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SPATIALLY EXPLICIT POPULATION MODELS: CURRENT FORMS AND FUTURE USES[1]

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Abstract. Spatially explicit population models are becoming increasingly useful tools for population ecologists, conservation biologists, and land managers. Models are spatially explicit when they combine a population simulator with a landscape map that describes the spatial distribution of landscape features. With this map, the locations of habitat patches, individuals, and other items of interest are explicitly incorporated into the model, and the effect of changing landscape features on population dynamics can be studied. In this paper we describe the structure of some spatially explicit models under development and provide examples of current and future research using these models. Spatially explicit models are important tools for investigating scale-related questions in population ecology, especially the response of organisms to habitat change occurring at a variety of spatial and temporal scales. Simulation models that incorporate real-world landscapes, as portrayed by landscape maps created with geographic information systems, are also proving to be crucial in the development of management strategies in response to regional land-use and other global change processes. Spatially explicit population models will increase our ability to accurately model complex landscapes, and therefore should improve both basic ecological knowledge of landscape phenomena and applications of landscape ecology to conservation and management.

Key words: dispersal; land management; landscape; mobile animal populations: population dynamics; population simulation models; spatially explicit population models.

INTRODUCTION

Population simulation models have evolved in complexity and sophistication in the past decade, increasing the potential utility of these models for a wide variety of applications. Simulation models have become important in the study of population dynamics in heterogeneous landscapes. In particular, population models that incorporate the habitat complexity of real-world landscapes can be used to examine possible population response to regional or global change. These models, therefore, show promise as tools for conservation biologists and land managers. In this paper we describe the current state of spatially explicit population models (SEPM), especially one class of spatially explicit models called **MAP** models since they are used to simulate **M**obile **A**nimal **P**opulations. We discuss how the models are being used and suggest some future directions in which research using these models might proceed.

In general, SEPMs are of interest for several reasons. First, these models give ecologists a technique for studying ecological processes that operate over local to landscape to global spatial scales and for estimating the possible responses of organisms to these processes. SEPMs may, therefore, be useful in predicting population and community responses to phenomena such as climate change or regional land-use that are difficult to study with traditional ecological techniques (e.g., Solomon 1986, Levin 1992, Murphy and Noon 1992). Spatially explicit approaches are also appropriate for

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modeling the impact of fire and other catastrophic events that can affect large portions of a landscape.

The second reason that SEPMs are of interest is that they may provide land managers with a method of examining possible responses of species of management interest to changes in local and regional management strategies. Comparison of modeling results with the results of field implementation of management strategies should be an important step in adaptive management strategies (Walters 1986, Conroy 1993). Finally, modeling population dynamics across complex landscapes should improve our ability to model in a realistic manner. SEPMs require habitat-specific information about demography, dispersal behavior, and habitat selection of the organism(s) being studied. Thus, the use of SEPMs will require a close interaction between ecological modelers and researchers conducting field studies of species' life history, behavior, and distribution.

In this article we will not review all published SEPMs. Instead, we will illustrate our points with examples of models that were discussed at a workshop on the use of SEPMs in conservation and management, held at the University of Georgia in November I992.

DEFINITION AND CURRENT STRUCTURE OF SEPMs

Spatially explicit models have a structure that specifies the location of each object of interest (organism, population, habitat patch) within a heterogeneous landscape, and therefore the spatial relationships between habitat patches and other features of the landscape (e.g., landscape boundaries, corridors, other patches) can be defined. Since the spatial layout of the landscape is explicitly incorporated, the models can be used to indicate how populations or communities might be affected by changes in landscape structure, including changes in landscape composition (the relative or absolute amount of habitat types or features in a landscape) or landscape physiognomy (the exact placement of habitat patches and other features within the landscape) (Dunning et al. 1992).

Models that are not spatially explicit can be very useful in studying some landscape processes. For instance, Pulliam and Danielson have used analytical models to examine the impact of a landscape composed of source and sink habitats on population dynamics and interspecific interactions (Pulliam 1988, Danielson 1991, Pulliam and Danielson 1991). These analytical models, however, cannot be used to examine aspects of landscape physiognomy, such as patch isolation, since the arrangement of the habitat patches is not specified. To model population dynamics in real-world landscapes where landscape composition and physiognomy are both likely to be important, one must use a spatially explicit modeling approach that includes the spatial and temporal arrangement of landscape features.

To project the impact of landscape change on wildlife populations, models must relate the demographics of the population explicitly to the landscape in which the organisms exist. MAP models do this by combining a landscape map describing the locations of suitable and unsuitable habitat patches with a population model incorporating habitat-specific demography and detailed dispersal behavior. Such models allow various landscape patterns to be evaluated when planning land management strategies that involve extensive alteration in the distribution and quality of habitat patches.

Structure

Two important components of the structure of any landscape model are the model's grain and extent (O'Neill et al. 1986, Wiens 1989). The grain of a landscape is the smallest patch size, which defines the lower limit of resolution of the landscape map (Wiens 1989). Each individual patch is usually assumed to be homogeneous in its local habitat characteristics. SEPMs are often constructed as grids of interconnecting square or hexagonal cells (Fahrig 1988, Noon and McKelvey 1992, Pulliam et al. 1992). The grain of these landscapes is therefore defined by the size of the cells, which is usually of a scale relevant to the organism being modeled, such as the species' home range or territory size. Heterogeneous landscapes are made by assigning different habitat characteristics to different cells. While the minimum patch size is limited by the size of an individual cell, habitat patches larger than an individual cell can be created by grouping contiguous cells with similar characteristics.

Some SEPMs reduce the size of the individual cells to a single pair of (x/y) coordinates (Palmer 1992, Pacala et al. 1993). In these models the shape or size of the individual cells is usually not explicitly specified. As with other SEPMs, the cells can be occupied by a single organism only, such as the single tree that is allowed per cell in SORTIE, a spatially explicit forest simulator (Pacala et al. 1993), or the (x/y) coordinates can be occupied by a population (e.g., Palmer 1992). Spatially explicit models that reduce cell size down to a single point are particularly useful in modeling general landscape impacts on hypothetical populations, where the size of the individual cells is not critical.

The extent of a landscape is defined as the largest scale being covered by the study (Wiens 1989) and is set by the size of the landscape map. Most SEPMs currently under development for relatively mobile vertebrate species examine individuals and populations that inhabit microscale to mesoscale areas (<1 ha to 10^4 km^2, Delcourt and Delcourt 1988). Other spatially explicit models are being developed to cover even larger areas, especially for the study of global climate change (e.g., Solomon I986).

Types of landscapes

The simplest landscapes used in spatially explicit modeling are those in which each cell has only a few character attributes, such as habitat type or age. The attributes can be assigned either randomly or in particular patterns to the cells in this type of "artificial landscape" to examine how landscape characteristics affect hypothetical populations. Artificial landscapes are especially useful for testing the potential importance of landscape variables that are difficult to isolate in real landscapes. For example, Lamberson et al. (1994) used artificial landscape maps to test the effects of patch size and spacing on the viability of the threatened Northern Spotted Owl (*Strix occidentalis*) in potential reserve designs.

With the use of more sophisticated technologies, it is possible to capture the heterogeneity of real-world landscapes. This is particularly true of landscape maps created with geographic information systems (GIS). Habitat maps for a given species can be created by overlaying a grid of cells onto a GIS map of a given region and then assigning all of the characteristics of the underlying habitat polygons to each cell of the grid. This approach was followed in creating realistic landscape maps for advanced versions of BACHMAP, the MAP model of Bachman's Sparrow *(Aimophila aestivalis)* populations in the southeastern United States (Pulliam et al. 1992, Liu et al., *in press b*) and OWL, the model developed for the northern and California subspecies of the Spotted Owl in the western United States (McKelvey et al. 1992, Murphy and Noon 1992, Noon and McKelvey 1992).

Landscapes also can be made more realistic by introducing temporal as well as spatial variation of the landscape. For instance, the landscapes in BACHMAP and OWL are altered with each time step (annually in the sparrow model, every 10 yr in the owl model). The age of the habitat in each cell is increased at the start of each time step, and age-related management practices are imposed to change the landscape in a way consistent with the management strategy being simulated. Thus, the distribution of suitable and unsuitable habitat patches changes with time, creating a dynamic landscape. On a smaller temporal scale, a foraging model being developed by Y. Cohen *(personal communication)* alters the quality of the forage in a small patch as the forage is harvested by a grazing moose. Moose move in response to the changes in forage quality across the landscape throughout the day.

Individual-based vs. population-based models

Many of the SEPMs under development are individual-based. In these models, the location of each individual across the landscape is monitored, and individuals acquire fitness characteristics associated with the cell type they occupy. The status of each individual is followed through an entire simulation. In models with an annual time step, individuals can undergo an annual cycle of breeding, dispersal, and mortality (e.g., Pulliam et al. 1992). In models with a daily time step, foraging, growth, and predator avoidance of each individual can be monitored. An example of the latter is Turner et al. (1993), which is a model that follows the movements, foraging activity, and mortality of individuals and small groups of wintering bison (*Bison bison*) and elk (*Cervus elaphus*) in Yellowstone National Park. The resource levels in occupied patches are depleted by foraging bison and elk, and therefore the distribution of depleted and nondepleted patches changes with time. This model provides an example of how habitat-specific demography or the behavior of organisms can be used to further define resource heterogeneity in the landscape. Population parameters in individual-based models are calculated by following the fate of all individuals through time and deriving estimates of total population size or extinction probability.

SEPMs can be population-based, where each cell contains a population (e.g., Satoh 1990, Hassell et al. 1991, Palmer 1992). This may be the most appropriate modeling strategy for abundant organisms such as rodents or insects in models where it may be difficult to follow each individual in a large population. In these models, patch-specific reproduction and mortality are measured by population growth rates, while movement between patches is measured by immigration and emigration rates. It may be possible to create population-based models on GIS landscapes by adapting existing metapopulation models that use artificial landscapes. In this adaptation, the subpopulation dynamics from the metapopulation model would be assigned to clusters of cells of suitable habitat from the real-world landscape.

Movement and dispersal rules

Perhaps the most important difference between SEPMs and other landscape models is that SEPMs can incorporate movement of organisms between specific patches across the landscape and quantify how this movement may affect population dynamics. Rules of movement can allow for both the temporary movement between patches for individuals searching for food, predator refuges, or mates; or the more permanent movements of dispersing individuals. Movement rules can specify boundary effects, dispersal mortality, and use of corridors or other landscape features.

When SEPMs are constructed, dispersal rules must be explicitly incorporated, for dispersal characteristics can be very important in determining how successfully a species will exploit a given landscape. Modeling dispersal is challenging, however, because we know so little about an individual's "perception" of the landscape or the factors that influence the transition from one spatial location to another. This lack of understanding is not always a major handicap, however. If the area being modeled is sufficiently small, then very few of the best habitat patches are likely to remain undiscovered regardless of how we simulate the dispersal process, and the details of dispersal in such a landscape will be relatively unimportant when measuring population size. In such a landscape, the physiognomy (arrangement) of the habitat patches will likely have little effect on local populations. Dispersal details will also be relatively unimportant in those instances where high-quality habitat patches tend to be temporally static. In such situations, long-lived patches will eventually be colonized regardless of whether the species is a "good" or "poor" disperser, and the landscape ultimately will become saturated to carrying capacity. In either of these cases, SEPMs are not usually required to model population dynamics.

One of the goals of many SEPMs is to examine long-term dynamics over areas large enough that, given an organism's dispersal and habitat selection ability, at least some high-quality patches may not be fully exploited. Under these conditions, dispersal ability may be the limiting factor in determining the size of the population that can be supported in the landscape. The rules that govern dispersal and settlement are critical in these situations. Given the lack of field data on dispersal for many organisms, modelers may need to turn to other approaches for approximating dispersal behavior. The field of optimal foraging theory, as applied to patchy resources, is a place where the search for reasonable dispersal rules may be profitable. To date, there has been little use of these ideas in determining which types of rules might be most appropriate under specific conditions. Field ecologists who wish to make quantitative predictions with SEPMs should recognize the need to invest a substantial effort toward gaining a better understanding of dispersal and the spatially explicit phenomena that may influence it.

SENSITIVITY ANALYSIS

For many species, the detailed natural history information required for parameterization of SEPMs is not available. To overcome this difficulty, parameter estimates based on published work are often used (e.g., Pulliam et al. 1992). To determine if the specific value used for a given parameter has a disproportionate impact on model results, many researchers depend on sensitivity analyses of the models' variables. In sensitivity analysis (Jorgensen 1986), multiple simulations are performed to determine if the model's results are sensitive to the exact value used for a particular variable. Interactions between variables can be determined by simulations that change several parameter values in a factorial design or by Monte Carlo randomizations.

These analyses can be used in at least two ways. First, the results can identify variables for which model results are relatively invariant over the range of parameter values tested. For these variables, the models can be run using a constant parameter value reasonable for the organism being studied, Second, modelers can use the results of sensitivity analyses as a guide for coordinating field research. Field studies can be used to improve estimates of parameters to which model performance is most sensitive. Sensitivity analyses do not tell us what variables drive ecological systems, however, or what management strategies would be most effective (Green and Hirons 1991).

Insights from sensitivity analyses

Formal sensitivity analyses of a number of spatial models of animal movements have provided several consistent and valuable insights. For example, major sensitivities arise for the unknowns of an animal's behavior (e.g., dispersal behavior, allocation of search effort in heterogeneous landscapes, and habitat selection ability). We expect a resurgence of interest in field studies of behavior, particularly habitat selection, as a result of spatial modeling results. One of the most significant observations has been that a species can be severely habitat limited, and in fact, go extinct even if suitable, but unoccupied, habitat is still present (Lande 1987, Pulliam 1988, Lamberson et al. 1992).

Population dynamics have been shown to be sensitive to factors such as the pattern of distribution of the habitat types, the habitat-specific birth and death rates, and dispersers' abilities to discriminate habitat patches on the basis of their quality. For example, the proportion of a landscape that is sink habitat, and its arrangement relative to source habitat, can have unexpected effects on population dynamics (Pulliam and Danielson 1991, McKelvey et al. 1992). Surprisingly, if a species is a poor discriminator among habitats of varying quality, it may be better to have distinct boundaries around reserves rather than gradual transitions into the surrounding matrix (McKelvey et al. 1992, Cantrell and Cosner 1993).

The results of sensitivity analyses are dependent upon the intervals over which the parameters are allowed to vary. For example, the average size of patches in a landscape may significantly affect the likelihood of species' persistence only over a small range of patch sizes (Thomas et al. 1990, Carroll and Lamberson 1992, McKelvey et al. 1992, Lamberson et al. 1994). Outside this range, however, population persistence may become increasingly sensitive to variation in another aspect of the landscape pattern or life history. The observation of changing sensitivities has important implications to management. No longer is there necessarily a single optimal management strategy to recover a threatened species. Rather, the optimal strategy will change through time as the quality, amount, and geometry of the habitat changes, emphasizing the necessity of management in an adaptive context (Conroy et al. 1995).

BASIC QUESTIONS THAT CAN BE ADDRESSED

SEPMs are being used to address a variety of questions in population and community ecology. Some of these questions have not been addressed widely by traditional ecological research, while others are germane to the central topics that have dominated much of ecology. Some examples of those topics were prominently discussed in the November workshop as being fruitful areas of investigation.

Dynamics of resources and organisms

Perhaps the most common use of SEPMs to date has been in the study of individual and population response to landscape change. Resource distributions are dynamic across landscapes; that is, the distribution of habitat patches containing necessary resources is changing through time and space in many real-world landscapes (Turner 1987, 1990, Turner and Ruscher 1988). Stochasticity in resource distribution across landscapes exists at different spatial and temporal scales (Levin 1992). Spatial and temporal autocorrelations in environmental factors such as weather, habitat quality, and predation also exist at a variety of scales. How do organisms respond to such variation? Our ability to test hypotheses of organism response has been limited by the difficulty in manipulating landscape variables. One solution to this limitation has been to use small organisms whose landscapes can be practically manipulated (e.g., beetles, Rykiel et al. 1988, Wiens and Milne 1989; and moths, Fahrig and Paloheimo 1988). SEPMs represent another approach in which a population's response to landscape changes can be modeled with stronger replication than usually possible in the field. It is still critical to verify the validity of simulation models with field tests, however, to help assess the applicability of model results to the real world (Conroy et al. 1995).

Many of the above studies have emphasized the final population size that results from a landscape change or manipulation. The path that a population takes to get to that final state is also an important result. The dynamics of a population during a time interval in which the population or its resources are changing in amount or distribution may be referred to as the population's transient behavior. An example of a nonequilibrium population estimated to be in transition between decline and stability is the Northern Spotted Owl, a species currently threatened by habitat loss and fragmentation (Simberloff 1987). A recovery plan (USDI 1992) is being implemented for this species, in which stabilization of its habitat distribution is a major goal. Prior to this stabilization, however, many population trajectories, including extinction, are possible. Which trajectory is followed depends in large part on the pattern and rate of recovery of its critical habitat. Several different map-based alternative management strategies, varying in amount and distribution of continued timber harvest, have been proposed in connection with a proposed reserve design (Thomas et al. 1990). Almost all of the alternatives reach the same static reserve structure at some time in the future, but habitat trajectories and time frames to recovery vary (Fig. 1). How do the risks to persistence of the owl population vary among the five alternatives during the transitional period? Do some alternatives have unacceptably high risks of crossing a habitat threshold, beyond which the population declines inescapably to extinction (Lande 1987, Thomas et al. 1990, Lamberson et al. 1992)?

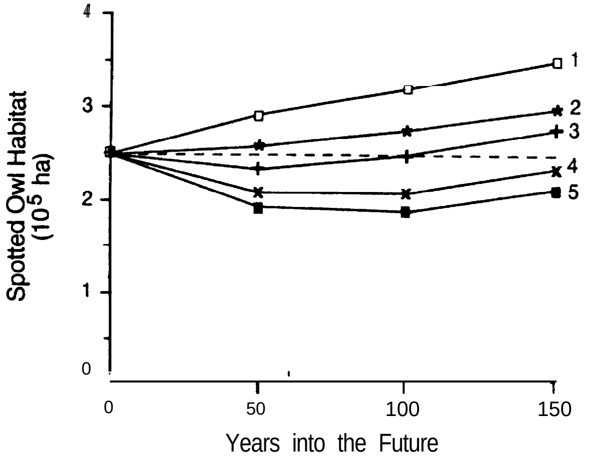

FIG. 1. Projected change in the amount of Spotted Owl habitat on National Forests for five alternative strategies (numbered solid lines) that establish a Spotted Owl reserve design in the Pacific Northwest (USDA 1992). The dashed line indicates the current amount of owl habitat. Note that alternatives 3-5 project a continuing loss of habitat during part or all of the simulated time span. This loss occurs even though the owl is currently listed as threatened due to past loss and fragmentation of its habitat (USDI 1992).

Questions such as these can be addressed only by considering the amount, geometry, and rate of change of habitat in a spatially and temporally explicit fashion. The transient behavior of the Spotted Owl population in Oregon is being examined using OWL, a SEPM integrated with a GIS mapping of the forested landscape in Oregon (McKelvey et al. 1992, Turner et al. 1995). Preliminary studies indicate that whatever management strategies are selected will significantly affect the population trajectory during the transition until the final reserve design is reached.

Habitat selection and population regulation

SEPMs are proving useful in linking behavioral and ecological studies that examine habitat selection to population studies that consider how populations are regulated. Analytical models of habitat selection have suggested that a landscape's composition can affect a population's probability of extinction (Pulliam and Danielson 1991). For example, rates of population decline may be greater than rates of habitat loss in landscapes dominated by sink habitat, with the result that some landscapes may fail to support viable populations even if some suitable habitat still exists. Such effects have also been found in SEPMs with artificial landscapes where the composition of the landscape can be varied in a controlled fashion (Liu 1992). Linking SEPMs with GIS-derived landscape maps provides a method for determining when such landscape effects might be important in the real world; the MAP model parameterized for the California Spotted Owl applies this method (Noon and McKelvey 1992). Ultimately, modeling may suggest conditions under which populations are regulated by local or by regional ecological processes.

Reserve design for threatened and endangered species

Models incorporating the spatial pattern of a species' habitat and the distribution of its population have provided insights into the design of reserves for threatened and endangered species (e.g., Thomas et al. 1990). For instance, most conservation plans need to consider the location, number, size, and shape of critical habitat patches (reserve elements) in an effort to provide for a species' persistence. Spatial models, structured and parameterized according to a species' life history, allow one to explore the efficiency of various reserve designs. The models can be used to estimate the potential effects on a species' persistence by systematically varying factors such as the percentage of the landscape that is suitable habitat, and the size, shape, and spacing of habitat patches. The addition of marginal (i.e., sink) habitat to a reserve can be assessed for negative effects on a managed population (Pulliam and Danielson 1991). These exercises can be done on artificial landscape maps to explore general reserve design principles (Lamberson et al. 1992, 1994) or on GIS-based maps that incorporate land-use and ownership constraints (Murphy and Noon 1992, Noon and McKelvey 1992).

BRIDGES TO OTHER FIELDS

One of the main reasons that SEPMs are an important tool for ecologists is because they allow ecologists to escape the bounds of spatial and temporal scales in which they typically have worked, and in doing so, bridge the gaps that currently exist between ecology and other fields. Ecologists can use spatially explicit modeling as a bridge in at least two ways. First, models can be used to integrate the study of ecological processes with other phenomena operating at scales that previously were not conducive to ecological research. Second, ecologists can use models to predict simultaneously both ecological responses and the responses of non-ecological variables studied in other disciplines.

Examples of both these approaches are found in recent modeling efforts. The use of SEPMs to bridge behavioral and population ecology is mentioned above. The use of SEPMs to link ecological research with applied fields such as wildlife management and conservation biology is discussed in Turner et al. (1995) and Conroy et al. (1995). An additional example of bridging between fields is the linkage of landscape ecology and population genetics. Many studies have demonstrated the importance of gene flow and metapopulation dynamics to the genetic structure of populations (Barrowclough 1980, Meffe and Vrijenhoek 1988, Burson 1990). The analytical models of Chesser (1991*a, b)* show that the incorporation of spatial movement of individuals between demes can have substantial effects on the genetic structure of populations. With their more realistic landscape capabilities, SEPMs could be a useful tool for population geneticists.

Another example of how SEPMs could bridge different approaches to ecological study is found in modeling approaches to climate change. Simulation models of successional forest structure are being used to examine how plant communities will change with global climate change (Shugart et al. 1992). Linkages between these models and SEPMs may allow the prediction of how animal populations respond to climate change and other global environmental processes (see Holt et al. 1995). Forest simulator models and animal SEPMs are often constructed at different' spatiotemporal scales; thus, a critical area for research in this linkage will be to understand better how information is transferred across hierarchical scales (Levin 1992).

Spatially explicit models can also include nonbiological parameters to examine response of non-ecological variables. An example of this second approach is provided by ECOLECON, developed by J. Liu (1992, 1993, Liu et al., *in press a),* who integrated the study of forest economics with the ecological consequences of land use in managed southern pine woodlands. In this model, forest economic indices such as land expectation value are calculated to determine the economic costs of management for conservation of species of management concern. This approach allows an integration of ecological and economic concerns in designing management strategies (Constanza 1991).

Finally, SEPMs represent a bridge between ecological research and field studies of the natural history of organisms in real-world landscapes. For model predictions to be accurate, the parameterization of the model must be based on life history and behavioral information accurate for both the organism and the landscape being modeled (see Conroy et al. 1995). This requires that the modeler understand the natural history of the species and places an important emphasis on basic natural history research in ecology. The lack of data on the demography, dispersal ability, and habitat use for even the most common species hampers the ability of ecologists to predict species' responses to any environmental change.

LIMITATIONS

SEPMs are not a panacea for population ecologists. At their present level of development, the models have limitations (Conroy et al. 1995). Currently, the best SEPMs cannot predict, with any high degree of quantitative accuracy, the eventual number of organisms that might be found in a particular landscape. Like any model, many simplifications must be made to make these models tractable and comprehensible. Furthermore, there are unknowns such as many aspects of dispersal behavior. These simplifications and unknowns make it impossible to predict the population size of species *X* at time *Y* in landscape *Z*. This is especially unfortunate for many conservation or endangered species situations. The best current applications of SEPMs are in making comparative and qualitative statements about the likely population responses to a set of potential or real landscape alterations. As SEPMs become more sophisticated and our ecological knowledge increases, we eventually will be able to narrow the zone of uncertainty associated with using these models as predictive tools. Even with the best knowledge, however, complex landscape structures are not deterministic entities, and we cannot expect to forecast new futures with a high degree of precision.

For some studies in landscape ecology, a researcher may wish to alter a specific aspect of a landscape's composition without changing other aspects such as the landscape's physiognomy. This is hard to do with SEPMs, since both the composition and physiognomy of a landscape are explicitly incorporated into the model. For these studies, analytical models such as those used by Pulliam and Danielson (1991) will be more useful. To fully understand the relative importance of all aspects of landscape structure, a set of carefully constructed comparative models using a variety of approaches is required.

FUTURE GOALS

We believe that modeling spatially explicit landscapes can improve our ability to do ecological research in two major ways. First, better development of SEPMs will improve our ability to model realistic landscapes, allowing us to better understand population and community responses to environmental change. Second, SEPMs will allow us to ask different questions and increase the impact that landscape approaches are already having on ecological research.

Currently, most SEPMs are capable of making qualitative predictions as to which environmental or life history variables are likely to have the biggest effect on population dynamics (see sections on *Sensitivity analysis* and *Limitations*). What is not generally possible at present are quantitative predictions of actual population responses to specific environmental changes. Therefore, a major focus of research needs to be on increasing the predictive ability of models (Conroy 1993, Conroy et al. 1995). Most current models also depend on types of demographic and behavioral data that are extremely difficult to obtain in the field. Analysis of parameter impact on model performance may suggest simple field parameters that are more easily measured and that contain the same information (at least in regard to the model) as more difficult to estimate field parameters (e.g., Vickery et al, 1992). Such an analysis would allow the modeling and field research to be more efficiently interactive and increase one's ability to devise a model that is both accurate and realistic.

SEPMs should also allow us to address new questions and design new approaches to our research. An excellent example of this can be found in the application of percolation theory, using spatially explicit models, to the study of landscape change and organismal response (Turner et al. 1989*a*, *b*, Johnson et al. 1992). SEPMs can provide a method of exploring (either through simulation or through the design of field tests) the predictions of theoretical and analytical models. Various authors have pointed out that the development of ecological theory often outpaces empirical testing of the theory (e.g., Kareiva et al. 1989). This is often due to the inability of researchers to design field experiments where the relevant environmental parameters can be controlled. This is particularly true of landscape experiments, where the relevant environmental variables are difficult to manipulate, especially for studies involving most vertebrates. Although they do not substitute completely for field experiments, SEPMs permit some exploration of landscape hypotheses. For example, SEPMs allow one to change environmental variables in the model while holding life history characteristics of the modeled population constant, or vice versa. Population models also allow simulated replication of scenarios of landscape change.

When combined with relevant field studies, SEPMs can help test the predictions of ecological theory with a spatial component. The predictions of Pulliam's (1988) analytical model of source and sink dynamics are currently being tested with field studies and simulation modeling of upland bird and mammal populations (Liu 1992, Pulliam et al. 1992; J. B. Dunning, *unpublished data*, B. J. Danielson, *unpublished data).* Non-intuitive modeling results, such as unexpected patterns of spatial distribution of organisms across different landscapes, can be tested by field studies. Computer models can be used to generate hypotheses concerning how fine-scale processes, studied with field experiments, interact with larger scale processes to produce broad-scale distributional patterns (Levin 1992). Again, simulation modeling incorporating realistic landscapes provides a framework for interactive research between theoretical ecologists and field biologists.

SEPMs are providing a mechanism for studying how large-scale patterns and processes affect populations. In this sense, we are gaining an increased understanding of how open populations are affected by their landscape context. Virtually all SEPMs are case-specific, however, in that the results of the modeling are specific to both the initial conditions and to the organism and landscape being simulated. For the most part, specific lessons learned from results of one model may not be extrapolated to other cases. Probably the most direct method of studying the general impact of landscape phenomena is to design general landscape models of hypothetical populations (e.g., Palmer 1992). Eventually, generality may also emerge, however, from the comparison of results across case-specific models. For example, if sensitivity analyses from a variety of modeling efforts indicate that the models show low sensitivity to a particular class of variables, then this low sensitivity could be identified as a general property of this class of models. Comparison of results across models may be an effective method of identifying emergent properties of landscape characteristics. Levin (1992) discusses the possibility of developing scaling laws to make comparisons among studies done at different scales.

Finally, SEPMs may allow researchers to identify the ecologically meaningful scales at which landscape processes operate. Organisms of different size or with different life histories will respond to the same landscape in different ways, if they operate over different scales. A small rodent lives and disperses over a much smaller portion of the landscape than does the fox that hunts the rodent. But the rodent is affected indirectly by factors that affect its predator (Holt 1977). What then are the appropriate landscape scales for studying the rodent: the smaller region over which the rodent itself lives and disperses or the larger region that includes the factors affecting the fox? Modelers could seek to explore this question by comparing simulations in which the spatial extent of the landscape map is varied systematically to determine the scale at which the most realistic population dynamics are attained. Thus, SEPMs should play a role in exploring the most basic scale-related questions in ecology.

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LITERATURE CITED

Barrowclough, G. E 1980. Gene flow, effective population size, and genetic variance in birds. Evolution 34:789-798.

Burson, S. L. 1990. Population genetics and gene flow of the Common Tern. Condor 92:182-192.

Cantrell, R. S., and C. Cosner. 1993. Should a park be an island? SIAM Journal of Applied Mathematics 53:219-252.

Carroll, J. E., and R. H. Lamberson. 1993. The owl's odyssey: a continuous model for the dispersal of territorial species. SIAM Journal of Applied Mathematics 53:205-218.

Chesser, R. 1991a. Gene diversity and female philopatry. Genetics 127:437-447.

——— 1991b. Influence of gene flow and breeding tactics on gene diversity within populations. Genetics 129:573-583.

Conroy, M. J. 1993. Testing hypotheses about the relationship of habitat to animal survivorship. Pages 331-342 *in* J. D. Lebreton and P. M. North, editors. The use of marked individuals in the study of bird population dynamics. Birkhauser-Verlag, Basel, Switzerland.

Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecological Applications 5:17-19.

Constanza, R., editor. 1991. Ecological economics: the science and management of sustainability. Columbia University Press, New York, New York, USA.

Danielson, B. J. 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. American Naturalist 138:1105-1120.

Delcourt, H. R., and F. A. Delcourt. 1988. Quaternary landscape ecology: relevant scales in space and time. Landscape Ecology 2:23-44.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.

Fahrig, L. 1988. A general model of populations in patchy habitats. Applied Mathematics and Computation 27:53-66.

Fahrig, L., and J. Paloheimo. 1988. Effect of spatial arrangement of habitat patches on local population size. Ecology 69:468-475.

Green, R. E., and G. J. M. Hirons. 1991. The relevance of population studies to the conservation of threatened birds. Pages 594-633 *in* C. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, United Kingdom.

Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. Nature 353:255-258.

Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. Theoretical Population Biology 12:197-229.

Holt, R. D., S. W. Pacala, T. W. Smith, and J. Liu. 1995. Linking contemporary vegetation models with spatially explicit animal population models. Ecological Applications 5:20-27.

Johnson, A. R., B. T. Milne, and J. A. Wiens. 1992. Diffusion in fractal landscapes: simulations and experimental studies of tenebrionid beetle movements. Ecology 73:1968-1983.

Jorgensen, S. E. 1986. Fundamentals of ecological modelling. Elsevier, Amsterdam, The Netherlands.

Kareiva, P. 1989. Renewing the dialogue between theory and experiments in population ecology. Pages 68-88 *in* J. Roughgarden, R. M. May, and S. A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. Conservation Biology 6:505-512.

Lamberson, R. H., B. R. Noon, C. Voss, and K. McKelvey. 1994. Reserve design for terrestrial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. Conservation Biology 8:185-195.

Lande, R. 1987. Extinction thresholds in demographic models of terrestrial populations. American Naturalist 130:624-635.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Liu, J. 1992. ECOLECON: a spatially-explicit model for ecological economics of species conservation in complex forest landscapes. Dissertation, University of Georgia, Athens, Georgia, USA.

———. 1993. ECOLECON: An ECOLogical-ECONomic model for species conservation in complex forest landscapes. Ecological Modelling 70:63-87.

Liu, J., F. W. Cubbage, and H. R. Pulliam. *In press a.* Ecological and economic effects of forest landscape structure and rotation length: simulation studies using ECOLECON. Ecological Economics.

Liu, J., J. B. Dunning, and H. R. Pulliam. *In press b.* Assessing alternative management strategies: an example coupling GIS with spatially-explicit models. Conservation Biology.

McKelvey, K., B. R. Noon, and R, H. Lamberson. 1992. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. Pages 424-450 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Boston, Massachusetts, USA.

Meffe, G. K., and R. C. Vrijenhoek. 1988. Conservation genetics in the management of desert fishes. Conservation Biology 2:157-169.

Murphy, D. D., and B. R. Noon. 1992. Integrating scientific methods with habitat conservation planning: reserve design for Northern Spotted Owls. Ecological Applications 2:3-17.

Noon, B. R., and K. S. McKelvey. 1992. Stability properties of the spotted owl metapopulation in southern California. Pages 187-206 *in* J. Verner et al., technical editors. The California spotted owl: a technical assessment of its current status. US Forest Service General Technical Report PSW-133.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Pacala, S. W., C. D. Canham, and J. A. Silander, Jr. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canadian Journal of Forest Research 23:1980-1988.

Palmer, M. W. 1992. The coexistence of species in fractal landscapes. American Naturalist 139:375-397.

Pulliam, H. R. 1988. Sources, sinks and population regulation. American Naturalist 132:652-661.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137:S50-S66.

Pulliam, H. R., J. B. Dunning, and J. Liu. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications 2:165-177.

Rykiel, E. J., R. N. Coulson, P. J. H. Sharpe. T. F. Allen, and R. O. Flamm. 1988. Disturbance propagation by bark beetles as an episodic landscape phenomenon. Landscape Ecology 1:129-139.

Satoh, K. 1990. Single and multiarmed spiral patterns in a cellular automaton model for an ecosystem. Journal of the Physical Society of Japan 59:4204-4207.

Shugart, H. H., T. M. Smith, and W. M. Post. 1992. The potential for application of individual-based simulation models for assessing the effects of global change. Annual Reviews of Ecology and Systematics 23:15-39.

Simberloff, D. 1987. The Spotted Owl fracas: mixing academic, applied, and political ecology. Ecology 68:766-771.

Solomon, A. M. 1986. Transient response of forests to CO_2-induced climate change: simulation modeling experiments in eastern North America. Oecologia 68:567-579.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl. Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl (USDA: Forest Service; USDI: Bureau of Land Management, Fish and Wildlife Service, and National Park Service). 1990-791-17l/20026. US Government Printing Office, Washington, D.C., USA.

Turner, M. G., editor. 1987. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.

———. 1990. Spatial and temporal analysis of landscape patterns. Landscape Ecology 4:21-30.

Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. Ecological Applications 5:12-16.

Turner, M. G., V. H. Dale, and R. H. Garner. 1989a. Predieting across scales: theory development and testing. Landscape Ecology 3:245-252.

Turner, M. G., R. H. Gardner, V. H. Dale, and R. V. O'Neill. 1989b. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55:121-129.

Turner, M. G., and C. L. Ruscher. 1988. Changes in landscape patterns in Georgia, USA. Landscape Ecology 1:241-251.

Turner, M. G., Y. Wu, W. H. Romme, and L. L. Wallace. 1993. A landscape simulation model of winter foraging by large ungulates. Ecological Modelling 69:163-184.

USDA (US Department of Agriculture, Forest Service). 1992. Final environmental impact statement on management for the northern spotted owl in the national forest. Portland, Oregon, USA.

USDI (U.S. Department of the Interior, Fish and Wildlife Service). 1992. Recovery plan for the northern spotted owl. Unpublished draft. Region 1, Regional Office, Portland, Oregon, USA.

Vickery, P.D., M. L. Hunter, Jr., and J. V. Wells, 1992. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. Auk 109:697-705.

Walters, C. 1986. Adaptive management of renewable natural resources. MacMillan, New York, New York, USA.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Wiens, J. A., and B. T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology 3:87-96.