Chapter 4

The Impact of Mathematics On Ecology and Evolutionary Biology

Ecology and evolutionary biology encompass a broad range of levels of biological organization, from the organism through the population to communities and whole ecosystems, and a tremendous range of spatial and temporal scales. Aspects of it have been discussed in the earlier sections, from phylogenetic reconstruction to organism-environment interfaces. The grand challenges identified earlier, in particular, analysis of structure-function relations and the integration of phenomena occurring at different scales are of particular relevance both to ecology and to evolutionary biology.

Autecology refers to the interaction of organisms with their environments, including aspects such as physiology, morphology, and behavior. Some related aspects of organismal biology have been covered in the preceding section. The need for enhanced mathematical and computational ability is most evident when one attempts to couple large numbers of individual units into highly interactive networks. Individual-based models of populations provide a case in point, as do spatially distributed analogues of simpler dynamic models. Computationally intensive areas of autecology include those linking neurobiology with behavioral models for tasks such as search, and the modeling of spatial pattern formation through interacting particle systems or partial differential equations.

Population biology deals with the basic and applied aspects of ecological and evolutionary change, including links to resource management, epidemiology, and demography. The rich theoretical literature in this subject, including the work of such giants as Lotka, Volterra, and Kostitzyn in ecology; Fisher, Wright, and Haldane in genetics; and Kermack and McKendrick in epidemiology, has greatly influenced the development of fields as diverse as dynamical systems theory on the one hand, and probability and statistics on the other (see the earlier section of this report). As already discussed, May’s demonstration of how chaotic behavior could arise in simple dynamical models was a catalyst for the development of that aspect of dynamical systems theory, and interest in the dynamics of epidemics has spurred research in differential-difference equations and integro-differential equations, an area pioneered by Volterra in the classical models of mathematical ecology.

Population biology thus includes a dauntingly diverse assemblage of topics, including, for example, the construction of phylogenetic trees from data sets, the interface of game theory and population genetics, the ecology and evolution of quantitative characters, molecular evolutionary dynamics, and human population genetics.

Among the critical computational problems in population biology are those that relate to data base management in the examination of risk groups for epidemiological models, for example, the classification of sexual behavior and its relationship to the spread of AIDS; categorization and analysis of information on the global environment, being collected by means of remote sensing techniques; and the manipulation of data bases, such as those derived from sequence analysis, and their use in interpreting phylogenetic histories. Dynamic aspects relate to models of the spread of disease in heterogeneous populations; the interaction between evolutionary biology and neural networks, as reflected in the view of evolution as a combinatorial optimization problem in a very high dimensional space; more sophisticated game theoretical approaches to evolution; and quantitative genetics.

Communities and ecosystems include the study of how assemblages of species are organized in space and time, and how these assemblages interact with each other and the physical environment. One area that has received great interest is the analysis of the organization of trophic webs Ñ the very compilation and storage of data from hundreds of webs collected by ecologists introduces substantial problems of data storage and retrieval. Cohen's analysis of the consistent patterns exhibited by these webs (Cohen 1978) demonstrates how sophisticated mathematical analysis can lay bare patterns in the balance of nature. Biogeochemical cycles represent a complementary aspect of the dynamics of ecosystems; and the analysis of patterns in these cycles, and how they respond to different stresses in different ecosystems is of fundamental importance. The analysis of ecosystems, and especially of the transfer of energy and nutrients within the biota and between the biota and its physicochemical environment, involves a class of problems of considerable applied importance.

Agroecosystems, ecotoxicology (the responses of ecosystems to chemical stresses), landscape ecology, and global change represent other areas of importance. The study of agroecosystems raises problems from the characterization of rates of spread of pest species (for which the mathematical results of Kolmogorov et al. (1937) provide the mathematical underpinnings, and for which models and approaches borrowed from percolation theory and interacting particle systems allow the extension to fragmented habitats) to issues of management, as represented by dynamic programming approaches to integrated pest management, among other problems. Ecotoxicology trades heavily on diffusion-advection models of spread, and on multivariate statistical methods for the analysis of the fate, transport, and spread of chemicals.

4.1 Accomplishments of the Past

For interdisciplinary work, such as theoretical and computational biology, a success occurs in one or more of three ways. First, new mathematics can develop from the biological problem. Second, the theory can affect in a fundamental way the world view of biologists, most of whom are not theoreticians. Third, the theoretical contribution can lead to modifications of practice. Ecology and evolutionary biology have had numerous instances of each kind of success.

The application of mathematical methods in this area is a very old enterprise; as already discussed, it spans a range of topics from the very basic to the very applied (Hallam and Levin 1986, Levin, Hallam, and Gross 1989, May 1981, Roughgarden 1979). Demographic methods have been applied to the study of human and nonhuman populations for centuries (see for example Keyfitz 1977) and form the basis both for population projections and for the understanding of the population consequences of life history phenomena (Cole 1954). The interface with population genetics, and more recent game theoretical approaches, have produced a rich mathematical literature that forms the basis for our understanding of the evolution of the living world. At the other extreme, mathematical models have been fundamental in describing the fate and transport of pollutants in the environment (Levin et al. 1989), the spread of agricultural pests, the dynamics and control of epidemics, the management of renewable and nonrenewable resources, and the response of ecological systems to stresses such as toxicants, acid deposition, and global climate change.

4.1.1 The Synthesis of Population Genetics and Evolutionary Biology

A major role of mathematical biology, and of biology in general, must lie in aiding our understanding of the evolution of the living world. The theory of evolution by natural selection, and the associated extensions that include the neutral theory, relate to the central organizing principle of modern biology. A key aspect of the elaboration of that theory lay in the mathematical contributions of Fisher, Haldane, and Wright, already discussed, and in relating evolutionary change to the underlying genetic mechanisms (see Provine 1971).

The suggestion that most molecular genetic variation within a species and between species is selectively neutral (i.e., has no adaptive or functional significance) stimulated a great deal of mathematical work on random changes in allele frequencies due to sampling effects in finite populations. Diffusion approximations to finite population models have been employed successfully to understand the amount and pattern of genetic variation in populations, including sampling properties (work by Kimura 1983, Ewens 1972, Watterson 1977, Griffiths 1979). The mathematical analyses of these models had an enormous impact on the biological view of molecular genetic variation and led to the development of statistical tests and estimation procedures useful in the analysis of enzyme polymorphism and sequence variation (see Nei 1987 for examples). This theoretical and empirical work also stimulated important work on models with random temporal and spatial variation of selection coefficients by J. Gillespie (1978).

Modern topics of fundamental interest that involve considerable mathematical content include punctuated equilibrium, coevolution, and sociobiology. Quantitative methods have been involved intimately in the development and logical structure of sociobiology, broadly construed to encompass all interactions among individuals that affect reproductive success. Quantitative theory has been instrumental both in establishing the hypothesis itself within an evolutionary framework (cf. Hamilton 1964, Cavalli-Sforza and Feldman 1981) and in testing and revising the fundamental theory (see developments of relatedness, e.g., Hamilton 1964, Uyenoyama and Feldman 1980.

4.1.2 Autecology

Classic studies in heat balance in leaves and plant parts (Raschke 1960, Gates 1965) and animals (Porter and Tracy 1973) were used to predict "climate space," the set of microclimate variables (exposure to sunlight, wind, etc.) consistent with maintaining body temperature within non-lethal limits, and to predict activity times of animals and whole plant water and gas exchange. Cowan (1965) used electrical circuit analogues of flow of water from roots to leaves and out through stomatal pores to predict the onset of wilting. More recently, plant physiologists have developed models to represent photosynthesis and carbon allocation at scales ranging from biogeochemical (Farquhar et al. 1980) to global. These models draw from studies of physiology, biophysics, and adaptation, and are important tools in theoretical and applied studies of plant biology. Similarly, a range of models exists for transpiration, many based on the Penman-Monteith formulation for surface energy balance (Monteith 1973), but with many versions including more sophisticated biology. Models include relationships between carbon assimilation and water use based on optimization principles (Cowan and Farquhar 1977) or on isotope discrimination during carbon assimilation. These models can be used in applications ranging from crop production, through evolutionary studies of plant adaptation, to examination of the role of vegetation in global climate change.

Other work of considerable importance in this area, focusing on the relationship between the structure of an organism and its ability to function in its environment (see for example, McMahon and Kronauer 1976, Wainwright 1976, Vogel 1988, Cheer and Koehl 1987) already has been discussed in the previous section.

4.1.3 Population Biology

Population modeling and population projection have been an important part of demography and ecology since the pioneering contributions of John Graunt (1662). Demographic methods have been applied to the study of human and nonhuman populations for centuries (see e.g., Keyfitz 1977) and form the basis for population projections and for the understanding of the population consequences of life history phenomena (Cole 1954). These mathematical methods provide organizing principles for collecting and analyzing data on the rates of fertility and mortality. Such analyses are now commonplace in many areas of population biology and are applied to numerous species, ranging from humans to insects of economic importance (Keyfitz 1977, Carey, in press). The theory of age structured populations, and the theories built on Leslie's matrix and the Perron-Frobenius operator theory are among the most elegant and important advances of mathematical biology. Recent advances treat other aspects of population structure (e.g., Nisbet and Gurney 1982) and open population systems (e.g., Roughgarden et al. 1985).

The seminal work of Volterra and Lotka on predator-prey mechanisms showed how simple assumptions could lead to sustained oscillations of predator and prey populations. The predator-prey models of Volterra and Lotka rarely are taken literally. Yet they have formed the cornerstone of the subject, being the point of departure for more sophisticated models, and stimulating both experimental studies of individual behavior and further mathematical studies of the bifurcation properties of systems of continuous time differential equations.

Related closely to these predator-prey models are complementary models of competing organisms; again, the original models assume a simple quadratic form but have stimulated more sophisticated approaches. The theory of the ecological niche (see for example, Whittaker and Levin 1975) and the associated theory of competitive exclusion, among the most influential concepts in community theory, derive in large part from the mathematical approaches. Other work dependent upon it has examined the limits to similarity and niche width of coexisting species (MacArthur 1972), studies of coevolution and character displacement (Roughgarden 1979, Slatkin 1980, Fenchel and Christiansen 1977), and stochastic models of competition and predation.

One of the greatest successes of mathematical theory has been the application of diffusion models and their extensions to the spread of populations. The methods have been available, of course, for over a century (Skellam 1951), and early successes in the theory of epidemics occurred shortly after the turn of the century (Brownlee 1911). But the first major advances came from population genetics, especially the work of Haldane (1937) and Fisher (1937), and later work by Mal cot (1969) and (in a discrete setting) Kimura and Weiss (1964), Maruyama (1977), and others.

Fisher modeled the spread of an advantageous gene through the use of diffusion-reaction equations, hypothesizing that, in the generic case, allelic spatial distributions would relax to ones characterized by fronts, spreading at the rate of twice the product of square root of the diffusion coefficient and the maximal selection coefficient. This remarkable insight was confirmed in simultaneous mathematical analyses by Kolmogorov et al. (1937), and has been a stimulus to much modern mathematical work (e.g., Bramson 1983, Aronson and Weinberger 1978). In ecology, there are direct analogues (Skellam 1951, Okubo 1980), and such models have been applied to study the rate of advance of invading species (Lubina and Levin 1988, Andow et al. 1990). Kareiva (1983), stimulated by the mathematical theory, examined the link between these population level descriptions and the individual movements of foraging insects.

Closely related to this work, and building upon it, has been the development of models to explain patchiness in the distribution of organisms (e.g., Steele 1978, Segel and Jackson 1972). This has stimulated research into critical patch size (Skellam 1951, Kierstead and Slobodkin 1953, Okubo 1980) and other mechanisms for generating and maintaining non-uniform spatial distributions (Levin 1979).

Evolutionary approaches to ecological problems have had a tremendous growth and influence over the past two decades. Maynard Smith (1982) applied theoretical approaches to evolutionary problems. Earlier, optimal foraging theory (Emlen 1966, MacArthur and Pianka (1966) linked behavior and optimization by the assumption that certain behaviors had been optimized by natural selection. Optimal foraging theory stimulated considerable biological research, including more than 100 empirical tests of the theory (through 1986, reviewed in Stephens and Krebs 1986). The most recent conceptual advance in this field involves the use of stochastic dynamic programming and computational methods to derive biological insights (Mangel and Clark 1988). This latter work shows one of the first instances in ecology (although common in physics and chemistry) of gaining biological insight through numerical computation.

Life history theory (Cole 1954) has been a fundamental and active area of research, providing a link between demographic and evolutionary theories. Problems of interest include senescence (evolution of the mortality schedule, Hamilton 1966), the timing of reproduction and tradeoffs with respect to mortality (Cole 1954, Caswell 1982), dispersal and dormancy (Cohen 1966, Cohen and Levin 1987) and density-dependent selection on equilibrium population sizes (Roughgarden 1979).

4.1.4 Epidemiology of Infectious Diseases

The mathematical theory of infectious diseases, pioneered by Ross, MacDonald, Kermack and McKendrick, and others, has been an important applied tool, especially for the establishment of vaccination strategies. (See various papers in Levin, Hallam, and Gross 1989.) Recently, Anderson and May (1979) and May and Anderson (1979) stimulated a renaissance of activity in this area, especially involving viral diseases such as influenza (Liu and Levin 1989, Castillo-Chavez et al. 1988, 1989); rubella (Hethcote 1989); myxoma (Dwyer et al. 1990); and AIDS (Anderson and May 1987, Castillo-Chavez et al. 1989, Castillo-Chavez 1989).

Models of gonorrhea transmission were used to evaluate the effectiveness of strategies to combat the rapid rise in gonorrhea incidence in the United States in the 1960's. The initial step was the formulation and analysis of a simple model (Cooke and Yorke 1973), which was later extended to incorporate a "core" group of highly sexually active individuals. Tracing and treating the sexual contacts of members of the core group was shown to be a more cost-effective control than random screening of asymptomatic women (Hethcote and Yorke 1984). The work of Hethcote and Yorke has been one of the success stories of the application of mathematical models in epidemiology to influence management practice.

4.1.5 Fisheries Management

Fisheries management has proved a fertile area for the interaction of mathematics and biology. Fisheries managers recognized early that the problems involved were not only difficult, but could benefit considerably from a quantitative approach. The biological side has contributed concepts of nonlinear maps such as the Ricker map. Many mathematical methods of optimal control and adaptive management (Clark 1985, Walters 1986) have been developed to solve problems in fisheries management. The recent work on non-classical control problems by Clark (1985) was directly motivated by the problems of irreversible investment in fisheries. The methods developed by Clark, Walters, Ludwig and their students and colleagues are currently applied worldwide to manage renewable resources.

A strong link also exists between fisheries management and evolutionary ecology. Although allozyme variation has been used for about 20 years in the study of evolutionary processes, in the last 10 years such variation also has been used to provide genetic "markers" that can be used to assess the composition of populations. This method, called Genetic Stock Identification, currently is used in Washington and California to determine the composition of oceanic mixtures of salmon in terms of the contributing source stocks. Because of the complexities of the analysis, the teams working on this problem always involve biologists and mathematicians. The calculations are done by use of the EM algorithm (Dempster et al. 1977).

4.1.6 Community and Ecosystem Processes

Historically, the applications of mathematics to community and ecosystem level processes have been of two types: the simplistic dynamic approaches patterned after the Lotka-Volterra theory, and descriptive multivariate methods, of which Whittaker (1975) was the most important practitioner. Recently, however, a number of directions that blend theory and data have proved promising.

Understanding the causes of vegetation change has been an important long-term goal of ecology. A recent class of models has linked individual-based simulations of populations to models of detritus composition and nutrient release. Because species differ in the chemistry of their detritus, and because this difference influences decomposition and nutrient release, this class of models exhibits a rich behavior that mimics real systems. It is becoming apparent that these models exhibit a rich array of dynamical behaviors, including deterministic chaos and multiple stable states. These models provide important information on plant community processes, constraints over selection and biogeochemistry. The development of succession/production/decomposition models is continuing with applications to paleobiology and global change.

One of the most important advances in community theory in the past decades has been the recognition of the patchy nature of most systems, and the importance of spatially localized disturbances in maintaining diversity. The seminal paper here was Watt (1947), but its influence was negligible for a quarter of a century. More recent work in the marine intertidal (Levin and Paine 1974, Paine and Levin 1981), in forests (Pickett and White 1985), and in other systems has made this one of the most active areas of research in ecology.

A number of important studies in biogeochemistry have relied heavily on simulation models. Dynamic watershed models simulate water movement and biogeochemical reactions affecting soil and lake water chemistry, and have been central to integrated assessment of aquatic effects of acid deposition. They have been used as heuristic tools to improve understanding of watershed dynamics and as bases for projecting regional responses of watersheds to changes in acidic deposition. The comparison of the mathematical basis of these models, their calibration and application to watersheds that differ in size, slope and geology, and the experiments that these models have stimulated have been a significant component of the national integrated assessment of acid deposition effects. Similarly, the Parton et al. 1988, Schimel et al. (in press), and Pastor and Post 1988 models have been used to analyze the effects of climate change on carbon and nitrogen biogeochemistry.

The early developments in ecosystem analysis also dealt with problems concerning the transfer of energy and materials among biota and their physico-chemical environment. The relevant models were composed of linear differential equations and, with the availability of computers, led to development of a suite of mathematical and simulation tools based on thermodynamics (Odum 1960), compartmental analysis (Patten 1971), and systems analysis (Watt 1966). The transfer of energy and nutrients among the biotic and abiotic components of ecosystems is one of the classic areas of application of mathematical models in ecology. Perhaps the most fruitful applications have been in nonlinear simulation models at levels from individuals (Botkin et al. 1972, Shugart and West 1977) to spatially explicit long-term ecosystem succession (Costanza et al. 1990).

Trophic webs describe the flow of energy among biological components in an ecological community, and are of applied importance because they help predict, for example, how environmental toxins propagate through living species, and which predators may help regulate weed species or pests. From the first monographs on food webs (Cohen 1978, Pimm 1982) have followed collections of hundreds of food webs (catalogued in machine readable form) from different habitats. These catalogues have led to the discovery of several new quantitative regularities, previously unsuspected, in the structure of food webs. These regularities, in turn, have led to the development and analysis of new mathematical models based on random directed graphs, which have made new and testable predictions about food web structure. A current general reference, the result of collaboration between an aquatic ecologist, a population biologist and a mathematician, is Cohen et al. (1990).

4.2 Grand Challenges

In this section, we identify two grand challenges, among the many confronting mathematical ecology and evolutionary biology. The first, global change, includes relations to biodiversity and sustainable development of the biosphere (see for example Lubchenco et al. 1991), as well as global changes in the carbon cycle, climate and the distribution of greenhouse gases. The second, molecular evolution, builds bridges between population biology and the problems of cellular and molecular biology, as discussed in an earlier section.

4.2.1 Global Change

Global change, with its great implications for the future of our biosphere, presents one of the grandest challenges to computational biology. The proliferation of information from remote sensing, as well as more traditional ground surveys, introduces the need for geographical information systems that provide a framework for classifying information, spatial statistics for analyzing patterns, and dynamic simulation models that allow the integration of information across multiple spatial, temporal, and organizational scales. Multigrid techniques, parallel processing, and other advances will be essential tools in interfacing general circulation models with ecological models, and will require substantive partnerships among physical scientists, biological scientists, and computational scientists.

The deficiencies of our knowledge about the patterns and processes of individuals, population and communities are serious enough even for static climatic conditions. But these shortcomings are magnified in any attempt to deal with long-term changes in global climate. Historical measures of production contain information on the variations in the climate, but the global increase in "greenhouse" gases portends a trend of unknown magnitude in climatic change. We are challenged to predict how such global changes will be reflected in the genetic structure of organisms, in biodiversity, in the behavior of individuals, in the recruitment and growth of populations, and in the behavior of communities, and to develop strategies for mitigation and sustainable development. Understanding and dealing with the biological implications of global climate change, from every perspective, requires a significant new initiative. One of the central challenges, as discussed many times in this report for other problems and again in more detail below, is the development of approaches for dealing with and relating phenomena across disparate scales of space, time, and organizational complexity.

4.2.2 Molecular Evolution

Many challenging and important problems remain to be solved in the application of population genetic theory to molecular evolution. The existing methods of population genetics, such as the neutral theory, which were developed to describe variation at single loci, require restructuring to address questions that arise in the analysis of DNA sequence data. For example, the implications of tight but incomplete linkage among nucleotide sites within loci present a serious challenge. Molecular evolution is an area of rapid growth in the acquisition of sequence data as well as in theoretical development, and an area with enormously important economic and political implications, ranging from the environmental release of genetically engineered organisms to improvements in biotechnology.

Although several methods are available for reconstructing phylogenies from sequence data (Cavalli-Sforza and Edwards 1967, Nei 1987, Felsenstein 1981), robust methods for assessing the reliability of the inferred phylogenies are not available. Realistic models of the evolutionary process that can form the basis for statistical inference are needed. Rapidly accumulating sequence data raise questions far ahead of current statistical methods. Progress in this area will be important for understanding the evolutionary relationships of virtually all organisms that lack a detailed fossil record, including bacteria and plants, as well as recently diverged human populations.

Molecular variation within populations and divergence between species contain information about the relative importance of evolutionary forces including mutation, recombination, natural selection, migration, transposition and gene conversion (e.g., Hudson 1990, and Hughes and Nei 1988). Efficient methods of extracting this information and for testing alternative models are needed, particularly since large amounts of DNA sequence data are becoming available. The task of characterizing the properties of sequence variation expected under neutral models is underway, but alternative models with various forms of natural selection interacting with genetic drift are only beginning to be developed and explored. Gillespie (1989) has begun the analysis of the evolutionary process in a highly structured molecular landscape. Takahata and Nei (1990) have obtained some results for a model with many alleles maintained by overdominant selection and frequency dependent selection. These studies indicate the possibility of progress, but much more effort in these directions is needed.

A promising area for further research, and one in which important progress already has been made, is in understanding molecular variation in populations has been made by consideration of gene genealogies. This research was spearheaded by the analysis of the coalescent process by Kingman (1982), and extended by Griffiths (1980), Tavare (1984), Watterson (1984), Kaplan et al. (1988), Tajima (1983), Takahata (1988), Slatkin (1989), and others. The analysis of measure-valued diffusions (Fleming and Viot 1979) represents another powerful approach for the study of multidimensional population genetic processes.

4.2.3 The Problem of Scale

An important factor motivating new developments in ecology is the expanding temporal and spatial scale of many critical environmental problems. Within a decade we have moved from forest and lake studies on the scale of tens of hectares, to acid precipitation and air pollutants operating on entire regions, to carbon dioxide problems on a global scale. The mathematical challenge will be to develop a theory of scale that can (1) guide the aggregation and extrapolation of fine-scale understanding to larger scales, and (2) suggest hypotheses and methods for the direct investigation of large-scale phenomena.

Fundamentally new approaches to studies in population biology will be made possible by an understanding of phenomena that occur at different spatial and temporal scales. For example, genes express their effect at the individual level, but the effect of individual variation on population dynamics is poorly understood. Some recent successes in this area include the expression of genes in individuals and the role of individual behavior and variation in population dynamics (Mangel and Clark 1988). New approaches (i.e., theory, models and data) are needed to link sub-populations that are intermittently connected by stochastic events mediated by fluid flow (e.g., water, wind) and even plate tectonics. The key problems are to: (1) determine the "characteristic scales" for various ecological processes, (2) formulate the corresponding models that capture scale-dependent effects, and (3) test this theory at the appropriate spatial and temporal scales.

Different dynamical characteristics are displayed by epidemiological systems depending on the level of spatial aggregation of observations. At the individual level, stochastic effects are very important. In a small group, a disease may enter and quickly disappear. However, in cities and counties as a whole, persistence is more likely and the patterns of incidence appear more regular. For larger aggregations, deterministic models have proved to be useful. An understanding of the appropriate ways to link small-scale and large-scale epidemic behavior is important for understanding the impact of disease. Greater access to powerful computers will make it possible to study the relationships between different scales.

The development of new models and innovative mathematical and statistical methods for addressing the interaction of social dynamics and epidemiology, at distinct biological and sociological levels of aggregation, and at distinct temporal and spatial scales, is a rapidly expanding area of research. Models and methods that follow the dynamics of pairs (or groups) of individuals in different "sociological spaces" are now being extensively studied.

Population biology and ecosystem ecology long have been disjunct subdisciplines. Challenges posed by environmental problems, including global change, are causing these two areas to pull together. Paleobiology, process studies, and theoretical examinations show that biogeochemical cycling imposes important resource constraints on populations. In return, patterns of resource use specific to populations, such as type of gaseous product, carbon element ratios and organic compounds, produce feedback to local and global element cycles. This linkage is central to our current understanding of plant populations dynamics, dynamics of species invasions and marine biogeochemistry.

Linking population biology to biogeochemistry involves some major challenges to mathematical representation. For example, species of phytoplankton that have highly contagious distributions affect global air chemistry, possibly influencing global climate. Soil carbon changes over time scales of hundreds to thousands of years, yet controls soil nutrients that control plant growth and competition over short intervals. In addition, the interactions take place in a spatial context, which requires large input data sets for realistic simulation. Better theory, more powerful computations, and large-scale field studies are all required to achieve the coupling of these subdisciplines. The requirement to predict the effects of human use of ecosystems and global climate change makes this coupling essential.

Global problems ultimately must be studied at global scales. This is especially true when linking spatial and temporal scales in the study of oceanic processes and global climate change. For example, zooplankton respond to the spatial and temporal distribution of their food resources (phytoplankton) and their predators (planktivores), while the planktivores respond to the temporal and spatial distribution of the zooplankton and their predators (piscivores). In order to predict the patterns of these organisms, one must deal with spatial scales that range from millimeters or less (phytoplankton), centimeters (zooplankton size), meters (zooplankton aggregation size), tens of meters (planktivore school size), to kilometers (planktivore school group size, piscivore group size and movement scale). Each of these spatial scales has its own temporal scale (Okubo 1980).

The concept of self-similarity, derived from fractal geometry (Mandelbrot 1977), implies that extrapolation of information across scales is possible as long as the underlying process remains unchanged. However, ecological processes (e.g., energy flow, nitrogen exchange, etc.) are not always self-similar at all scales, because processes often change abruptly between locations. Relatively uniform areas might be measured with a few samples and extrapolated to large regions with little error, while heterogeneous regions with complex gradients of soils, light and moisture might produce major differences within a single watershed (i.e., not self-similar) and thus be difficult to extrapolate. The principal questions are: (1) How does one identify self-similar processes? (2) How can situations that are not self-similar be anticipated? (3) Can extrapolation methods be developed for these situations?

Many ecological processes occur in spatially patterned environments. Plant succession, biodiversity, foraging patterns, predator-prey interactions, dispersal, nutrient dynamics, and the spread of disturbance all have important spatial components. Many theoretical studies (e.g., Levin and Paine 1974, Steele 1974, Clark et al. 1978) have demonstrated the significance of spatial considerations in processes such as energy flow, nutrient cycling, and population growth rates. However, the difficulty of analyzing these processes often has caused the spatial dynamics to be ignored.

Models based on percolation theory (Stauffer 1985) recently have been used to relate the spatial distribution of resources to the propagation of disturbance (Turner et al. 1989) and the dynamics of species dispersal and habitat utilization (Gardner et al., in press; O'Neill et al. 1988). Other ideas from the theory of interacting particle systems are being applied to ecosystem problems. For instance, models that simulate the change in critical thresholds of disturbance propagation as a result of climatic change (i.e., drier forests), previous disturbance history, and the effects of human intervention will be useful for unravelling the issues associated with global change. Studies of the percolation "backbone" (a connected series of sites that transports material, energy, or organisms through a spatial system) may provide an objective view of critical habitats for the design and management of conservation areas.

Spatially explicit models can be very useful in addressing the problem of linking scales. The spatial resolution (grain) can be manipulated and changed in modeling studies. Evaluation of model predictions against spatial data available in geographical information systems allows the uncertainties of model predictions to be evaluated and key processes and parameters to be identified. It is expected that measurement of these parameters will significantly improve the accuracy and reliability of spatial predictions.

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