Theoretical Ecology: Beginnings of a Predictive Science

Ecologists have been known for their exhaustive field studies in which they describe and catalog species in a given area and search for patterns in the interactions among the species. Although some ecologists still undertake such studies, many are analyzing systems with theoretical models and are using descriptive studies to confirm and extend their models.

Ecological systems are being analyzed in two ways: with computer models of entire ecosystems and with mathematical models of particular phenomena. The computer models, simulations of specific environmental situations, incorporate the unique characteristics of environments [*Science* **175**, 46 (1972)]. E. O. Wilson of Harvard University believes that, because these computer models are so specific, they do not often lead to general laws. The mathematical models have as their purpose the discovery of general laws.

In conjunction with field studies, mathematical models form the basis of present-day theoretical ecology. By isolating the key components of a system and treating them as much as possible in isolation, ecologists attempt to produce models that describe broad classes of phenomena. Various types of mathematics are used in the construction of the models. For example, some models consist of systems of differential equations that describe competition among species, and others consist of statistical measures that describe species diversity. This approach to ecology, strongly influenced by the late Robert MacArthur of Princeton University, is now providing insight into fundamental problems, including the problems of explaining species distributions, community structure, and competitive interactions among species. Although the models are highly idealized, they have led to some results of great generality. One such result is the theory of species equilibriums on islands.

The theory of species equilibriums on islands, one of the first theories to be both tested and applied, influenced scientists to study island populations in their investigations of community structure and species competition and is now being applied to problems of conservation. The realization that national parks can be treated as islands has enabled researchers to predict the rate that species in national parks will become extinct, to predict the number of species that will eventually survive, to describe the type of species most likely to survive, and to specify park designs that will minimize extinctions.

Islands support fewer species than large land masses, smaller islands support fewer species than adjacent larger islands, and remote islands support fewer species than islands nearer a source of colonists. MacArthur and Wilson proposed that these patterns of species distribution result from a dynamic equilibrium between immigrations of species to an island and extinctions of species on the island. They assumed that immigration rates increase with island area and with proximity of the island to the mainland. Extinction probabilities, which they assumed to result from random fluctuations in population sizes, decrease as the population increases in size. Thus they assumed that extinction rates decrease as island area increases. They used these assumptions as a basis for a mathematical model consisting of differential equations that describe species equilibriums on islands.

The MacArthur-Wilson model permits several predictions: For example, the number of species on recently depopulated islands will increase approximately exponentially as species return to those islands and, at equilibrium, as many species will become extinct as will arrive on an island. The highest extinction rates are predicted to occur among rare species and on small islands. Wilson points out that these high extinction rates were previously not appreciated and that they augur grave consequences for wildlife conservation in national parks.

Predictions Are Verified

Several predictions of the theory have been verified by periodic surveys of species on islands. In one such study, Jared Diamond of the University of California in Los Angeles surveyed birds on the nine Channel Islands off the coast of California and compared his survey taken in 1968 to the records of surveys taken in the years up to 1917. Both the earlier and Diamond's surveys showed that none of the islands supported as many species as comparable areas on the mainland. On each island, the number of species in 1968 remained about the same as before 1917, but about 17 to 62 percent of the bird species present on a given island before 1917 were absent in 1968 and had been replaced by other species. Diamond, John Terborgh of Princeton University, and others have performed similar studies of species on other islands. Their results qualitatively confirm the predictions of the MacArthur-Wilson theory.

The prediction that the number of species on recently depopulated islands will increase exponentially can also be tested. The first test came from Wilson and Daniel Simberloff, who is now at Florida State University. After surveying the arthropods on six small mangrove islands off the west coast of Florida, Wilson and Simberloff fumigated the islands and monitored the subsequent return of arthropods to the islands. During repopulation the number of species grew exponentially until an equilibrium was reached. At equilibrium the number of species of a given island was the same as that before fumigation, although many of the individual species were different.

MacArthur and Wilson's theory also yields the prediction that, when an island is newly formed from the mainland, the number of species on that island should decrease approximately at an exponential rate until a new equilibrium is attained. It is this aspect of the theory that is directly applicable to wildlife preservation in national parks.

Diamond and Terborgh have independently applied MacArthur and Wilson's theory to specific islands in order to develop a model that predicts the number of species that will become extinct on a land bridge island of a given area as a function of time. Their model is based on studies of the return to species number equilibrium of land bridge islands formed about 10,000 years ago from New Guinea and from Central America when the sea level rose after the most recent Pleistocene glaciation caused inundation of former land bridges.

Diamond and Terborgh stipulate that, by definition, a species population of a land bridge island is at equilibrium when the number of species on that island equals the number of species on a nearby oceanic island that has the same area and that was never connected to the land. Since the land bridge islands are fairly far from the mainlands, the rate of migration to the islands is assumed to be negligible. Knowing both the time elapsed since the islands were formed and the expected numbers of species on the island at equilibrium, Diamond and Terborgh proposed a relaxation time or a constant of decay to species equilibrium that is a function of island area. Terborgh tested his model on Barro Colorado Island in Gatun Lake.

Barro Colorado Island, a former hilltop, was formed 60 years ago when the Panama Canal was constructed and surrounding valleys were flooded. It was set aside as a wildlife refuge and, 50 years ago, its birds were surveyed by Edmund Willis of Princeton University. Terborgh found that 13 to 18 forest species became extinct between that first survey and surveys made recently. The species that became extinct on the island are still present on the mainland. According to Terborgh's calculations, based on data from the land bridge islands, 16 to 17 species would have become extinct on Barro Colorado in the past 50 years. Terborgh is careful to point out that one field study is insufficient to confirm his results, but he is nonetheless encouraged by his ability to estimate extinction rates.

Terborgh, Diamond, and Wilson warn that, since national parks are isolated areas often surrounded by urbanization or disturbed habitats, planners of national parks should be aware of these predictions of the rate of species extinctions as a function of island area. Wilson believes that the observance of certain precautions can minimize extinctions in national parks. For example, since those species that are present in smallest number, such as large mammals, are most likely to become extinct, the extinction rate for such species should be estimated, and the parks should be planned so that their initial extinction rates will be as low as possible. (Since the curve of species extinction is one of approximately exponential decay, the initial extinction rates are the highest rates.) Terborgh believes that tropical rain forest parks would have to cover at least 1000 square miles if extinction rates are to be acceptably low. He defines an acceptable extinction rate as one in which less than 1 percent of the initial species becomes extinct per century. Even with parks this large, he doubts that the largest predators, such as the jaguar and the harpy eagle, can be saved.

Since park areas are, of necessity, restricted, Willis, Wilson, Diamond, and Terborgh point out ways to design parks so that extinctions would be minimized. For example, if parks must be divided, the fragments should be connected by corridors of natural habitat. Wilson also proposes that extinctions could be minimized if it were known how resources are allocated among species in communities (species packing). If species packing were well understood, certain species that are close to extinction in one habitat may be fitted successfully into other communities.

Community Structure Is Investigated

Species packing has been studied by MacArthur and Robert May of Princeton University and by Diamond. MacArthur and May approached the problem theoretically by investigating the differences among competing species, whereas Diamond approached the problem empirically by investigating rules that govern community structure.

The principle of competitive exclusion is fundamental. According to this principle, two species cannot coexist if they do exactly the same things (such as obtain the same food in the same places in the same way). MacArthur and May investigated the question of how competitive exclusion determines community structure by studying the stabilities of communities whose members have overlapping niches. A niche is operationally defined by the way in which the species utilize resources. For example, Diamond has documented bird species with nonoverlapping niches that are defined by altitude on a mountain. All of the species in one group take berries for food but one species lives only in an altitude range of sea level to 3,200 feet, a second from 3,200 to 4,500 feet, and a third from 4,550 to 11,000 feet. Other species have niches that overlap.

MacArthur and May investigated the magnitude of niche separation, which they found to be determined by the requirement that a community maintain a stable equilibrium in spite of environmental fluctuations. They define a population that is at equilibrium to be at a stable equilibrium if that population can be perturbed and yet will return, after a period of time, to its former equilibrium. For example, the arthropods on the mangrove islands were at a stable equilibrium since the number of arthropod species on the islands at equilibrium was the same after the fumigation as before.

MacArthur and May showed that, if the environment never changes, a community can be at a stable equilibrium, and there is no limit to the amount that their niches can overlap. If random variations in the environment are taken into account, there must be a minimum distance between niches of a community at stable equilibrium. For example, assume that the sizes of the food eaten by each species are normally distributed. (The graph of the probability that a species eats food of a given size as a function of food size is bell shaped and symmetrical.) Then if species are ordered according to the sizes of their foods (a resource spectrum), the assumption of stable equilibrium leads to the prediction that the average food sizes of two species that are adjacent on the resource spectrum differ by approximately 1 standard deviation in the food size taken by either individual species. MacArthur and May cite several field studies that support this model, such as work on bird niches by Diamond and by Terborgh.

Another approach to the species packing problem is taken by Diamond, who is developing assembly rules for species. The assembly rules are based on the fact that species fit into communities in different ways. Some species fit well into communities with many species but fit poorly into communities with few species. Conversely, some species, such as the "super-tramp" bird species that are always among the first to colonize a defaunated island, fit well only in communities with few species. Other species can only fit in communities when combined in certain ways. A combination of three species may fit together in a community (a permissible combination), but any two of them alone may be unable to fit in (a forbidden combination).

From investigations of the structure of bird communities, Diamond has constructed incidence functions that describe the probability that a given species will occur in a community in terms of the other species already present in that community. He has derived certain rules that govern community assembly. One such rule states that permissible combinations of species will resist invaders that would transform them into forbidden combinations. Diamond believes that, in addi-

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tion to their application to wildlife conservation, assembly rules may be applied to a major unsolved problem in theoretical ecology—the problem of coping with complexity.

Theoretical ecology has dealt mainly with one-dimensional systems. Competition studies model one species competing against another although, as evidenced by Diamond's work on community structures, this model is not always appropriate. Many species act together to compete against other groups of species. Niches may also depend upon several variables rather than upon a single variable (such as food size) analyzed by MacArthur and May. The development and analysis of multidimensional models presents a challenging problem for theoretical ecologists.

Theories of community structure and island biogeography are now being extended to other fields of research such as anthropology and epidemiology. John Terrell of the Field Museum of Natural History in Chicago is applying results from theoretical ecology to studies of the evolution of human populations. Joel Cohen of Harvard University has developed a probabilistic model of malaria epidemics based on the concept that species already on an island (in this case, the host for the malaria protozoa) affect the subsequent establishment of other species on that island. Such applications of theoretical ecology promise to enrich both other fields of research and theoretical ecology. For example, Montgomery Slatkin of the University of Chicago and his colleagues have extended Cohen's model to describe colonization by species with high extinction rates (such as insects) in situations where the colonists come from other habitats within the system.

The unsolved problems in theoretical ecology are many, but Diamond, for one, is optimistic about the future. He compares the state of theoretical ecology today to molecular biology 15 years ago—new concepts and techniques for research have recently been developed, and, he believes, the next two decades will see the completion of a revolution in the study of ecosystems.

—Gina Bari Kolata

Additional Reading

1. R. H. MacArthur, *Geographical Ecology* (Harper & Row, New York, 1972).
2. R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, N.J., 1973).
3. J. M. Diamond, *Science* **179**, 759 (1973).
4. J. Terborgh, *Ecology* **52**, 23 (1971).