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Spatial Models of Ecological Systems and Processes: The Role of GIS

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This overview provides a foundation for discussion of methods and techniques to integrate spatial ecological models with the technology of geographic information systems (GIS). The discussion of models is limited to those that simulate ecological dynamics in two-dimensional (horizontal or vertical) or three-dimensional space. We briefly review historical modeling approaches for terrestrial, freshwater, and marine ecosystems that have some spatial component or can be extended into space. Examples of current spatial models are discussed for these ecosystems, and the use of distributional mosaic models for the simulation of broad-scale landscape disturbances such as fire and pests is examined. We exclude models of organisms in patches, animal dispersion models, and insect- and disease-dispersion models that consider space without location (coordinates) or configuration of subareas. This distinction is important for the application of GIS techniques to spatial ecological models (Baker, 1989). Future needs and directions that will enable ecological models to capitalize on the capabilities of GIS are discussed with regard to database management; remotely sensed data; landscape-level models; model-base management systems; data and model sensitivity, errors, and uncertainties; and environmental risk assessment.

Ecological processes operate at a variety of scales in space and time. Historically ecologists focused on changes in time and single sites or small geographic areas; however, during the past two decades ecological modelers have worked on incorporating spatial pattern into models and applying models to large geographic areas (Okubo, 1975; Levin, 1976). Currently much of this work is being championed by the new discipline of landscape ecology, which tends to combine work from many disciplines including geography, physics, biology, and ecology. A better basic understanding of the spatial aspects of ecosystem processes is needed. As Hunsaker et al. (1990) point out, effective long-term management and protection of valuable natural resources require a better understanding of how the scale of the environmental hazard affects ecological processes and over what scales the effects should be monitored and examined.

Not all ecological topics require models that are explicitly spatial; progress has been made, as we will review, with models that have no explicit spatial interactions. In deciding whether spatial aspects are necessary in a model, one must consider two conceptual questions: (1) What are the spatial units and their interactions, and (2) how do the relative sizes and locations of these spatial units affect such state variables as biomass and population size and such ecosystem functions as energy flow, biological productivity, and population change?

Several issues are involved. First, what are the "natural" units of a landscape? Sometimes the answer is obvious to the human observer, but other times the spatial units can be determined only after detailed analyses of plant and animal distributions. Sometimes there may be no correct single unit since units differ for different organisms. Once spatial units are defined, we next must consider how the state of one type of unit can affect the future state of another. The null hypothesis is that the future state of a

landscape unit is independent of adjacent units. When substantive spatial interactions occur, this is not true.

We know of cases in which there are spatial effects of one unit on another. Sprugel (1985), for example, showed that upwind trees protect other trees from wind and frost damage. It follows that the removal of an exposed, upwind forest plot can alter the future condition of a previously interior plot. Woodby (1991) found that future forest composition was affected by seed tree availability in neighboring locations. Such results suggest that spatial models are needed to address questions related to forest growth and regeneration. However, where we are confident that there are no substantive spatial influences, spatial components to models may not be necessary.

The development of models with spatial processes is one way to examine landscape effects. Another is to analyze existing landscape patterns. A third is to develop an understanding of processes, such as seed dispersal and wind effects on forests, that create spatial patterns. Although most of this chapter emphasizes methods and approaches for the integration of ecological models with GIS, questions about spatial units and their interactions underlie the discussion.

HISTORICAL MODELING APPROACHES

In the past, ecological modeling has had a temporal emphasis, that is, projections of state changes at one location over time. Different approaches were necessary for terrestrial, aquatic, and marine models. Terrestrial plant models did not consider organisms moving over the ground, whereas animal models did. Aquatic models had to consider that organisms were embedded in a medium (water) that moved; only rarely was movement of the terrestrial medium (the soil) an important factor in terrestrial models (e.g., models of organisms on eroding or disintegrating landscapes). Also considered in aquatic models was the notion that animals and plants in oceans and lakes are always immersed in some form of chemical solution. As a result, aquatic models often incorporated chemical and toxicity submodels. It was necessary in aquatic models to integrate time and spatial processes (two dimensional and three dimensional) for as many as ten species or more and hundreds of model grid cells. Many aquatic models are linked to water circulation models. These models are good examples of the linkage of process models and GIS.

The simplicity of the basic relationships represented in models often leads to incomplete perceptions of nature. Most models are based on a series of differential or difference equations, Markov chains, or Leslie matrices, without spatial considerations and with explicit steady-state assumptions. Early ecologists viewed spatial heterogeneity as a "problem," whereas more recently heterogeneity is viewed as an important and tractable source of spatial variation in biophysical processes (Kolasa and Pickett, 1991; Levin, 1974). Also recently, some ecologists have questioned this steady-state or "balance of nature" concept; they claim that nature is better characterized by dynamic change with large fluctuations in magnitude of state variables (Egerton, 1973; Botkin and Sobel, 1975; Botkin, 1990). In order to set the stage for the discussion of the role of GIS in spatial ecological modeling, we briefly discuss the historical background of ecological modeling, but the reader should understand that we cannot possibly do the topic justice in a few pages. A tremendous amount of ecological modeling has taken place since the late 1960s, and to aid the reader we refer to published reviews of models. Spatial statistics is not reviewed here, but the reader is referred to Patil et al. (1971), Cliff and Ord (1973), Pielou (1977), Sokal (1979), Turner et al. (1989a), S.J. Turner et al. (1991), Cressie (1991) and the spatial statistics section of this volume.

Terrestrial plant models

There are a large variety of highly developed nonspatial models of grasslands, shrublands, and forests (e.g., Lauenroth et al., 1983), as will be covered in the following sections:

Dynamical systems models

"Dynamical systems models" refer here to those models that use both discrete and continuous mathematics. Solutions to a partial differential equation in continuous space have been used to model changes in age–size distribution of patches of mussel beds in Washington (Paine and Levin, 1981). This approach might be scaled up to the landscape level and incorporated with GIS. However, it may be more practical to determine states of landscape subareas using discrete mathematics.

Difference equation models

All difference equation landscape models use discrete state spaces (Baker, 1989). The most common forms of difference equation models use stochastic Markov models or the deterministic Leslie matrix models. In the Leslie matrix model, the matrix contains values that are rates of change, not probabilities. This approach uses explicit birth functions for modeling biological populations, and modifications have been used to model populations with nonstationary transition probabilities and spatial effects (see Rees and Wilson, 1977). One forest succession model was linked with a highly modified Leslie matrix to predict moose population changes in relation to changes in forest composition and structure through time (Botkin and Levitan, 1977).

The Markov chain models calculate changes in state by matrix multiplication, where the column vector repre-

senting the population's age classes is multiplied by a transition matrix containing birth and death change probabilities. Markov chains have been used to model succession (Horn, 1975) and vegetation-type changes on small plots (Lough et al., 1987), and on large areas (Lippe et al., 1985). However, the assumption in Markov chains that the transition probabilities are stationary (do not change over time) is questionable. Markov chains cannot easily accommodate higher-order effects (interactions in time and space) and have difficulty in accounting for spatial heterogeneity (Baker, 1989). Transition probabilities between ecological states can be estimated from time-series remotely sensed data, and these estimates can be used in Markov models. For example, Hall et al. (1991) examined disturbance frequencies in wilderness and managed areas in northern Minnesota boreal forests in this manner. The steady-state solution of the model (e.g., percentage of the landscape in different states) was determined by the frequency of disturbance.

Some of the more complex ecosystem models were developed by teams of scientists during the 1960s and 1970s as part of the International Biological Program. The grassland ecosystem model, ELM, for example, has submodels for water, temperature, nutrients, producers, plant phenology, decomposers, insect consumers, and mammalian consumers that change on daily time steps through the growing season (Innis, 1978). The model has been used to analyze the effects of variation in weather, herbivory, and nutrients at several grassland sites. Grassland succession models, in contrast, typically have one trophic level and biomass changing at seasonal or yearly time steps (Bledsoe and Van Dyne, 1971). Forest photosynthesis models usually consider only one trophic level with model flows of carbon during daily time steps (Sollins et al., 1974), but more complex forest ecosystem models have also been developed (Swartzman, 1979). Forest succession models usually consider only one trophic level and population levels changing at yearly time steps (Botkin et al., 1970; Horn, 1975).

A group of stochastic difference equation models (the JABOWA family of models) has been used to model forest growth in many parts of the world (Botkin et al., 1972; Shugart and West, 1977; Prentice, 1986). The JABOWA-type forest growth models use difference equations to model diameter increment of individual trees (the states). The models use explicit, stochastic birth and death functions. Death (mortality), for example, is driven by a random function, affected by tree age and stress. Competition among trees for light on a small plot (1/100 to 1/10 ha) is modeled as a function of total leaf weight (proportional to leaf area index). Several simplifying assumptions eliminate the need for large amounts of data on growth changes over time and environmental conditions in the forest canopy. Extrinsic variables (temperature and moisture) control soil water balance and tree growth. The use of the JABOWA-type model as a landscape submodel will be discussed here under mosaic landscape models, and Nisbet and Botkin present a case study in Chapter 23.

The development of terrestrial plant models led to finer temporal resolution, increasing complexity of process modeling, multispecies models, and increasing attention to the effects of changes in exogenous variables, like climate. Simultaneously, a surge of interest in spatial processes in ecology, such as "gap dynamics" in forest canopies on a landscape scale, has set the stage for the expansion of spatial modeling to be discussed later.

During the past 20 years, much has been learned from models about the dynamics of single species and multispecies vegetation associations. However, vegetation response in space has only recently begun to be analyzed. One lesson ecologists have learned is that more is often not better. Analyses of some complex terrestrial ecological models are constrained by large data and computational requirements. Extension of these models to the landscape level greatly magnifies these constraints. One solution to the problem is to simplify the models; differences distinguished by high-resolution nonspatial models may have far less significance at the landscape level. Another solution is offered by recent developments in computer technology that greatly increase model processing speeds. Soon desktop workstations will be as fast as today's supercomputers, and computational speed will be far less of a hindrance on the development of complex spatial ecological models.

Freshwater models

Ecological models for lakes and streams often consider not only the plants and animals within several trophic levels but also the uptake of chemical nutrients and the regeneration of detrital materials. Early aquatic models were empirical steady-state models of nutrient input and primary production (Vollenweider, 1965). The concept of mass balance (i.e., accounting for the loss and gain of the biological and chemical variables by considering different physical, chemical, and biological processes) was widely used in aquatic models. In the simplest case, nutrient loading (chemical) balances algal production (biological) for a given lake's retention time (physical). Over the past two decades, most aquatic models have evolved into complex ecosystem models emphasizing interactions among all chemical, physical, and biological components. Some models emphasize only the biological component (Jorgensen, 1978). Ecological models usually include a spatial component, whereas biological models may not.

Several state-of-the-art reviews on aquatic ecological models are available (e.g., Straskraba and Gnauck, 1985; Sonzogni et al., 1986; Booty and Lam, 1989). We discuss two types of aquatic models, fish yield models and nutrient/plankton models, that were developed without the use of GIS.

Fish yield models

Fish yield models are mostly empirical ones (e.g., Matuszek, 1978; Lee and Jones, 1982) that were designed for a whole lake, and they use a seasonal or yearly time step. Typical inputs are lake retention time, nutrient load, and total dissolved solid concentration. The output includes fish yield, population abundance, and commercial catch. Some detailed simulation models were also developed, using such factors as food consumption, metabolism, swimming speed, ingestion, and excretion (Stewart et al., 1983).

Nutrient/plankton models

Nutrient/plankton models were developed to answer questions about eutrophication (excess algal overgrowth resulting from rich nutrient conditions). Model equations were a set of differential equations with state variables covering, in some cases, 4 to 6 phytoplankton species, 3 to 6 zooplankton species (in 3 or 4 life stages), 1 to 2 benthic animals, and 1 to 4 fish groups (in 3 or 4 life stages) (DiToro et al., 1981; Park et al., 1975). These were developed for a variety of one-, two-, and three-dimensional representations of the lake or water body (Lam et al., 1982). The time step was hourly, daily, or seasonal. In the 1970s, nutrient/plankton models were at their peak of development. Hundreds of horizontal grid cells with several vertical layers were used, sometimes directly adapted from ocean/lake hydrodynamic models, which provided transport mechanisms between cells (Lam and Halfon, 1978). These spatially complex models preceded the advent of GIS. The dynamic presentation of the two- and three-dimensional results of so many variables would pose serious challenges even to current GIS.

There are two major lessons learned from the past two decades of experience in developing aquatic models. One lesson is that a spatially or ecologically complex model was not necessarily better than a simpler one in terms of predictive capability (Lam and Halfon, 1978). The choice of model complexity depends on the questions being asked and the availability of knowledge and data. The other lesson is that an ecosystem model that includes biological, chemical, and physical components can provide broader answers than a simple biological model. Lam et al. (1983), for example, used an ecosystem model to simulate the effect of plankton production/decay that resulted from changes in water level, nutrient loading, and weather (climate).

Marine models

Ecological models developed for marine systems include ecosystem models, migration models, spatial stochastic models, regression-based models relating abundance to variable environmental factors, colonization models, and multispecies models. Although we focus on ecosystem models applied to fisheries, we also present some discussion of spatial models applied to fisheries.

Ecosystem models

Multitrophic-compartment marine ecosystem models have been developed to evaluate the effect of fishing on fish stocks. Development has been along three pathways: static energy or materials budgets (Polovina, 1984; Christensen and Pauly, 1991); dynamic simulation models (Andersen and Ursin, 1977; Browder, 1983); and dynamic spatial simulation models (Laevastu and Favorite, 1981; Longhurst, 1978). Marine ecosystem models have had limited acceptance in fisheries research, possibly because traditional fishery biologists distrust complex models with large numbers of state variables, coefficients, and assumptions. The advancement and refinement of ecological modeling techniques for marine systems have been slow because of lack of support. Static models are better represented than dynamic models in the marine fishery literature (i.e., Cohen et al., 1982; Christensen and Pauly, 1991). Only a few dynamic spatial marine ecosystem models exist. Until recently, the computer core and run time required for the execution of models of this type have hampered their development.

Marine ecosystem models that emphasize primarily plankton also have been developed (Kremer and Nixon, 1977) but have not emphasized spatial heterogeneity.

Other spatial models in marine systems

The earliest spatial models in fisheries science were simple conceptual models that attempted to explain seasonal fish movements on the basis of seasonal changes in temperature. More recently numerical models of fish migration have been developed, such as a stochastic compartmental model of the migration of juvenile salmon (Lee, 1991) and a stochastic compartmental model for the migration of marine shrimp (Grant et al., 1991). Migration models also have been developed for marine mammals—for instance, to describe the movements of the northern fur seal (French et al., 1989) and the sperm whale (Botkin et al., 1978). These models move animals through space, although they do not examine the effect of spatial heterogeneity or organization of spatial subunits on migration patterns or condition of stocks.

Spatial models have recently been developed to test the validity of common procedures for estimating stock abundance indices in a spatially heterogeneous marine environment. Along parallel lines, remote sensing and statistical analysis techniques are being used to examine fish and marine mammal distributions in relation to oceanographic and bathymetric features (e.g., Podesta et al., in review). Therefore, there are many needs for spatial

information in fisheries apart from those required for ecosystem modeling.

Summary

In their review article, Sklar and Costanza (1991) make the following observations. Animal population models in ecology are similar to the demographic models in geography in that both deal with birth, death, and diffusion. Ecologists, however, have spent more time on temporal density-dependent interactions. Plant ecologists have long recognized the correlation between abundance and spatial heterogeneity. Although plant ecologists use demographic principles to model spatial dynamics, they have a tendency to emphasize community-level rather than population-level interactions and have attempted to deal more explicitly with spatial–time processes than animal ecologists. In the past, ecological modelers have rarely combined geometric, statistical, or mechanistic approaches with the incorporation of spatial characteristics or processes into a model.

CURRENT STATE OF SPATIAL MODELING

We review the current state of spatial models for ecological processes by ecosystem type—terrestrial, freshwater aquatic systems, and marine systems—and by general types. This approach produces a fairly dramatic contrast among disciplines. To date much more attention has been given to spatial relationships and the use of GIS in the first two ecosystems than in marine systems. In Chapter 25 Johnston discusses the use of GIS and spatial models from the viewpoint of population, community, and landscape ecology. The complexity of many modern concerns such as climate change and cumulative effects from one or more hazards begs for more holistic ecological models, and the discipline of landscape ecology and research on "integrated modeling" are moving ecological models in that direction (see Chapters 26–29).

Terrestrial models

Modeling for terrestrial ecosystems usually involves simulation over time of landscape-level ecological attributes related to the location and configuration of area subunits or cells. The classification of terrestrial spatial models follows Baker (1989). The discipline of landscape ecology (Forman and Godron, 1986) attempts to describe dynamics and interactions of biological resources in a spatial context and thus provides the "where" aspect of reality to add to the "when" and "how" aspects of temporal mechanistic modeling. Although not restricted to terrestrial systems, most of the modeling work in landscape ecology has occurred in terrestrial ecosystems; thus our discussion of landscape ecology is included in this section. Baker (1989) and Sklar and Costanza (1991) provide reviews of landscape models.

A very promising approach to landscape-model development appears to be the incorporation of nonspatial distributional models (sometimes called process-based models) into spatial landscape models with GIS (Baker, 1989). A distributional model is one in which the distribution of values of a variable (e.g., distribution of land area among landscape elements) is modeled without regard to location. Evaluation of distributional models requires determination of the states of such variables as vegetation type, species population density and size, and elevation. In the past some have tried to estimate the change in state variables over time by Markov analysis (Shugart et al., 1973; Horn, 1975; Marsden, 1983) or by one or a series of differential or difference equations. Interactions in space may use continuous or discrete mathematics, but a description of discrete state space may be easier in landscape ecology than a description of continuous space.

True spatial models use the location and configuration of landscape subareas to project change in the landscape. These models may be raster based (grid cell maps) or vector based (polygon maps defined by coordinates). Most spatial landscape maps are mosaics of subareas (either cells or polygons). Each cell or polygon is characterized by a single value per layer (single discrete state) or a distribution of values even though the values may be taken from a continuous state space (e.g., topographic map). Spatial models with multiple layers are also possible in which each layer is composed of cells whose states are characterized by variables mapped in two-dimensional space. Mosaic spatial models can be classified as whole mosaic models or distributional mosaic models.

Whole mosaic models

Cells in whole mosaic models have only one value per data layer rather than a distribution of values. Browder et al. (1985) used this approach to simulate the spatial configuration of land and water in a disintegrating marsh. They first used a probabilistic spatial model to develop a knowledge base that was then used by an expert system to select clustering coefficients best approximating the observed pattern of land and water in specific Louisiana marsh sites. The appropriate clustering coefficients were subsequently employed to model the entire sequence of land disintegration in the GIS raster representation of each specific marsh. The project objective was to determine how the length of the ecologically important shoreline (land–water interface) changed over time as a function of stage of disintegration and degree of clustering or spatial dependence in disintegrating coastal marshes. Influences of neighboring cells have also been incorporated into a

whole landscape model of land-use changes (Turner, 1987).

Another type of a whole mosaic model is a cartographic model in which values for environmental or ecological variables are accorded to each cell in a GIS data layer (Tomlin, 1991). Each variable is represented by a data layer in the GIS and treated as a component in an equation that simulates some ecological response. For example, the locations of present and potential sage grouse strutting grounds (leks) in Pine Valley, Utah, were simulated in a cartographic model that incorporated multivariate analyses of existing lek sites and mapped variables representing elevation, temperature, water sources, and vegetation type (Nisbet and Reed, 1983). A Bayesian model can also be used with data layers in a GIS to make spatially explicit projections. Milne et al. (1989) used this approach to predict winter deer habitat independently at each of 22,750 grid cells based on 12 variables stored in a GIS. A grid-cell-based model was used to explore the effects of vole and deer herbivory in slowing the invasion by trees of a utility right-of-way (Hyman et al., 1991). This model used a unique approach in which data layers with different spatial resolutions were used to simulate differently scaled processes. This approach also increased computational efficiency and decreased computer storage requirements. Johnston gives additional examples of habitat suitability modeling in Chapter 25.

The final type of whole landscape model is based upon a "cellular automaton," an array of cells whose dynamics are determined only by interactions with neighbors (Wolfram, 1984). This approach has been used to model hypothetical plant populations competing in a landscape subject to fires (Green, 1989; Green et al., 1990).

Distributional mosaic models

In these models, sometimes referred to as process-based landscape models (Sklar and Costanza, 1991), each cell (or group of cells) contains a distributional landscape submodel. Several models have used a JABOWA-type model as a submodel in landscape-level analyses. The biggest problem with this approach is the difficulty in scaling up from the plot level to the landscape level.

One approach to scaling up from cells to the landscape is to simulate growth for a small number of stand types characterized by different climate and soil conditions, and extend the results geographically for each stand type to all areas of similar type (Shugart and Noble, 1981; Pearlstine et al., 1985; Dale and Gardner, 1987; Pastor and Post, 1985). A JABOWA-type model (BRIND), for example, was used to simulate forest response in 16 conditions of elevation and fire probabilities, from which landscape-level inferences of fire probability were made, although this was not an explicitly spatial model (Shugart and Noble, 1981). In another application, bottomland forest growth was projected by a version of the JABOWA model (FORFLOW) for various flood elevations of the Santee River in South Carolina (Pearlstine et al., 1985). Results from simulations before river diversion and from two diversion options were noted for changes in vegetation type and mapped into a GIS for display.

The other approach to scaling up is to simulate state changes (growth of individual trees) in a grid of plots in a landscape. This requires extensive computing resources and characterization of climate, soil, and initial forests for all plots. Smith and Urban (1988) used this approach with ZELIG, a JABOWA derivative that incorporates spatial interactive effects on the establishment, growth, and death of trees in a grid of 900 plots in an east Tennessee forest. In another application, which considered interplot dynamics in a riparian corridor, a version of the FORFLOW model was used to predict rates of seed dispersal by gravity, mammals, and birds (Hanson et al., 1990).

An interesting mosaic landscape model (CELSS) was constructed of differential equation submodels that determined exchanges of water, salts, and suspended sediments among 1 km cells in a Louisiana coastal marsh (Costanza et al., 1990). Analysis of landscape-level flows showed that past and future climate, ecological variables (e.g., primary productivity), and past activities (e.g., canal construction) significantly affect landscape evolution. A related model (Boumans and Sklar, 1990) used fixed subareas (polygons) rather than grid cells to model succession in a degrading Louisiana wetland. In another wetland application a model called ISLAND was developed using difference equation (Markov chain) submodels to simulate the response of a barrier island landscape to changes in rates of sand deposition, seaward erosion, and loss of a grass species (Rastetter, 1991). In an ecosystem-oriented application, a grid-cell model of nitrogen dynamics in the Walker Branch Watershed in Oak Ridge, Tennessee, was constructed (Bartell and Brenkert, 1991). Difference equations were used to model 50-year changes in the distribution of nitrogen among soil, litter, understory vegetation, and overstory vegetation pools.

One of the most successful groups of models that has been linked to a GIS simulates effects of fire on chaparral shrublands and coniferous forests (Kessell and Cattelino, 1978; Kessell, 1979; Kessell, 1990). Data are input from the GIS and manipulated by gradient analysis submodels to estimate vegetation and fuel data for each grid cell. These models have been extended to predict the effects on mammals of changes in landscape structure (Kessell et al., 1984). Kessell's models are important in the development of landscape modeling applications because they incorporate environmental and vegetation data with explicit modeling of landscape-scale natural disturbances in a form useful for resource managers (Baker, 1989).

Distributional mosaic models have been used extensively in the simulation of broad-scale landscape disturbances (e.g., fire, pests, pathogens, exotic species, and

windthrow). Prediction of disturbance spread is important in terms of both a practical standpoint (e.g., concerning how far and how fast a pest species might spread) and a more general understanding of the dynamics of the vegetation mosaic in disturbed landscapes (Turner and Dale, 1991). Some models use a simple probabilistic relationship to determine whether a disturbance will spread spatially from one site to another (Turner et al., 1989b). Probabilistic models of fire spread, which require no knowledge of physical mechanisms, have been used to explore the conditions under which a fire spreading through a simple, homogeneous, two-dimensional space can become "critical"—spread from one end of the space to the other, for instance (Albinet et al., 1986; Ohtsuki and Keyes, 1986; Hirabayashi and Kasahara, 1987; von Niessen and Blumen, 1988). To apply a probabilistic fire model to an actual landscape, predictions from empirical models of fire spread can be used to develop probabilities of spread, perhaps based on thresholds of wind speed and fuel moisture (Turner et al, in press; Turner et al., 1992), for various fuel categories across a landscape. Mechanistic detail and temporal dynamics have been incorporated in a probabilistic fire spread model developed by Baker et al. (1991) in which a set of data layers stored in a GIS are linked with a disturbance-spread model that incorporates the effects of temporally varying weather conditions on fire size.

Key strengths of the probabilistic modeling approach are its generality and the ability to produce testable hypotheses (Turner and Dale, 1991). The approach can be applied to numerous types of disturbances that spread spatially across heterogeneous landscapes. Even when an initial landscape pattern is constant, replicated simulations of a stochastic model can be used to project both the magnitude and range of potential disturbance effects. However, the simulations must often be interpreted and evaluated at the scale of the whole landscape rather than on a site-by-site basis. Because the model is probabilistic, it is not designed to predict whether a particular hectare or plot will be disturbed; rather, the objective of the model is to predict disturbance patterns over a large area. Physically based models that will predict the actual location and other properties of individual disturbances are available, however (e.g., Rothermel, 1972; Kessell, 1979).

Another distributional mosaic model links a forest growth model and a Leslie matrix insect-dynamics model and applies the coupled model across interacting patches that vary in elevation and other site-specific environmental conditions (Dale et al., 1990). This model couples biotic dynamics that occur at vastly different temporal scales, emphasizes the importance of fine-scale dynamics in generating broad-scale patterns (Turner and Dale, 1991), and demonstrates the potential of making simple and stochastic difference equation models spatially explicit.

Models of other processes, such as foraging dynamics, can also be distributed across a landscape and linked with a GIS. A spatially explicit winter foraging model, for example, was developed to explore interactions between the abundance and spatial distribution of resources and ungulate densities in Yellowstone National Park (Turner et al., 1990; Wu et al., 1991). During the simulation, ungulates search the landscape and move on the basis of the distribution and arrangement of resources represented in a GIS, and foraging is simulated by using a differential equation. Forage intake, ungulate energy balance, and ungulate survival are projected under alternative resource distributions and winter severity.

Freshwater aquatic models

Aquatic models use similar methodologies as described here for spatial model development. Although some models use the Markov process and stochastic treatment of random (heterogeneous) spatial patterns, the majority of models fall into the mass balance category by using partial differential equations in time and space that are solved by finite difference and finite element techniques (Gray, 1986). It is not possible to describe all types of aquatic models in this discussion. Some ecological models are of significant importance in advancing ecological theories. Other models have practical importance, including those on benthic and groundwater biology (MacQuarrie et al., 1990). The potential to make use of GIS technology is greater when the spatial component in these models is well developed. The following are two examples of aquatic spatial models that have been linked with GIS.

Biological/toxics models

The issues of toxic waste, chemical pollution, and human health have gained much attention. Two types of models have been developed: toxicity models and contaminant pathway and fate models. In toxicity models (Minns et al., 1991), threshold values were used to establish survival rates for several taxa of aquatic biota (fishes, algae, zooplankton, zoobenthos, invertebrate, amphibians, wetland birds, etc.). Toxicity is commonly measured by the concentration of the pollutant (metals, organic and inorganic chemicals, acidity, and radionuclides, etc.) needed to achieve a 50% mortality rate of a species (e.g., rainbow trout over a given period, such as 4 days). This empirical indicator is known as the LC50 and is widely used in toxicity models. One interesting use of the model is to back-calculate the loading of the toxicant needed to achieve a safe guideline or water quality objective for all the lakes over a large region. For example, critical values of sulfate deposition load were derived from watershed acidification models (Lam et al., 1989) for a number of species (Minns et al., 1991) in more than 2000 lakes in eastern Canada.

In contaminant pathways and fate models, chemical equilibria are usually assumed among the media, which for a lake or sea normally include water, suspended solids, and biota. The toxicant often goes through various media before accumulating in the higher trophic animals such as fish and humans. Thus, it is not possible to run the model for one particular medium by itself and expect the computed concentration to be at equilibrium with the concentration in other media. The model equations and equilibrium conditions have to be solved for all media simultaneously. For example, Thomann and Connolly (1984) adopted this approach for computing the dynamic equilibrium concentration of polychlorinated benzenes in water, plankton, and fish. A more comprehensive approach for contaminant pathways and fate models is proposed by Brewers et al. (1991). As in the case of nutrient/plankton models, GIS techniques can be used to present the spatial patterns of the computed results and to input detailed spatial information (e.g., satellite data) for model enhancement.

Habitat models

GIS technologies have been applied to simulate the home range and habitat of water-based plants (algae) and animals (fish, waterfowl, turtles, etc.). Data on temporal and spatial distribution of the animal can be collected by various methods, including radar transmitters and remote sensors. Such habitat data as depth, light, and temperature are converted from point measurement to interval classes by statistical clustering and contouring. GIS overlay analyses and modeling can then be performed to relate the biological data with the habitat variable (Painter, 1991).

Marine models

Dynamic spatial ecosystem models

Spatial models are needed in marine resource studies because the marine environment is spatially heterogeneous, biomass varies as a result of the heterogeneity in environmental variables, and fish and marine mammals move from one environment to another. Pola (1985) stated that "Migrations are an important feature of marine ecosystem dynamics because they cause temporal changes in the spatial distribution of biomass and influence prey availability and vulnerability to predation, accessibility to fishing gear, and exposure to environmental conditions." Fish and marine mammals migrate to feeding grounds, to spawning grounds, or to areas of improved environmental conditions. At least four types of periodic movements can be observed in marine ecosystems: (1) seasonal long-distance migrations, usually along a latitudinal gradient, between summer feeding grounds and winter spawning grounds; (2) seasonal onshore–offshore migrations; (3) ontogenetic onshore–offshore movements in which the different life stages move in different directions; and (4) daily excursions between resting and feeding grounds. Marine mammals also make long-distance migrations in connection with their feeding and reproduction. In some species, separate populations occupy adjacent habitats such as coastal nearshore and offshore waters.

Despite the importance of fish and marine mammal migrations to energy flow in ecosystems, few marine ecosystem models are constructed to take into account spatial variation and movements of animals and material between systems. For the most part, ecosystem modelers have avoided consideration of the effects of spatial heterogeneity by defining system boundaries so that the flows across boundaries are minimal. This means the averaging of state variables and conditions across the entire area, which could lead to erroneous estimates of environmental effects and prey–predator interactions.

Spatial marine ecosystem models are needed to (1) estimate biomass from results of resource surveys, (2) quantify prey–predator and other interspecies interactions, (3) estimate effects of variable environmental factors on recruitment and stock size, and (4) estimate effects of fishing. Laevastu et al. (1982) emphasized the critical importance of installing the appropriate spatial and temporal resolution in ecosystem models. We discuss three types of spatial models for marine ecosystems: multitrophic-compartment models that compute change in the magnitude and distribution of fish biomass over time; a dynamic simulation model for carbon and nitrogen flow; and a simple spatial biomass model.

Multitrophic-compartment models

Laevastu and associates developed DYNUMES, a gridded model that computes change in the magnitude and distribution of fish biomass over time in the eastern Bering Sea, and PROBUB, a simplified version of DYNUMES that computes equilibrium biomasses for larger spatial units (polygons rather than grid cells) and covers the Gulf of Alaska and the Bering Sea (Laevastu and Larkins, 1981).

Initial inputs of the DYNUMES model are depth, sea–land table, surface and bottom temperatures, and nature of the bottom. Covering an area of 1,500,000 km^2, DYNUMES has a spatial resolution of 63.5 km to a cell side. Overlaid grids represent different depth layers (surface and bottom). There is a biomass submodel for each point in a cell.

The DYNUMES model is "process oriented" with rate variables that determine state variables. The emphasis is on fish. Standing crops of phyto- and zooplankton are simulated with a harmonic formula to represent seasonal variability. Consumption of fish by marine mammals and

birds is included in the model, based on their respective estimated biomasses, which vary seasonally but not as part of the simulation. Growth of fish biomasses, fishery yields, mortalities, consumptions (predation), and migrations are computed at each time step. Feeding is food-density dependent. Distributions affect predation and the availability of food. Growth influences migration. Temperature has an impact on both growth and migration.

In simulating migration, biomass is moved from one grid point to another according to season or specified events (i.e., changes in currents, temperature anomalies, etc.) (Pola, 1985). Finite difference equations such as those employed in estimating diffusion (Laevastu and Larkins, 1981) are used to approximate migrations. There are two migration components: a predetermined, or fixed, component based on season; and a variable component based on temperature change with time. The four-dimensional DYNUMES model can simulate the distribution of any species or species group in space and time.

Such models as DYNUMES ideally should be coupled to hydrodynamical–numerical models, but because of the large computer core memory and run time required for both model types, the environmental models have to be run separately and their output fields stored at locations from which they are read into ecosystem models in the desired time steps (Laevastu and Favorite, 1981).

In PROBUB (Prognostic Bulk Biomass Model), the area modeled is separated into nine regions, each of which is treated as internally homogeneous (Laevastu and Larkins, 1981). The regions roughly conform to fishery statistical areas that have distinct differences in biomass density and landings. Separate, linked models are created and initialized for each region. In the initialization of the model, an estimate is made of the biomass of a top predator. Then biomasses of other species under equilibrium conditions are determined iteratively, while the original input of biomass remains fixed (Laevastu and Favorite, 1981). Results of this initialization stage of a dynamic simulation model correspond to a static model or budget. Once equilibrium biomasses are computed, the model can be executed to simulate long-term and cyclic changes in the ecosystem caused by the fishery and other factors, such as climate change. In PROBUB, migrations across boundaries are computed empirically.

GEMBASE (General Ecosystem Model for Bristol Channel and Severn Estuary) is another example of a dynamic ecosystem simulation model (Longhurst, 1978; Longhurst and Radford, 1978). It simulates the carbon and nitrogen flow between ecological state variables and seven geographic regions. The model contains about 150 equations and 225 parameter values. It uses hydrodynamical models to transfer materials between adjacent geographic regions. NORFISK, a biomass model with six spatial subcomponents, has recently been developed for the North Sea (Bax et al., 1984).

Proposed marine ecosystem models

As stated earlier, few marine ecosystem models have been constructed to take into account spatial variation and movements of animals and materials. We propose three systems in which the application of spatial marine ecological models is especially relevant: coral reefs, estuaries, and migrations of large pelagic fish in the Atlantic.

Coral reefs are one spatial component of shallow-water tropical marine systems. The fish biomass of coral reefs is supported not only by the primary production of the reef but also by the primary production in nearby seagrass beds and mangroves. The carrying capacity of a marine area may be determined by the mosaic of reef, seagrass, and mangrove area rather than by reef area alone or by the total area of all three habitats. Initially a comparative biomass budget could be prepared for several locations having different mosaics of reef, seagrass, and mangrove area. Results of such studies would (1) provide help in educating resource managers and the public about the importance of seagrass and mangrove areas, (2) guide the effective placement of artificial reefs, and (3) provide a perspective for selecting "source" areas to establish as preserves to protect reef fish species from overfishing.

The estuary is the most spatially heterogeneous part of the marine environment. Physical habitat usually consists of coastal wetlands, shallow tidal creeks, submerged shoreline (the littoral zone), seagrass beds, mud bottom, and open water, all of which are important to the production of estuarine-dependent fishery species. The chemical variation of an estuary is best characterized by salinity, in which a gradient is established from its freshwater source to its outlet to the sea. Both physical characteristics and salinity determine suitability of habitat (Browder and Moore, 1981). Freshwater flow determines the relationship between salinity contours and physical habitats. A continuing challenge for marine ecologists is for each estuary to (1) demonstrate the relationship between freshwater runoff and fishery production for an estuary and (2) answer the question "How much water does the estuary need to best maintain fishery production?" These are complex tasks that can best be addressed with ecological landscape models.

Both large-scale and small-scale spatial variability are characteristic of the ocean. On the large scale, the equatorial convergence zone and regions of upwelling, continental margins receiving terrestrial nutrients are much more productive than the ocean at large. Even within such regions, boundaries between water masses, denoted by discontinuities in temperature or salinity, are much more productive than adjacent areas.

The spatial heterogeneity of the ocean is an important factor in the ecology of tunas and other large oceanic pelagic fish, which migrate long distances between spawning grounds in the tropics and subtropics and feeding grounds in northern temperate waters. The tunas appear

to have strong temperature preferences. Furthermore, studies suggest that they are attracted to temperature discontinuities, or fronts, where prey are thought to concentrate. Persistent and recurrent fronts and upwelling areas appear to correspond to topographic features of the ocean floor—the shelf break, islands, and seamounts, for example. Fronts also occur on the boundaries of major current systems like the Gulf Stream. Although upwellings and fronts recur in the same general area, they are not always in the exact location but may be displaced by several kilometers seasonally or annually. Year-to-year variation in the timing and rate of seasonal temperature change could affect migration patterns and the availability of prey.

Year-to-year variations in the location, strength, and persistence of frontal and upwelling systems that stimulate primary productivity and concentrate prey also could affect food availability for tunas. Dynamic spatial bioenergetic–migration models could systematically test the potential effects of extreme feeding conditions in various parts of tuna range on bioenergetics and recruitment. The model also could test the potential effect of variable migration patterns on annual abundance indices.

Stock assessment problems caused by the uneven spatial distribution of fish have led to the development of other types of spatial models in fisheries research. For instance, Farber (1990) developed the stochastic spatial simulation model BILSIM to examine how the aggregation of fish along environmental attractants affected the reliability of relative abundance estimates based on catch rate (catch per unit effort). Edwards and Kleiber (1989) used a spatial model to investigate how the nonrandom distribution of dolphin in the Pacific Ocean affected estimates of relative abundance based on dolphin sightings by observers on tuna vessels. Results of both studies focus attention on the need to (1) improve the general understanding of small-scale spatial and temporal distributions of large pelagic fish and marine mammals and (2) develop data stratification methods that are more robust to the effects of small-scale randomness. Such stratification might require detailed spatial data on ocean surface and bottom features.

The future in marine modeling

The future of spatial ecological models in the marine system is strongly tied to the future of ecosystem models, other spatial models, and other approaches to spatial analysis. The spatial marine models by Laevastu and associates were pioneering efforts. Recently applied in Norway and in the Black Sea, these ecosystem models provide a rich source of useful information on spatial approaches to marine modeling. The work of Pauly, Christensen, and others (e.g., Pauly et al., 1987) and the symposium publication edited by Christensen and Pauly (1991) are generating new interest in marine ecosystem modeling as well as strengthening the conceptual basis of model development. Although the models are neither spatial nor dynamic, they strengthen the foundation of marine ecosystem modeling in general by improving the estimation and comparison of critical ecosystem parameters between areas and species. Furthermore, this volume represents an encouraging interest in ecosystem modeling by those who have a strong foundation in traditional fishery biology. The increased power of personal computers and the recent development of workstations with large memory capacity and fast processing speed will rapidly increase the progress of ecosystem modeling in the marine environment. Geographic information and image analysis systems are other technological advances that will improve the opportunities for marine ecosystem modeling by making these models easier to develop.

FUTURE NEEDS AND DIRECTIONS

GIS is not necessary for all ecological modeling. Indeed, some ecological studies are mainly concerned with temporal aspects of ecological processes. Only those models that have a spatial component or that have the potential to be incorporated into a spatial modeling framework should be linked with a GIS. For this discussion, a spatial model can be loosely defined as one that has either one or more state variables that are a function of space or can be related to other space-dependent variables. The three factors that primarily have limited the use of GIS by ecological modelers are the difficulty and expertise required to link models with GIS, the time required to develop the necessary databases, and the cost of software and hardware. These are not necessarily unique to ecological modeling, although some of the databases may not be of interest to other scientists. However, many novel and challenging research concepts will shape future spatial model development using GIS as well as ideas for GIS enhancement to meet the research needs.

Landscape-level models

Many mechanistic ecological models exist, but new tools are needed to extend these models to the landscape level and to use GIS technologies. Landscape models have the potential of: (1) mapping the flows of energy, materials, and information; (2) designating source, sink, and receptor areas; (3) predicting succession in two- and three-dimensional space; (4) determining cumulative thresholds for anthropogenic substances; and (5) addressing questions of scale (Reiners, 1988). Models could be reduced into modules that can be related explicitly to location or configuration of subareas on the landscape (Baker, 1989; Sklar and Costanza, 1991). However, to manage these modules a modular system requires an interface (with

BASIC, FORTRAN, "C," etc.) within the computer system or GIS or, even better, a macro language facility (Lam and Swayne, 1991). Such an improvement is needed particularly when temporal models are generalized from one location to many locations with spatial interactions and feedbacks. The problem of integrating models with different temporal and spatial scales is not trivial and requires special methodologies (Turner and Gardner, 1990).

Sensitivity, errors, and uncertainties

When site models are generalized to regional models, it is usually necessary to interpolate data, and hence the data uncertainty increases. The majority of so-called map data are generated by contouring methods based on a finite number of observations. Propagation of uncertainties from input and boundary conditions based on map data will pose new problems for spatial models. In particular, data generated from GIS are often given as ranges or class intervals, not point values. Indeed, some spatial models now use intervals and classes as the measure for state variables (Camara et al., 1990). Sensitivity analysis and model calibration must consider pattern statistics and new techniques to display and compare computed and observed results (Turner et al., 1989a; Cai, 1991). These should be nested as a library of functions within GIS systems. GIS vendors should consider more sophisticated contouring methods with optimization constraints and error estimation using kriging and semivariogram methods to enable modelers to track down the GIS-generated interpolation errors. Future GIS will probably require fast, large-memory computers with parallel processors.

Database management

Spatial models require a large set of mapped landscape data. An effective database management system (Cowen, 1988) is needed to pass two- and three-dimensional data between models and GIS. Currently many GIS can archive and retrieve various types of data including cartographic (map), satellite (image), and digitized (raster and vector) data from different sources. A user-friendly (for modelers) interface is required to access and integrate these data. Standardization of data format by the GIS industry will facilitate easy transfer of data but must incorporate data integrity control (e.g., in computer networking). In particular, ecological modeling requires a GIS that can store time-varying data and include/exclude data according to specified regions or time periods. Common GIS usage includes applying overlay delineation, contouring and plotting, calculating energy budget and transport gradients between grid cells, and computing influence or probability zones. A demand exists for high-resolution maps (oceans, lakes, forests, and land use) and detailed zoom-in powers.

Remotely sensed data

Traditionally ecologists have focused on the manipulation of satellite and radar images in GIS for terrestrial vegetation data and phytoplankton chlorophyll-density data; more research is needed in the design of fully interactive image analysis software and in the area of optical modeling (e.g., relating optical spectral density to chlorophyll concentration and the presence or absence of organisms). The use of radar tracking of organisms is unique in the field of ecological habitat and home range modeling. Future model development with these and other GIS technologies through the inclusion of more landscape information will broaden the scope of application in habitat management.

Model-base management system

A GIS is often used as only a display device for the presentation of model results. However, graphical presentation is a fundamental and mundane function for GIS. On the other extreme, some GIS offer a modeling capability themselves and make the models GIS subroutines. One has to learn a new modeling protocol within the GIS and follow special procedures and database structures to program an ecological model. Although this GIS-driven modeling capability is an excellent tool for overlaying map variables and deriving relationships among them, it is strictly limited to the methodologies defined by the GIS and not suitable for complex models.

Therefore, what is needed is something between the extremes of just a display device and a GIS-specific modeling protocol. Expert systems with GIS capability (Lam and Swayne, 1991) and expansion of GIS capability with artificial intelligence (Coulson et al., 1987) are integrative solutions. Such systems provide an open architecture (e.g., complete with such modeling languages as DYNAMO) and could allow the user to decide which models should be resident within or outside the GIS. (DYNAMO is a continuous-time simulation model, useful for modeling flows of material between compartments.) Interfaces for GIS data to be transferred to the models and vice versa through a complete library of GIS functions are essential. An example is the GIS system called GRASS (USA-CERL, 1988), which consists of a set of some 300 GIS programs and functions for GIS operations that can be called directly from external simulation programs, making the GIS and all its capabilities effectively available as subroutines for environmental models. GRASS's map functions, for example, have been used in a spatial model of natural disturbances in landscapes (Baker et al., 1991), using a driving program written in the popular simulation

language SIMSCRIPT II.5 (CACI, 1987). Unlike DYNAMO, SIMSCRIPT has an event-related language that permits analysis of discrete time models. However, most simulation languages can make "system calls" to external routines or use external libraries of functions and can thus directly use GRASS capabilities. This capability for open, direct, command-line access to a library of GIS functions provides a unique and powerful link between environmental models and GIS capabilities.

Expert systems provide a simple query-and-answer interface so that choices of data, models, or model parameters can be made according to a set of expert rules (Lam and Swayne, 1991; Lam et al., 1989; Crowe and Mutch, 1992). An example is the RAISON system (Lam and Swayne, 1991), which is also programmable and can integrate external components of database, spreadsheet, graphics, statistics, simulation models, and expert systems. In Chapter 24 Lam presents a case study of a fish species richness model that uses GIS and expert systems. Coulson et al. (1991) discuss intelligent GIS that contain an artificial intelligence component capable of using qualitative information. An intelligent GIS is a powerful tool because it can blend methodologies for representation, analysis, and interpretation of quantitative, spatially referenced data with heuristic knowledge of experts. Open architecture systems are rapidly emerging and will probably form an integral part of future GIS.

Environmental risk assessment

Ecological risk assessment provides a framework to enable (1) a quantitative basis for balancing and comparing risks associated with environmental hazards and (2) a systematic means of improving the estimation and understanding of those risks. Graham et al. (1991) show that the spatial heterogeneity of the landscape is especially important for regional ecological risk assessment and identify GIS as an important tool for regional assessments (Hunsaker et al., 1990). Society needs a quantitative and systematic way to estimate and compare the impacts of environmental problems at various spatial scales, and future ecological models must provide probabilistic numerical and graphical estimates of change for issues as varied as marine fish migration, forest production and succession, non-point-source pollution, fire and pest movement, climate change, and identification of sensitive and unique ecological areas. Those models that consider the dynamic interactions of species populations with extrinsic variables such as sea levels and climate (Botkin et al., 1991) will be most useful if there is a built-in GIS component.

CONCLUSIONS AND RECOMMENDATIONS

Ecological modeling differs greatly among the subdisciplines of ecology, but it is developing in the same general direction—integration of temporal and spatial effects. Most advances in the past concerned temporal effects, and considerable progress has been made. The next logical step is to consider spatial phenomena. As stated, the null hypothesis in spatial analysis is that the future state of a unit on a landscape is independent of adjacent units. This assumption is often implicit in many ecological models, but the degree to which it is true remains unclear. Most demonstrations of spatial aspects in ecological models just display independent effects as if they were integrated in space, but there is no spatial interaction between cells or subareas. True integration of spatial aspects in ecological models is more an ecological problem than a display problem. Sklar and Costanza (1991) ask ecological modelers to give explicit and concentrated attention to the modeling of larger geographic areas (regional and global), and GIS technology will be important in making the transition from local models to larger areas. The next step for ecologists is to test the null hypothesis to determine at what scale it is true or false, and this test is particularly important when considering issues at regional and global scales.

From a pragmatic viewpoint models are developed for two purposes: to better understand ecological processes; and to help make resource-management and policy decisions. Often these two purposes correspond to the classification of model approaches into stochastic (probability-based) and process-based models, although these are not mutually exclusive. Grant (1988) reminds ecologists of two important points to keep in mind as ecological models are improved and GIS technology is better incorporated:

> One is that the quality of a model does not depend on how realistic it is, but rather on how well it performs in relation to the purpose for which it was built. The other is that the level of resolution included in a model must fit the resolution required by the problem at hand. Modelers must learn to compromise between the known complexity of ecosystems and the need to address a problem with limited data and time.

In light of the limited use of GIS by ecologists during the past 10 years, GIS technology offers a relatively untapped potential for ecological modeling of spatial processes. One future direction is to design ecological models to accommodate spatial analysis by using GIS modules as subroutines for data storage, manipulation, and display. Another approach is to code future ecological models in a GIS modeling language that can take full advantage of GIS spatial analysis and display.

Most GIS systems are still relatively expensive. A system of software and workstation hardware can cost $100,000 or more; however, some GIS are available for less than $1000. These include both workstation and PC versions such as the GRASS system developed by the U.S. Army Corps of Engineers; the pMAP cartographic modeling package, available from Spatial Data Systems; RAISON, available from Canada's National Water Research Institute; and IDRISI, developed by Clark University. Widespread use of GIS in ecological studies could be encouraged greatly by the availability of less expensive GIS software.

Future integration of GIS and ecological modeling will require close cooperation between modelers and GIS vendors. Vendors of GIS should be encouraged to develop: (1) open software architectures that provide access by model subroutines to GIS modules, such as in the GRASS GIS; (2) comprehensive modeling languages (e.g., the RAISON Programming Language) that permit complex spatial analyses, such as calculation of gradients between cells and movement of materials based on gradients and probabilities; (3) the ability to store, analyze, and display time-varying data by pixel or polygon; and (4) libraries of commonly used data, such as regional and national topography, temperature, and rainfall. Such close cooperation between developers of ecological models and GIS is necessary to accomplish the huge task of modeling the current state of regional and global ecological phenomena. The products of such cooperation will provide the tools to assess the effects on ecological phenomena and conditions from regional and global changes.

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