
Theoretical ecology

The use of mathematical models to provide a conceptual framework for the analysis of ecological systems. Ecology, the study of the relationship between organisms and their environment, deals with an inherently diverse array of complex systems, rich in idiosyncratic details of natural history. Mathematics is a language that makes it possible to express and think clearly about complex relationships. Thus, mathematical models are considered the essential tools of theoretical ecology. If mathematical ecology is defined as the application of mathematical theory and techniques to ecology, theoretical ecology is the use of such theory and techniques to develop broad conceptual insights into ecological systems. *SEE MATHEMATICAL ECOLOGY.*

Tactical versus strategic models. In contrast with other disciplines, ecology is rather diffuse. Theoretical physics, for example, is conceptually unified by the existence of fundamental laws governing all physical systems. Theoretical ecology cannot as yet rely on universal ecological laws, other than those same physical laws and the general notion of evolution by natural selection. Rather than aiming at all-inclusive laws, much theoretical work in ecology has more modest goals, for instance clarifying verbal concepts arising from field studies, or sharpening intuition about the possible reasons for qualitative similarities among disparate systems. A wide spectrum of models is used in ecology, ranging from complex tactical models describing specific empirical systems to simpler strategic models that (while admittedly caricaturizing real systems) can be understood in some depth by virtue of their relative simplicity. The term theoretical ecology usually denotes strategic rather than tactical models.

In addressing practical problems, where quantitative predictions are essential, large-scale computer models that mimic the behavior of particular systems in a detailed manner are often necessary. The very specificity permitting such models to be good descriptors, however, may also make it difficult to draw general conclusions from them, or to see where they fit into broader conceptual schemes. The more abstract models of theoretical ecology can provide guidelines for interpreting the qualitative behavior of complex simulation models. Moreover, there has been a great deal of theoretical work tied closely to applied problems such as pest control, epidemiology, and fisheries management; partly as a result of this development the long-standing division between theoretical ecology and systems or simulation ecology has begun to blur. Instead of trying to incorporate into an applicable model all the details of a system, the aim is to include just enough significant detail to capture its essential behavior, without making the model so complicated that it cannot be understood clearly by a combination of analysis and judicious numerical studies. The diversity of ecological systems is becoming reflected in a corresponding diversity in ecological theories tailored to those systems. *SEE ECOLOGY, APPLIED; SYSTEMS ECOLOGY.*

Hierarchy of models. The diversity in ecological theories may be categorized in various ways. One obvious way is by the level of organization in the traditional hierarchy of living systems. A given theory may focus on individual organisms, populations, communities, ecosystems, or even the entire bio-

sphere. Particularly rich bodies of theories exist at the organismal, population, and community levels. At the individual level, theoretical models examine the consequences and ultimate evolutionary causes of individual design features, such as leaf size in plants and diet breadth in animals. (A design feature is an organismal trait that can influence rates of death and reproduction, and hence Darwinian fitness.) Such models provide an important link between ecological theory and evolutionary biology. At the population level, theoretical work aims at understanding patterns in distribution and abundance, such as causes for population cycles. Theoretical community ecology is concerned with the factors determining the species composition and functional organization of communities, with a particular emphasis on interspecific interactions such as competition, predation, and mutualism. Theoretical analyses at the ecosystem level attempt to analyze flows of energy and material in entire ecosystems.

Ecological theories at any level may be phenomenological or mechanistic. An example of a phenomenological model is the logistic model of population ecology, which describes how the growth rate of a population declines as the population approaches its carrying capacity, without explaining why this occurs. By contrast, a mechanistic model would incorporate assumptions about the causal processes that depress growth rate near carrying capacity.

Much work in theoretical ecology attempts to bridge these traditional levels by using low-level models as building blocks in constructing higher-level models. For instance, the foraging strategies of individual consumers have been studied by using optimization and game theoretic techniques. Insights gleaned from such studies can be exploited in refining models of resource competition. An advantage for this modeling strategy is that lower-level models are more readily open to experimental evaluation. Many ecosystem ecologists are uneasy with this bottoms-up, reductionist approach. On the one hand they fear that important emergent properties of entire systems may be lost by a myopic concentration on the separate pieces; on the other hand, they note pragmatically that there are just too many lower-level pieces to keep track of in complex ecosystems. A number of top-down approaches to ecosystem theory have been proposed, but it has not been determined which, if any, will provide viable theoretical alternatives to more reductionist theories. *SEE GAME THEORY; OPTIMIZATION.*

Even firm believers of the reductionist approach admit that complex behaviors arise at higher levels that cannot readily be predicted from the behavior of isolated units at lower levels, and that the causal arrow can point down, as well as up, the hierarchy. The carrying capacity of a population, for instance, reflects not just the life history and foraging strategies of the individuals in the population (these traits themselves being the product of a population process, namely, evolution by natural selection) but also the web of interaction among species in which that population is embedded, as well as ecosystem-level determinants of renewal rates of abiotic resources. *SEE ECOLOGICAL COMMUNITIES; ECOLOGICAL INTERACTIONS; ORGANIC EVOLUTION.*

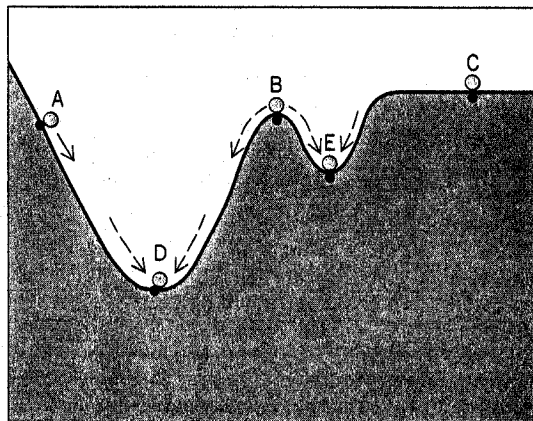
Ecological theories. Ecological theories may be static or dynamic.

Static. A static theory does not include time as an explicit variable. Static theories describe compactly

the structure of large bodies of information; for that reason they have been particularly common in community ecology, which deals typically with complex, multivariate data sets. For instance, considerable attention has been given to describing the structure of food webs. Static models specifying the probability that species pairs are trophically linked have been used with great success to predict statistical properties of food webs. Theoretical ecologists view static models as useful way stations toward the development of dynamic models. *SEE FOOD WEB.*

Dynamic. In a dynamic theory, variables change through time because of forces embodied in the mathematical structure of the theory. The mathematical formalism may be difference equations, in which variables are computed at discrete time intervals, or differential equations, which are appropriate when variables change continuously. The variables themselves may be continuous (such as leaf temperature) or discrete (such as the number of eagles on an island). It is often appropriate to approximate discrete variables with continuous ones, particularly when numbers are large. A model may be deterministic, so that specification of the system's state at one time fixes its states for all future times, or stochastic, such that each state can give rise to an array of future states, each with a specified probability. Stochastic models tend to be quite complex mathematically compared to their deterministic counterparts. However, there are some ecological questions, such as understanding the dynamics of colonizing species, that clearly require stochastic analyses, and others, such as analyzing the coexistence of competing species, where traditional deterministic approaches have been greatly enriched by incorporating the effects of stochastic temporal variation. *SEE DETERMINISM; ECOLOGICAL MODELING; STOCHASTIC PROCESS.*

A particularly important cluster of concepts in theoretical ecology centers around the notions of equilibrium (or steady state) and stability. Although these ideas are formalized in the language of dynamic systems theory, they relate to the earlier notion that there is a balance of nature. For instance, a population is at a point equilibrium when its size does not change over time. (Other possible equilibria include regular cycles and more complicated patterns of numerical fluctuations, which can be produced by time lags and strong nonlinear feedbacks.) For this equilibrium to



Stability concepts illustrated by balls under the influence of gravity on a hilly landscape. The solid arrow denotes current motion; the broken arrows, motion following small perturbations from the indicated points.

be stable, the population when pushed away from equilibrium must return to it. The illustration shows balls placed on a hilly landscape to illustrate several stability concepts. A ball at position A is not at equilibrium, because it is rolling downhill. Balls at points B through E would all be at equilibrium. But B is a point of unstable equilibrium; once a ball at B moves slightly, it continues to move away from its equilibrium position. A ball at C is neutrally stable; if it is moved slightly, it will stay at its new position, neither returning to its old position nor moving farther away. Points D and E are locally stable positions; a ball at either of these points tends to return to its original position (possibly with oscillations) when moved by a small amount, but can be pushed into a new equilibrium position if the perturbation is sufficiently large.

Analyses of equilibrium states and their stability properties permeate theoretical ecology at all levels. For example, at the individual level, the models of evolutionary ecology often lead to functions relating individual fitness to individual traits (such as body size), coupled with the proposition that over evolutionary time (all else being equal) populations evolve toward trait values that maximize fitness (at least locally in a phenotype space), and once a population reaches that state it does not change. The parallel with the balls and landscape in the illustration is strong. More generally, the population stabilizes at the phenotypic value (or combination of phenotypes)—the evolutionarily stable state of the population—such that alternative phenotypes have lower fitness. Likewise, the regulation of population abundance around an equilibrium value is a central feature of many population models. Much of theoretical community ecology has been devoted to elucidating how the destabilizing influence of some interspecific interactions constrains the number of coexisting species and the pattern of their interactions, and how other interactions buffer communities against external perturbations. *SEE SYSTEMS ANALYSIS.*

Extensions to traditional theories. A model is dynamically insufficient if it leaves out variables that are qualitatively important to the behavior of a system. Extensions to traditional ecological theories are essential if theoretical ecology is to inform attempts to solve important human problems, such as checking the spread of infectious diseases, managing renewable resources, and mitigating the damage of environmental stresses. In modern theoretical ecology, researchers are actively examining three distinct kinds of dynamic insufficiency in the classical models of ecology: the assumption of constant parameters, the omission of key variables, and the aggregation problem.

Constant parameters. Parameters assumed to be constant may in fact be varying with time. For instance, traditional theories about the role of competition in communities concluded that the number of coexisting consumer species must not exceed the number of distinct resource types supporting them. However, work on competition in variable environments has revealed that sometimes a number of consumer species may be sustained by a single, fluctuating resource population. If environmental fluctuations are sufficiently great, the notion of stability in a deterministic landscape (as in the illustration) may be seriously misleading.

Omission of key variables. There may be key variables left out of the models that are involved in feedback relationships with the included variables. An im-

portant class of examples, again from community ecology, is the study of indirect interactions. For instance, in a community composed of three species, A, B, and C, if A increases the abundance of B, and B decreases the abundance of C, A indirectly depresses the abundance of C. This indirect effect may exceed any direct effect of A on C. Leaving B out of a model of the community would lead to a serious misunderstanding of the interaction between A and C.

Aggregation problem. The theoretical variables may aggregate subsidiary variables and thereby obscure crucial facets of the dynamics. Ecology at the ecosystem level, in particular, is plagued by the aggregation problem, but the problem may arise at any level. Most populations, for instance, are internally heterogeneous; models using total numbers may be defined too coarsely. Individuals differ in birth and death rates and in their interactions with other species: this results from differences in genes, age, size, and so forth. Such heterogeneities can crucially affect population dynamics.

Another generic source of heterogeneity in population and community ecology is spatial structuring, which occurs at both large and small scales. Within a generation in a given population, different individuals may reside in different microhabitats and may interact with a limited number of individuals of their own and other species. This can have important consequences for population size and stability. Over several generations, most populations and communities are open to dispersal, receiving immigrants from other populations as well as sending forth emigrants. Understanding the long-term persistence of an ecological system may require an understanding of the dynamics of metapopulations, spatially dispersed open populations coupled by dispersal; this ultimately will require an integration of ecological theory with biogeography and the earth sciences. *SEE ECOLOGY; ECOSYSTEM.*

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Theoretical physics

The description of natural phenomena in mathematical form. It is impossible to separate theoretical physics from experimental physics, since a complete understanding of nature can be obtained only by the application of both theory and experiment. *SEE PHYSICS.*

Purposes. There are two main purposes of theoretical physics: the discovery of the fundamental laws of nature and the derivation of conclusions from these fundamental laws.

Discovery of fundamental laws. Physicists aim to reduce the number of laws to a minimum to have as far as possible a unified theory. When the laws are known, it is possible from any given initial conditions of a physical system to derive the subsequent events in the system. Sometimes, especially in quantum theory, only the probability of various events can be predicted. *SEE DETERMINISM; NONRELATIVISTIC QUANTUM THEORY; QUANTUM MECHANICS.*

Conclusions from fundamental laws. The conclusions