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COMMENTARY

Spatial Uncertainty and Ecological Models

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ABSTRACT

Applied ecological models that are used to understand and manage natural systems often rely on spatial data as input. Spatial uncertainty in these data can propagate into model predictions. Uncertainty analysis, sensitivity analysis, error analysis, error budget analysis, spatial decision analysis, and hypothesis testing using neutral models are all techniques designed to explore the relationship between variation in model inputs and variation in model predictions. Although similar methods can be used to answer them, these approaches address different questions. These approaches differ in (a) whether the focus is forward or backward (forward to evaluate the magnitude of variation in model predictions propagated or backward to rank input parameters by their influence); (b) whether the question involves model robustness to large variations in spatial pattern or to small deviations from a reference map; and (c) whether processes that generate input uncertainty (for example, cartographic error) are of interest. In this commentary, we propose a taxonomy of approaches, all of which clarify the relationship between spatial uncertainty and the predictions of ecological models. We describe existing techniques and indicate a few areas where research is needed.

Key words: spatial sensitivity analysis; geostatistics; neutral model; spatial decision analysis; error budget analysis; error analysis.

INTRODUCTION

Ecological models are diverse in purpose and structure. Early models were simple theoretical models designed to produce general predictions unconstrained by the details of a particular time or place. The growth of public interest in solving environmental problems has since provided a new impetus for the development of applied ecological models (Goodchild and Case 2001). Meanwhile, advances in computing and the availability of remotely sensed environmental data have made it possible to develop models of specific, realistic situations with spatially resolved processes. Spatially explicit population models emerged as part of this trend. This type of model has been used, for example, to help understand how human alterations of river flow can influence bird and fish populations (for example, Jager and others 1993, Wolff 1994, DeAngelis and others 2000). In these models, the aquatic environment is represented as a grid of cells with daily changes in water depth and/or velocity. The success of individual animals in terms of feeding, reproduction, and survival, depends on local hydrology.

All ecology emerges from interactions among individual organisms that co-occur in time and space. One way to represent ecological interactions is to use a spatially explicit model with distance constraints on the ability to find food, mates, or refuge. Many ecological phenomena deemed impossible by aspatial models, become possible when illuminated by a spatial persective. Models that consider spatial heterogeneity are able to produce

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realistic behaviours sush as the coexistence of competing species, the coexistence of predators/parasites with their prey/hosts (refuges), the persistence of metapopulations (the rescue effect), and speciation (allopatric). Cormack (1988) summed up the importance of spatial heterogeneity to ecosystems as follows: "Without variability there would be no biology. Without space, no environment."

Geo-referenced spatially explicit models rely on spatial data, generally in the form of digital maps from geographic information systems (GIS). For population models, these input maps usually provide information about habitat (for example, land cover, vegetation, soil, habitat suitability index). The influence of uncertainty in spatial data on model predictions is therefore a concern (see, for example, Hansen and others 1999; Bennett and others 2000).

Because many ecological models now depend on spatially distributed information, methods have been developed specifically to evaluate the role of spatial uncertainty, which has been defined as the difference between phenomena in the world and the description of these phenomena (Edwards and Fortin 2001). In this paper, we present a classification scheme for questions about the relationship between predictions of an ecological model and variation in its spatial inputs. The approaches explored here address six distinct but closely related questions about this relationship (Figure 1). This taxonomy could serve to organize the expanded methods that are expected to accompany the increased use of spatially explicit models in ecology. These approaches include:

1. Uncertainty analysis. How does uncertainty in spatial data influence uncertainty in model predictions?
2. Sensitivity analysis. Which spatially distributed input variables are the model most sensitive to?
3. Error analysis. How do measurement and cartographic errors propagate through the model?
4. Error budget analysis. What sources of error in the processes used to obtain spatial input data cause the largest variation in model predictions?
5. Decision analysis and risk assessment. Given the variation known to exist among realistic alternative input maps, what is the optimal decision (or, alternatively, the ecological risk) predicted by the model?
6. Hypothesis testing using neutral models. What influence does variation in spatial structure have on model predictions?

An analogy with painting helped us to understand the distinctions among these six approaches. Like the simulation of alternative landscapes, painting is used to describe and understand the real world, but not always be reproducing it exactly.

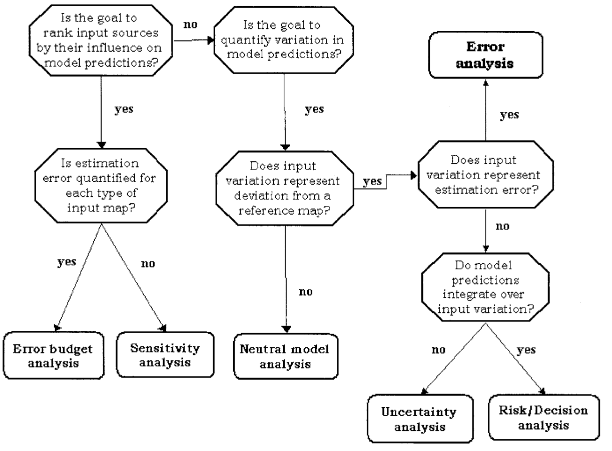

Figure 1. Decision tree used to identify the appropriate spatial Monte Carlo method among those that require alternative spatially distributed input variables.

Uncertainty Analysis

Uncertainty analysis seeks to quantify the variation in model predictions, Var(Y), caused by uncertainty in parameters, Var(X_i), where Y = f(X). The variation generated by each parameter depends on (a) how sensitive the model is to the parameter and (b) parameter uncertainty (Hambry 1994). If the parameter is measured very precisely, it may not generate much uncertainty, even though the model is sensitive to it. In the nonspatial case, Monte Carlo simulation (that is, multiple evaluations with random inputs) (Manly 1997) of the model is used to conduct uncertainty analysis. Parameter vectors are drawn from a specified multivariate distribution that includes correlations among parameters (Dale and others 1988). According to O'Neill and others (1982), the multivariate distribution should describe the actual distribution of values in the ecological system represented by the model.

Spatial uncertainty analysis is similar to that of nonspatial input parameters except that each parameter is a georeferenced lattice, **X**, rather than a single value. A stochastic model is often used to describe spatial uncertainty in **X**. The variation described includes spatial variation within a lattice cell and temporal variation. Monte Carlo simulation can still be used to propagate a collection of alternative inputs through the ecological model, but the distribution of parameter values is multivariate (all spatial locations). Stochastic simulation can be used to "draw" alternative landscapes (Heuvelink 1998; Wang and others 2000). A stationarity assumption makes it possible to use the same distribution at all locations. Spatial autocorrelation among data is also described (for example, Heuvelink 1998). Stochastic simulation generates alternative landscapes based on a probabilistic model of the input field, including its distribution and autocorrelation structure. In rare situations where the ecological model makes independent predictions at each location, and there is no aggregation or spatial pattern analysis of model predictions, non-spatial methods for propagating uncertainty can be applied independently at each location (Goovaerts 2001). If distributional requirements are met, simulation can be replaced by a simpler analytical approach (Heuvelink 1998).

For multinomial data, probabilities for classifying each location can be conditioned on surrounding data either by minimizing differences between higher-order (conditional) frequency distributions of simulated and actual landscapes (Johnson and others 1999) or, more commonly, by assuming a geostatistical model. In the case of categorical data, indicator simulation is the appropriate geostatistical method (Isaaks 1984). Conditional simulation, which uses a subset of data from the reference landscape, ensures that local information will be preserved in the landscapes generated (for example, Kyriakidis 2001; Jager and others forthcoming (unpublished)).

Sensitivity Analysis

Sensitivity analysis seeks to rank input variables by their influence on predictions of a model. Sensitivity is purely a property of the model; the nature of uncertainty in the input variables is irrelevant. In a nonspatial model, sensitivity to a parameter is the partial derivative of model response, Y, with respect to the input parameter, X_i. A normalized index, $\frac{dY}{dX_i} \times X_i$, is often used to compare parameters with different units. Because sensitivity is evaluated at the current parameter values, sensitivity rankings can change from one region of parameter space to another. Sensitivities can be calculated analytically (Dale and others 1988; Railsback and Jager 1988).

The main distinction between sensitivity analysis and the other approaches is that sensitivity is a property of the ecological model and not of its spatial inputs. Sensitivity analysis compares the influence of small variations within multiple spatial inputs on model predictions. The statistical model for sensitivity analysis simply perturbs each value in a reference map independently by equivalent amounts to facilitate comparison and is not concerned with the actual properties of input uncertainty (for example, its magnitude or correlation structure). However, local sensitivities can be used to generate an integrated uncertainty index by integrating sensitivities over the multivariate distribution of parameters.

To be consistent with the way sensitivity analysis is defined for nonspatial parameters, Monte Carlo methods used to generate alternative landscapes should superimpose a standard amount or percentage of variation on each reference input map. Because input values at different locations are independent, alternative landscapes can be constructed simply by adding a deviate to each location on the reference map, where the deviate is drawn from a single univariate distribution. This process is repeated for each type of input map (for example, elevation and land cover), and variation in model predictions is later partitioned among the input maps. Alternatively, Crosetto and others (2000) recommend performing spatial sensitivity analysis using variance-based techniques.

Error Analysis

The objective of error analysis is to quantify errors in model projections propagated from different sources of input estimation error (Parysow and others 2000). Parameter variation in error analysis represents estimation error (O'Neill and others 1982). Spatial error analysis focuses on the contributions of georegistered input data used by a spatial model. The uncertainty among alternative landscapes used to conduct spatial error analysis should reproduce errors inherent in the process by which maps are created. For example, spatial data obtained by interpolating field measurements (Wang and others 2000) are likely to have a different error structure than spatial data obtained by classification of remotely sensed imagery (Ehlschlaeger and Goodchild 1994; Soares and others 1997). Therefore, spatial data derived by different means require different statistical models, derived from replicate maps produced by the appropriate cartographic process (McGwire and Fisher 2001). Using our analogy with painting, maps produced for the purpose of error analysis are reproductions obtained by analyzing and modeling variations among paintings of the same landscape by different artists.

Spatial error analysis is often carried out with spatial data (locations and values) obtained by remote sensing. Error exists in both the location and the value assigned to each cell. For categorical data, classification (assignment of values) can be supervised (the model is based on measured ground-truth data) or unsupervised. Map accuracy is summarized by a confusion matrix (Friedl and others 2001). Element *i*, *j* of the confusion matrix contains the number of pixels classified into category *i* that were observed to be category *j* in independent ground-truth data. This matrix can be converted to an error matrix containing probabilities of misclassification.

Alternative maps can be generated from a reference map and an error matrix. The category assigned to each map cell in the reference map may be altered in a new realization based on multinomial probabilities taken from the error matrix. This approach does not consider spatial variation in accuracy because the error matrix no longer contains spatial information (Congalton 1988; Steele and others 1998; McGwire and Fisher 2001). Developing Monte Carlo methods for generating landscapes with realistic spatial variation and autocorrelation in error is an active area of research (McGwire and Fisher 2001).

Error Budget Analysis

The ultimate goal of error budget analysis is to reduce uncertainty in those spatial inputs that have the largest influence by more accurate measurement or higher spatial resolution in sampling. Construction of a spatial error budget is similar to spatial sensitivity analysis in that it has a backward focus, highlighting important sources of error. It differs from sensitivity analysis in that the variation among input maps reflects variation introduced by the cartographic process.

Parysow and others (2000) describe error budget analysis as a method of systematically partitioning the contributions of different sources of error via an ANOVA-like table. Parysow and others fit a polynomial regression between the variance of model output and the standard errors of model inputs.

Gertner and others (2002) generated spatial error budgets for erosion (soil loss) by modeling the propagation of error from slope, up-slope contributing area, and model parameters with a variance partitioning method. Error was quantified for each grid cell by comparing detailed ground-truthing measurement of parameters with available soil maps. This budget identified two different measurements that contributed most to the uncertainty in predicted erosion. In areas with flat topography, slope contributed most to uncertainty. In steep areas, up-slope contributing area contributed most to uncertainty.

In the example above, spatial variation in error was represented. Developing an error budget for a particular model and site requires intensive effort, the results of which may not generalize to other sites. However, the example provides a nice illustration of a generalizable result drawn from a site-specific analysis.

Decision Analysis and Risk Assessment

Ecologists are typically interested in predicting the distribution of likely outcomes to ensure that management decisions incorporate uncertainty. Both spatial decision analysis and risk assessment consider spatial uncertainty. Most ecological problems will require a suite of alternative landscapes produced by stochastic simulation. However, probability kriging may be a simpler alternative (Goovaerts 2000) for simple GIS models that do not involve movement of animals or materials. In risk assessment, spatial models have been used to represent heterogeneity in the exposure of animals to toxic chemicals (Clifford and others 1995; Pastorok and others 1996; O'Connor 1996). Spatial uncertainty can influence estimates of ecological risk (Rossi and others 1993), and this may be particularly important in population viability analysis, which seeks to quantify the risk of future extinction for declining populations.

Spatial optimization of ecological models, which can account for spatial uncertainty, is gaining popularity as a management tool. An example of a typical optimization problem is to identify the optimal number and configuration of land parcels to be included in a wildlife reserve, where the objective is to maximize the benefits to a listed population (for example, see Hof and Bevers 1998; Pressey and others 1997). Spatial uncertainty can be incorporated into spatial decision analysis by defining a stochastic objective. For example, one's goal might be to choose areas for contaminant remediation that minimize humans risk of exposure (Massemann and others 1991) or to configure the smallest wildlife reserve with a less than 95% chance of extinction over the next century.

Hypothesis Testing Using Neutral Models

Neutral models play an important role in landscape ecology, where they are used to study theoretical effects of spatial pattern on populations (for example, Gardner and others 1987; With and others 1997; Wiegand and others 1999). Neutral models are used to formulate and test hypotheses about spatial effects in a virtual setting that extracts them from the extreme complexity of the natural world. This is accomplished by creating alternative landscapes with only minimal constraints. In the simplest case, neutral models assign landscape categories to individual grid cells at random, constraining only the overall proportion of each category. The underlying multinomial model for generating alternative categorical landscapes is similar to that used in error analysis, except that they do not represent deviations from a reference map. Other neutral models have been designed to test hypotheses involving contagion or spatial autocorrelation—for example, the modified random clusters method of Saura and Martinez-Millan (2000) and the fractal generation methods of Hargrove and others (2002) and With and King (2001).

In general, neutral models do not attempt to mimic error structure in a cartographic process or preserve properties of a reference landscape. For example, patches are free to be positioned at different locations on the landscape and in different configurations relative to one another. If landscapes produced by neutral models were paintings, they might resemble Picassos.

Future Directions

We envision two directions for future research aimed at improving on current techniques. First, the simulation methods currently used to generate alternative landscapes for spatial uncertainty analysis do not preserve the patch-size distribution of the reference landscape. Generated landscapes differ from the reference landscape in that they tend to be highly fragmented near the boundaries of large patches, and they tend not to have inclusions (small patches) within the interior of large patches. Keitt and others (1997) suggested that overestimation of small patches is a real feature of error in classified imagery. It may therefore be appropriate to retain this feature when conducting error analysis or error budget analysis; however, for uncertainty analysis, the uncertainty near patch boundaries should be a feature of among-map, rather than within-map, variation. That is, boundaries delineating patches within a particular map should be drawn such that the overall patch-size distribution is preserved, but boundaries should differ among maps. This is important because many ecological models are sensitive to fragmentation. Artificial fragmentation might be reduced by designing a heuristic swapping algorithm to bring the patch-size distribution of landscapes using existing methods close to that of the reference landscape (for example, conditional simulation).

Another promising direction for simulating uncertainty in categorical data would be to devise a method that accounts for the hierarchical structure in land-cover classification. An approach that first generates higher-level classes, followed by the subclasses within them, would reflect the fact that two subclasses are less likely to be mistaken for one another if they belong to different superclasses. For example, a hierarchical approach to classifying land cover might first assign areas as either forest or grassland. Next, patches within areas of forest would be classified as either deciduous or coniferous forest, and patches within areas of grassland would be classified as either tallgrass and shortgrass prairie.

Conclusions

Analysis of spatial models and their responses to geographic inputs will no doubt continue to be important. As tools continue to be developed, ecologists will be better equipped to address questions about the influence of uncertainty in spatial input data and model robustness. The six approaches reviewed here differ, sometimes subtly, in the questions that they address. Even when the method for generating spatial variability is the same, the data required to characterize that variability, as well as interpretations of the resulting variation in model output, can be quite different. For example, does variance in spatial data represent natural variation, lack of knowledge about the correct value, known measurement error, or cartographic error? New methods are needed to reveal relationships between ecological model predictions and spatial uncertainty, but careful consideration of the relevant question(s) is a paramount concern.

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