lower colonization rates. Small crop islands from a source of colonizing insects are possible only in a diverse ecosystem. Of course, a major trend in agriculture has been to reduce diversity to increase the efficiency of mechanization; but when pest problems need control, careful cost accounting is necessary to establish whether simplicity or diversity will yield the greatest long-term benefit. We have already discussed the influence of diversity on pests and beneficial insects in Section V.

As a very general conclusion, agricultural ecosystems can be viewed in terms of two central concepts of ecology: island biogeographical theory and the succession of communities. Current thinking and developments in these fields should have an heuristic influence on research in the improvement of pest-management strategies.