Simulating Ecological Complexity Using the Example of Pesticides in Ecosystems

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Many ecological questions are not amenable to investigation with traditional laboratory experiments because the phenomena are too fragile, complex, large or take place over long time scales. Yet it is important that students, both biology majors and nonmajors, be exposed to complex ecological questions and to the methods that can be used to investigate them. An increasing number of ecological problems are highly political, such as acid deposition, global climate change and deforestation. Our citizens need to be well-informed about these problems, including the methods used to reach conclusions about them, to enable them to participate wisely in vital decision-making processes.

An alternative to direct experimentation with such complex systems is simulation modeling. A simulation is a formal representation of a system that changes through time. The system is composed of parts ("compartments") that are interconnected with mathematical equations. The equations represent our understanding of the connections or transfers between the compartments. Each compartment is assigned a starting condition, and the model uses those starting conditions, plus the equations representing compartment interactions, to project the state of the compartments in the future. Such models can readily be used in biology laboratories to give students insights into the workings of the system being studied. On a socio-political level, use of such models in biology laboratories familiarizes students with a tool that is commonly used by scientists and politicians for trying to predict the consequences of alternative future scenarios (e.g. what are likely climatic consequences of a doubling of CO_2 equivalents?).

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Many recent critiques of science education in the United States suggest that teachers and texts focus excessively on memorization of facts at the expense of conceptual understanding and development of higher order intellectual skills, such as critical thinking and problem solving (AAAS 1989, Uno 1990). Allowing students to explore ecological problems with the aid of simulation models can foster development of these reasoning skills. The models provide students with a system about which they can ask questions and develop hypotheses, manipulate in a variety of ways, and then observe and interpret the varied outcomes to understand how the system works. Use of models that simulate current ecological problems can also help students realize that science (its methods as well as its findings) is relevant to their daily lives.

We describe a simulation exercise developed for use in an introductory biology course for nonmajors at Oregon State University. The simulation focuses on control of western spruce budworm (*Choristoneura occidentalis*) in forests of the western United States, however the concepts and educational strategies can be adapted to a wide variety of ecological systems. We use a nonlinear, multivariate simulation model, which gives rich and complex results from a series of simple mathematical equations. The exercise fosters appreciation of the complexity of ecological problems. Further, it introduces the uses and limitations of models, and provides students with an opportunity to improve their problem-solving and reasoning skills.

Recent reviews of educational software have pointed out that, while computers have potential utility for helping students to develop higher order reasoning skills, in practice computers are most commonly used in education for drill/review or tutorial programs (Duhrkopf 1989; Duhrkopf & Bell 1988, 1989). While drill/review and tutorial programs can be useful in helping students to master specific information, such programs do little to strengthen process skills (Duhrkopf 1989; Duhrkopf & Bell 1988, 1989). The exercise described here provides an example of a simulation that is simple to use and that is designed to foster development of the integrative reasoning skills that our students need.

Context for Using the Budworm-Forest Model

The budworm-forest model is introduced after students have been exposed to the basic concepts of ecosystem, community and population ecology, and when they are beginning to explore human impacts on the biosphere. The exercise begins with a question: Why have losses to pests in agriculture and forestry generally not diminished significantly over the last four to five decades, while use of chemical pesticides has increased greatly over that time interval (Pimentel et al. 1984)? The students are given a handout, which provides general background information about western spruce budworm in western forests, including the basic life cycle of the insect, its effects on forests, the history and causes of outbreaks and control attempts in the Pacific Northwest, and the natural regulators of budworm populations (Dolph 1980, Fellin 1983, Fellin et al. 1983).

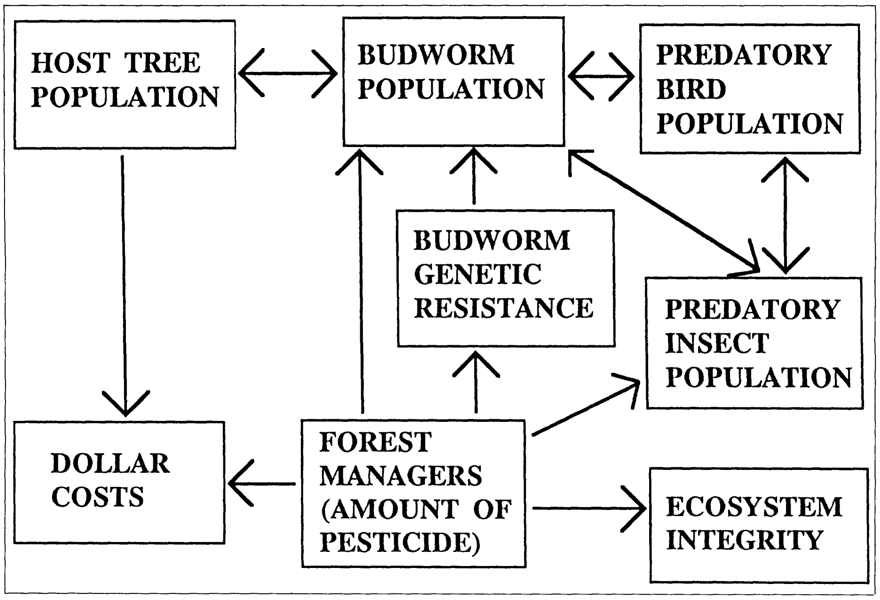

Figure 1. Conceptual model of the western spruce budworm—forest system. Arrows represent the compartment interactions simulated by equations in the model. (For example, budworms influence trees by defoliating them, and trees influence budworms by being their food supply.) The forest manager's decision about how much pesticide to apply is influenced by all compartments, but the decision is reached subjectively, rather than by a formal equation.

How the Model Works

The model represents the spruce budworm-forest system using eight compartments (Figure 1), with equations representing connections between the compartments. The compartments are:

1. Spruce budworm population
2. Host tree population
3. Population of insects that are predatory or parasitic on spruce budworms
4. Population of birds that prey on budworms
5. Budworm genome (represents the proportion of budworms that are genetically resistant to the pesticide)
6. Ecosystem integrity (represents the health of nontarget ecosystem components other than those already represented by compartments
7. Dollar value of losses to budworms plus control costs
8. Forest managers (who decide whether and how much pesticide to use each year).

Technically, the model is based on seven difference equations, most of them nonlinear, with a time step of one year. Most of the equations controlling the compartments are modifications and combinations of logistic equations. [The logistic equation is a simple mathematical model of a population growing from a small initial number to an upper limiting population (the carrying capacity) in a finite environment. For derivation and description of logistic population equations, see Begon et al. 1986 or any introductory ecology textbook.] Equations for most compartments include terms for:

1. The amount in that compartment at the start of each year (= time t)
2. The influences of other compartment(s) on that compartment
3. The potential rate of reproduction of organisms in the compartment.

The equations allow students to calculate the amount in compartments after the passage of one year (= time t + 1), and iteratively into the future. The outcome each year is influenced by the amount of pesticide applied in that year and by compartment interactions.

For population compartments, the next year's population size is affected by survival from the previous year [which is influenced by the amount of pesticide applied and by other compartments (Figure 1)], and by reproduction. For example, the equation for the budworm population compartment is:

The size of the budworm population at the start of the next growing season equals the proportion of budworms that survive due to their genetic resistance to the pesticide and due to chance, times the proportion that survive due to availability of hosts and due to predation by birds and by other insects, times its population size at the start of the previous year plus reproduction within the population.

Survival probabilities are approximations, based, where possible, on information available in literature on western spruce budworm in western forests (Carlson et al. 1983). Nonlinearity results from using the logistic equation to calculate intrinsic population growth for each time step.

Students run the model, first using hand calculators, and later working with a computer version of the model. The computer version allows students to explore outcomes of alternative pesticide spray strategies over many years, while they can only simulate a few years with hand calculations. Nevertheless, we find that the hand calculation portion is invaluable in giving students a dynamic visualization of the compartments and their interactions, as well as an appreciation for the advances enabled by computer simulation.

Running the Model—Hand Calculations

In our laboratory, students work in eight groups, and a group structure is necessary for the first part of the exercise. To demystify the model (and to provide students with practice in simple calculations, which many need) each group represents one of the compartments in the spruce budworm-forest system (Figure 1).

Each compartment (group) is given a starting amount and the equation that represents the influences of compartments that directly affect it, including pesticide spray (Figure 1). Using hand calculators, each group projects its compartment size into the future, with outcomes depending on the pesticide spray strategy used and the responses of the other, interacting compartments.

The equations are generally simple, although they vary in complexity depending on the number of compartments influencing the subject compartment (Figure 1). Freshmen, nonscience majors are able to perform the calculations without undue stress.

As an example, the equation for calculating host population sizes is:

$$H_{t+1} = (1 - 0.05B_t)\left[H_t + rH_t\left(\frac{K - H_t}{K}\right)\right]$$

Where: H_{t+1} = size of host population at start of next growing season (= time t + 1); H_t = size of host population at start of current growing season (= time t); B_t = size of budworm population at start of current growing season; r = intrinsic rate of increase of host population; and K = carrying capacity of the environment for the host.

Compartments that influence one another exchange information about their sizes at each yearly time step, and thus the simulation moves forward in time. Essentially, the room functions as a living computer, with eight parallel processors (the eight student groups, each group hand-calculating parts of the model). Each year, the "forest managers" decide how much pesticide to use in the current year, based on last year's outcomes.

The process works best when the class decides in advance, as a group, what the goals of their control strategy will be. Will they try to completely eliminate the budworms? Will they simply try to reduce the populations to some acceptable level? Will economics be a consideration? Will they consider consequences for other compartments, such as birds or ecosystem integrity? The criteria for "success" are virtually infinite and will usually be different for each group of students. In practice, the class as a whole usually decides on the amount of pesticide to be used each year, keeping their goals in mind, rather than leaving that decision to one compartment or to the instructor. At each yearly time step there is an opportunity for each compartment to analyze its outcome (Why did it increase or decrease, considering what happened in the previous year to the compartments that affected it?), and for the instructor to facilitate a discussion of the changes that occurred in all compartments.

Computer-Assisted Modeling

In a one-hour session, students are usually able to complete only two to three years of the simulation using the hand calculations. During this time, they have usually thought of other pesticide regimes that they would like to simulate, and they have become well-acquainted with the compartments and interactions in the model. Thus, they are primed to begin running the entire simulation using the computer. Each group has its own computer, can devise its own goals and strategies, and can run the entire model for many years, using a variety of spray strategies limited only by their imaginations (and the range of allowable spray amounts; from 0 to 1 kg ha^{-1}). They follow results for every compartment over time, rather than focusing only on one compartment.

Students use the program BUDWORM, an interactive simulator of the spruce budworm-forest system written by Bruce McCune, for use in General Science 101 at Oregon State University. (The program is available from the authors.) The model is written in FORTRAN-77, compiled by Microsoft FORTRAN version 3.2 for MS-DOS-based machines. The program requires very little disk space or memory, but it does require CGA-compatible graphics. (It will run on CGA, EGA or VGA machines.) Because the computations are numeric-intensive, execution is speeded by using a computer with a math coprocessor, but a coprocessor is not required.

The computer model differs in one way from the hand calculations. Realism is improved in the computer model by making budworm outbreaks cyclical, with an outbreak occurring about every 20 years in the absence of spraying. [Western spruce budworms are not strictly cyclical, but they do resurge and wane over variable periods (Johnson & Denton 1975, Carlson et al. 1983, Swetnam & Lynch 1989)]. Cycling is accomplished in the model by varying *r* (the intrinsic rate of increase of the budworm population) in a sine-wave pattern with a period of 20 years. (Because the biological basis of the variations in western spruce budworm populations is not understood, the cycle could not be built mechanistically into the model.) The model begins near the beginning of an outbreak.

The model is simple to run. The model is called by typing, "BUDWORM," and begins in year one. Each year, the user is prompted to enter how much insecticide to spray (by typing a number ranging from 0 to 1), and a graphical representation of results for the various compartments is displayed (Figure 2). Cumulative dollar costs, over the simulation, are also displayed each year. (These costs are approximations based on lost revenues due to budworm-induced death and growth losses of budworm-susceptible tree species, plus the cost of applying pesticide spray.) Beyond the choice of an insecticide amount, the only other option students have in the present version is deciding what to do after 30 years have elapsed. They can continue the simulation where they left off (for 30 years or more), reset everything back to the starting point and run the model again, or quit. The computer prompts them, asking which option they want. More complex versions could allow students to manipulate population parameters, such as *r*, *K* or starting population sizes. For our students, however, such manipulations would probably confuse the central issues addressed by the model.

As with the hand calculations, students benefit most if they decide within their group what their management goals are. A game element can be added if the class sets an overall goal, such as minimizing both cumulative dollar costs and spruce budworm populations over a 30-year simulation, with groups competing to achieve the lowest values. Each group of students records its various strategies and results, and after running several 30-year simulations, presents its best simulation to the rest of the class, including an explanation of why it worked as it did.

Follow-up Questions & Discussion

After running several 30-year simulations using the computer (in practice, for about one hour), the students answer a series of questions about the model and about general issues that it raises. First they are asked to choose one of the spray regimes that their group followed through time and to write an explanation of one compartment's dynamics during that simulation, considering what was happening to the other compartments. In writing their response to this question, their awareness of the multivariate and interactive nature of the system is enhanced. For example, if they answer that the bird population declined in part because its insect prey declined, then they are led to wonder why the decline in its insect prey occurred, and so on through the entire system. They are also asked to list some factors that probably would influence the dynamics of their compartment, yet were ignored by the model. (For example, climatic variations undoubtedly influence bird populations yet were not included in the model.)

Then, we ask them how such a

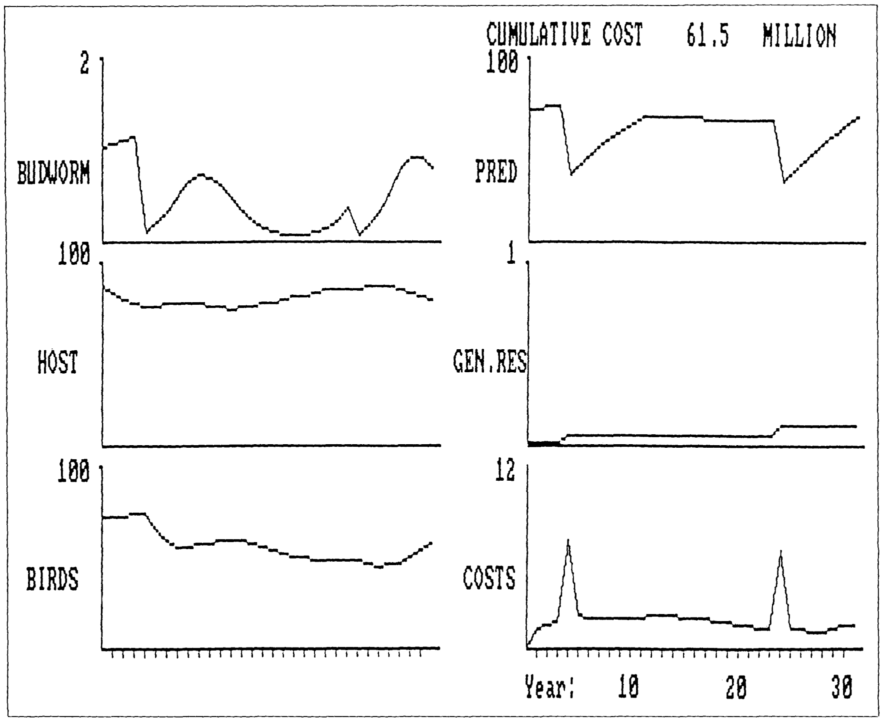

Figure 2. Graphical output from program BUDWORM. The dynamics of each compartment across 30 years are illustrated. In this simulation, pesticide was applied at the maximum possible rate (1 kg ha^{-1}) in years 4 and 24, and no pesticide was applied in other years. The X-axis is time (t to t + 30 years), and the Y-axis is the amount in each of the compartments. Compartments and possible ranges for each are: BUDWORM = budworm population, 0–2 million larvae ha^{-1}; HOST = host tree population, 0–100% of maximum; BIRDS = predatory bird population, 0–100% of maximum; PRED = predatory and parasitic insect population, 0–100% of maximum; GEN.RES = budworm's genetic resistance to pesticide, as a proportion (0–1) of the population; COSTS = dollar costs of losses to budworms and of budworm control projects. (The compartment representing ecosystem integrity is not pictured.) Cumulative dollar costs over the 30-year simulation are displayed at the upper right.

model could be useful to a land manager, such as a regional forester. This usually leads them to the generalization that models are useful in ecology in part because they allow results of various manipulations to be predicted without endangering the ecosystems, without much expense and with freedom from the temporal constraints of real life.

They are asked to use a box-and-arrow systems diagram to summarize the model as a whole (constructing their version of Figure 1, not having seen it), and each group contributes its insights about compartments or interactions that were included in, and ignored by, the model. This helps them to see the complexity of the system visually and to appreciate the difficulties experienced by land managers in integrating diverse considerations into their management decisions.

Using their system diagram, students are asked to identify two examples of negative feedback systems that operate to exert controls over the budworm populations in nature. (For example, budworm population increases cause predatory insect populations to increase, which causes budworm population to decrease.) They are then asked to identify ways in which attempts to control budworms with pesticides might interfere with these negative feedback controls. (For example, pesticides also affect some of the predatory insects, decreasing their importance as a natural control on the budworms.) Thus, they arrive at one of many answers to the question posed in the beginning of the exercise, concerning why chemical control of pests has often not resulted in significant reductions in losses to pests, despite increased rates of pesticide use.

By the end of the three-hour exercise, they have acquired insights about some advantages and disadvantages associated with use of chemical pesticides, about the evolution of genetic resistance, about the role of natural control agents, about economic costs of losses to the budworm and of pesticide application, and about the complexity of ecological systems. They are then asked to pretend that they are attending a public hearing on a plan to spray a national forest for western spruce budworm and to make a list of the questions they would want to ask at the hearing. If they haven't already grasped the relevance of modeling and of understanding complex ecological systems to their lives away from the classroom, this role-playing helps to make those important connections apparent.

We have been using and refining this model for three years, and the graduate teaching assistants who instruct the laboratories have consistently given the exercise very high ratings. It challenges students to think about the issues and processes in a fun and provocative manner, and the students gain factual information about the ecology of the situation, as well as conceptual and reasoning skills. The students also enjoy the activity, usually preferring the computer simulation over the hand calculations. We retain the hand calculations, however; without them, the model would be too much of a black box, and the group interactions and practice at calculation are worthwhile. The students particularly enjoy the game element associated with groups competing to reach the goal(s) set by the class, and this makes the learning process more fun.

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