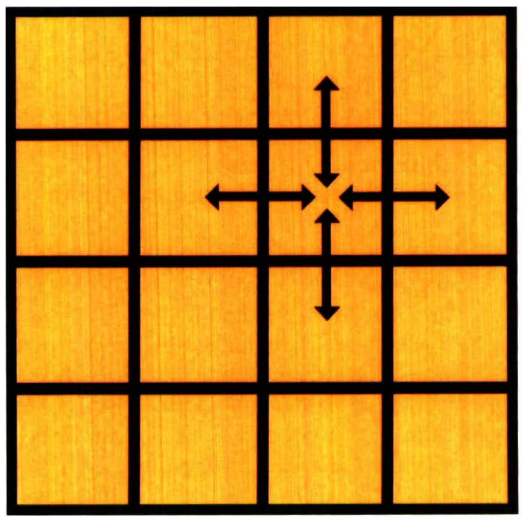
A Tutorial for Understanding Ecological Modeling Papers for the Nonmodeler



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MODELING PAPERS PLAY A CRUCIAL ROLE in furthering the science of entomology. In complex ecological systems, modeling can be used to predict outcomes, clarify questions, facilitate computer experiments, and manipulate key variables that would be impossible to do experimentally because of cost, logistics, or ethics. Yet, to many entomologists, models remain the domain of mathematicians, statisticians, and others from more quantitative disciplines. As a result, modeling papers sometimes are ignored by the biologists for whom these papers are written. This is unfortunate because a particular model can provide insights that might help those working on an empirical problem. Conversely, modelers can always benefit from those working closely with the biology of the systems that they are trying to model by fairly assessing the results and assumptions the modelers have used to describe the systems. It is important that both modelers and nonmodelers speak to one another. Modelers, however, seem to have a language of their own: analytic models? simulation models? individually based models? stochastic models? Readers unfamiliar with modeling might wonder how these terms relate to the modeling paper they are trying to understand.

Becoming familiar and comfortable with any subject is often a matter of getting to know the terminology and basic tools associated with the discipline. If you do modeling on a regular basis, there is little need to read on. This article is not for you. Some of the more arrogant modelers might even feel a wave of condescension, believing that such things ought to already be a part of the tool kit of every entomologist. Nevertheless, we all approach entomology from a different perspective and often use a different set of tools to pursue our science. Many of my colleagues shudder at the thought of anything mathematical, and, in their circles, it is rare that such tools are ever used. This primer is for them.

Statistical Versus Process Models

Models can be classified in several different ways. Like any taxonomist, we would like a nice, neat dichotomous key, but modeling can be an amalgam of many different elements. Although there is overlap between model types, with one blending smoothly into the next, there are some general rules and some dichotomies. We will work through these. But keep in mind that these many models might all be combined to produce a more complex model. A list of definitions of all the model types is given in the glossary.

The first distinction that needs to be made is between statistical models and process or descriptive models, which are the kind of mathematical models I describe here. Statistical models are used to give a probabilistic interpretation of the data. Familiar statistical models include techniques such as simple linear regression that fits a line through a series of data points. Statistical models do not try to describe underlying processes through an understanding of biological mechanisms but rather attempt to find a set of parameters that can be used to predict relationships that are described by the data. The science of statistics is one of the most valuable tools we have for understanding data. It can help us find hidden patterns, predict future trends, find differences between one set of biologi-

A Glossary of Model Types

Analytic Model: A model for which a specific mathematical form for the model can be written in an equation or set of equations. The ability to write an equation for a model allows the use of many techniques developed to examine the prediction and behavior of these models. (Compare with *Simulation Model*)

Cellular Automata Model: A spatial model where both time and space are discrete.

Computer Model: See *Simulation Model*.

Continuous Versus Discrete: Continuity refers to the values that may be represented in three aspects of the model: time, space, and model parameters. For example, in continuous-time models, time can take on any value between the time when the model begins and when it ends, including all fractional times. In discrete-time models, time can only take on a finite number of values (e.g., $t = 1,2,3 \ldots T$). Likewise, in continuous space, the model explicitly incorporates all possible locations on an x, y grid. When continuous model parameters are used, the model can take any value within the full range of that parameter value. For example, if one of the parameters was the size of a population, N, then N might be 0.004 in a model with continuous parameters. If N is discrete, however, it only can take on integer values (e.g., 153).

Coupled-Map Lattice Model: A spatial model where time is continuous and space is discrete.

Descriptive Model: See *Process Model*.

Deterministic Model: A model in which there are no random events. In a deterministic model, the same input will always produce the same output. Examples of deterministic models include ordinary differential equations and partial differential equations. (Compare with *Stochastic Model*)

Discrete: See *Continuous*.

Eulerian Model: A spatial model that examines the distributional movement of a population.

Individual-Based Model: A model where each individual insect, plant, or field is modeled and population processes arise through the interaction of individuals in the model. Often used with Rule-based modeling.

Island Model: A spatial model in which every population can exchange individuals with every other population in the model.

Island-Continent Model: A spatial model in which discrete smaller populations receive individuals from a large population (called the *mainland pool*).

Lagrangian Model: A spatial model that follows the movements of individuals within a population.

Object-Oriented Programming: A type of programming in which objects can be defined with specific attributes and functions that modify those attributes. This is a very useful programming environment for individual-based models. For example, a popular object-oriented programming language is C++ (pronounced "C plus plus").

Ordinary Differential Equations: Used in continuous time analytic mathematical models.

Partial Differential Equations: Used in analytic mathematical models in which both time and space are continuous.

Process Model: A model that explicitly incorporates aspects of the biological processes found in the natural system being represented by the model. (Compare with *Statistical Model*)

Rule-Based Model: Where the behavior of entities (e.g., individuals, plants, fields) are governed by a set of rules and conditional statements; often used in individual-based models. For example, to model parasitoid movement on a leaf, a set of rules might be as follows:

Step 1. Move forward until host larva is detected or edge of leaf is reached.
Step 2. If host is found, then deposit eggs.
Step 3.If edge of leaf is reached turn 160° and go to step 1.

Simulation Model: In contrast to analytic models, this term refers to models that use computer programs rather than mathematical equations to describe the biological process. It also may be used to describe a model where several mathematical equations are combined to follow the results of linked systems. (Compare with *Analytic Model*)

Spatial Model: Any model that incorporates a spatial dimension explicitly or implicitly. In spatially explicit models, the specific locations of processes are tracked. In implicit models, locations are not defined and, typically, the number or proportion of spatial sites with a given attribute are specified.

Statistical Model: A model that examines distributional properties of the data. This type of model typically does not incorporate biological processes explicitly in the model. (Compare with *Process Model*)

Stepping-Stone Model: A spatial model in which individual populations form an array in which each population can exchange individuals only with its neighbor.

Stochastic Model: A model in which random events play a role in the model. In stochastic models, a given input may produce many different outputs because some of the parameters in the model are random variables. (Compare with *Deterministic Model*)

cal conditions and another, and provide a measure of the probability that such differences are significant. Still, typical statistical models do not try to add "biology" in their description. There is no attempt to describe the underlying mechanisms that might produce the data that we have obtained. The same statistical model can be used both for looking at a relationship between labor and costs in an economic model and between larval and pupal weights in an entomological setting.

Although process or descriptive models often share many of the goals of statistical models, such as prediction, they differ because they achieve that prediction by incorporating a biological description of relevant processes found in the system one is studying. These types of mathematical models attempt to describe the pertinent aspects of the biology behind the behavior one sees in the real system and to reproduce the data that one might collect from biological processes. The focus of this article is on these types of mathematical models, and when I use "model," it is in this limited sense. In addition, the emphasis is on models used to study ecological processes, but much of what I say applies to other types of models as well (such as models used to examine physiological processes).

Ecological models can be constructed for several purposes and can vary from the specific [e.g., How does the parasitoid *Tetrastichus giffardianus* Silvestri affect the population dynamics of *Bactrocera dorsalis* (Hendel) on wild guava?] to the very general (e.g., How do local extinctions affect regional population stability in spatially connected systems of subpopulations?). They may be used to conduct theoretical experiments on systems for which manipulation is impossible for logistic or ethical reasons. They allow one to speed up time and provide a level of control over the system that would be impossible in the field. They also may be used to generate hypotheses for testing in the field or laboratory. For example, the model might suggest that under condition A, and given assumption B, the system should behave like X, Y, and Z. The model provides a standard against which the real system can be compared. If the model and biology do not agree, it affords the opportunity to explore what might be missing from the model or examine what we do not understand about the biology of the system. By reducing the complexity and by focusing on only certain aspects of a system, models help us determine which factors are most important in driving the system of interest. And, finally, models also can be used to decide which biological data are most important to gather. For example, perhaps a model of a specific system suggests that movement rates influence population dynamics more than fecundity (perhaps an attribute already well studied), suggesting that future research should be directed to movement.

Thus, models complement and support basic research into the ecology, behavior, and other aspects of natural systems. Modeling makes predictions, generates hypotheses, and allows us to explore questions that otherwise would be impossible to examine.

Assumptions

Models are always an incomplete description (they even might be called a caricature) of reality and because of this, a choice must be made on which aspects of reality to include and which to exclude. Examples of questions that could be asked

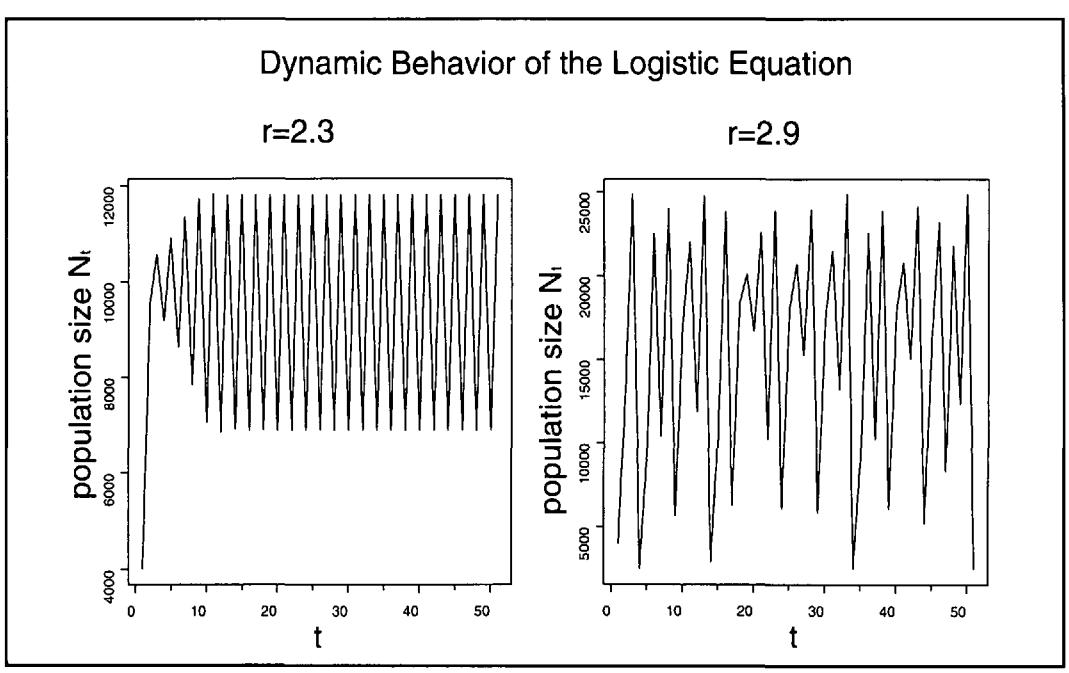

Fig. 1. The behavior of a model using the deterministic logistic equation $N_{t+1} = N_t + rN_t \frac{K - N_t}{K}$ to predict the size of an insect population through time. The behavior of the model differs depending on the value of the growth parameter r (see text for details). When $r = 2.3$, the population has predictable oscillations. When $r = 2.9$, the behavior of the model is very erratic and enters into the realm known to mathematicians as "chaos."

would be as follows: What influences the dynamics that I am trying to capture in my model? Do I need to include space in the model? Do the insects migrate first and then mate, or do they mate and then migrate? Are actual population numbers important or will tracking simple proportions be adequate? Which components of the real ecological system are important to include in the model to capture the processes I am interested in examining? Although all of these types of questions could be addressed, it is how they are addressed that is the most important step in deciding if a model is meaningful because how they are addressed comprises the assumptions of the model. Examining assumptions is arguably the most important contribution nonmodelers can make in helping modelers decide if they have created an adequate description of the biological process they are trying to capture. Because a model can never capture every aspect of a natural system, some aspects of the actual ecological system must be omitted, and this is where modeling becomes more art than science. From my perspective, deciding on what things to include in a model, what processes I am trying to capture, and determining the salient components of the biology that need to be represented are among the hardest parts of building a useful model.

Examining what is to be included in the model and what will be omitted is one way the person familiar with the biology of an insect can be helpful to the modeler. Is the modeler making a contribution or just flexing his or her computational muscles without adding anything relevant to our science?

Assumptions often are not stated explicitly and, at times, can be difficult to sort out. When examining a paper, if there are things that are unclear or you cannot find the assumptions, it is time to give the author a call. Assumptions make or break a model. Often, the inner workings of the model, what tools were used to evaluate the model, and other details of the modeling process can be evaluated by mathematicians and must take a back seat to the importance of evaluating biological assumptions.

Types of Mathematical Models

Models can be classified by what role random events play in the model. If nothing is random in the model, it is said to be *deterministic,* if random events are included in the model, it is called *stochastic* (discussed below). In a deterministic model, a given set of inputs will always result in the same answer. For example, the simple model $N_{t+1} = 2N_t$ states that if the population at a certain time t is N, then at the next time $t+1$, it will have doubled. This is deterministic. If you put in the number 100, you will always get 200 back. This is a simple example, but deterministic models can be complex. For example, one deterministic model I worked with contained more than a thousand lines of computer code, modeled more than 2,500 crop fields, and tracked the genetics and population dynamics of the insects living in each field (Peck and Ellner 1997). The most typical deterministic models that you will encounter are difference equations or differential equations. These two modeling types also suggest another way in which models might differ based on how time is handled in the model. In discrete-time models, such as difference equations, time takes on values only at certain time-points (i.e., time is broken into discrete segments, usually of fixed length). In differential equations, time is continuous. We will first look at discrete-time models, then at continuous time models.

One of the most famous difference equations is the Fibonacci sequence:

$$N_{t+2} = N_t + N_{t+1}$$

For this equation, we need two starting times: N_0 and N_1. If we start with 0 and 1, we get the famous Fibonacci series: 0, 1, 1, 2, 3, 5, 8, 13, 21, . . . Fibonacci assumed that if you started with a pair of rabbits that gave birth when they were 1 month old to a single male-female pair for each of two consecutive months, and all the rabbits survived long enough to mate and then died, the number of pairs after 8 months would be as follows:

Month 1: 0 + 1 = 1
Month 2: 0 + 1 = 1
Month 3: 1 + 1 = 2
Month 4: 1 + 2 = 3
Month 5: 2 + 3 = 5
Month 6: 3 + 5 = 8
Month 7: 5 + 8 = 13
Month 8: 8 + 13 = 21

The first number on each line represents the number of rabbits born 2 months ago; the second number gives the total born last month; and the last number, after the equal sign, the number alive this month (i.e., the number of rabbits born 2 months ago + the number of rabbits born last month = population size in the current month).

Now, examine the assumptions of this model: exactly one pair replaces the old pair each month, rabbits are always born in opposite sex couples, and only two pairs are born per parental pair each generation. Are these assumptions realistic? How could the model be made more realistic? What part of rabbit biology does this capture? What part does it ignore? Take some time to work through this example with the assumptions given. How the numbers work out might not jump out at you until you work through it with pencil in hand.

Another famous difference equation is that of the discrete logistic:

$$N_{t+1} = N_t + rN_t \frac{K-N_t}{K},$$

where N_t is the population size of female insects at time t, r is the growth parameter, and K is the carrying capacity (the highest number of insects that can be supported in the location of the population). If we start with 100 females, the carrying capacity is 200, and the growth rate of the population, r, is 1.5 per generation, and we assume a gen-

eration time of one month, after three months the population size would be as follows:

Month	Population size
Month 0: 100	
Month 1: 100 + 100•1.5•(200-100)/20 =	175
Month 2: 175 + 175•1.5•(200-175)/200 =	207.8
Month 3: 207.8 + 207.8•1.5•(200-207)/200 =	196.9

Notice that when the population is above the carrying capacity the term in brackets becomes negative and the population shrinks. This equation is especially interesting because it demonstrates three special kinds of population behavior, depending on the value that r takes: constant, cyclic, and chaotic population dynamics. Figure 1 shows the population size for this model plotted for two different values of r. Chaos is a property of certain deterministic dynamic systems in which final outcomes are sensitive to small differences in initial conditions. In the equation, chaos occurs for values of r greater than 2.6. For values of r less than 2.6, you will see stable (although cyclic) behavior. These systems, although completely deterministic, can mimic stochastic dynamics (discussed below) in a model because of their unpredictability. A difference equation implies (1) time is modeled discretely in steps, (2) the model is completely deterministic, (3) the equation completely describes the process, and (4) specific mathematical tools exist for evaluating the model.

The other type of deterministic modeling you are likely to see is the differential equation model. In modeling with ordinary differential equations, we assume that time is continuous. For example, the classic Malthusian growth model is written thus:

$$\frac{dN}{dt} = rN ,$$

where and the population size N is a function of time. Here we see that the change in the population size (dN/dt) during any instant is the size of the population multiplied by the parameter r, which gives the growth rate of the population. We can go further by "integrating" both sides, which allows us to find the population size at any time t:

$$N_t = N_0 e^{rt},$$

where N_0 is the initial population size at time 0 (the starting time) and e is an analytic number, such as p, which has a value of 2.7183 if taken to 4 decimal places. Therefore, if the initial population is 100, and r = 1.5, and time is being measured in years, then after 5 years the population will be as follows:

$$100 \bullet 2.7183^{1.5 \bullet 5} = 180{,}804.24 .$$

By plugging in a few values for t, you can see that the population rises quickly so that in just a few years, it rises above the ability of your calculator to handle the large size of the number.

Ordinary differential equation models can be more complicated, as in this system of three coupled differential equations from Anderson and May's (1981) insect-pathogen model:

$$\frac{dS}{dt} = r(S + 1) - \upsilon SP$$
$$\frac{dI}{dt} = \upsilon SP - (\alpha = b)I$$
$$\frac{dP}{dt} = \lambda I - (\mu = \nu(S + I))P ,$$

where S is the number of susceptible insects in the population, I is the number of infected individuals, P is the number of parasitoids, r and l are the growth rate of susceptible and parasitoid individuals, respectively, n is the rate of parasitism, a and b are mortality sources for the parasitized individuals, and m is the mortality rate of parasitoids. The analysis of this set of equations goes far beyond the scope of this paper, but, because we can write down a formula, there are several well worked-out methods for understanding the long-term behavior of the system. We can find stable points where host and parasitoids can coexist and find a set of parameter values where one or both populations become extinct. When you see a differential equation, you know at least four things: (1) time is modeled continuously, (2) the model is completely deterministic, (3) the equation completely describes the process, and (4) there are specific mathematical tools for evaluating the model.

In short, the difference between difference equations and differential equations is that the former evaluates the population at discrete time-points whereas in the latter, time is considered continuous. In general, continuous models are handled more easily mathematically. In reality, however, we usually have to examine the populations we are studying at specific time points so discrete models may be closer to what we might expect to examine in the field.

Unlike deterministic models in which there are no random events, stochastic models explicitly contain randomness. Even simple processes rarely are understood well enough to predict the outcome with complete accuracy. For example, the physics of flipping a coin are fairly well understood, but tiny variations in the coin's initial velocity, the angle of its launch, and the air currents surrounding its spin all provide enough variation to make it a wonderful way to randomly choose who gets to kickoff first in a soccer game. Comparatively, the complexity of an ecological system is enormous, and stochastic forces play a major role. Almost every aspect of any measurable system will vary because of natural variation and complex interactions. One way to mimic these effects in a model is to add randomness to some of the parameters; this adds a degree of realism that is lacking in deterministic models. Adding random variables also allows us to examine how the natural variation in parameter values affects the overall behavior of the system. For example, if you know that a pest moves an average of 4 m and individuals overall move between 1 and 7 m, you can incorporate both pieces of information

into the model to explore the effect of that variation on the rate an insect population disperses throughout a region.

A stochastic model implies that there is something random in the model. For example, to decide how many eggs are laid per female, in a model that follows the dynamics of a simple population, a random number might be chosen between 1 and 20. The randomness in the model might come from any number of statistical distributions and may be very sophisticated, but the basic idea is that there are events in the model that cannot be predicted. At one time you might put in N insects and get out $2N$, and the next time you might put in N insects and get out $4/9N$ insects. The kinds of stochastic models that you will see in the entomological literature generally require that you run them many times so that you can get a feel for the variation and average behavior of the model (just as in biological systems, modelers often will talk about "model behavior" meaning the output pattern through time) and how much it varies from time to time. If an author of a stochastic model presents only one run, or there are no error bars on the plots, it is a red flag that the model may not have been explored thoroughly. An exception might be if it is a model based on stochastic equations (which are beyond the scope of this article) in which some of the model parameters are defined as random variables and from these equations, distributional properties of the model, such as its mean and variance, might be derived using certain mathematical techniques for dealing with these kinds of equations. This brings us to still another way to split models: analytic versus simulation models.

Analytic Models. Analytic models usually have a specific mathematical form (i.e., you can write an equation for the model). They may be either deterministic or stochastic. If the model is stochastic, some of the parameters in the model will be defined as random variables (i.e., parameter values come from a probability distribution)—rather than just taking on a fixed number, as do the parameters in deterministic models. Analytic models are the sort used to describe gravity in your high school physics classes, or the famous $E = mc^2$. Analytic models are not simple necessarily, and they include everything from large systems differential equations to large, spatial arrays of interacting equations called coupled-map lattices. They are especially valuable because there are well-developed mathematical tools that can allow the modeler to explore the behavior of these models in great detail. For example, with analytical models you can find the particular value of model parameters where the model behavior changes. The drawback of analytic models is that they often cannot handle the complexity of real biological systems.

Simulation Models. The popularity and growth of simulation models, or as they are sometime called computer models, has followed the advance in modern computer technology. Simulation models (Table 1) are the most likely type of model that a reader will encounter in the entomological literature. Computers allow us to model very complex processes and, often, are limited only by the imagination of the modeler. This can be problematic because the complexity of simulation models can quickly rise to the level of that found in the biological process itself. Among the principal reasons to model a system is to reduce the complexity so that underlying processes can be understood more clearly. When a simulation model becomes too complex, this advantage is lost. Understanding computational models requires much more work, and interpretation of these models must be examined carefully. These models can, however, handle the biological complexity that would have been unheard of in the years before the development of modern computer technology.

Two kinds of simulation models, rule-based and individual-based, can be particularly valuable to entomologists. Rule-based modeling is characterized by having the computer follow the same rules that an insect, or insect population, might follow when faced with given environmental factors or natural situations. There are now computer packages that require little, if any, mathematical know-how that will allow one to define rules and relationships for a system and run simulations from rules one has defined. Individual-based modeling, often a kind of rule-based modeling, follows the activities of individual insects through time and/or space. This allows "computer insects" to interact with their computer environment and other members of the population, providing the opportunity for a detailed description of the original system in the model. It allows one to look at how individual behaviors may influence population-level processes.

There are computer packages available for rule-

Table 1. A sample of modeling papers published in *Environmental Entomology* between 1989 and 1998 classified by whether they are analytic or simulation, and deterministic or stochastic.

Model	Deterministic Models	Stochastic Models
Analytic models	Schaalje 1990, Yu et al. 1992, Brewster and Allen 1997	Munholland and Dennis 1992
Simulation models	Culin et al. 1990, Geden et al. 1990, Berry et al. 1991, Besin et al. 1991, Wilhoit et al. 1991, Flinn et al. 1992, Follett et al. 1993, 1995, DeGrandi-Hoffman et al. 1994, Korzukhin and Porter 1994, Flinn and Hagstrum 1995, Gribko et al. 1995, Hagstrum 1996, Regniere 1996, Carter et al. 1998, Throne et al. 1998, Weseloh 1998	McCann et al. 1989, Kemp and Dennis 1991, McKibben et al. 1991, Provencher and Riechert 1994

Nonspatial models are in black; spatial models in blue (see *Spatial Models* section).

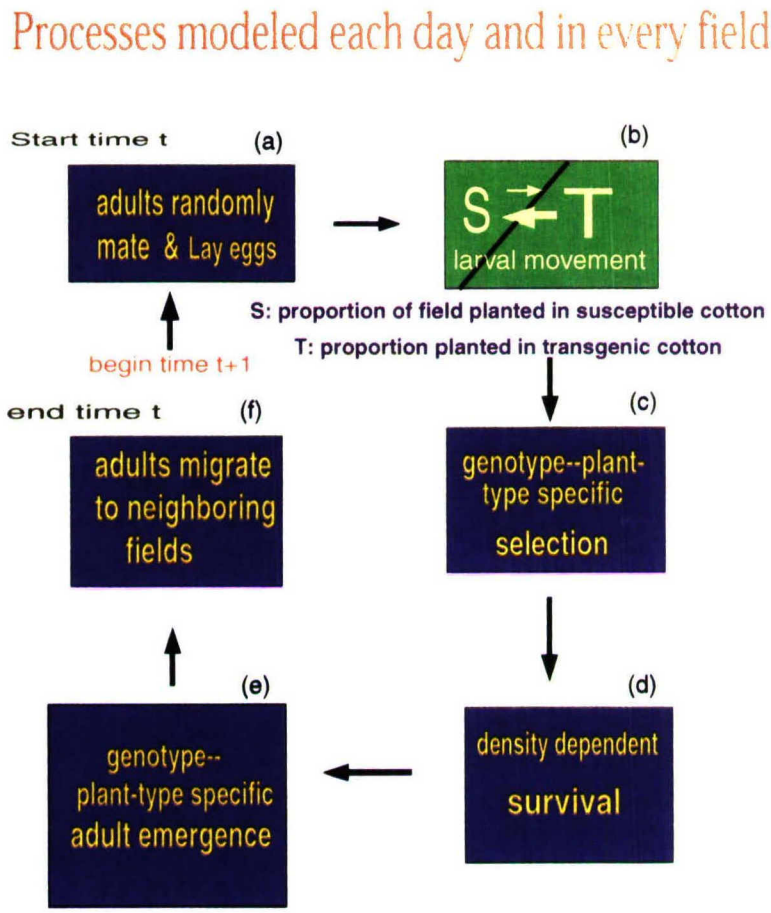

Fig. 2. This spatial model (Peck et al. 1999), which explores the regional development of resistance in *Heliothis virescens* (F.) to a *Bacillus thuringiensis* Berliner (Bt) d-endotoxin in transgenic cotton, has several compartments. In each day and within every field, the activities of the insects are represented in the model by using compartments to handle the separate aspects of their life history. Starting in the upper left-hand corner (a), the insects randomly mate and lay eggs, which are then divided among the plantings of susceptible and transgenic cotton in the field. These eggs hatch and the larvae move between the two crop types (b); the size of the arrows indicate that most movement is from the transgenic crop to the susceptible plants because larvae are more likely to drop once they have tasted the Bt-containing leaves. These events are followed by (c) selection through mortality (based on their allele type and what kind of plant they are on), (d) density dependent survival (if the population is large), (e) plant-type (transgenic or susceptible) specific adult emergence, and (f) migration to neighboring fields, after which a new day begins and the same processes are repeated. Each of these compartments is a separate model that captures a particular life history stage of the insect and then passes the information it has generated to the next compartment. By sharing information among the compartments, the entire life history of the insect can be modeled.

based modeling, but, often higher level languages like C, C++, FORTRAN, PASCAL, or BASIC are used. In particular, object-oriented programming, which is available in some newer computer languages such as C++, provides an excellent environment for rule-based programming. Object-oriented programming languages allow one to define objects with certain attributes and functions that are associated with these objects. For example, I developed a program in C++ that defined insects as one class of objects. Associated with an insect object was its sex, genetic makeup, location on a plant, and its fecundity. Rules associated with the insect-object included how the insect should respond when it met another insect, or move when it was living on a dying plant. The insect objects foraged and moved among plant objects that, in turn, had attributes such as health and a location in the field. It was like having a minimicrocosm in my computer!

Simulation models are relatively easy to produce, largely because they typically are computer programs designed to mimic aspects of a biological system. Nevertheless, their testing and interpretation can be time-consuming. For example, in a complex simulation model of *Heliothis*'s resistance to transgenic cotton (Peck et al. 1999), the model was constructed in just over 1 month, but testing and refining took more than 1 year, thousands of runs, and a substantial investment of time to convince us that the model was doing what we hoped it would do. Most of the hard thinking started *after* the model was written as we devised ways to test the model and sort out its complexities.

The amount of effort to develop the *Heliothis* model is typical of what is required to develop a simulation model. Never let their simplicity to construct lull you into thinking that they are a quick-and-dirty method of exploring complex questions. When done correctly, they can be among the most time-consuming methods of modeling. There has been a lively debate on simulation versus analytic modeling, and the role of population dynamics modeling (Berryman 1991, 1997; Onstad 1991; Logan 1994; Hess 1996a). These articles in the *American Entomologist* describe in detail some of the issues and problems with these two types of models.

Often one will see several of the model types described in this article combined into a larger more complex model. For example, a compartment model will consist of several analytic, and/or simulation models combined to produce a single model. Typically, these are explored through simulation. The analytic models are run in "compartments," and the information from these runs is passed on to other compartments, which in turn model different aspects of the system. The flow of such a model is illustrated in Fig. 2. Each of the compartments is controlled by a mathematical or simulation model that passes information to the next compartment after modeling the processes represented inside the individual compartment.

The Representation of Space in Models

Increasingly, it has been recognized that the spatial dimension in which organisms move plays a major role in ecological processes (Levin 1989, Karieva 1990). Living things move. Individuals, populations, and even entire ecosystems change their location at spatial scales ranging from millimeters to thousands of kilometers. This annoying fact has plagued ecological studies since the time that insects first descended upon our ancestors' plantings of domesticated crops. If living things would just stay put, they would be so much easier to study, understand, and quantify. But they do not—and we just have to deal with it. To understand what effect space has on the dynamics of a population in the field can be challenging. Models,

however, allow the addition of spatial manipulation with comparative ease.

Spatial Models. An important decision for developing spatial models is how space is handled in the model. Space usually is incorporated either implicitly or explicitly. With spatially implicit models, we look at the proportion of sites with a specific attribute but track nothing about actual location or spatial relationships. The most famous of these is Levins' (1969) metapopulation model. A metapopulation is a group of subpopulations connected by the dispersal of individuals among the patches that make up a regional population. Levins proposed a model that followed the change in the proportion of patches that is occupied:

$$\frac{dp}{dt} = mp(1-p) - xp\ .$$

In this model, p is the proportion of patches that is occupied. The parameter m is the movement rate between patches, x is an extinction rate, and t is time. The term on the left, you will recall from calculus, dp/dt is the derivative operator (and if you have forgotten calculus, this gives the slope of p as a function of t, so we know how fast and in which direction p is changing with t). This model predicts that the proportion of occupied patches will stabilize over time to the value $1\text{-}x/m$. For example, if the extinction rate is $x = 0.10$ per time period, and the movement rate is $m = 0.50$, the proportion of occupied patches in this region over the long term would be $1\text{-}(0.1/0.5) = 0.8$. In this model, we do not actually know anything about the location of the patches, and there is nothing in the model about the distances between patches. We only know the proportion occupied—hence, space is implicit, rather than explicit. In these kinds of models, there is no measure of distance or direction between sites.

Spatially Explicit Models. These models incorporate the idea of distance as an aspect in the model (i.e., some places are further away than others). Fig. 3 illustrates several ways space may be represented in a spatially explicit model. All of these models are discrete. In stepping-stone models (Fig. 3 a and b), insects may disperse only to adjacent patches. This implies that for a member of a population at one location, it may take several steps to reach a more distant patch. In an island-continent model (Fig. 3c), all dispersing individuals come from a mainland source and movement among the islands typically is ignored; in an island model (Fig. 3d) the interaction of interest is among islands. Notice that in each of the spatial representations illustrated in Fig. 3, the idea of distance is inherent in the model. Some things are closer to others and this affects the dynamics and behavior of the model.

Metapopulation Models. These models may be implicit or explicit. Metapopulation modeling recently has generated much interest, especially in conservation biology (Hanski and Kuussaari 1995). Formally, a metapopulation (Fig. 3e) is defined as a set of populations distributed over a number of patches that are connected by dispersal

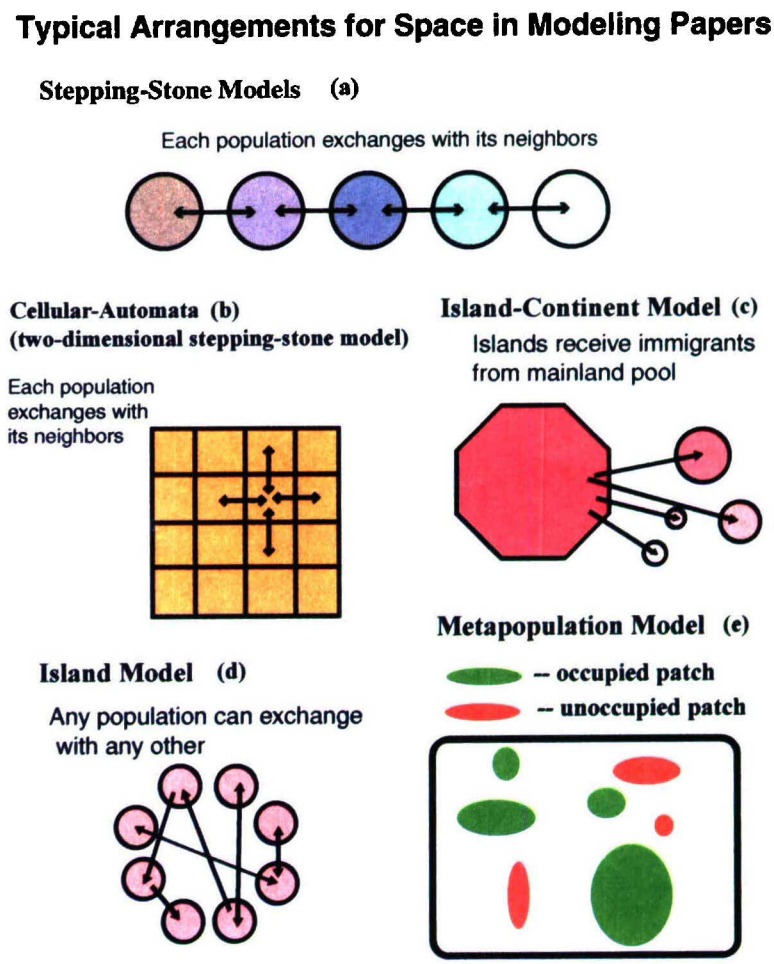

Fig. 3. Space can be handled in a number of different ways. The spatial structure that is used in a model should match the biological process one is trying to capture with the model. In a stepping-stone model (a), populations can exchange individuals with neighboring populations but not with more distant populations. Cellular automata (b) is a two-dimensional spatial model that also incorporates discrete time to signify the model's behavior. These two models (a and b) consider local processes so that changes that start in one population spread more slowly to the rest of the other populations in the region. In an island-continent model (c), exchanges in population only happen in one direction— a large population (the continent) sends out individuals that arrive on the islands. In an island model (d), each of the spatially separated populations can exchange with any other population; however, the rates of exchange can vary among the different populations. In typical metapopulation modeling (e), one is concerned with a population of habitat patches of varying sizes, some of which are occupied and some of which are not.

(Hess 1996b). In metapopulation models, the question of interest often is about exploring the interaction between habitat patches with a viable population and habitat patches in which the population has become extinct. For example, how many metapopulation patches must be occupied with viable populations, and what movement rates among patches are necessary to avoid extinction of the regional population for a given number of years? Moilanen and Hanski (1995) used a metapopulation model to explore the relationship between habitat destruction and the coexistence of two competing populations of butterflies.

Continuous spatial models also play an important part in modeling space. These types of models typically use partial differential equations to express the dynamics of population movement in the model. As with ordinary differential equations de-

scribed earlier, partial differential equations assume that both time and space are continuous, and they have the following form:

$$\frac{\delta b}{\delta t} = \mu \frac{\delta^2 b}{\delta x} + rb ,$$

where b is the population density at location x and time t, m is the dispersal rate, and r is the growth rate. I illustrate this only to give an example of what the equations look like should you come across one while reading a modeling paper. Their full analysis is beyond the scope of this article, but many of the same assumptions hold as in ordinary differential equations and should be stated in the paper. The assumptions should be examined as carefully as any other type of model. The model is deterministic (although stochastic versions do exist) and there are specific tools for evaluating these types of equations.

Tackling the Modeling Paper

Table 1 lists a selection of articles from *Environmental Entomology* classified according to some of the criteria mentioned above. In examining these articles, one should explore their assumptions: Are they clear? What should be added or deleted from the model? What assumptions strengthen the modeler's case? What things weaken it? This table makes it clear that the most common kind of modeling is deterministic simulation models. From a probability standpoint, therefore, these likely are the kinds of models that will cross your desk. These also are the models that require the most careful review from entomologists familiar with the system being modeled.

The first step in evaluating a modeling paper is to determine what questions the authors are trying to address. Why did they write the model? Was it to make predictions for insect control programs? Was it to conduct computer experiments that would be impossible for the real system? Were the authors exploring theoretical questions? How general or specific did they hope to make their results? The answers to these questions will help in assessing the modeler's goals and how well they met them.

The next step is to identify the modeler's assumptions. First, look for the assumptions offered up front (i.e., look for explicit statements about the assumptions). There typically will be statements such as "We assume that the number of eggs laid per female is . . ." Next, list the variables used in the model. This gives you a picture of what aspects of biology are supposed to be included in the model. Determine if important processes appear to be missing. How did the modeler handle space and time? Remember, however, the model always will be a simplification of the real system. The question is thus: Were critical processes omitted?

Next, look at the flow of the model, (i.e., the order that events take place). For example, determine if reproduction precedes or follows movement, which can have profound repercussions on the results (Alstad and Andow 1995). Does feeding come before or after reproduction? Does the order of events mirror the way things really happen in the system being modeled?

Exploring a modeling paper does not mean you need to understand everything about the workings inside of the model. But you should not be intimidated to the point that you ignore the paper because your modeling background is weak (or nonexistent). You can make a real contribution by looking over the details of a modeling paper. It may be that the model never has been explored by someone with your biological insight into the processes being modeled; your comments and questions about how the model works can be a valuable aid to the modeler. The role of the biologist's view of the model cannot be overstated. Otherwise, a model may end up being an exercise in computation only, and of little practical value.

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