methods, as shown in the following outline, modified from Metcalf et al. (1951).

Inventory of Methods of Applied Insect Control (arranged in approximate order of complexity)

- I. Cultural methods or the use of agronomic practices
  - A. Use of resistant varieties of domestic plants and animals
  - B. Crop rotation
  - C. Crop refuse destruction
  - D. Tillage of soil
  - E. Variation in time of planting or harvesting
  - F. Pruning or thinning
  - G. Fertilization
  - H. Sanitation
  - I. Water management
  - J. Planting of trap crops
- II. Mechanical methods
  - A. Hand destruction
  - B. Exclusion by screens, barriers
  - C. Trapping, suction devices, collecting machines
  - D. Crushing and grinding
- III. Physical methods
  - A. Heat
  - B. Cold
  - C. Humidity
  - D. Energy—light traps, light regulation, irradiation
  - E. Sound
- IV. Biological methods
  - A. Protection and encouragement of natural enemies
  - B. Introduction, artificial increase, and colonization of specific parasitoids and predators
  - C. Propagation and dissemination of specific bacterial, virus, fungus, and protozoan diseases
- V. Chemical methods
  - A. Attractants
  - B. Repellents
  - C. Insecticides
  - D. Sterilants
  - E. Growth inhibitors

VI. Genetic methods
  A. Propagation and release of sterile or genetically incompatible pests
  B. Genetically engineered crop plants
VII. Regulatory methods
  A. Plant and animal quarantines
  B. Eradication and suppression programs.

The incorporation of some of these techniques into pest-management programs is discussed in subsequent chapters of this book.

REFERENCES

Adkisson, P. L. 1969. How insects damage crops. Pages 155–164 in *How crops grow: a century later*. Conn. Agric. Exp. Stn., New Haven. Bull. 708.

Allee, W. C., O. Park, A. E. Emerson, and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders, Philadelphia. 837 pp.

Allen, W. A., and E. G. Rajotte. 1990. The changing role of extension entomology in the IPM era. *Annu. Rev. Entomol.* **35**:379–397.

American Chemical Society. 1969. *Cleansing our environment: the chemical basis for action*. American Chemical Society, Washington, DC.

Apple, J. L., P. S. Benepal, R. Berger, G. W. Bird, A. P. Gütierrez, F. Maxwell, W. G. Ruesink, P. Santelmann, and G. B. White. 1979. *Integrated pest management: A program of research for the state agricultural experiment stations and the colleges of 1980*. A study conducted by the Intersociety Consortium for Plant Protection.

Barfield, C. S., and J. L. Stimac. 1981. Understanding the dynamics of polyphagous, mobile insects. *Proc. Int. Con. Plant Prot.* **1**:43–46.

Bartlett, B. R. 1956. Natural predators: Can selective insecticides help to preserve biotic control? *Agric. Chem.* **11**:42–44, 107.

Brown, A. W. A., and R. Pal. 1971. *Insecticide resistance in arthropods*. World Health Organization, Geneva.

Bruce, W. N., G. C. Decker, and J. G. Wilson. 1966. The relationship of the levels of insecticide contamination of crop seeds to their fat content and soil concentration of aldrin, heptachlor, and their epoxides. *J. Econ. Entomol.* **59**(1):179–181.

Bruce, W. N., G. C. Decker, and W. H. Luckmann. 1967. Residues of dieldrin and heptachlor epoxide found in pumpkins growing on soil treated with aldrin and heptachlor. *J. Econ. Entomol.* **60**(3):707–709.

Burns, A. J., T. H. Coaker, and P. C. Jeppson, eds. 1987. *Integrated pest management*. Academic, London.

Feder, G. 1979. Pesticides, information, and pest management under uncertainty. *Am. J. Agric. Econ.* **61**:97–103.

Geier, P. W. 1966. Management of insect pests. *Annu. Rev. Entomol.* **11**:471–490.

Geier, P. W., and L. R. Clark. 1961. *An ecological approach to pest control*. 8th

Proc. Tech. Meet. Int. Union Conserv. Nature Nat. Res., 1960, Warsaw, pp. 10–18.

Glass, E. H., and S. C. Hoyt. 1972. Insect and mite pest management on apples. Pages 98–106 in *Implementing practical pest management strategies*. Proceedings of a national extension pest-management workshop. Purdue University, Lafayette, IN.

Gould, F. 1983. Genetics of plant herbivore systems: interactions between applied and basic study. Pages 599–654 in R. R. Denno and M. S. McClure, eds., *Variable plants and herbivores in natural and managed systems*. Academic, New York.

Gould, F. 1988a. Evolutionary biology and genetically engineered crops. *Biol. Sci.* **38**:26–33.

Gould, F. 1988b. Genetic engineering, integrated pest management and the evolution of pests. *Trends Ecol. Evol.* **3**:S-15–S-18.

Graebner, L., D. S. Moreno, and J. L. Baritelle. 1984. The Fillmore Citrus Protective District: a success story in integrated pest management. *Bull. Entomol. Soc. Am.* **30**(4):27–33.

Grieshop, J. I., F. G. Zalom, and G. Miyao. 1988. Adoption and diffusion of integrated pest management innovations in agriculture. *Bull. Entomol. Soc. Am.* **34**(2):72–78.

Harcourt, D. G. 1970. Crop life tables as a pest management tool. *Can. Entomol.* **102**(8):950–955.

Hare, J. D. 1983. Manipulation of host suitability for herbivore pest management. In R. R. Denno and M. S. McClure, eds., *Variable plants and herbivores in natural and managed systems*. Academic, New York.

Headley, J. C. 1972. Economics of pest control. Pages 180–187 in *Implementing practical pest management strategies*. Proceedings of a national extension workshop. Purdue University, Lafayette, IN.

Headley, J. C. 1982. The economics of pest management. Pages 69–91 in R. L. Metcalf and W. H. Luckmann, eds., *Introduction to insect pest management*, 2d ed. Wiley, New York.

Higley, L. G., and W. K. Wintersteen. 1992. A novel approach to environmental risk assessment of pesticides as a basis for incorporating environmental costs into economic injury levels. *Am. Entomol.* **38**(1):34–39.

Hunt, E. R. 1966. Biological magnification of pesticides. Pages 251–262 in *Scientific aspects of pest control*. Nat. Acad. Sci. Publ. 1402.

Kennedy, G. G., and D. C. Margolies. 1985. Mobile arthropod pests: management in diversified agroecosystems. *Bull. Entomol. Soc. Am.* **31**(3):21–27.

Kogan, M., and D. E. Kuhlman. 1982. *Soybean insects: identification and management in Illinois*. Bull. 773. Illinois Agricultural Experiment Station, University of Illinois, Urbana.

Luckmann, W., and G. C. Decker. 1952. A corn plant maturity index for use in European corn borer ecological and control investigation. *J. Econ. Entomol.* **45**(2):226–232.

Luckmann, W. H., W. M. Bever, B. J. Butler, H. J. Hopen, R. L. Metcalf, H. B. Petty, and F. W. Slife. 1971. Pesticides and pest control systems. In *Agriculture's role in environmental quality*. Proceedings of the 1st Allerton conference. University of Illinois College of Agriculture Special Publication 21.

Mathews, G. A. 1984. *Pest management.* Longman, London.

Metcalf, C. L., W. P. Flint, and R. L. Metcalf. 1951. *Destructive and useful* 3d ed. McGraw-Hill, New York.

Meyer, R. H. 1974. Management of phytophagous and predatory mites in Illinois orchards. *Environ. Entomol.* **3**(2):333–340.

Mumford, J. D., and G. A. Norton. 1984. Economics of decision making in pest management. *Annu. Rev. Entomol.* **29:**157–174.

National Academy of Sciences. 1969. *Insect pest management and control.* Publ. 1695. Washington, DC.

National Extension Insect Pest-Management Workshop. 1972. *Implementing practical pest-management strategies.* Purdue University, Lafayette, IN.

Pedigo, L. P. 1989. *Entomology and pest management.* Macmillan, New York.

Pedigo, L. P., and L. G. Higley. 1992. The economic injury level concept and environmental quality. *Am. Entomol.* **38**(1):13–21.

Pedigo, L. P., S. H. Hutchins, and L. G. Higley. 1986. Economic injury levels in theory and practice. *Annu. Rev. Entomol.* **31:**341–368.

Pesticide Review. 1979. Annual. USDA, Washington, DC.

Petty, H. B. 1972. Corn insect pest management. Pages 107–115 in *Implementing practical pest management strategies.* Proceedings of a national extension pest-management workshop. Purdue University, Lafayette, IN.

President's Science Advisory Committee. 1965. *Restoring the quality of our environment.* The White House, Washington, DC.

Rabb, R. L. 1972. Principles and concepts of pest management. Pages 6–29 in *Implementing practical pest management strategies.* Proceedings of a national extension pest-management workshop. Purdue University, Lafayette, IN.

Reynolds, H. T. 1972. Practical application of suppression methods in pest management. Pages 30–36 in *Implementing practical pest management strategies.* Proceedings of a national pest-management workshop. Purdue University, Lafayette, IN.

Smith, R. F. 1969. The new and the old in pest control. *Proc. Acad. Nazion. Lincei, Rome (1968)* **366**(128):21–30.

Stern, V. M. 1965. Significance of the economic theshold in integrated pest control. *Proc. FAO Symp. Integrated Control* **2:**41–56.

Stern, V. M., R. F. Smith, R. Van den Bosch, and K. S. Hagen. 1959. The integrated control concept. *Hilgardia* **29**(2):81.

Via, S. 1990. Ecological genetics and host adaption in herbivorous insects: the experimental study of evolution in natural and agricultural systems. *Annu. Rev. Entomol.* **35:**421–446.

WATERlines. 1993. University of Illinois Cooperative Extension Service, 122 Mumford Hall, Urbana, IL 61801. February 1993.

Weires, R. W., and H. C. Chiang. 1973. *Integrated control prospects of major cabbage insect pests in Minnesota: based on the faunistic, host varietal, and trophic relationships.* University of Minnesota Agricultural Experiment Station, Technical Bulletin 291.

2

ECOLOGICAL ASPECTS OF PEST MANAGEMENT

Peter W. Price and Gilbert P. Waldbauer

The purpose of this chapter is to form a conceptual basis with which to examine agricultural systems, and to introduce the reader to some ecological concepts that seem to be particularly useful in suggesting ways in which we might analyze these systems with a view to developing efficient pest-management procedures.

I. THE ECOSYSTEM CONCEPT

Individual organisms of the same species live together as a population, populations of different species live together and form a community, and the community is influenced by its physical environment. We call such a complex system of biotic and abiotic factors an ecosystem—for example, an experimental ecosystem in a laboratory, an urban area, an agricultural system, or a natural ecosystem such as a woodland, a watershed, or a hot spring. An expanse of any convenient size may be chosen for study.

The value of the ecosystem concept is that it emphasizes the interaction of all factors in a given area and that it forces us to look farther than studies of isolated pockets or aspects of biological activity. The danger is that we become blinded by the complexity of the interactions and we are led to superficiality in our studies. However, it must be emphasized that the individual, the population, the community, and the physical factors are the building blocks of the ecosystem, and that understanding each level of organization is essential to understanding the whole system.

The fundamental components of an ecosystem are the individual organisms. We must remember that natural selection works principally on repro-

---

Introduction to Insect Pest Management, Third Edition, Edited by Robert L. Metcalf and William H. Luckmann.
ISBN 0-471-58957-8

ducing individuals; through this selection populations become adapted, and the results of adaptation lead to evolutionary change. Thus, the study of individuals is of prime importance—their biology, behavior, physiology and morphology, and response to other members of the same species, to other organisms, and to abiotic factors in the environment. The study of individuals offers a potent method for the analysis of population change, and until we understand the basic needs and responses of individuals, we are ignoring the major forces of selection that influence the whole population and community.

Just as the individual is a natural and basic unit for study, so is the population. While the recognition of a population is more difficult, and its limits harder to discern, such recognition is nonetheless critical to any study of population dynamics. Study methods should be designed to permit the detection of populations—that is, groups of interbreeding individuals—the extent of the populations as well as their degree of isolation, sources from which emigration can proceed, and areas for colonization in the event that dispersal should occur. Even so, each individual organism must be considered unique, carrying its own genetic contribution to the gene pool of the population. Thus, when we consider populations, the genetic contributions of individuals and the consequent individual qualities (behavioral, physiological) that contribute to variation within the population are no less important than numbers of individuals. It is on this variation that natural selection acts, and without it evolution stagnates. Since populations must constantly adapt to changing conditions, either biotic or abiotic, and since population size depends to a large extent on the success of this adaptation, we must place equal emphasis on the study of qualitative and quantitative change in populations.

Populations of different species coexist and interact with each other, thus demanding study at the community level. As we see later, any given habitat seems to have a finite saturation level for species, and this limitation forces an organization within the community that could not be recognized other than by the study of the whole system. Here both intra- and interspecific competition play an important role, and comparative studies between species that are closely related either taxonomically or ecologically contribute greatly to data interpretation. Environmental effects on different organisms can be compared, and then interaction through competition for a limiting resource observed. Changes in species numbers, relative abundance, and diversity in space and time can be compared. The distribution of individual species may reveal differences in niche occupation or niche breadth (see definition later) and the extent to which species overlap and interact. These considerations bear directly on the understanding of population fluctuations.

Naturally, each individual, as well as all interactions between individuals and populations at the community level are influenced by physical factors. Temperature and humidity, soil or water conditions, topography, drainage, aspect, and shading may all influence community members, and certain members may modify these factors to the benefit or detriment of other members. Since physical factors act directly on the physiology of the organism, much information can be obtained from physiology texts (e.g., Blum, 1985; Chapman, 1982; Heinrich, 1993; Tauber et al., 1986). Therefore, we consider mainly biotic factors, which we feel have received too little attention in relation to pest management.

These considerations bring us, by logical steps, to the only conclusion possible for understanding insect populations: the need for studying them at the ecosystem level, not forgetting that all components of the ecosystem provide insight into the basic mechanisms involved in insects and agricultural ecosystems. Since insects are such mobile creatures, and humans have increased their mobility and that of their food plants, interactions are extensive; thus, we must define our ecosystem for study as a similarly extensive area. Therefore, the minimum size we should consider probably involves several crop fields plus the neighboring uncultivated areas. But we will see that interaction sometimes comes from far beyond this local area in the form of migrating insects on the same land mass, and even invaders from other continents.

Thinking in terms of the ecosystem concept and its component parts dictates certain approaches to the sampling and general study of insects. If variation within a population is to be identified, many sample stations must be employed. If the movement of organisms must be studied, extensive sampling is necessary. In view of these needs, the use of single-plot studies is not satisfactory where mean abundances are derived from random samples. Such randomization suppresses information on population variation and is an inefficient way of testing hypotheses (see also Price et al., 1990). Samples sited on transects through areas occupied by populations or across extensive tracts of land covering at least a field and its adjoining areas are commonly more useful. Stratified random sampling may be used, with strata carefully selected in order to test a hypothesis. With the adoption of extensive sampling methods, we are more likely to reach an understanding of pest insects at the ecosystem level. Examples of the different scales worth investigating are illustrated well in the studies of rangeland grasshoppers by Kemp and associates (1989; 1990a, b).

II. THE ECOLOGICAL NICHE CONCEPT

Each individual—the smallest natural unit in the ecosystem—requires a variety of resources in certain quantities, neither too much nor too little, in order to survive and reproduce. By looking at many individuals of a species in a community we can determine what these resources are for the species. Major resources are food, breeding site, space, time, temperature, humidity, and a habitat that provides protection from predators. Species, of course, differ in their quantitative and qualitative utilization of these basic resources. The ecological niche of a species can be defined as the set of resources that provides a species with all its requirements for existence and reproduction. Species that can reproduce over a broad range of conditions are said to have a broad niche, and those that tend to be specific in any requirement are said to have narrower niches.

Once we realize that each species has a definite set of resources essential to its perpetuation, it becomes clear that there must be a limit to the number of species that can occupy any given area. In other words, there must be a saturation level for numbers of species, set by the abiotic and biotic components of the area. It appears that the more heterogeneous the physical environment, particularly in terms of soil quality and topography, the more plant species occupy an area.

Insects have more latitude than one might think in exploiting the resources in their niches. They can, for example, pick and choose among available foods so as to consume a balance of nutrients more favorable than would be supplied by any one food alone. Grasshoppers grow better when they are allowed to eat a mix of three plant species than when they are allowed to eat only one. When corn earworm larvae feed in maize ears they eat a favorable mix of germ and endosperm. This ability to self-select a favorable nutrient balance has been demonstrated experimentally. For example, several species are known to select a favorable balance of casein and sucrose when they are offered two pieces of synthetic diet, one lacking only its sucrose component and the other lacking only its casein component (Waldbauer and Friedman, 1991).

Of course, when we deal with insects, which tend to be host-specific, the more plant species there are in the community, the more kinds of insect herbivores there are likely to be, and these in turn support a greater variety of parasitoids and predators. Thus, the complexity of the community increases rapidly with the number of plant species in coexistence.

But the variety of plant species is not the only component of the community that sets limits on its carrying capacity for insect species. As plants pass through their various growth stages, they may produce completely new resources that can be exploited by insects. For example, in the rosette stage the lesser knapweed, *Centaurea nigra* L., is exploited by only one herbivorous insect (Morris, 1971a), but when the plants send up stems and flowers, another seven species are able to exploit them (Fig. 2.1). Here the complexity of the community is increased not by adding more species, but by increasing *structural complexity*. Thus, we should expect a plant community's carrying capacity for insect species to be determined by two components: the number of plant species, or species richness, and the structural complexity the plants provide. As these two components increase in a plant community, so does the number of ecological niches for insects.

One herbivore may be an important part of the niche of another herbivore (Waldbauer et al., 1980). The rice leaf folder, *Cnaphalocrosis medinalis* (Guenée), requires sugar to lay eggs, but nectar-producing plants are generally very scarce in wetland rice fields in Asia. However, in the laboratory rice leaf folders can mature eggs on a diet of honeydew produced by another common rice pest, the brown plant hopper, *Nilaparvata lugens* (Stål). There

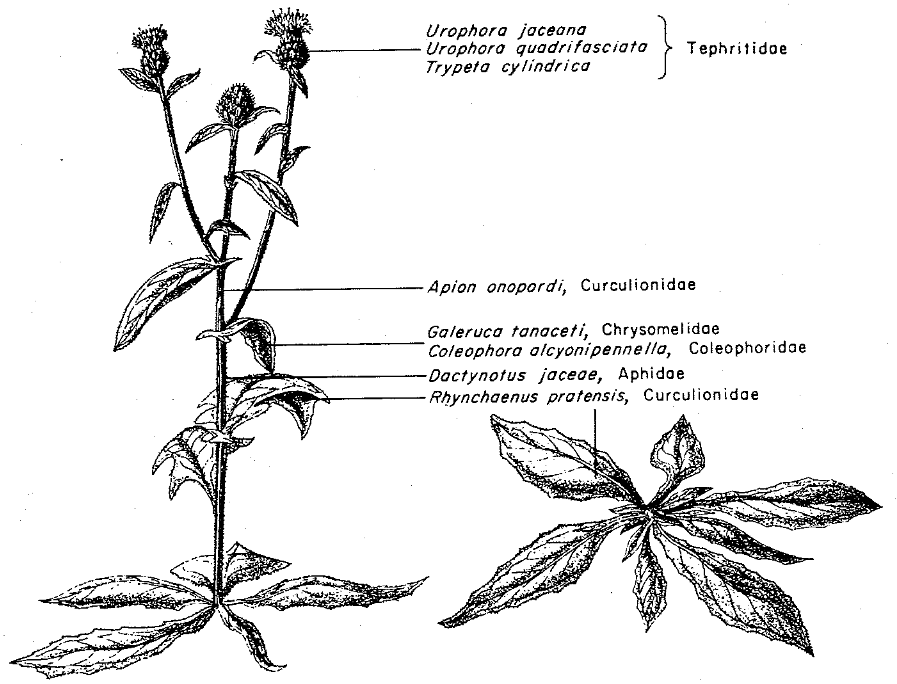

Figure 2.1 Lesser knapweed, *Centaurea nigra* L., before and during flowering, showing the change in structural diversity due to flowering, and the increase in insect species that this permits. The insect herbivores, the family to which they belong, and the positions in which they feed are indicated. Grazing maintains the plant in the nonflowering condition. (After Morris (1971a).)

is no reason to doubt that this relationship holds in the field, although this has not yet been determined.

Field data that support the effect of both these components on insects, species richness and structural complexity, were collected in old fields in Michigan, where the relationship between the community structure of plants and the community structure of plant bugs (Homoptera) was examined. The species diversity of the plants (see the appendix for a discussion of diversity) and their structural diversity were equally well correlated with insect species diversity; together they accounted for 79% of the variance in insect species diversity (Fig. 2.2) (Murdoch et al., 1972). Price (1976) and Mayse and Price (1978) found that the number of insect species in soybean fields increases with the structural complexity of the plants. Thus, we can conclude that the plant community has a profound influence on the insect community that exploits it (see also Price, 1984; Strong et al., 1984).

Perhaps a more dramatic method of demonstrating that each plant community has a natural limit for species is to remove all insects from an area and to observe how many species eventually recolonize the area. This has been

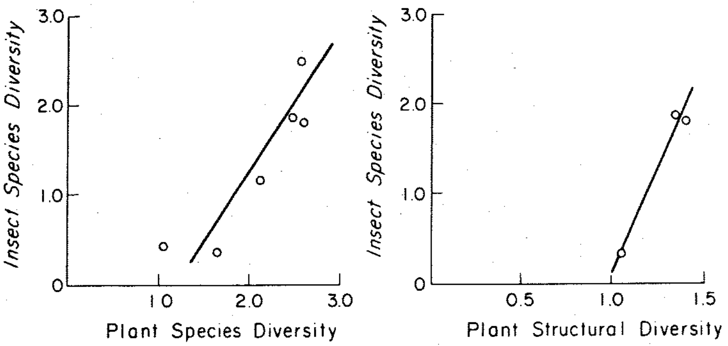

Figure 2.2 The relationships between plant species diversity and insect species diversity (left), and plant structural diversity and insect species diversity (right). Plant-sucking bugs (Homoptera) were studied in old-field communities by Murdoch et al. (1972), from whom the data are taken.

done with small, red mangrove, *Rhizophora mangle* L., islands of similar size in Florida Bay (Wilson and Simberloff, 1969; Simberloff and Wilson, 1969). After a detailed census had revealed the number of arthropod species originally present, each island was covered with a tent and fumigated with methyl bromide. A subsequent census revealed that the islands had been almost completely defaunated; only a few individuals of two species of wood-boring beetles survived, but the mangrove trees had received only minor damage. Frequent censuses monitored the recolonization of these islands. Immigration was rapid (Fig. 2.3), and it was soon evident that the rate at which additional species became established declined rapidly and reached almost zero when the number of species established was about equal to the number of species present before defaunation (cf. islands E2, E3, ST2) (Simberloff and Wilson, 1970). Only on the island most distant from the mainland—the major source of colonists—had the predefaunation numbers not been reached after 720 days.

We will look at these colonization curves in more detail later, but the important thing to notice now is that each island had its own limit for species, and this limit did not change even after nearly complete defaunation. Since these islands had only one species of plant, the plant communities of each island must have been essentially the same, both in species and structure, and therefore also in saturation level. Therefore, we must look for another explanation for the differences in species numbers among the islands seen in Fig. 2.3. Actually, island E2 was only 2 m from the Florida mainland, island E1 was 500 m from the mainland, and E3 and ST2 were at intermediate distances. We see that E2 supported the most species, and E1 the fewest. Clearly, distance from the source of colonists is a third important factor in determining the number of species that occur in a plant community. The theoretical explanation for this is given in Section III.

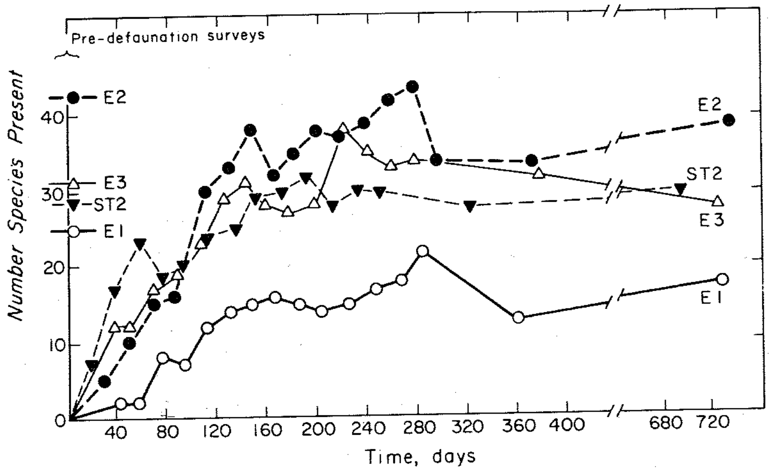

Figure 2.3 The progress of colonization by arthropods on four small mangrove islands with time, after defaunation. Species numbers before defaunation are indicated on the ordinate by the position of the island's symbol. Note that, apart from the most distant island from the mainland (E1), the species numbers were similar before defaunation and after 720 days. E2 was the nearest island and supported the most species, while E3 and ST2 were intermediate in distance and species supported. (After Simberloff and Wilson (1970). Copyright 1970 by the Ecological Society of America. Reprinted by permission of Duke University Press.)

Before leaving the niche concept, we must examine another organizing influence within the community—energy flow. In green plants the sun provides energy that drives the photosynthetic process. Herbivores derive their energy by feeding on plants, and carnivores feed on herbivores or other carnivores. Thus, the community can be divided into levels composed of organisms of a certain feeding category, called trophic levels. The primary producers are the plants that actually produce food by photosynthesis; next come the herbivores, then the primary carnivores, then the secondary carnivores, and so on. Energy passes from one trophic level to another along a series of feeding links—the food chain. One example is the following:

Food chain	Sun →	Corn	→ Corn borer	→ Nabid bug	→ Wren	→ Hawk
Trophic level		Primary producer	Herbivore	Primary carnivore	Secondary carnivore	Tertiary carnivore

The biomass of the hawk population is much smaller than the biomass of the corn population and therefore contains much less energy. As energy passes from trophic level to trophic level there is an inevitable loss with each transfer; the organisms in the food chain use some of the energy to support their own activity and physiological functions, and much energy remains unutilized and is lost to the food chain by decay. Thus, energy flows through the community from trophic level to trophic level, being rapidly depleted until there is not enough to support an additional feeding link.

This food chain is an oversimplified example, for there are many organisms that feed on corn, and many predators that in turn feed on them. The interactions are complex and it is more realistic to consider the passage of energy through a community as traveling along a food web rather than along a unidirectional food chain. We will return to these concepts later.

III. COLONIZATION OF ISLANDS

The application of the studies on island defaunation to agricultural ecosystems is obvious. We can regard annual crops, for example, as islands that may have a life-span of as little as one growing season and are colonized by arthropods from the surrounding area. We must regard crops as islands on both a short time scale and a long, evolutionary time scale (Janzen, 1968). Each growing season an annual crop becomes available for colonization, and we may see colonization curves similar to those on the mangrove islands. In addition, in evolutionary time new plant species evolve and become available to insects that can adapt to exploiting them. As evolutionary time progresses, more and more species adapt, and we are again likely to see a rate—in this case of adaptation to the new plant species—that is rapid at first and falls off as the new ecological niches provided by the plant are filled. As humans change the genetic makeup of their crop plants, the spectrum of insects adapted to exploit these plants also changes. In this way we can exercise some control over the colonization rates and colonizing species that affect the productivity of our crops. It is worth studying some theoretical considerations of the colonization of islands, so that we may understand the colonization process better. Thus we turn to the theory of island biogeography (MacArthur and Wilson, 1967; see also MacArthur, 1972).

As we have seen in the defaunation studies, each island or each community has its own limit for species of arthropods, and once this has been reached, an equilibrium exists. This equilibrium is not static, but dynamic, in the sense that new species may arrive and resident species may become extinct, but the number of species remains at equilibrium. Thus, the equilibrium number clearly depends on the immigration rate of arthropods into the community and the rate of loss from the community by emigration and extinction. In this context we consider immigrants to be those species represented by individuals capable of reproduction, either because an inseminated female arrives or because both sexes colonize, that is, they are capable of founding a colony.

Naturally, the rate at which new species become established is rapid at first, when many niches are vacant, but declines as the niches are filled (Fig. 2.4). In the early stages of colonization most of the species that arrive are new to the island. At this stage the rate of colonization also tends to be