CHAPTER 3

Introduction to Models

Models are essential tools in landscape ecology, as they are in many scientific disciplines. Spatial models, in particular, play a prominent role in evaluating the consequences of landscape heterogeneity for ecological dynamics. Because we refer to models throughout this book—and because we are aware that many students have had little training in modeling or systems ecology—the first part of this chapter presents an elementary set of concepts, terms, and caveats for students to understand what models are, why they are used, and how models are constructed and evaluated. We also define what we mean by a spatial model and indicate the circumstances where spatial models will be most useful. The second part of this chapter introduces neutral landscape models (NLMs) and illustrates the utility of simple models for understanding landscape heterogeneity and testing hypotheses linking pattern with process. There are many excellent texts that address modeling issues in greater depth. Students interested in the modeling process are referred to the recommended readings at the end of the chapter.

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WHAT ARE MODELS AND WHY DO WE USE THEM?

What Is a Model?

A model is an abstract representation of a system or process. Models can be formulated in many different ways. Physical models are material replicas of the object or system under study, but at a reduced size; for example, models of ships and airplanes are developed to better understand the forces that act upon them, and architectural models allow the space and structure of a building to be visualized. Physical models are used in many branches of engineering, but ecologists also build physical models of streams, ponds, and even whole ecosystems (Perez et al. 1991; Macilwain 1996; Petersen et al. 2003) providing an important bridge between experiments in natural systems and theoretical models (Stewart et al. 2013). In contrast, abstract models use symbols rather than physical devices to represent the system being studied. For example, verbal models are constructed out of words, graphical models are pictorial representations, and mathematical models use symbolic notation to define relationships describing the system of interest. We focus here primarily on mathematical models, which have played an important role in ecology since the beginning of the twentieth century (Fig. 3.1).

Why Landscape Ecologists Need Models

George E. P. Box (1979) stated in this oft-repeated quote, "All models are wrong, but some are useful." Models are useful because they allow us to precisely define the problem, articulate the relevant concepts, and then provide a means of analyzing data and communicating results. Most importantly, models allow us to predict the logical outcomes of how we think a system works and then explore the suite of conditions that vary in time and space. Because knowledge is always incomplete, and all data needed to build a model are never available, all models require assumptions to "fill in the blanks." Therefore, most models are used to explore the consequences of our assumptions and hypotheses rather than to represent system structure and dynamics definitively. Models should always be regarded as one of the scientific tools for achieving a specific end rather than as goals unto themselves.

When ecologists are faced with answering questions in a large and complex landscape, it is difficult—sometimes impossible—to sample every possible combination of conditions or to conduct experiments at the ideal spatial and temporal scales. The cost of landscape experiments in time and money is often prohibitive. Some management options have been evaluated using experimental methods (see Bowers et al. 1996; Mabry and Barrett 2002; Haddad et al. 2003; Joshi et al. 2006) while manipulations of microlandscapes have provided valuable insights into the

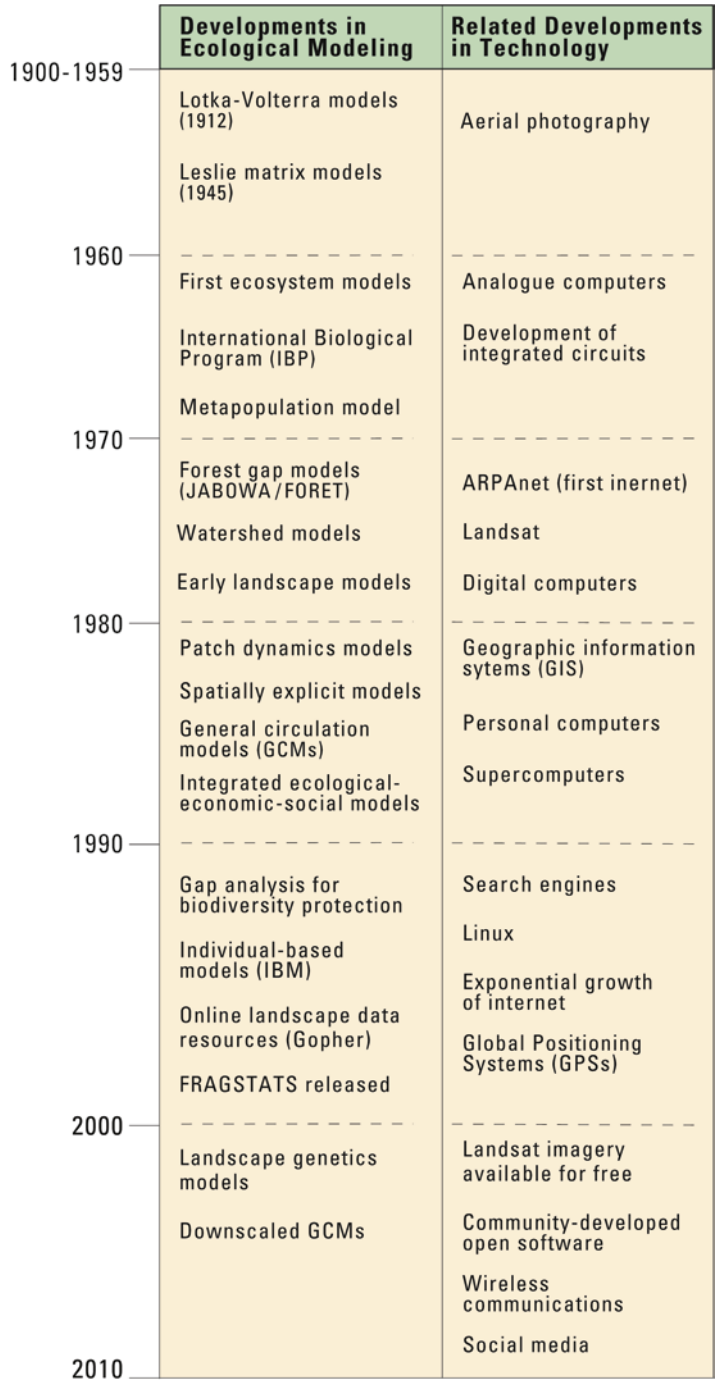

FIGURE 3.1.

Timeline of the development of models in ecology, with important technological and programmatic developments that influenced ecological modeling highlighted. Developments shown are not comprehensive but selected for illustration.

response of insects, small mammals, and some plants to alternative patterns (e.g., Johnson et al. 1992; Glenn and Collins 1993; Imes et al. 1993; Wiens 1995; Wiens et al. 1995; With et al. 1999; Brinkerhoff et al. 2005; Johnson and Haddad 2011). However, extrapolation of these results to large regions remains a perplexing problem (see Chap. 1). Landscape ecologists more commonly use field studies to provide correlative relationships—for example by comparing locations that vary in their degree of land-cover or connectivity of a specific habitat type. Natural disturbances have also been used as "uncontrolled experiments" with their effects expressed in quantitative terms (see Chap. 6). However, all these approaches are limited in the range of conditions, replication, or control. Under these circumstances, the unique features of each landscape or disturbance event may dominate results. Models can be used to relax empirical constraints, providing a means of systematic comparison across a broad range of conditions, but they do so at the cost of increased levels of unknowns and uncertainties.

It has been more than 20 years since Baker (1989a) and Sklar and Costanza (1990) first reviewed landscape models. Focused reviews on specific topics have been published since then (e.g., Turner et al. 1994b; Lambin 1997; Fries et al. 1998; Perry et al. 2004a; Perry and Enright 2006; Keane et al. 2007; Scheller and Mladenoff 2007), but the ambitious task of assembling a comprehensive overview of the broad range of topics and applications found in landscape ecology has not been attempted. An informal survey of papers listed in ISI's Web-of-Science (2011) over the last 10 years (2001–2011) referencing both "landscapes" and "model" for a subset of journals (American Naturalist, Biological Conservation, Conservation Biology, Ecology, Ecological Applications, Ecological Modelling, Landscape Ecology, and Oikos) showed that over 1167 papers have been published within this topic area in the last 10 years. These papers represent a wide diversity of topics and approaches and illustrate the difficulty of placing landscape models into simple, discrete categories necessary for a coherent review. The volume and diversity of approaches are healthy signs of the continued growth of this field of research, but both also make a judicious choice of modeling approach even more challenging. A clear and simple paradigm for addressing this issue has yet to emerge. Consequently, useful modeling strategies and examples for studying pattern and process in changing landscapes will be presented throughout the remainder of this book.

Models may be used to formalize understanding, define unknowns, guide field studies, develop theory, or make predictions. All these objectives will require a careful strategic and tactical approach. *Strategic issues* are those concerned with setting objectives and selecting an approach that minimizes errors; *tactical issues* are those concerned with the details of model construction, testing, and application.

STRATEGY FOR DEVELOPING MODELS

All models are simplifications of real systems (Risch et al. 2005; Hunt et al. 2007). Therefore, the first strategic issue is to define the purpose and scope for the model, the inherent limits of available information and measurements, and to consider the consequences of model error on results.

Define the Problem and Develop a Conceptual Model

A specific statement of model objectives provides the framework for model development and the context within which simulation results must be interpreted. Definition of the problem should be as specific as possible, allowing one to determine the form of the model, the degree of complexity needed, and the spatial and temporal scales at which it will operate (Grant et al. 1997). Once the problem is stated, a conceptual or qualitative model can be developed. The conceptual model identifies system boundaries (the temporal and spatial scales and associated inputs and outputs), the model components (state variables), and the relationships among the state variables. A conceptual model of sufficient detail allows the important variables and parameters (coefficients that control model processes), the system drivers (driving variables, see Table 3.3 in Appendix) and the required inputs and outputs to be defined. The appropriate level of spatial and temporal resolution for the model (i.e., model scale) is a key consideration in a conceptual model (Fig. 3.2). Once formally stated, the model developer should consider the following three issues that affect the adequacy of the approach defined by the conceptual model.

Trade-offs Among Generality, Precision and Realism

Levins (1966) stated that no model can be completely realistic, always precise, and generally applicable (but see Orzack and Sober 1993). Levins's provocative paper stated: "It is … desirable to work with manageable models which maximize generality, realism, and precision [in order to reach the goals] of understanding, predicting, and modifying nature" (Fig. 3.3). Consequently, a strategic approach to model development is one that is cognizant of these trade-offs. Levins used familiar models of population biology to illustrate this problem. We review Levins' list here, providing parallel examples from the recent literature of landscape modeling.

Sacrifice generality to realism and precision. Most models that trade generality for realism and precision produce place-based results. By specifying particular cases (or scenarios), a reduced parameter space may be defined and relevant measurements made. Models that emphasize realism and precision are often closely calibrated so that they closely mimic observed dynamics of the focal landscape.

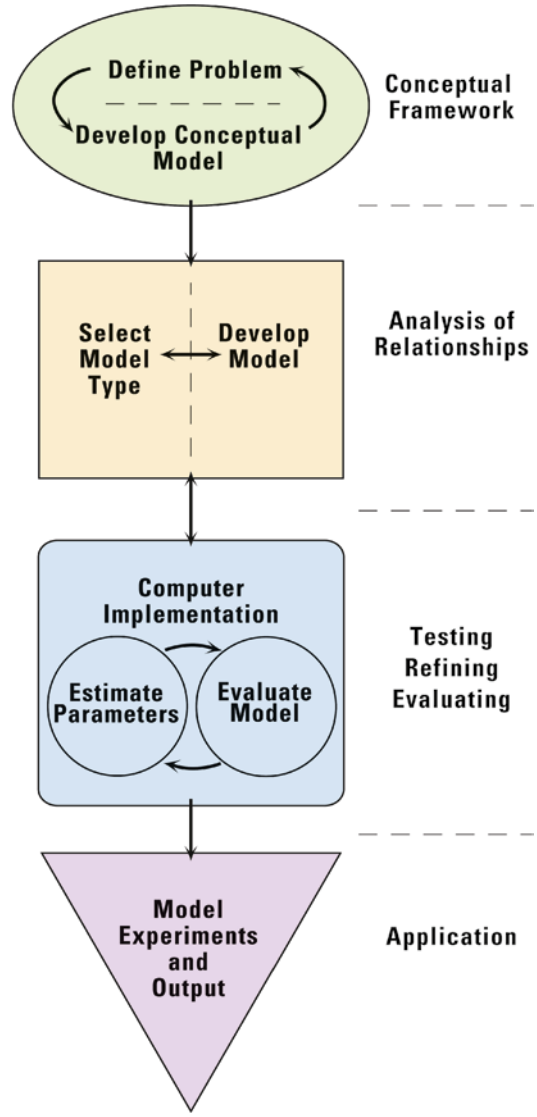

FIGURE 3.2.

Flowchart illustrating the major steps in building a model.

Results may be tested (i.e., confirmed or rejected), but general conclusions across a broad spectrum of landscapes will be limited. Examples of this approach include landscape models that focus on specific locations where precisely measured parameters may be obtained (e.g., Jantz et al. 2004; Ferrari et al. 2009). Iterative application across a suite of conditions (e.g., Scheller et al. 2007; Sturtevant et al. 2009) may be used to introduce stochastic effects and increase generality.

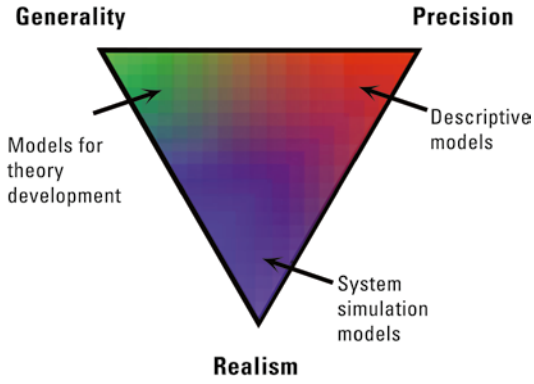

FIGURE 3.3.
Schematic representation of Levins (1966) conceptualization of the trade-offs between a model's generality, precision and realism usually encountered in the development and use of ecological models.

Sacrifice realism to generality and precision. Landscape models often adopt this trade-off and strive for a correct average result rather than a specific prediction of what will happen at a particular time or place on a given landscape. Such models ignore highly detailed interactions and usually employ equations with a reduced parameter set. If the details excluded from the model have a minor effect on the results, or the sum of all ignored details cancel out, then a simple model may be more general and more precise. Examples of this approach include models that propagate disturbance over large areas and long time periods (e.g., Gardner et al. 1999; Keane et al. 2007). Models predicting equilibrium conditions may also sacrifice reality for generality (e.g., Chave and Norden 2007), using this theoretical endpoint as a measure of the effect of changing processes. The simple NLMs presented later in this chapter also exemplify this trade-off.

Sacrifice precision to realism and generality. This trade-off is often adopted when the desired result is qualitative rather than quantitative. Many theoretical models fall into this category, and they make very general predictions that are not directly applicable to a particular place or set of measurements. Examples include GAP models (Scott et al. 1993; Kiester et al. 1996), island biogeography, and neutral theory (Hubbell 2001) and extinction debt (Tilman et al. 1994).

It is the general consensus that Levins' trade-offs are general and may not be easily avoided. The form of the model and quality and quantity of available data define the domain over which model results may be reliably used for understanding, prediction, and/or management. The comparison of alternative models that differ in their assumptions and simplifications (see Gardner et al. 1999; Keane et al. 2007; Yang et al. 2008 for examples from the fire literature) are the best means for checking the limits and broadening the scope of conclusions drawn from a single model (Levins 1966).

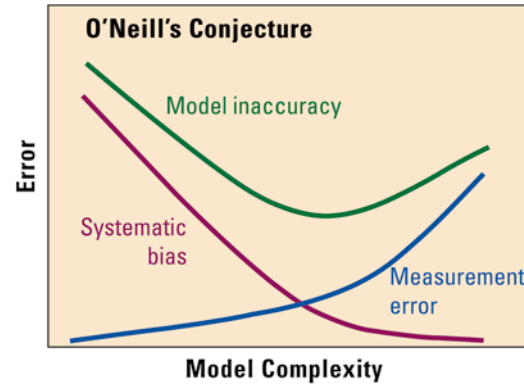

FIGURE 3.4.
A conceptual representation of the conjecture by O'Neill (1973) that simple models may have significant errors due to absence of important processes (*red line*) while complex models have error associated with unmeasured (or unmeasurable) parameters and processes (*blue line*). The conjecture is that there is an optimum level of model complexity that minimizes total error (*green line*).

TRADE-OFFS BETWEEN MODEL COMPLEXITY AND MODEL ERROR

It has often been assumed that complex models are more accurate and simple models are more general because simple models may lack essential details, causing systematic bias in predictions—but adding detail to a model does not guarantee an increase in reliability unless the added processes are essential, well understood, and reliably estimated. The potential trade-off between complexity and error was first discussed by O'Neill (1973) who speculated that for any given problem and level of knowledge there may be an optimal level of model complexity (Fig. 3.4). Strayer et al. (2003a) also present a thoughtful discussion of the level of detail to include in models of heterogeneous systems.

Landscape models are often developed with the implicit assumption that the results will only be useful if they are completely realistic (i.e., highly detailed). Because landscapes are diverse and complex, a fully realistic model will be complex with significant data requirements for estimating all model parameters. A counterstrategy for reducing complexity while also improving model reliability is nearly always necessary (Beven 2002). The development of hierarchy theory (Allen and Starr 1982; O'Neill 1989) has shown that the aggregation of similar components into a single unit (i.e., numerous species into fewer functional types; Lavorel and Garnier 2002) reduces the number of parameters that must be estimated and may, therefore, substantially improve results. One may also take advantage of "the law of averages" by setting the realistic temporal and spatial scales for model resolution: If final results can be expressed in hectares and years, then the average values of fine-grained values (e.g., hours to days, meters to hectares) can be used to produce more precise results (Peters et al. 2004a).

In all cases, it is important to evaluate model error. The first step should be to compare model output with available data graphically, testing whether results fall within the confidence limits of empirical results. These comparisons should specifically focus on the model objectives: If the purpose of the model was to

assess the direction of change (i.e., an increase in urbanization) then only the direction of change needs to be assessed; if the purpose was to locate areas where change has occurred (a more difficult task), then spatial statistics may be required to verify model response. The strategic issue is that model-data comparisons are most meaningful when objectives have been clearly and precisely defined. More formal methods of sensitivity and error analysis (Gardner et al. 1981; Jager and King 2004) are useful for identifying model components and parameters that most contribute to model errors.

When Should Models Be Spatially Explicit?

Most generally, a model should be spatially explicit when the inputs, the outputs, or the processes required by the modeling objectives and conceptual formulation vary spatially (Strayer et al. 2003a). If spatial pattern is a driving variable—that is, the model needs to predict the consequences of alternative configurations of *input* conditions or forcing variables—then a spatially explicit model is warranted. Examples include models of the effect of habitat arrangement (not simply amount) on population dynamics; the effect of arrangements of riparian buffer habitats on nutrient loading to surface waters; of the effects of alternative distributions of resources on the movement or foraging patterns of animals; and the positive (or negative) effects of pathways or corridors for animal dispersal (Lookingbill et al. 2010; Sullivan et al. 2011). A spatially explicit model is also warranted if predicting changes in spatial pattern is required—that is, the model *output* must be spatial. Examples include models that predict the distribution and abundance of animals in a landscape at a future point in time; future spatial patterns of habitat in response to animal movements and foraging patterns; and land-cover patterns that respond to alternative land-use activities or management strategies. Lastly, a spatial model is needed when the *processes* themselves interact within a local neighborhood to generate patterns, such as when competition between neighboring organisms generates distribution patterns, or when the process itself has a spatially explicit response, such as the actual flow path of water or nutrients, or the actual migration or dispersal pathway of an organism (Fig. 3.5). Thus, the model goals determine whether a spatial model is needed.

A fully spatially explicit model will have explicit spatial locations for all variables and inputs. Nonspatial or spatially implicit models may produce maps as output, making these approaches appear to be spatially explicit when, in fact, they are not. For instance, maps produced by a table look-up process (e.g., nutrient dynamics; Burke et al. 1991; 1999) do not consider location-specific effects and, hence, are spatially implicit predictions. The complexity required to develop and test a spatially explicit model is significantly greater than a spatially implicit model, making spatially explicit approaches only desirable when local effects are known to dominate results measured at landscape scales (Peters et al. 2004a).

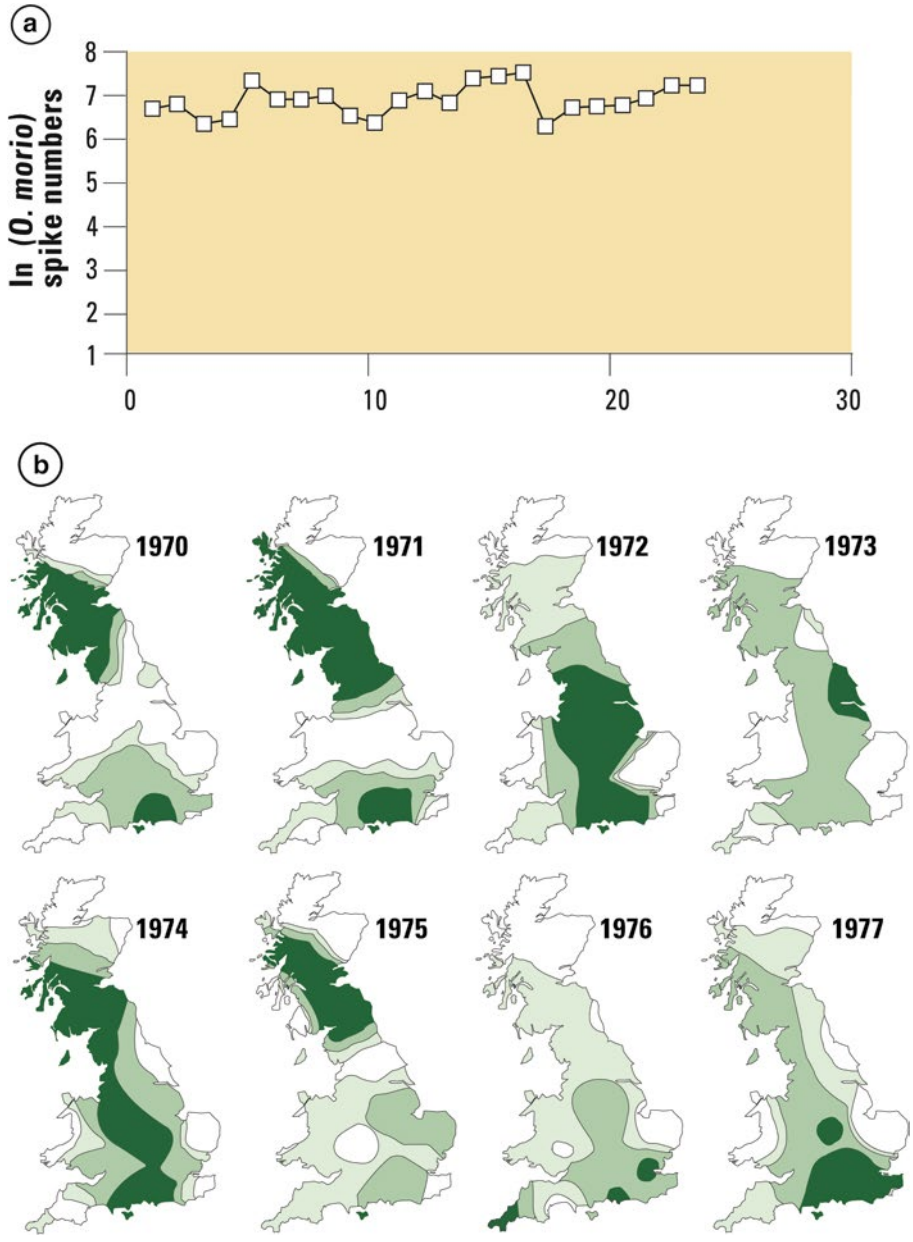

FIGURE 3.5.

Comparison of temporal vs. temporal + spatial population dynamics. (**a**) Shows the change through time in a population of the green-winged orchid, *Orchis morio*, at one locality. In this case, changes are temporal only. (**b**) Shows the change in the spatial distribution in Great Britain of elder aphid (*Aphis sambuci*) between 1970 and 1977, where the density of the shading represents local population density. This illustrates changes through both space and time; predicting such dynamics would require a spatial model.

ADAPTED FROM GILLMAN AND HAILS (1997.)

To summarize the strategic issues: One should apply the law of parsimony when developing a model by precisely defining the models purpose, developing the simplest conceptual model possible, adding complexity only when it is necessary and supported by data, use a hierarchical approach to define model variables and processes; and planning on revisiting these strategic steps when model errors indicate the need for improvement.

TACTICS FOR MAKING THE MODEL WORK

The tactical steps for developing a working model are derived from the systems ecology approach to ecological modeling (Fig. 3.2) developed primarily by engineers for characterizing the dynamics of complex physical systems. The success of the systems approach had a strong influence in the early development of landscape ecology in both Europe (Opdam and Schotman 1987; Naveh and Lieberman 1990; Zonneveld 1995) and North America (Johnson et al. 1981; Gardner et al. 1987; Opdam 1987; Sklar and Costanza 1990) and continues to be the dominant paradigm for model development today (Wu and David 2002; Costanza and Voinov 2004; Lookingbill et al. 2008). The basic principles of the systems approach go back to the philosophy of holism formulated by Smuts (1926) and developed more rigorously by Von Bertalanffy (1968, 1969). Numerous works written more than 30 years ago describing the principles of general systems theory and their application to ecological systems are still relevant today (e.g., Watt 1968; Van Dyne 1969; Patten 1971). Here, we draw from the sequence of modeling steps outlined in Kitching's (1983) text on systems ecology. We also provide a reference table for terms commonly used in modeling (see Appendix, Table 3.3). Readers may wish to refer to Swartzman and Kaluzny (1987) and Haefner (2005) for excellent introductions to the tasks associated with model development.

Once the conceptual model has been developed, a wide variety of mathematical formulations may be used to transform the "concept" into an operational model. A wealth of model types has been used in landscape ecology (as discussed throughout the book), but it is beyond our scope to review and describe these techniques here.

The programming language or simulation software for implementing a model is usually selected based on local resources, experience and expertise. Often, a decision must be made between whether to program a new model or to use an existing model. For example, a number of existing models, such as the forest landscape simulator LANDIS (Mladenoff and He 1999; Sturtevant et al. 2009) and the ecosystem model Century (Parton et al. 1992; Gilmanov et al. 1997), have been used widely. The use of an existing model eliminates the need for massive amounts of programming and analysis, but the existing structure (and the developer's strategic decisions that led to this structure) may constrain the questions that a new user desires to

ask. Furthermore, it is difficult for new users to become deeply familiar with the workings of complex models. Regardless of the software decision, all model implementations require systematic checking for the adequacy of relationships represented and the accuracy of methods employed. This phase, often referred to as *model verification*, may require more time and energy than any other step represented in Fig. 3.2. An important adjunct to this stage is the production of adequate *model documentation* and the ultimate public availability of the final source code.

The specification of values for the model parameters, model inputs, and initial values of the state variables within the model (see Appendix, Table 3.3) are typically estimated from data or obtained from published values. The process of parameter estimation differs from model *calibration*—the iterative adjustment of parameters to improve model fit to measured output variables. Calibration may be required when direct estimates of parameters are not available but net changes in system dynamics have been measured, providing the objective criteria for parameter adjustments. The errors associated with calibrated values are unknown unless a second data set is available to test the adequacy of calibrated (but unmeasured) parameters.

Once operational, a model must be evaluated for its utility. Does model behavior agree with empirical observations? Are the underlying assumptions reasonable? Do those assumptions result in realistic behavior? Objective comparison of model results with data, sometimes referred to as *model validation* (Rykiel 1996) provides the necessary confidence in predictions to make models useful and define the conditions over which the model will be most reliable. Although the term "validation" continues to be widely used (e.g., Scheller and Mladenoff 2004; Nuttle and Haefner 2007), because this term connotes "truthfulness," its unqualified use can be confusing and is generally discouraged (see Mankin et al. 1975 for a thoughtful discussion of validation issues).

When the steps illustrated in Fig. 3.2 have been completed, the ecologist has a tool that may be used to conduct experiments and predict outcomes. The verification of predictions across a range of conditions confirms or rejects the model hypotheses and assumptions, providing new insights into system behavior. As confidence builds, model applications may move from hypothesis testing to more serious applications such as conservation planning and planning. Care must be taken at each stage of model development to assure the accuracy and adequacy of the model. In spite of the availability of software that eases the process of model development, there is always the danger that insufficient attention to each step of development will produce unreliable results. Because no amount of care will guarantee that a model is a perfect representation of the ecological system it was intended to mimic, the comparison of results with alternative models (Levins 1966) continues to be sage advice for the careful scientist (Box 3.1).

Box 3.1
CAVEATS IN THE USE OF MODELS

Wise application of modeling tools recognizes the pitfalls and problems of model development and interpretation. We review here, in concise form, what we consider to be the most important caveats for modeling in landscape ecology:

1. *Know thy model*. The performance of each model is the logical consequence of the hypotheses and assumptions upon which that model is based. Alternative assumptions regarding systems behavior might be equally viable, but produce dramatically different results. Comparison among alternative model formulations is extremely desirable, and should be attempted where possible (see Kittel et al. 1996; Pan et al. 1998; Miranda et al. 2009 for examples).
2. *Errors propagate*. Small errors in sensitive parameters can lead to large errors in outputs (Rose et al. 1991). Techniques for the analysis of effects of parameter errors are available (Metzgar et al. 1998) and should always be employed before predictions are made. Assessment of errors of spatially explicit models remains a challenge (Khan et al. 2006; Minor et al. 2008), largely because of the added complexity of evaluating qualitative and quantitative spatial predictions.
3. *All models are simplifications of reality*. This is not a casual philosophical statement! It simply means that no single model will ever be a completely adequate description of reality. Therefore, the goal of model studies should be to define the applications for which a given model provides reliable and useful results. New applications of old models are not released from this requirement.
4. *There are never enough data*. The incomplete nature of data often requires parameter values to be estimated from a diversity of sources. Inconsistency in the methods of data collection and parameter estimation may result in model biases that are difficult to identify. Gaps in empirical information that do not allow adequate estimation of key parameters are often the greatest source of uncertainty in model predictions.
5. *High tech methods do not guarantee a "good" model*. Technologically advanced methodologies, including the availability of higher level programming languages that facilitate model coding, do not assure the accuracy or reliability of results. When developing or interpreting models, it is critical for the user to understand fully the structure of the model, the assumptions that went into its development and the constraints (such as spatial or temporal scales) on its appropriate use.
6. *Keep an open mind*. There is no single paradigm for spatial modeling of landscapes. Model development and testing requires a broad perspective of landscape ecology and systems analysis techniques.

NEUTRAL LANDSCAPE MODELS

As development of landscape ecology accelerated and spatial heterogeneity received increased attention, new models that could represent explicit spatial patterns and allow different aspects of pattern to be varied were needed. Also needed was a

yardstick against which the potential influence of different spatial patterns could be evaluated. NLMs were developed in the late 1980s to fill this gap (Gardner et al. 1987).

Neutral Models in Ecology

The sequential development and testing of hypotheses is essential for progress in science (Platt 1964; Quinn and Dunham 1983). The simplest hypothesis that one should first construct is the null hypothesis of no effect (Fisher 1935)—i.e., landscape processes are not responsible for the observed pattern. A properly formed null hypothesis provides the required reference point against which alternatives may be contrasted. Because landscape analysis involves relating ecological patterns to complex histories of natural forces and events (e.g., climate, terrain, soils, water availability, biota, natural disturbances, etc.) as well as the consequences of human alterations (e.g., urbanization, agriculture, forestry management, etc.; see Chap. 2), the specification of appropriate null hypotheses is a challenge. Consequently, observational and correlational approaches tend to dominate over the experimentation and hypothesis testing more typical of sciences studying simpler systems (see Strong 1980 for further discussion). The difficulty with corroborative studies is that the uniqueness of each landscape (Phillips 2007) limits the use of experimental designs and the possibility of replicate measures. When treatment effects (i.e., processes dependent change in landscapes) are tested without true replication, the validity of these comparisons is often suspect (Hurlbert 1984; Hargrove and Pickering 1992).

Neutral models, which simulate dynamics *in the absence of specific processes*, have been widely used in ecology for testing the corresponding null hypothesis of statistics (the terms "null" and "neutral" are distinguished here, but are often used interchangeably). For instance, Cole (1951, 1954) used random numbers to construct cycles similar to those observed in natural populations; Simberloff (1974) used island biogeographic theory to examine community patterns; Istock and Scheiner (1987) used random landscapes to test patterns of species diversity; and Nitecki and Hoffman (1987) produced an edited volume on the subject. Other examples include niche shifts in *Anolis* communities (Haefner 1988a, b); community formation in fishes (Jackson et al. 1992); plant migration rates (Higgins and Richardson 1999); hemlock regeneration and deer browsing (Mladenoff and Stearns 1993); bird assemblages in fragmented landscapes (Sisk et al. 1997); tests of Holling's hypothesis of discontinuities in landscape pattern causing clumps and gaps in the distribution of body sizes within animal communities (Siemann and Brown 1999); and the continued investigations of the formation of structure in natural communities (Wilson 1995). Perhaps the most notable use of neutral models has been Hubble's provocative theory of biodiversity (Hubbell 2001, 2006) which continues to be widely discussed in ecology (e.g., Lowe and McPeek 2014; Warren 2012).

A simple standard for landscape pattern—and thus the basis for testing differences between landscapes—is a random map (Fig. 3.6) which lacks all factors that might organize or structure pattern (Gardner et al. 1987; Gardner and Urban 2007). Tests of observed landscapes against replicate random maps reveal the magnitude and significance of differences due to the structure of actual landscapes. Therefore, random maps are *neutral landscape models* (*NLM*) against which effects of processes that structure actual landscapes may be tested. Studies of NLMs have shown that surprisingly rich patterns can be generated by random processes alone—and their use has shown that actual landscapes may not always be measurably different from these random patterns (Gardner et al. 1993; Li et al. 2004).

With and King (1997) reviewed the use of NLMs and separated their uses into two categories: (1) to determine the extent to which structural properties of landscapes (e.g., patch size and shape, amount of edge, connectivity, autocorrelation) deviate from some theoretical spatial distribution, and (2) to predict how ecological processes, such as animal movement, seed dispersal, gene flow, or fire spread, are affected by landscape pattern. A third important use has also emerged: to evaluate new methods of numerical analysis, including the development and testing of landscape metrics (Li et al. 2005; Gardner and Urban 2007; Wang and Malanson 2007). We next provide a brief overview of the methods behind the generation of random maps and uses in landscape studies.

Random Maps: The Simplest Neutral Model

The simplest method of generating a map is to randomly locate sites within a 2-dimensional grid. This may be efficiently accomplished by using a uniform random number generator (URN) found within most computer languages and mathematical software tools. The URN function typically produces numbers that vary randomly over the interval of 0.0–1.0. The generation of a random map with a single land-cover type is accomplished in two steps: (1) An array of m columns and n rows with $m \cdot n$ elements (sites) is constructed; (2) For each map site a single URN is generated: If the URN is less than a prespecified probability value, p, the site is set to 1; if not, the site is set to 0. For instance, if $p = 0.4$ the grid site will be set to 1 if URN ≤ 0.4, or to 0 if the URN is >0.4. For maps of sufficient size (m and n each >250) the proportion of sites set to 1 will be very close to the value of p while the number of sites set to 0 will be approximately $1 - p$ (e.g., $1.0 - 0.4 = 0.6$). The total number of matrix elements (i.e., grid sites or cells) occupied by the habitat (land-cover) type of interest will be approximately equal to $p \cdot m \cdot n$ while the number of sites of "nonhabitat" will equal $(1 - p) \cdot m \cdot n$.

As the grid is filled with 0's and 1's, *clusters*, or *patches*, of the land-cover type will form (Fig. 3.6). Clusters are identified with rules defining contiguous sites. The simplest rule defines clusters as groups of sites of the same land-cover type with at

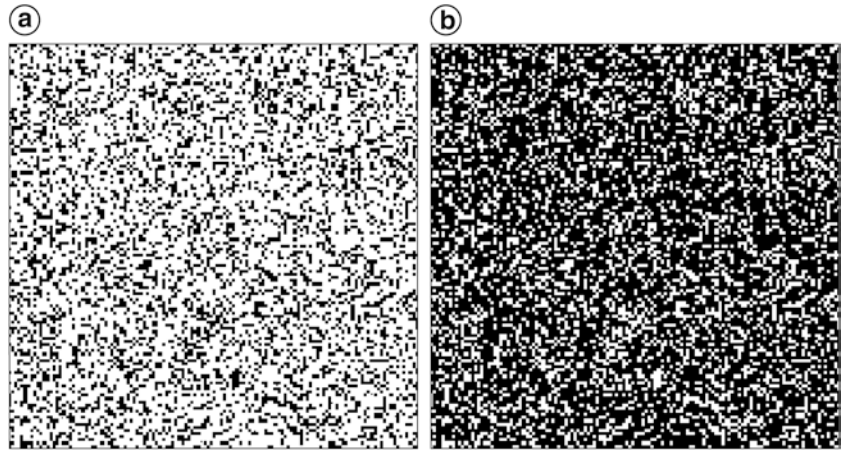

FIGURE 3.6.
A random map (m, the number of rows and columns equals 64) generated with the probability, p, that grid cells contain the land-cover type of interest. The black cells represent (**a**) 0.3 and (**b**) 0.7 of the landscape. The user may determine, by hand, that the largest cluster of the black cover type percolates in (**b**).

least one horizontal or vertical (but not diagonal) edge in common. This rule for cluster (patch) identification is usually referred to as the "four-neighbor" or "nearest-neighbor" rule, and it is a conservative estimate of habitat adjacency (also see discussion in Chap. 4 and Fig. 4.9). When a series of maps is generated with increasing values of p, the number of patches increases over the interval $0.0 < p < 0.3$; as p continues to increase small patches coalesce into larger ones and the total number of patches declines (Gardner et al. 1987; Gardner 2011; Fig. 3.7a). The amount of edge on the map is also affected by p, with the maximum amount of edge occurring when $p = 0.5$ (Gardner et al. 1987; Fig. 3.7b).

The total extent of the map (i.e., the value of m and n representing the number of rows and columns, respectively) also affects measures of pattern. Smaller maps (i.e., lower values of m and n) will cause patches to be truncated by the map boundary. This effect is most noticeable when p is >0.6 (Gardner et al. 1987). Table 3.1 illustrates the truncation effect for a variety of map types and sizes ($m = n = 64$, 128, 256). For random maps with $p < 0.5$ the size of clusters in smaller maps is approximately 80 % of the size of clusters in the larger maps—indicating that truncation effects due to map size result in systematic underestimation of patch size. The truncation effect becomes more noticeable as the value of p increases. At $p = 0.5$ clusters are approximately 70 % that of the next largest map size; and at $p = 0.7$ and 0.9 (Table 3.2) cluster sizes of the smaller maps are approximately 25 % the size of the next largest map!

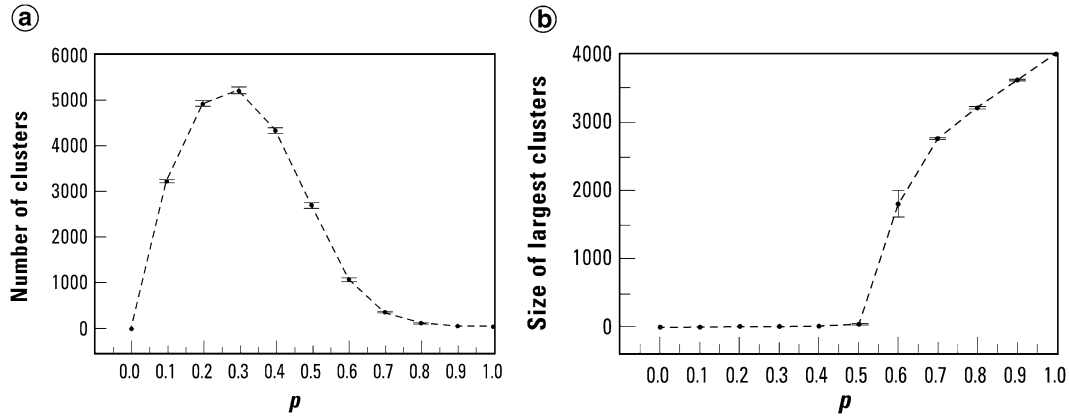

Figure 3.7.

(**a**) The number of clusters and (**b**) size the largest cluster for random maps that vary in the probability, p, that a grid cell contains the habitat type of interest. Plotted from data reported in Tables 1 and 2 of Gardner et al. (1987) for maps with 200 rows and columns.

Table 3.1.

Percolation thresholds for 2-dimensional maps with different neighborhood rules.

Lattice geometry	Neighboring sites	p_c
Square	4	0.59275
	8	0.40725
	12	0.292
	24	0.168
	40	0.098
	60	0.066
Triangular	**6**	0.5
	12	0.295
	18	0.225
Honeycomb	3	0.6962
	12	0.3

Table adapted from Plotnick and Gardner (1993)

TABLE 3.2.
AVERAGE NUMBER OF SITES COMPOSING A CLUSTER (I.E., PATCH SIZE IN GRID CELL UNITS) AS A FUNCTION OF MAP SIZE (NUMBER OF ROWS AND COLUMNS) AND p, THE FRACTION OF SITES OCCUPIED.

Map size	Map type[a]	p 0.1	0.3	0.5	0.7	0.9
64×64	Random	5.2	21.4	167.0	2780	3680
	$H=0.2$	124	574	1360.0	2620	3660
	$H=0.8$	216	908	1760.0	2760	3670
128×128	Random	6.3	27.4	255.0	11,200	14,700
	$H=0.2$	482	2140	5600	10,500	14,600
	$H=0.8$	1110	3720	7160	11,100	14,700
256×256	Random	7.6	33.4	350	44,900	58,900
	$H=0.2$	1760	9190	21,800	42,200	5860
	$H=0.8$	4450	15,000	28,400	44,300	58,800

AVERAGES BASED ON 100 INDEPENDENTLY GENERATED MAPS (MAPS WERE GENERATED AND ANALYZED USING RULE (GARDNER 1999). ALTHOUGH THE DOCUMENTATION OF RULE IS RECENT, THIS IS THE SAME PROGRAM ORIGINALLY USED TO GENERATE NEUTRAL MODELS (GARDNER ET AL. 1987)).

[a]MAP TYPES ARE: RANDOM = SIMPLE RANDOM MAP; $H=0.2$, A MULTIFRACTAL MAP WITH THE VALUE OF H OF 0.2; $H=0.8$, A MULTIFRACTAL MAP WITH THE VALUE OF $H=0.8$. SEE TEXT FOR DISCUSSION OF MULTIFRACTAL MAPS.

Why does the truncation effect depend on the value of p? Are there general rules of pattern formation in simple random maps that provide insight into the analysis of landscape patterns? It is these types of question that have been a primary focus of percolation theory (Stauffer and Aharony 1992) from which the first NLM were derived (Gardner et al. 1987). A central concept to emerge from percolation theory was the strong dependency of pattern on the choice of value for p and the existence of a *critical threshold* where small changes in p would result in sudden changes in pattern. The existence of a critical threshold (symbolically defined as p_c) equals 0.59275 when maps are sufficiently large and clusters are defined by the nearest-neighbor rule (Table 3.1). The reason for this threshold is that above p_c occupied sites are so abundant that nearly all sites contact neighbors along one of their four edges causing a single cluster to extend, or "percolate," from one edge of the map to the other. In our previous example (Table 3.2), maps with values of $p > 0.59275$ *will always* result in truncation of the largest cluster on the map. If $p > p_c$ the percolating cluster will continue to increase in size as map dimensions increase. This

truncation effect leads percolation theorists to develop the concept of the *infinite cluster*—a cluster that will continue to grow as map dimensions are increased. Thus, there is no finite map dimensions that will fully contain the cluster when $p > p_c$. Although no landscape will have infinite bounds, the practical implication of the "infinite cluster" is that a map 1/2 the size of another will have an average cluster size that is only 1/4 as large.

The general dependence of cluster size on p, and the existence of a critical threshold where small changes in p produce sudden changes in cluster sizes, has important implications for both material systems (the original focus of percolation theory) and pattern and process relationships within landscapes. The effect of a critical threshold may be easier to visualize by imagining the process of habitat loss and fragmentation. If a landscape exists with $p = 1.0$—that is a landscape entirely composed of a single land-cover type, say forest—then a gradual reduction in p on a random map is equivalent to poking holes in the forest. As the value of p slowly declines (i.e., the forested lands are randomly converted to other land-cover types) from 1.0 to 0.90, isolated gaps in the continuous forested landscape occur with little effect on the overall landscape pattern. As random clearing continues (i.e., values of p further decline from 0.9 to 0.6), forest gaps become more frequent and larger, the amount of edge increases, but never-the-less a single large forest cluster still dominates the landscape. It is still possible for organisms restricted to forests to move across the landscape—that is, the single large cluster still percolates. However, the single large cluster becomes more and more dendritic as the critical threshold is approached. It is now possible to find numerous sites that would disconnect the percolating cluster if they were converted from forest. The sudden disconnectance of the forest habitat resulting from the disturbance of a single site is most likely to occur when $p = p_c$.

The numerical value of a critical threshold depends on the neighborhood rule used to identify clusters (Plotnick and Gardner 1993). When an "eight-neighbor" rule is used to identify clusters, the value of p_c drops to 0.40725 (Table 3.1). Because diagonal neighbors are now also counted as cluster members, potential neighbors are further away from each other. With the inclusion of more distant neighbors within the cluster, large dendritic structures form and "percolate" across the grid at lower values of p. The ecological justification for the analysis of landscape pattern with different neighborhood rules should be process dependent. For instance, if the spread of a disturbance is slow and via immediate contact (e.g., some fungal diseases), then the nearest-neighbor rule might be applied and a critical threshold of the spread of the fungus would occur at $p = 0.59275$. However, short distance dispersal of large seeds might cover a neighborhood of considerable area, resulting in a revised definition of connectance among neighboring sites. It may also be necessary to change the neighborhood rule if the resolution of the map were to change. For instance, a four-neighbor rule applied to maps with 90-m grid cells might be

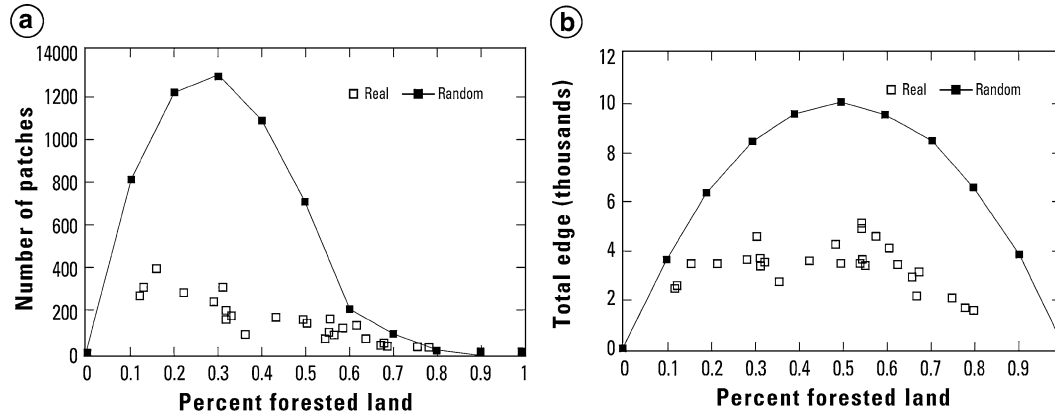

FIGURE 3.8.

Comparison of (**a**) the number of clusters and (**b**) total number of edges for random and actual landscapes. ADAPTED FROM GARDNER ET AL. (1992B).

changed to a 21-neighbor rule if map resolution were increased to 30 m (other alternatives exist and may be explored in the lab exercises associated with this chapter). The value of the critical threshold has also been shown to vary with map geometry (Table 3.1) primarily because different map geometries have different number of neighbors (e.g., a triangular grid has three neighbors associated with each site while a honeycomb grid would have eight neighbors). Even though the value of the threshold may change, the general response of the system is similar no matter what rule is applied.

One of the initial misunderstandings in the use of random maps as NLMs was the idea that NLMs were intended to represent actual landscape patterns. That was never the case! *NLMs do not represent actual landscapes, but provide the standard against which actual landscapes may be compared*. The NLMs control for the amount of a land-cover type, allowing consequences of particular spatial patterns to be evaluated against the random pattern given comparable habitat abundance. The level and kinds of deviation in spatial pattern compared to random expectations may also help elucidate factors that generate patterns. Thus, it is valid to compare NLMs with actual landscapes—that is, compare patterns generated at random with patterns structured by landscape processes. For example, aerial photographs for nine counties in Georgia taken at three different times and representing different physiographic regions (Turner and Ruscher 1988) were used to develop 27 landscape maps. The number of clusters and total edge of forested areas were compared to NLMs (Gardner et al. 1992; Fig. 3.8). A number of points illustrated by this comparison have been subsequently confirmed by analysis of data from other areas (Gardner et al. 1993). The key points are:

1. It is trivially true that patterns of random and real landscapes are identical when p is equal to either 0.0 or 1.0. It is important to remember that the nearer the value of p is to these limits the more similar random and real landscapes become.
2. The total number of clusters of actual landscapes and NLMs is greatest when p is within the range of 0.1–0.3. Over the range of $p = 0.1$–0.5 the total number of clusters in actual landscapes is noticeably less than that of NLMs.
3. In actual landscapes and NLMs the total amount of edge is at a maximum near $p = 0.5$, but like the cluster numbers, the amount of edge in actual landscapes is much less than in random ones.
4. The degree of connectivity (as measured by the presence of a single cluster spanning the map) was equivalent to the NLMs in 25 of 27 actual landscapes. The two landscapes which differed from NLMs either percolated at $p = 0.43$ or failed to percolate at $p = 0.68$. The cause of this deviation was due to the interaction of topography (ridge and valleys) and the process of human land-use conversion.

The qualitative trends in pattern in actual landscapes and NLMs are similar although the magnitude (e.g., number of clusters, amount of edge) is less and the variability greater in actual landscapes. These differences are produced by a complex suite of factors that organize patterns on actual landscapes (Chap. 2).

An important and very practical application of NLMs has been their use to test the performance of different landscape metrics (Li et al. 2005; Gardner and Urban 2007; Wang and Malanson 2007) across a range of conditions (i.e., number of habitat types, map sizes, values of p). The evaluation of spatial indices by NLMs before they are applied to actual landscapes, and the systematic comparison among similar landscape indices, provides important information on the reliability of different metrics to identify unique patterns on actual landscapes (Gardner and O'Neill 1990; Gustafson and Parker 1992; Gardner and Urban 2007; Nesslage et al. 2007). We revisit this topic in Chap. 4, but several lessons from these studies are worth highlighting here. The first is that the value of p (i.e., the amount of any land-cover type of interest) affects the value of nearly all landscape metrics. Indeed p often enters directly into the calculation of the metric itself (e.g., diversity, contagion) or indirectly as an indication of the amount of habitat found on the map. As p increases, the number of possible arrangements of land-cover decreases. Obviously, differences in landscape pattern as a result of differences in p are not surprising. But, the key point is that interpreting the patterns or relating them to processes must first account for the value of p! The second caveat is that the critical threshold causes a transition from many small to fewer large clusters on the map. Therefore, large differences in landscape metrics should be expected above and below this critical threshold. It is questionable whether metrics insensitive to this transition will provide useful insight into

landscape pattern and process. Finally, it is quite clear that the introduction of new indices without prior testing by a series of neutral models should be regarded as a serious omission.

Correlated Patterns from Fractal Maps

Landscapes composed of multiple habitat or land-cover types may require a more complex neutral model to characterize these patterns. Often the arrangement of multiple land-cover types is directly linked to the topography of the region; wetlands and riparian forests are usually associated with rivers and floodplains and found at lower elevations, whereas drier conditions and habitats occur along ridge tops. Conditions between these extremes are intermediate in elevation and usually intermediate in soil moisture and temperature levels. Because habitat characteristics (land-cover types) vary with these elevational gradients, many landscapes with multiple cover types are characterized by a strong autocorrelation between habitat types. Methods that can generate patterns of continuous change would provide a useful neutral model for landscapes with multiple land-cover types.

One method for representing continuous, autocorrelated variation of patterns is the generation of maps via fractional Brownian motion. A fractal Brownian motion in one dimension is produced by creating a series of steps, X_t, whose distance from the previous step $(X_{t+1} - X_t)$ is randomly determined from a Gaussian distribution. A 3-dimensional map may be produced by allowing steps to occur in both the X and Y directions with the random displacements recorded as elevation (the Z direction). The midpoint displacement method (MPDM) for creating fractal surfaces has been extensively used to model 3-dimensional patterns (Barnsley et al. 1988). The "fractal" of fractional Brownian motion is controlled by two parameters: The variance of displacement of points, σ^2 (usually set to 1.0), and H, which controls the correlation between successive steps (Saupe 1988; Plotnick and Prestegaard 1993). Because the successive displacement of points results in an expected difference between any two points equal to $(E[X_1 - (X_1 - d)] \propto d^{\mathrm{H}}$ (Plotnick and Prestegaard 1993), the difference between two points will be proportional to the square of the distance, d, and the correlation, $C(d)$, between the points $[C(d) = 2^{2\mathrm{H}-1} - 1]$ (Mandelbrot 1983; Feder 1988). The fractal dimension, D, of maps generated by the MPDM is equal to $\mathrm{D} = 3.0 - H$ (Saupe 1988). When $H = 0.5$, successive displacements in the Brownian walk are not correlated; when $H < 0.5$, successive displacements are negatively correlated and maps appear to have a very rough surface; and when $H > 0.5$ steps are positively correlated and the maps have a smooth surface (Fig. 3.9). Habitat maps may be generated from the continuous numbers produced by the MPDM by scaling the real numbers and assigning ordinal values to each grid square proportional to the fraction of the map, p_i, occupied by each habitat type (Gardner 1999, 2011). This process of generating a neutral

model with fractal maps is summarized in three steps: (1) generation of a topographic map with roughness controlled by H; (2) slicing the topography into contours with the area of each contour equal to the proportion of the map occupied by that habitat type; and (3) assigning ordinal habitat (land-cover) values to sites within each contour.

The realistic nature of the fractal maps is the direct result of the autocorrelated process of map generation (Fig. 3.9) which results in realistic associations between habitat types (i.e., riparian forests will not be found along ridge tops). Although the patterns are constrained by this autocorrelation resulting in frequency distributions of cluster sizes that differ from those of simple random maps, the map patterns produced by fractal methods are still random. The creation of multiple maps with the same set of parameters (map size, H, number of habitat types and the value of p for each habitat) produces dramatically different patterns. However, successive habitat types will always be associated with each other. The positive autocorrelation of maps with high values of H creates larger average cluster sizes than maps with smaller values of H when $p < p_c$ (Table 3.2). Above the critical threshold average cluster sizes are similar among all map types.

The generation of spatial patterns with fractal maps has had a number of applications. Fractal landscapes have been used to represent the degree of spatial dependence of actual landscapes (Milne 1991a, b; Palmer 1992); the effect of landscape fragmentation on population and community dynamics (With et al. 1997; With 2002; With and King 2004); the invasive spread of exotics (Lavorel and Chesson 1995; With 2002, 2004); and landscape disturbances (McKenzie et al. 2006; Wimberly 2006). In most of these examples the effect of "structure" on habitat arrangement was quantified by comparison of fractal maps with simple (nonstructured) random maps. For instance, the objective of With et al. (1997) was to examine how landscape structure affected the patterns of population dispersion of mobile organisms. Variation in landscape structure was created by generating maps that differed in the number and proportion of habitat types and the methods used to generate the spatial patterns. Simple random maps created pattern without an underlying structure, while fractal maps with different values of H created differently structured maps. The results showed that landscape structure had a large effect on the distribution of simulated patterns of species distributions. Although population size remained fairly constant over all simulations, patterns of distribution shifted owing to the aggregation of individuals within specific habitat types. The control of landscape structure created by the comparison of neutral models allowed the effect of pattern and scale to be evaluated.

Pearson and Gardner (1997) used randomly generated fractal landscapes for an entirely different purpose—to determine the consequences of spatial variation in the patterns of ^{137}Cs contamination in a Tennessee reservoir. The spatial

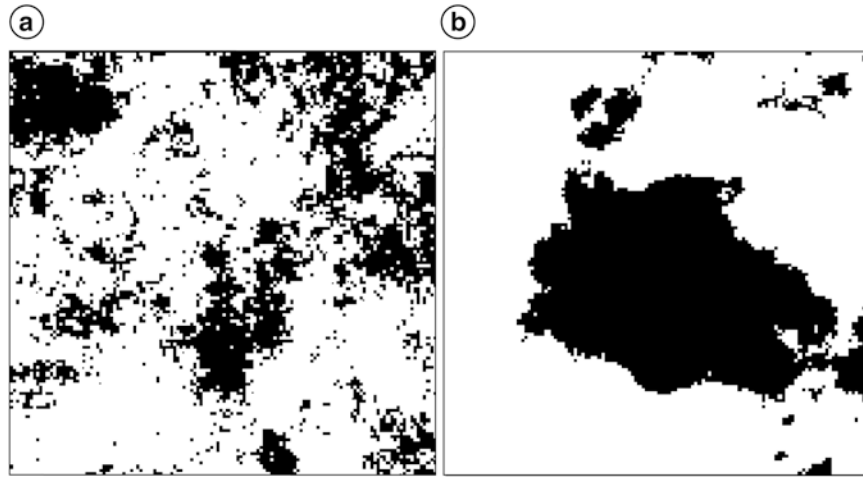

FIGURE 3.9.
Two examples of fractal maps with: (**a**) $H = 0.2$ and (**b**) $H = 0.8$. Each map has 128 rows and columns and the value of p (*green cells*) for each landscape type equals 0.33.

pattern of contamination was important because sites within the reservoir with high contaminant levels ("hot spots") could affect cleanup strategies. It was believed that contaminant hot spots should be spatially correlated, but the degree of correlation was not known. Fractal maps with varying levels of H were produced to assess the effectiveness of various sediment sampling schemes on the detection of these hot spots. The results showed that spatial patterns could be detected accurately in maps with a large degree of spatial autocorrelation using relatively few samples. However, as autocorrelation declined, the number of samples required to achieve the same degree of accuracy increased dramatically. A comparison of fractal maps with ^{137}Cs distributions estimated by a sedimentation model showed that contaminant levels were positively correlated within deposition zones (i.e., areas with similar hydrodynamics), but uncorrelated across different deposition zones.

Other applications of fractal landscapes as neutral models have included the effect of pattern on dispersal (Walters 2007), exploration of edge effects (With 1997; With et al. 1997) and source-sink relationships (Milne 1992; With 1997). Because multiple realizations of these neutral models can be generated, systematic application allows the effect of one component of landscape structure—the autocorrelation among habitat types—to be determined.

INSIGHTS AND APPLICATIONS OF NLMS

The most influential conceptual contribution of NLMs to landscape ecology revolves around the existence of critical thresholds—and the implications of these thresholds for relating landscape pattern to ecological processes (Homan et al. 2004; Groffman et al. 2006b). Although landscapes are not random, there are critical thresholds in connectivity where sudden changes in landscape pattern may occur with small shifts in disturbance regimes or changes in land-use. The factors that organize actual landscapes are not random making the prediction of the exact value of p_c for any given landscape uncertain (see Discussion Question 6.3). Never-the-less, critical thresholds for real landscapes do exist! Thus, above p_c we can expect landscape pattern to be dominated by a single very large cluster, while landscapes with values of p below p_c will be characterized by numerous, smaller, fragmented patches. Shifts in pattern that result from small changes in land-use may cross this threshold and have important implications for metapopulation dynamics and conservation of species diversity (Dale and Zbigniewicz 1995; Pearson et al. 1996; Gardner and Engelhardt 2008; also see Chap. 8). Metapopulation dynamics are possible in landscapes below p_c, while a single, large population dominates can occur in landscapes where the amount of habitat is above p_c. Conservation efforts should be cognizant of the implications of critical thresholds and connectivity in actual landscapes. Because small changes in available habitat near the critical thresholds result in disproportionately large changes in the degree of landscape fragmentation, efforts to preserve continuous tracts of habitat are highly vulnerable to disturbance effects when the amount of habitat is near the critical threshold.

A second key insight from NLMs is that the amount of habitat on a landscape (so the value of p) will strongly influence the values of a wide array of landscape metrics (see Chap. 5). Stated simply, habitat amount constrains habitat pattern, or composition affects configuration. Other related lessons learned from NLMs include:

- *Map dimensions*: Map boundaries affect pattern by the truncation of map patches. The truncation effect becomes more serious as map dimensions decline and p increases. Patterns for maps that are smaller than 100 rows and columns may be seriously impacted by these truncation effects.
- *Patch Structure*: Simple random maps have the greatest number of patches, with the number of patches determined by p. When patterns with contagion are generated (i.e., positive or negative associations between sites on the map), then the number of patches decreases. For instance, curdled maps generally have fewer patches than random maps because the hierarchical structure of map generation affects the contagion between map sites.

- *Thresholds of Connectivity*: Simple random maps are likely to have a single cluster which spans the map (percolates) when $p \sim 0.6$. Random maps with very high or very low contagion will percolate at $p > 0.6$. Random maps with moderate levels of contagion will percolate at $p < 0.6$. When a landscape is above the threshold of connectivity, patches tend to be large and contiguous and there is less difference among patterns. When a landscape is below the threshold of connectivity, patches tend to be small and fragmented and there may be greater differences between different maps. For instance, curdled maps can percolate when the overall value of $p \sim 0.6$, but each level must also percolate. On all maps (random or real), the probability of percolation is directly related to the size of the largest patch.
- *Connectivity and Scales*: Connectivity of sites across a map is defined by the relationships between map pattern and the process of interest, which "connects" adjacent sites. Therefore, connectivity is directly related to habitat abundance (p), the spatial arrangement of suitable habitat, and the resource utilization "rule" of the process being considered. On random maps, thresholds in connectivity occur near 0.6, 0.35, and 0.25 for successively larger neighborhoods of 4, 8, and 12 neighbors, respectively. Connectivity may be expected to vary most at intermediate levels of habitat abundance (e.g., 0.3–0.6).

Practical applications of NLMs often involve their coupling with dynamic ecological models that seek insight into the relationships between pattern and process within heterogeneous landscapes. The NLMs provide replicated manifestations of patterns from which measures of central tendency and variance can be obtained. The ability to generate replicate maps creates a control over the variation in spatial heterogeneity that simply is not possible with traditional sampling. The application of NLMs to landscape issues seems limited only by imagination, and is certainly an economical precursor to more expensive empirical studies. However, the use of NLMs for landscape studies also generated misunderstandings, and several caveats for the use of neutral models (with and King 1997; Gardner and Urban 2007) are important:

- Agreement of a NLM with a set of observations is not proof that the NLM is true (Caswell 1976). Agreement may suggest hypotheses that can be experimentally tested to establish their validity.
- The lack of agreement between an NLM and a set of observations does not prove that the excluded processes are responsible for the observed pattern (Caswell 1976).
- NLMs are theoretical constructs that may not be directly applicable to actual landscapes. For instance, it would be a misuse of NLMs to design a conserva-

tion reserve with the proportion of habitat equal to 0.59275. "On the other hand, approaching the design of the reserve with an appreciation of the importance of connectivity … would be an appropriate application (With and King 1997)."

- It is a misunderstanding of the role of NLMs to reject them as "artificial" and hence misleading simply because they fail to be good predictors of a particular ecological process (see Schumaker 1996; Gardner and Urban 2007). No single NLM will be appropriate for all situations. Rather the NLM should be designed to provide the appropriate null hypotheses against which actual patterns may be tested.

SUMMARY

A model is an abstraction or representation of a system or process. There are many different kinds of models, and mathematical models are commonly used in ecology. In landscape ecology, model development is an important tool that complements empirical techniques. Models permit the landscape ecologist to explore a broader range of conditions than can usually be set forth experimentally. Landscape models help to formalize our understanding and develop theory about how spatial patterns and processes interact, producing general insights into landscape dynamics.

Models are characterized in various ways: for example, models may be deterministic or stochastic; analytical or simulation; dynamics or static; and represent time as continuous or discrete. A model is spatial when the variables, inputs, or processes have explicit spatial locations represented in the model. A spatial model is only needed when explicit space—what is present and how it is arranged—is an important determinant of the process being studied.

The process of building a model is multifaceted and includes the following steps illustrated in Fig. 3.2: (1) Define the problem. (2) Develop the conceptual model. (3) Select the model type. (4) Develop the model by writing out the mathematical equations and relationships. (5) Computer implementation, including verification and documentation of the code. (6) Estimate the parameters, and calibrate if necessary. (7) Evaluate the model by comparison with empirical observation and perform a sensitivity or uncertainty analysis. (8) Use the model for experiments and prediction.

Models are and will remain extremely important tools in landscape ecology. Wise application of these models requires care, however, particularly to the following points: (1) Performance of any model results from the hypotheses and assumptions on which it is built. Comparing alternative model formulations is extremely valuable. (2) Understanding the sensitivity of models to error in estimating

parameters is critical; however, assessing error propagation in spatial models remains challenging. (3) All models are simplifications of reality, and the domain of applicability for each model must be defined. (4) Gaps in empirical data for estimating key parameters are often a great source of uncertainty in model predictions. The empirical database that contributes to a model must be understood. (5) Technologically advanced methodologies do not assure the accuracy or reliability of model results!

A NLM is any model used to generate pattern in the absence of specific processes being studied. Predictions from NLMs are not intended to represent actual landscape patterns, but rather define the expected pattern in the absence of a specific process. Comparison of the results of NLMs against actual landscapes provides a standard against which measured departures may be compared. If real landscapes do not depart from a NLM then there may be no need for a more complex model. The types of NLMs that may be generated are diverse (see Keitt (2000) for a unified approach to the generation of NLMs). Random maps provide the simplest NLM, but more complex neutral methods including hierarchical random maps and fractal maps have been used to provide insight into the effect of structured patterns of land-cover on ecological dynamics.

Studies utilizing NLMs have been important in the development of theory and the testing of methods for the analysis of landscape patterns. Results of these studies have been helpful for exploring the implications of landscape patterns for ecosystem processes, population dynamics, disturbances, management decisions, and conservation design. Neutral models are particularly useful for testing differences between landscapes when experimental manipulation and/or replication is not feasible and also serve as an economical means for designing expensive empirical studies. NLMs also played an important role in the development of theoretical landscape ecology by identifying critical thresholds in landscape connectivity, and they have been crucial for understanding the behavior of metrics of landscape pattern NLMs will continue to have a role in landscape studies because of the challenges associated with manipulating spatial patterns in broad-scale empirical studies.

DISCUSSION QUESTIONS

1. What are the distinguishing characteristics of landscape models? What is the difference between a spatially explicit and spatially implicit landscape model? Must all landscape models be spatially explicit?
2. What are the trade-offs (advantages and disadvantages) to using simple vs. complex models?

3. The survey of recent models presented in this chapter provides an overview of current modeling activities. Are models being applied in a balanced manner to the broad spectrum of landscape issues? What areas of landscape ecology are missing from the list of topics reviewed? Why?
4. Technological advances now allow complex spatial simulations to be easily performed and often linked with GIS software to produce mapped output. What should be the key concerns of landscape ecologists for the development, analysis, and application of these methods?
5. The statement was made in the text that "…it is not surprising that a (simple random) map one-half the size of another will have an average cluster size that is only one-quarter as large." Provide an algebraic proof that this will always be the case for simple random maps when $p > p_c$. Is this a scaling rule? Explain why this is not the case for simple random maps when $p < p_c$ (see Table 3.2).
6. Can theoretical or empirical rules relating pattern to map size be defined for fractal maps? If not, how would you go about establishing an empirical scaling rule for fractal maps?
7. Percolation theory predicts a critical threshold when $p \geq 0.59275$. What are the assumptions behind the use and application of this value? Do these assumptions apply to actual landscapes?
8. Table 3.2 shows that average cluster sizes of random and fractal maps are nearly the same when $p = 0.7$ or 0.9. Why is this true? Will other measures of landscape pattern also be similar for these values of p? Will the effects of landscape change be undetectable unless p falls below the critical threshold?

APPENDIX: CLASSIFICATION OF MODELS

Models may be described or classified in various ways, and it is helpful to understand some commonly used terms. We review the terms often used to describe ecological models; similar distinctions are also presented by Grant et al. (1997).

Deterministic vs. *stochastic*. A model is deterministic if the outcome is always the same once inputs, parameters, and variables have been specified. In other words, deterministic models have no uncertainty or variability, producing identical results for repeated simulations of a particular set of conditions. However, if the model contains an element of uncertainty (chance), such that repeated simulations produce somewhat different results, then the model is regarded as stochastic. In practice, the heart of a stochastic simulation is the selection of random numbers from a suitable generator. For example, suppose that periodic movements of an organism are being simulated within a specified time interval. It may be likely that the organ-

Table 3.3.
Terminology for model components and common procedures.

Term	Definition
Parameter	A constant or coefficient that does not change in the model
Variable	A quantity that assumes different values in the model
State variable	Major elements of the model whose rates of change are given by differential equations
Initial conditions	The values of the state variables at the beginning of a simulation
Forcing function, external variable, or driving variable	Function or variable of an external nature that influences the state of the system but is not influenced by the system
Output variables	Variables that are computed within the model and produced as results
Sink	A compartment in the model into which material or flow goes, but from which it does not return
Source	A compartment from which the material flowing in the model flows, but to which it does not return
Dimensional analysis	The process in which the units in a model are checked for consistency
Calibration	The process of changing model parameters to obtain an improved fit of the model output to empirical data
Corroboration	The process of determining whether a model agrees with the available data about the system being studied
Sensitivity analysis	Methods for examining the sensitivity of model behavior to variation in parameters
Validation	Term commonly used for the process of evaluating model behavior by comparing it with empirical data; we prefer corroboration because it does not imply "truth"
Verification	The process of checking the model code for consistency and accuracy in its representation of model equations or relationships

ism will move, but it is not certain when this event will occur. One solution is to represent the movement event as a probability, say 0.75, and the probability of not moving as (1.0–0.75) = 0.25. Selection of a random number between 0.0 and 1.0 is done to "decide" randomly if movement occurs during a specific time interval. If the simulation is repeated, the time-dependent pattern of movement will be differ-

ent, although the statistics of many movement events will be quite similar. Inclusion of stochastic events within a model produces variable responses across repeated simulations – a result that is quite similar to our experience of repeated experiments.

Analytical vs. *simulation*. These terms refer to two broad categories of models that either have a closed form mathematical solution (an analytical model) or lack a closed form solution and therefore must rely on computer methods (a simulation model) to obtain model solutions. For analytical models, mathematical analysis reveals general solutions that apply to a broad class of model behaviors. For instance, the equation that describes exponential growth in a population is an example of an analytical model (Table 1), as are many of the model formulations used in population ecology (May 1973; Hastings 1996).

In contrast, the complexity of most simulation models means that these general solutions may be difficult or impossible to obtain. In these cases, model developers rely on computer methods for system solution. Simulation is the use of a model to mimic, step by step, the behavior of the system we are studying (Grant et al. 1997). Thus, simulation models are often composed of a series of complex mathematical and logical operations that represent the structure (state) and behavior (change of state) of the system of interest. Many ecological models, especially those used in ecosystem and landscape ecology, are simulation models.

Dynamic vs. *static*. Dynamic models represent systems or phenomena that change through time, whereas static models describe relationships that are constant (or at equilibrium) and often lack a temporal dimension. For example, a model that uses soil characteristics to predict vegetation type depicts a relationship that remains the same through time. A model that predicts vegetation changes through time as a function of disturbance and succession would be a dynamic model. Simulation models are dynamic.

Continuous vs. *discrete time*. If the model is dynamic, then change with time may be represented in many different ways. If differential equations are used (and numerical methods available for the solution) then change with time can be estimated at arbitrarily small time steps. Often models are written with discrete time steps or intervals. For instance, models of insects may follow transitions between life stages; vegetation succession may look at annual changes, etc. Models with discrete time steps evaluate current conditions and then "jump" forward to the next time while assuming that condition remains static between time steps. Time steps may be constant (i.e., a solution every week, month, or year) or event-driven, resulting in irregular intervals between events. For example, disturbance models (e.g., hurricane or fire effects on vegetation) may be represented as a discrete time-step, event-driven model.

Mechanistic, *process-based*, *empirical models*. These three terms are frequently confusing. A "mechanism" is "…the arrangement of parts in an instrument." When used as an adjective to describe models (i.e., a *mechanistic* model) the term implies a model with "parts" arranged to explain the "whole." In the best sense of the term, a "mechanistic" model attempts to represent dynamics in a manner consistent with real-world phenomena (e.g., mass and energy conservation laws, the laws of chemistry, etc.). Although there has been waning support for mechanistic approaches to ecological modeling (Breckling and Muller 1994), the use of "mechanistic" in the strictest sense distinguishes these models from "black box" models which grasp at any formulation which might satisfactorily represent system dynamics. Confusion arises when the term "mechanistic" is loosely applied to distinguish less detailed models from more detailed ones. Often the implication is that mechanistic models are more desirable than less mechanistic(less detailed) models. Unfortunately, the assertion that additional detail produces a more reliable model must be demonstrated on a case-by-case basis (Gardner et al. 1982).

A "process-based" model implies that model components were specifically developed to represent specific ecological processes—e.g., equations for birth, death, growth, photosynthesis, and respiration are used to estimate biomass yields rather than simpler, more direct estimates of yields from the driving variables of temperature, precipitation, and sunlight. Although this concept seems clear, there is no a priori criterion defining formulations which qualify (or conversely do not qualify) as process models. Thus, depending on the level of detail, it is possible to have a "mechanistic process-based" model or an "empirical process-based" model.

An "empirical" model usually refers to a model with formulations based on simple, or correlative, relationships. This term also implies that model parameters may have been derived from data (the usual case for most ecological models). Regression models (as well as a variety of other statistical models) are typically empirical because the equation was fitted to the data.

The problem of distinguishing between types of model is illustrated by the simulation of diffusive processes based on well-defined theoretical constructs (Okubo 1980). These formulations of diffusion allow simple empirical measurements to define the coefficients estimating diffusive spread. Thus, there is a strong theoretical base along with empirically based parameters. Is such a model considered empirical or theoretical? Should complex formulations always be considered more theoretical or simply harder to parameterize?

The essential quarrel with each of these three terms is that most ecological models are a continuum of parts, processes, and empirical estimations. Separating models into these arbitrary and ill-defined classifications lacks rigor and repeatability. One person's mechanistic model is the next person's process-based model, etc. There does not appear to be a compelling reason to use these vague and often confusing terms to distinguish between alternative model formulations.

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