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Modeling for Synthesis and Integration: Forests, People, and Riparian Coarse Woody Debris

Monica G. Turner

Summary

Many of the most challenging questions in ecosystem science today are posed at intersections between disciplines, scales, and paradigms. Addressing such questions requires synthesis and integration, to which quantitative models can make important contributions. "Synthesis" is derived from the Greek *syntithenai*, meaning "to put together"; integration is the process through which synthesis is achieved. Synthetic or integrative quantitative models are developed to enhance understanding of the system, which can be fostered by formulating appropriate questions. Four ways in which quantitative models contribute to integration and synthesis are: (1) facilitating creative and critical thinking about relationships in a system, (2) comparing alternative ways of conceptualizing a system, (3) identifying principles or relationships that are general across systems, and (4) initiating an iterative process in which models and empirical observation constantly inform one another by developing models at the beginning of a research project. A new simple model integrating land use, natural disturbance, and the dynamics of riparian coarse woody debris (CWD) in northern Wisconsin (USA) was developed as an example. The model simulated relationships among three state variables: the density of live trees in the riparian forest, the density of standing snags, and the density of CWD. Four scenarios were simulated: (1) nominal, (2) single timber harvest, (3) large infrequent wind disturbance, and (4) lakeshore development. Results suggested that riparian CWD could be enhanced and maintained by large infrequent disturbances. Shoreline development always reduced riparian CWD, but the relationship was nonlinear. Shoreline development also had a more persistent negative impact on riparian CWD than did a single large clearcut. The model illustrated the approaches to question formulation; the combination of data and per-

spectives usually considered separately; and the use of synthetic modeling at the beginning of a research project. Synthesis and integration are critical to scientific progress and to finding solutions to many environmental problems facing society. Ecologists should continue to combine quantitative models with observations and experiments in their search for general understanding of ecological systems.

Introduction

Many of the most challenging questions in ecosystem science today are posed at intersections between disciplines, scales, and paradigms. For example, pressing questions regarding global change require integration of natural and anthropogenic processes over a wide array of spatial and temporal scales (Vitousek et al. 1997, National Research Council 2000). Understanding landscape dynamics requires synthesis of knowledge about the environmental template, natural disturbance regimes, successional change, and past, present, and future patterns of human land use (Turner et al. 2001). Improving our understanding of the complex relationships between the land and water, particularly as it influences eutrophication of aquatic ecosystems, is an important goal of both basic and applied ecological research (Carpenter et al. 1995, 1998; Naiman et al. 1998; Naiman and Turner 2000). Synthesis and integration are required to address these and many other fundamental challenges in ecology, and both are also highly prized in science (Pickett et al. 1994).

Simulation models can make important contributions to synthesis and integration. Many scientists have considered the role of models in science in general and ecology in particular (e.g., Holling 1978, Kitching 1983, Swartzman and Kaluzny 1987, Starfield and Bleloch 1986, Starfield et al. 1994, Grant et al. 1997, Ford 1999). Methods of problem solving, including models, were categorized by Holling (1978) relative to level of understanding and data availability (Figure 6.1). Mathematical models can often be developed and solved analytically if the structure and general dynamics of a system are well understood and there are good data on the important processes occurring within the system. Statistical analyses can be used to search for patterns that will lead to hypotheses about the nature of the underlying processes when good data are available but understanding is lacking. Systems analysis and simulation can be used to investigate hypotheses about how a system works if there are relatively few data but at least some understanding of system structure and dynamics (Figure 6.1). Models were also identified, along with long-term observation, ecosystem experiments, and comparative studies, as one of four key approaches to learning about ecosystems (Carpenter 1998).

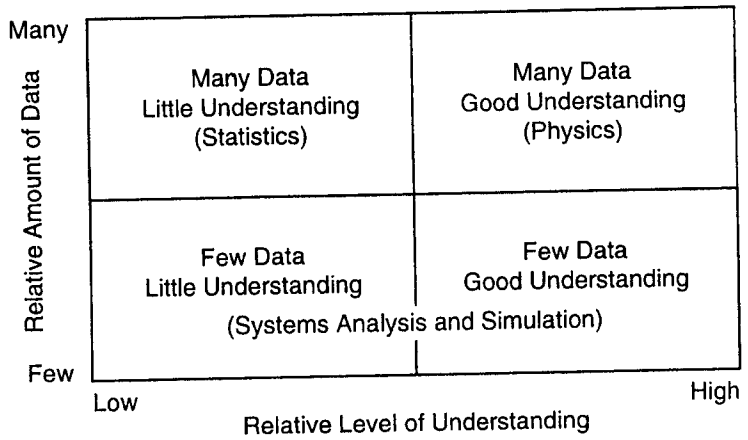

Figure 6.1. Comparison of methods of problem solving in terms of the relative level of understanding and the relative amount of data available about the system. (Modified after Holling 1978; Starfield and Bleloch 1986; and Grant et al. 1997.)

In this chapter, I will emphasize the use of simulation models in synthesis and integration while recognizing the importance of other approaches and models to problem solving. I will begin by defining synthesis and integration, then discuss ways in which questions can be formulated such that the likelihood of achieving synthesis is enhanced. I will next consider four ways in which quantitative models can contribute to synthesis and integration in ecology, using a variety of examples from the literature. Finally, to illustrate these points, I will present a new model developed to explore the dynamics of riparian coarse woody debris for lakes of northern Wisconsin, USA, in response to alternative land-use and disturbance scenarios.

Synthesis, Integration, and Question Formulation

What are synthesis and integration, and how do they differ from other goals of ecological models? The terms are defined in *Webster's New Collegiate Dictionary* (1981) as follows:

> Synthesis: [from Greek *syntithenai*, to put together] 1: a: the composition or combination of parts or elements so as to form a whole, b: the combining of often diverse conceptions into a coherent whole. 2: a: deductive reasoning, b: the dialectic combination of thesis and antithesis into a higher stage of truth.

Deductive reasoning: the deriving of a conclusion by reasoning, specifically, inference in which the conclusion follows necessarily from the premises.

Dialectic combination: any systematic reasoning, exposition, or argument that juxtaposes opposed or contradictory ideas and usually seeks to resolve their conflict; an intellectual exchange of ideas.

Integration: the act or process of integrating, which means 1: forming or blending into a whole. 2: a: uniting with something else, b: incorporating into a larger unit.

These definitions are consistent with those of systems ecology, systems modeling, and simulation modeling (von Bertalanffy 1968, 1969; Watt 1968; Van Dyne 1969; Patten 1971; Ford 1999). In ecology, integration entails the combination of existing data, perspectives, approaches, models, or theories that are apparently disparate (Pickett et al. 1994) and is the process through which synthesis is achieved. Integration may be additive or extractive (Pickett et al. 1994), but it requires the combination of two or more different areas of understanding to produce new understanding. Integration can occur at any scale or breadth of scope, but many novel attempts in ecology have involved larger scales or levels (e.g., landscape ecology). Integration will be limited if theory in one or more areas is not well developed or if no common currency can be found between the two areas (Pickett et al. 1994).

How can models be developed such that the likelihood of achieving integration and synthesis are enhanced? All models must be question-driven, and models developed for synthesis and integration are no exception. One cannot just "do synthesis" without a clearly stated purpose. Therefore, question identification is a key step in the modeling process—perhaps *the* key step. Model objectives provide the framework for model development, the standard for model evaluation, and the context within which simulation results must be interpreted. Thus, stating questions clearly is arguably the most crucial step in the entire modeling process (Grant et al. 1997).

I suggest three general ways to formulate questions to enhance opportunities for integration:

1. Questions posed at the intersection of two or more phenomena require integration of different lines of inquiry. For example, how does x influence, constrain or alter y, where x and y are different ecological phenomena? What are the feedbacks from y to x?

2. Questions exploring a wide range of conditions often require integration and recognize multiple outcomes. For example, what combinations of conditions might produce particular outcomes (i.e., states, flows, or dynamics)? Can multiple pathways produce the same result? Are there thresholds that produce qualitatively different outcomes? A state space can often be used to depict alternative ways of obtaining particular outcomes, as done by Turner et al. (1993) for the effects of disturbances of different size and frequency for landscape dynamics.

3. Questions about the relative importance of different factors require synthesis of existing knowledge. For example, what is the relative importance of two or more potentially influential drivers on the outcome of a system? Under what conditions are some processes more important than others? Such formulations allow a model to be exercised in an experimental mode (e.g., factorial simulation experiment) and the output analyzed similarly to experimental data. The relative importance of fire size, fire spatial pattern, and winter severity for wintering elk and bison in Yellowstone National Park were evaluated by using an integrative simulation model (Turner et al. 1994). Results from such models can also identify important avenues for empirical study.

Question identification and the subsequent development of the conceptual or qualitative model are perhaps the most intellectually challenging phases of modeling. This phase includes identification of system boundaries, defining model components, identifying the relationships among them, and describing expected patterns of behavior. These are key phases of model development in which opportunities for synthesis and integration can be created.

Quantitative Models in Synthesis and Integration

Simulation models have been widely used in many areas of ecosystem ecology for several decades. In this section, I will highlight four ways in which quantitative models have contributed to synthesis and integration in ecology. Examples are presented to illustrate these uses; these examples are illustrative rather than exhaustive.

Creative and Critical Thinking

Creative and critical thinking about the relationships among parts of a system that might otherwise be considered separately can be represented in a model so that the logical outcome of the representation can be explored. Models of the causes and consequences of land-use change provide excellent examples of the synthesis of subject areas typically considered separately. Understanding land-use changes and their ecological implications presents a fundamental challenge to ecologists, but it requires integrating knowledge from both the social and natural sciences; humans respond to cues from the physical environment and from sociocultural contexts (Riebsame et al. 1994). In addition, forecasting the

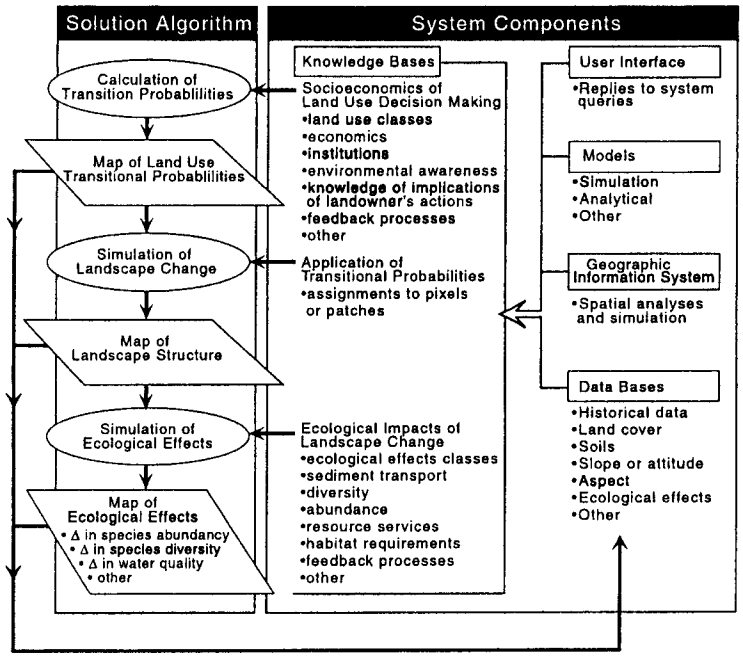

Figure 6.2. Conceptual model of land-use change and ecological responses in temperate forested landscapes of the United States (modified from Lee et al. 1992; reproduced from Turner et al. 2001.)

ecological consequences of land-use change demands integration among traditionally distinct subdisciplines in the natural sciences.

A conceptual model (Figure 6.2) developed by an interdisciplinary group of scientists laid the framework for addressing the causes and consequences of land-use change in temperate forested landscapes in the United States (Lee et al. 1992). This model set the stage for a group of studies in the southern Appalachian Mountains (USA) that quantified land-cover changes (e.g., Turner et al. 1996), related land-cover changes to other ecological response variables (e.g., Harding et al. 1998; Pearson et al. 1998; Wear et al. 1998; Pearson et al. 1999), and explored simulation methods for projecting future landscape patterns (e.g., Wear and Flamm 1993; Flamm and Turner 1994; Wear et al. 1996; Wear and Bolstad 1998). Results demonstrated strong interactions among environmental gradients and social, economic, and aesthetic variables in explaining and prediction land-use patterns. In addition, the likelihood for development to concentrate in riparian areas was suggested (Wear and Bolstad 1998), with important implications for water flow and quality (Wear et al. 1998).

A common theme underlying many studies of land–water interactions is the degree to which upland land uses and their spatial arrangement influence water quality. A simple model of phosphorus (P) transformation and transport for the Lake Mendota watershed, Wisconsin (USA) has provided useful insights into these relationships (Soranno et al. 1996). The watershed of Lake Mendota is dominated by agricultural and urban land uses, and the lake itself has a long history of limnological study (Brock 1985, Kitchell 1992). Soranno et al. (1996) developed a Geographic Information Systems (GIS)-based model of phosphorus loading in which phosphorus-export coefficients varied among land uses. The model was used to compare phosphorus loadings in Lake Mendota under current patterns of land use, presettlement land use, and projected future land use in which the urban area increased nearly twofold. Because rainfall events drive runoff, simulations were conducted for both high- and low-precipitation years. Results demonstrated that most of the watershed did not contribute phosphorus loading to the lake; most P came from a relatively small proportion of the watershed, ranging from 17% of the watershed contributing during low-precipitation years to 50% during high-precipitation years. A six-fold increase in phosphorus loading was estimated to have occurred since settlement.

Land-use models that truly integrate social, economic, and ecological considerations are in their infancy, and there is no consensus on how to best approach this task (Dale et al. 2000). Recent models of land-use change (e.g., Lee et al. 1992; Dale et al. 1993, 1994; Riebsame et al. 1994; Turner et al. 1996; Wear et al. 1996, Wear and Bolstad 1998) often seem simplistic, but they are at the forefront of integration between disciplines that are usually treated separately. Understanding how many diverse factors interact to determine land-use patterns and how ecosystems respond over a range of temporal scales remains a key challenge facing the scientific community and for which models must play an important role.

Alternative Ways of Conceptualizing a System

Seemingly contradictory alternatives, or the implications of alternative ways of conceptualizing a system, can be studied using quantitative models. The same questions or phenomena are often addressed very differently by different modelers. Which models will be most consistent or perform well under what conditions? How much information must be represented in each formulation? Can information be integrated across scales?

The Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) offers an example of the comparative use by many investigators of different models that were developed to address the same general phenomena. In one set of planned comparisons, the responses of net primary productivity (NPP) to doubled CO_2 concentrations (from 335 to 710 ppm) were projected using three biogeochemistry models (Pan et al. 1998). Results found projected increases in NPP of 11% using BIOME-BGC (Running and Coughlan 1988, Running et al. 1989), 5% using CENTURY (Parton 1988), and 8% using the Terrestrial Eco-

system Model (TEM; Raich et al. 1991; Melillo et al. 1993). The models found a negative relationship between precipitation and NPP in all three models, but the relationship between temperature and NPP differed among the models. Each model contained slightly different mechanisms, reflecting, in part, conceptual uncertainty about what controls NPP. Thus, the model comparison project required a highly coordinated, integrated research effort, and results were instrumental in identifying key areas of scientific uncertainty.

Identifying General Principles or Relationships

Models can be used to identify principles or relationships that are general by applying the same model (or suite of models) to different ecological systems. Because of the time required to develop and test complex ecological models, other researchers often apply existing models to new study areas. Models that have been widely used include the JABOWA and FORET models (Botkin et al. 1972; Shugart and West 1977, 1980), CENTURY (Parton et al. 1988), BGC (Running and Coughlan 1988; Running et al. 1989), and many others. Widespread applications of the same model offer opportunities for synthesis of patterns or processes in many different ecosystems or geographic locations within the same ecosystem type. In particular, situations in which the model fails may be most instructive in identifying the limits of applicability of the processes or boundary conditions represented in the model.

One example of widespread application of an ecosystem model is that of CENTURY (Parton et al. 1988), which has been used in many ecosystem types and many locations worldwide. Along a boreal forest transect study in Canada, predictions from CENTURY were tested against field data to explore the sensitivity of carbon dynamics to climate change (Peng et al. 1998; Peng and Apps 1998). The study found that the effects of climate change and enhanced CO_2 concentrations were not simply additive and that they varied along the gradient. Climate change alone would increase total carbon in vegetation but decrease total soil carbon. Increased CO_2 concentrations under current climate would increase total carbon in both vegetation and soil. When both effects were combined, NPP and decomposition both increased, resulting in a decline in soil carbon. Application and testing of the model in varying locations produced qualitatively different insights that could not be obtained by exercising the model at only one location.

Given the widespread use of several influential ecological models, there is a paucity of attempts to synthesize the general knowledge that has been obtained from these many applications. As for many areas in ecology (Baskin 1997), there are numerous opportunities for synthesis and integration of existing modeling results.

Developing Models Early in Research

Models can be used effectively as an exploratory tool at the beginning of a research project, even when data are scarce, to draw inferences about the logical outcomes that follow from the premises. Modeling can then be used to guide empirical study, beginning an ongoing interplay between the model and the data. Developing the conceptual model and exercising it provide a foundation upon which knowledge of the system can build. In this way, the model is not considered to represent final understanding but rather serves as a heuristic device designed to be modified iteratively as research continues. The model presented next illustrates this use of models.

Case Study: Modeling the Dynamics of Riparian Coarse Woody Debris

Coarse woody debris (CWD) is a critical linkage between terrestrial and aquatic ecosystems (Harmon et al. 1986; Murphy and Koski 1989; Gregory et al. 1991; Naiman et al. 2000). Riparian CWD is produced when trees die and fall into a lake, and it provides critical habitat for fishes and other aquatic organisms. In particular, recruitment dynamics of dominant fishes may depend on the physical heterogeneity provided by CWD, which in turn affects entire food webs (Carpenter and Kitchell 1993). The amount of CWD in lakes is determined by the balance between inputs (which depend upon the presence of riparian forest and its composition and structure), decomposition, and removal processes. Tree death may be gradual, as individuals age and senesce, or punctuated by events such as fires, blowdowns, or other natural disturbances that affect large areas and produce pulsed inputs of CWD. The natural dynamics of CWD accumulation are slow, with inputs and decomposition operating over time scales of decades to centuries (Stearns 1951; Hodkinson 1975; Harmon et al. 1986).

Development pressure has increased housing density in many areas that offer appealing natural amenities, such as mountains, coastal areas, and lakes. Land-use development in Vilas County, northern Wisconsin (USA) is one example. Vilas County contains over 1,300 lakes ranging in size from 0.1 to greater than 1,500 ha and covering 16% of the county's surface area. Housing density in Vilas County has increased rapidly since the 1960s, and over half of the new homes were built on the lakeshore (Schnaiberg et al. in press). Furthermore, if the current building rate persists, all undeveloped lakes not in public ownership could be developed within the next twenty years (Wisconsin Department of Natural Resources 1996).

Lakeshore development is negatively related to riparian CWD at the whole-lake scale (Christensen et al. 1997). Humans affect riparian CWD by direct removal to maintain beach areas and boating access. In addition, studies of aesthetic preferences in riverine landscapes have shown preferences for wooded stream channels that do not contain in-channel debris (e.g., Gregory and Davis 1993). Humans also alter the riparian vegetation, for example, by thinning the forest or removing snags, thereby modifying inputs to CWD (e.g., Harmon et al. 1986; Maser and Sedell 1994). The net effect of lakeshore development is

the uncoupling of the natural relationship between riparian vegetation and aquatic CWD (Christensen et al. 1997).

The forests surrounding the lakes of Vilas County have changed significantly since European settlement. Much of the northern forest was a hardwood-conifer mix of Eastern hemlock (*Tsuga canadensis*), birch (*Betula* spp.), and maple (*Acer* spp.), with pines (*Pinus* spp.) occurring on the sandy glacial-outwash plains (Curtis 1959). The presettlement disturbance regime was characterized by small gap disturbances along with infrequent, large disturbance events (Canham and Loucks 1984, Frelich and Lorimer 1991). Timbering began in the mid-nineteenth century and increased dramatically during the 1880s with construction of railroads. Most of the forest had been cut by 1900, and timber production declined rapidly due to resource exhaustion (Bawden 1997). Paleoecological studies suggest that this forest harvesting altered the physical structure of the lakes and disrupted the primary producer communities for more than 100 years (Scully et al. 2000). Tourism developed alongside reforestation, beginning with wealthy urban vacationers in the 1920s and evolving to include large numbers of recreational homes and retirees (Gough 1997; Voss and Fuguitt 1979). A long-term and retrospective study of the forest community indicates substantial shifts in composition of riparian forest in Vilas County (Stearns and Likens 2002).

Relatively little is known about the long-term dynamics of production and accumulation of riparian CWD in lakes. A recent modeling study suggested that natural catastrophic disturbances (severe, large-scale events that result in replacement of the riparian forest) could significantly bolster riparian CWD recruitment in streams (Bragg 1997). Compared to undisturbed old-growth forest, large natural disturbances increased the temporal variability and net delivery of CWD, whereas clearcutting reduced both delivery and net amount for many years (Bragg 1997). Natural disturbances in north temperate forests (e.g., large blowdowns in northern Wisconsin occurred in July 1977 and in the Boundary Waters Canoe Area in July 1999) produce large quantities of CWD that may persist in lakes for many centuries.

Question Identification

Predicting the dynamics of CWD requires integrating knowledge of the riparian forest, the natural disturbance regime, human settlement patterns and land-use practices, and the fate of downed wood. A new collaborative, inter-disciplinary study is addressing these issues for lakes in Vilas County using comparative studies, whole-lake experiments, and simulation modeling (see http://biocomplexity.limnology.wisc.edu). To explore the logical outcomes of hypothesized relationships among key components of the riparian system, I developed a prototype of a simulation model that will address the following questions. These questions also illustrate the approaches to question formulation described earlier in this chapter.

1. Is accumulation of riparian CWD a function of small, continuous inputs (e.g., small frequent disturbances), or is it dominated by occasional large pulses (large infrequent disturbances)? I hypothesize that under presettlement natural disturbance regimes, CWD will increase because rates of inputs (both pulsed and gradual) will exceed rates of decomposition and loss to depth by physical transport.

2. What is the effect of timber harvesting and shoreline development on the long-term rhythm of forest development and CWD? I hypothesize that a single timber harvest, such as the turn-of-the-century clearcut, will produce a period of several decades during which the source of CWD will be absent. CWD will decline but then gradually recover. However, with lakeshore development, CWD removal by humans will deplete the long-term resource of CWD while simultaneously reducing the source habitat. Christensen et al. (1997) estimated that it would take approximately 200 years to replace the deficit in CWD density in densely settled lakes. Therefore, I hypothesize that shoreline development will produce long-term declines in CWD abundance that are proportional to the amount of lakeshore developed. Alternatively, particular spatial locations such as sheltered coves may be the primary sources of CWD for the lake as a whole. Loss of riparian forest cover in these critical locations may result in dramatic losses of CWD for the lake, even if other areas of riparian forest remain intact.

3. Under what conditions will CWD fall below critical densities for fish populations? The abundance of CWD required to sustain fish populations over the long term is not known. Detecting such a threshold is complicated because there may be considerable time lags before the effect on fish populations are detected. Depending upon interactions between the slow and fast variables controlling the system, CWD may be pushed below the critical depensation level for fishes. There is evidence from the physical and ecological sciences for nonlinearities in pattern and process related to the thresholds in the area occupied by an entity of interest, such as a land cover type (Stauffer 1985; Stauffer and Aharony 1992; Gardner et al. 1987; Turner et al. 1989; With and King 1997). If gradual changes in riparian land use cause a threshold to be passed either in proportion of lakeshore that is forested or by removal of critical source areas, the fisheries may collapse. Such responses may show strong time lags related to tree life spans and the persistence time of CWD in the lake.

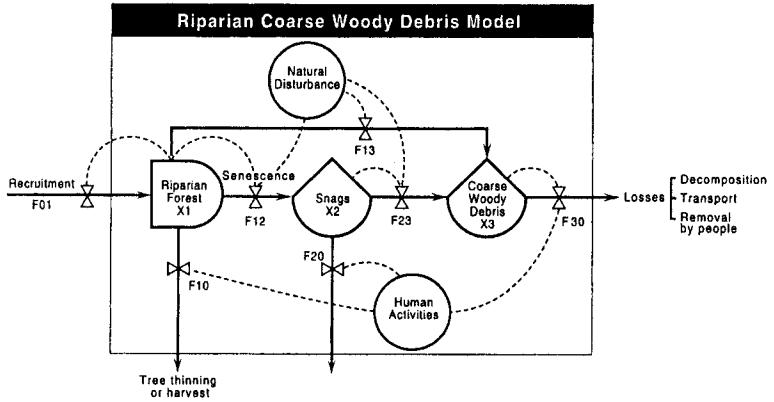

Figure 6.3. Conceptual diagram of the model developed to simulate the dynamics of riparian coarse woody debris (CWD). Flows from compartment i to compartment j are labeled Fij.

Model Structure

The model was purposefully designed to be a simple representation of forest dynamics and the production and accumulation of riparian CWD through time as influenced by natural disturbances and by changes in land use and land cover. Major state variables, flows and controls represented in the model are depicted in the model diagram (Figure 6.3). Spatially, the model considers only the riparian zone of a single lake, defined as the area extending 10 m upland of the lake perimeter; variables and parameters are normalized for 1 km of lake perimeter or 1 ha of riparian shoreline (e.g., 1000 m × 10 m). The model formulation does not vary with lake size. Temporally, the model employs a discrete time step of 1 yr and is run for 200 yr. Initial conditions for the model assume a well-developed forest (not early succession) with live-tree density at steady state.

Three state variables are represented: X1, the density of live trees in the riparian forest; X2, the density of standing snags in the riparian zone; and X3, the density of CWD in the riparian zone. Flows between compartments link these three variables (Figure 6.3). Riparian forest development (F01) is represented deterministically, and these trees may have several fates. They may die and become snags (F12), be blown down, thus bypassing the snag phase and becoming CWD directly (F13), or be removed by humans (F10). Similarly, snags may also be removed by humans (F20) or be converted to CWD when they fall to the ground (F23). Thus, CWD has inputs from the snags and live trees (F23 and F13, respectively). Losses of CWD (F30) occur through decomposition, physical transport to deeper locations in the lake, and direct removal by people.

Changes in the state variables are represented by three equations:

$$dX1 / dt = F01 - F12 - F10 - F13 \quad (6.1)$$
$$dX2 / dt = F12 - F23 - F20 \quad (6.2)$$
$$dX3 / dt = F13 - F23 - F30a - F30b - F30c \quad (6.3)$$

Each flow in the model is represented as follows, with parameter values and sources as shown in Table 6.1.

F01 = RECRUIT * X1, unless time since disturbance or clearcut is less than STAND_RECOV, in which case F01 = 0. Thus, there are no successional processes represented in this initial model. Rather, recruitment of trees into the forest is assumed to occur at a steady rate as a function of the current density of trees.

F12 = X1 * SENES, where tree death is also assumed to be a steady rate that is balancing tree recruitment. However, if a large, infrequent disturbance is simulated, then SENES increases during that event such that 25% of the remaining trees are killed but not toppled and become snags.

F10 = X1 * THINNING * P_DEVEL, representing the thinning of the forest by humans in the presence of shoreline development. A constant rate of thinning is applied until a threshold stand density is reached, after which no more thinning occurs. Thinning is applied only to the proportion of shoreline developed. However, if a clearcut event is simulated, then there is a pulsed event in which a large proportion of the standing forest is removed around the entire lake.

F13 = X1 * TREEFALL. Under nominal conditions, this flow is zero. However, when a large, infrequent disturbance is simulated, there is a pulsed flow of live trees directly to the CWD component, X3.

F23 = X2 * SNAGFALL. Under nominal conditions, snags fall to the ground and become CWD at a steady, relatively low rate. However, if a large infrequent disturbance occurs, snagfall increases during the event.

Table 6.1. Variables and parameters used in the initial model of riparian coarse woody debris dynamics.

Variable	*Description*	*Units*	*Initial Condition*	*Source*
State Variables				
X1	Density of live trees > 5cm dbh	number/ha	Random value ranging from 1000–2000 ha	Christensen et al. 1996; range of densities for undisturbed lakes.

Table 6.1. *Continued*

Variable	*Description*	*Units*	*Initial Condition*	*Source*
X2	Density of standing snags	number/ha	100/ha	Christensen et al. 1996, for undisturbed lakes.
X3	Coarse wood debris > 5cm dbh	number/km of shoreline (~ha)	500/ha	Christensen et al. 1996, for undisturbed lakes.
Rates of Natural Processes				
RECRUIT	Annual recruitment rate of stems > 5cm dbh under steady-state	yr^{-1}	0.005	Set to balance senescence (Frelich and Lorimer 1991, Runkle 1982, 1985); assumed 200-year return interval for gap formation.
SENES	Tree senescence rate	yr^{-1}	0.005 as nominal rate; set to 0.25 with a LID	Set to balance recruitment (Frelich and Lorimer 1991; Runkle 1982; 1985).
SNAGFALL	Rate of snags falling over and becoming CWD	yr^{-1}	0.04 as nominal rate, but set to 0.90 if a large, infrequent disturbance (LID) occurs	Estimated; Christensen et al. (1996) report that ~2.52 pieces of CWD were added per year to the undisturbed lakes; if a major windstorm occurs, this assumes that 90% of the standing snags will fall over.

Table 6.1. *Continued*

Variable	*Description*	*Units*	*Initial Condition*	*Source*
TREEFALL	Rate at which live trees fall to the ground and become CWD, bypassing the snag stage	yr^{-1}	0.0 as nominal rate, assuming trees die, remain snags for some time, then fall over; 0.75 when a LID occurs	Estimated based on windstorm events elsewhere (e.g., Turner et al. 1997).
STAND_ RECOV	Time for stand to re-cover to its predisturbance density of trees > 5cm dbh	yr	60	Estimated.
DECOMP	Rate at which CWD decomposes	yr^{-1}	0.01 yr^{-1} as nominal rate, reduced to 50% of this rate following a LID	Estimated; decomposition is very slow, but rates are not known; assumes 100 years.
TRANSPORT	Rate at which CWD is transported to depth by wind, currents, etc.	yr^{-1}	0.01 yr^{-1}	Estimated; some logs are moved around and transported out of the littoral zone.
Rates of Human Processes				
CWD_ REMOV	Rate at which humans remove riparian CWD	yr^{-1}	0.00 yr^{-1} with no development, 0.10 yr^{-1} for developed lakeshore	Assumed that humans remove 10% CWD per year from the riparian when development occurs; thus, all CWD is removed within 10 years.

Table 6.1. *Continued*

Variable	*Description*	*Units*	*Initial Condition*	*Source*
THINNING	Rate at which live trees are thinned from the surrounding forest, occurring only when land-use development has occurred	yr^{-1}	0.0 if there is no development; 0.01 yr^{-1} for areas that are developed if tree density is ≥ 800/ha	Christensen et al. (1996) report tree densities of at least 800/ha within the forested areas even of lakes that are developed.
SNAG_ REMOV	Rate at which human cut and remove standing snags	yr^{-1}	0.00 yr^{-1} with no development, 0/01 for developed lakeshore	This assumed that people would remove 10% of the standing dead trees annually, assuming they don't want them to fall on their structures.
P_DEVEL	Proportion of the lake that is developed	Unit less	Varies between 0–1.0	Set by the user for simulation.

F20 = X2 * SNAG_REMOV * P_DEVEL. If shoreline is developed, then this flow represents the removal of snags by people only in the proportion of shoreline that is developed. People remove snags that may endanger their buildings or property. However, if a clearcut is simulated, then F20 = X2 during that event, which assumes that all snags are removed during the clearcut.

Losses of CWD are represented by three flows:

F30a = X3 * DECOMP
F30b = X3 * TRANSPORT
F30c = X3 * CWD_REMOV * P_DEVEL

Decomposition and transport are modeled as constant proportions of the CWD present during a given time period. However, if a large infrequent disturbance occurs, then DECOMP is reduced by 50% because much of the wood will be elevated and not in contact with the soil, thereby slowing decomposition. Direct losses of CWD due to human actions are simulated when some proportion of the shoreline is developed. A constant rate is assumed but applied only to the proportion of shoreline developed.

Scenarios

The model was used to simulate the abundance and temporal dynamics of riparian CWD under four scenarios: (1) nominal, assuming small, frequent gap disturbances that represent the dominant natural disturbance regime; (2) a single extensive timber harvest as occurred during nineteenth-century logging; (3) a single large, infrequent wind disturbance (e.g., a tornado or the 1999 storm in the Boundary Water Canoe Area, Minnesota); and (4) lakeshore development, with proportions of the lakeshore developed varying from 0.10 to 1.0. Small frequent disturbances were modeled to produce gradual inputs and losses of CWD, and stochastic catastrophic disturbances were modeled (e.g., Canham and Loucks 1984; Frelich and Lorimer 1991; Cardille et al. 2001) to produce large pulses of CWD and reset the riparian forest to a pioneer stage. Human settlement influenced the abundance and structure of the riparian forest by reducing the proportion of the lakeshore in riparian forest, reducing tree density, and eliminating standing snags in the remaining forest.

Sensitivity Analysis

A simple sensitivity analysis was conducted to assess model response to variation in the parameter set. Parameter values (Table 6.1) were estimated using existing literature or by assigning reasonable estimates based on expert opinion; none were derived directly from empirical data obtained specifically for this model. Field studies begun during summer 2001 will be used for these purposes in the future. Sensitivity of model results to parameter values was determined by varying selected individual parameter values while holding all other parameter values constant. The initial density of the forest was fixed at 1,500 stems/ha for all sensitivity analyses.

Results

Nominal scenario. Depending on the initial tree density obtained at random, snags and CWD both increased to varying degrees during the simulation. The model was stable, by design. A steady-state condition was generally obtained before 100 yr (Figure 6.4a), with that time being slightly longer for higher initial values of X1 and shorter for the lower values. Higher tree densities in the forest produced a greater abundance of CWD, but CWD always remained at or above initial conditions.

Single extensive timber harvest. Immediately following the single clearcut simulated in model year 50, the density of live trees and snags declined dramatically (Figure 6.4b). After the recovery period, during which I assumed the trees had regrown and achieved a minimum dbh of 5 cm, the density of snags and CWD both began to increase. The CWD recovered from the clearcut scenario in approximately 90 yr. Standing snags took a bit longer to recover. Interestingly, the steady-state density of CWD achieved after the clearcut was always greater than the initial value of CWD.

Large, infrequent disturbance. The occurrence of a single catastrophic blowdown during model year 50 caused a dramatic decrease in the density of live trees and snags and a very large increase in the abundance of CWD (Figure 6.4c). Levels of CWD remained elevated for a relatively long time. Following a decline of CWD for about 150 yr through decomposition and transport to depth, CWD density reached a new steady state that was maintained at or above initial values. Riparian forest and snag density returned to and maintained levels comparable to their initial conditions.

Lakeshore development. CWD always declined with simulated lakeshore development, but the temporal dynamics and steady-state value of snags and CWD varied with the proportion of shoreline development. Furthermore, the relationship between steady-state CWD abundance and shoreline development was nonlinear. If only 10% of the shoreline was developed, CWD declined but stabilized within about 75 yr (Figure 6.5a). With 20% developed, snags and CWD declined quickly, but remained above zero. With 30% developed, CWD was reduced to very low levels within 75 yr, as were snags. As increasing proportions of the lake were developed, the low (near zero) values of CWD were obtained in shorter and shorter time intervals (Figures 6.5b and 6.6). The model still produced stable outcomes (Figure 6.6a) because live forest tree density was maintained well above zero, providing a constant source for CWD and snags. However, CWD density approached zero asymptotically as the proportion of lakeshore developed neared one, and CWD density was very low when 60% or more of the shoreline was developed.

The threshold densities of CWD required to maintain fish populations are not known. However, I examined the conditions under which CWD densities declined to less than 100/ha as a means to explore the potential for threshold dynamics. If the developed shoreline was less than 30%, CWD did not fall below this threshold. If the developed shoreline was greater than or equal to 30%, then this threshold was exceeded in varying amounts of time, ranging from 47 yr with 30% developed to 11 yr with the entire lakeshore developed. These results suggest the potential for complex responses to occur within the system, driven in part by time lags in cause and effect that may be amplified by fish population dynamics.

Model sensitivity. Among the parameters tested, the model was very sensitive to the rate of CWD removal by humans, suggesting that this rate should be estimated with reasonable confidence in future empirical studies. Model results were not sensitive to variation in the decomposition loss parameter or physical transport loss parameter. For example, varying the rate of CWD removal from 0.02/yr to 0.20/yr produced variation from 50 to 175/ha in the steady-state value of CWD. In contrast, variation in the decomposition rate from 0.01 to 0.12/yr produced variation of only 80–90/ha in steady-state CWD.

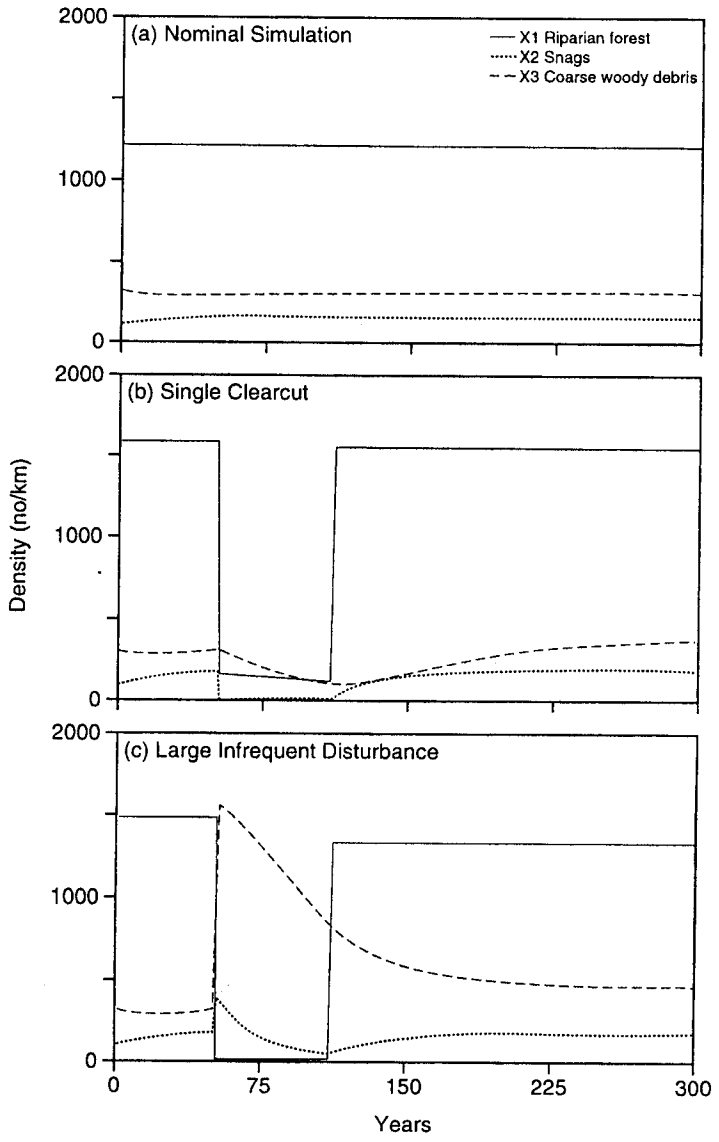

Figure 6.4. Representative simulations from each of three model scenarios: (a) the nominal scenario, which assumes small gap disturbances; (b) the single large clearcut, which occurs during model year 50 and is not repeated; and (c) occurrence of a large, infrequent disturbance (e.g., large blowdown) during model year 50.

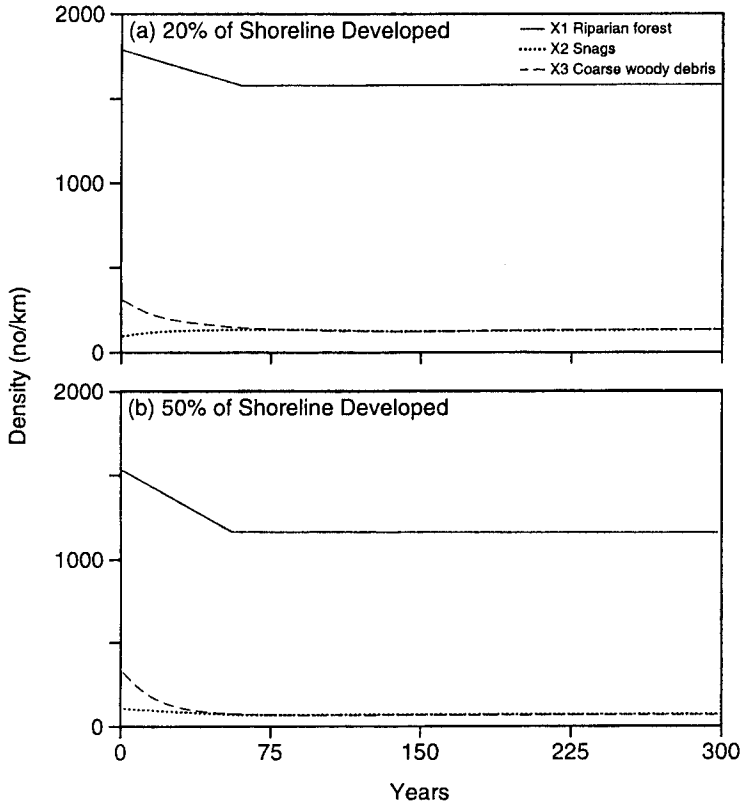

Figure 6.5. Representative simulations of lakeshore development occurring on 20% or 50% of the riparian zone surrounding a lake.

Discussion

The riparian CWD model illustrates several points regarding the use of models for synthesis and integration. First, the questions driving the model were formulated purposefully to require integration of existing data and knowledge. These questions addressed the intersection of different phenomena, allowed exploration of a wide range of conditions that might produce the same or different outcomes, and explored the relative importance of different phenomena for an ecological response. Second, this simple model of riparian CWD dynamics combined data and perspectives that usually are considered separately. These included the riparian forest, disturbance dynamics, human behaviors and

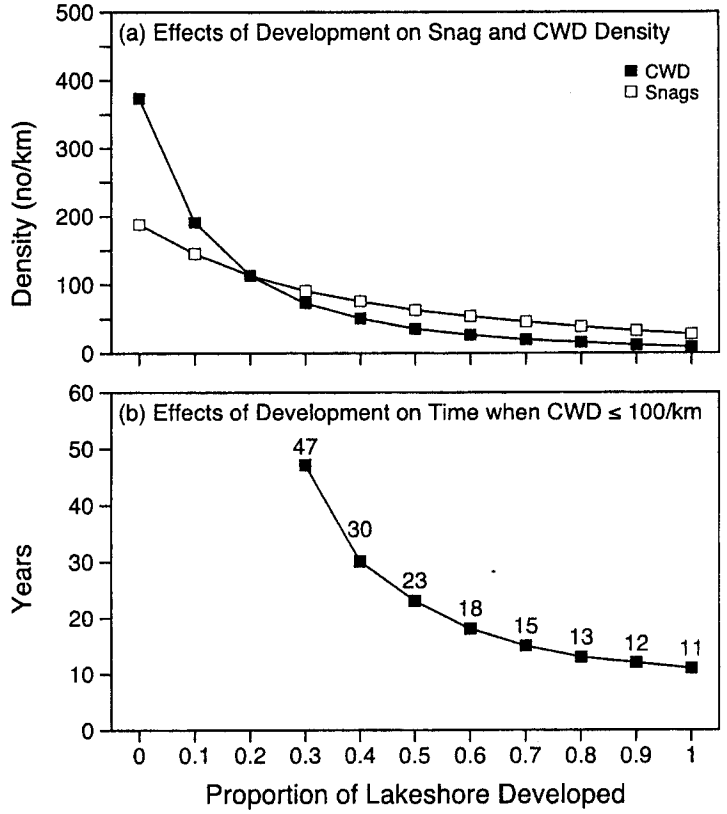

Figure 6.6. (a) Steady-state snag and CWD density for simulated lakeshore development occurring from zero to 100% of a lakeshore. (b) Number of years before simulated CWD abundance drops below 100/km shoreline as a function of the proportion of shoreline developed.

settlement patterns, ecosystem processes (e.g., decomposition), and physical processes (e.g., movement of logs by wind, waves, and ice). Eventually, links to in-lake dynamics and fish population dynamics will also be included. Third, the model was developed at the outset of a large multifaceted research project as comparative and experimental approaches were also beginning. The model predictions can inform the field studies and experiments, and the empirical data will be used to modify the model. Therefore, the model will continue to be integral to the overall research and will facilitate ongoing synthesis of the understanding developed throughout the project.

Clearly, much of the richness of the biological intricacy of the riparian forest ecosystem was excluded from the model. State variables and flows were selected to abstract the essence of hypothesized key interactions, but additional detail or complexity could be added to address other questions or make predictions for particular lakes. For example, successional processes could be modeled, along with variation in forest community composition through time and space. Different stand ages and functional groups of trees (e.g., conifers vs. deciduous trees) will differ in many important characteristics—for example, longevity, susceptibility to disease or windthrow, and decomposition rate—all of which influence CWD recruitment and fate. Other biota, particularly beaver (*Castor canadensis*), can be locally important influences on riparian forest dynamics and CWD, and their effects could be included. The model could also be made spatially explicit, representing the importance of particular landscape positions for CWD, the effects of slope and aspect, or the difference between sheltered and exposed locations. In addition to CWD density, the basal area and geometric complexity of CWD could be simulated. Some parameters, such as physical transport of logs to depth and the rate of CWD removal by humans, will also be influenced by lake type (e.g., seepage or drainage lake) and lake size. Finally, interactions among whole disturbance regimes could be explored rather than simple comparisons among single disturbance events.

Simple as it is, this model still produced interesting dynamics and hypotheses that can be tested empirically. The model suggests that riparian CWD can be maintained by large infrequent disturbances because the pulsed input is substantial and will persist for many decades, even centuries, in the absence of physical removal by humans. This result is consistent with that reported by Bragg (1997), in which natural catastrophic disturbance inflated long-term recruitment of CWD above the level expected in an old-growth forest. The model also suggests nonlinear relationships between lakeshore development and the abundance of riparian CWD, with the potential for thresholds to produce surprises for scientists, managers, and anglers. In addition, despite its acute effects, clearcutting once had a less persistent damping effect on riparian CWD than does moderate to extensive lakeshore development.

Modeling for Synthesis and Integration: Some Take-Home Points

Quantitative models are one of several different approaches to achieving ecological understanding (Carpenter 1998). They can be particularly effective in facilitating the combination of data, perspectives, approaches, or theories that are apparently disparate—that is, integration—to produce new understanding. That models must be question driven, even when synthesis and integration are the goals, cannot be overstated. It is not possible to synthesize everything for all questions, over all scales. Therefore, as with all types of modeling, question identification and selection is key.

Ideally, modeling for synthesis and integration is best begun early and continued throughout a research project. It should be an iterative process in which the models and empirical observation constantly inform one another. Using models as tools for synthesis and integration does not imply that the modeling gets done at the end after the data are all collected and the research project is charged with "synthesizing what has been learned." Modeling should not be an afterthought, an add-on at the end.

Modeling is always a process of abstracting key information and relationships from a system. Synthetic or integrative models require that the *important* processes and details be represented, not that *every* detail or process known about the system must be included. Synthetic models may still be highly abstracted representations of the system. Simple models can, of course, always be expanded as needed based on new questions, but synthetic models need not be encyclopedic.

In conclusion, synthesis and integration are critical to scientific progress and to finding solutions to many environmental problems facing society. Modeling has long been an integral part of ecosystem studies, and ecosystem scientists must strive to strengthen that connection and to exploit the insights that can be derived from modeling (Carpenter 1998; Lauenroth et al. 1998). Ecologists should continue to combine quantitative models with observations and experiments in their search for general understanding of ecological systems.

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7

The Role of Models in Prediction for Decision

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Summary

The processes of science and decision making share an important characteristic: success in each depends upon researchers or decision makers having some ability to anticipate the consequences of their actions. The predictive capacity of science holds great appeal for decision makers who are grappling with complex and controversial environmental issues by promising to enhance their ability to determine a need for and outcomes of alternative decisions. As a result, the very process of science can be portrayed as a positive step toward solving a policy problem. The convergence—and perhaps confusion—of prediction in science and prediction for policy presents a suite of hidden dangers for the conduct of science and the challenge of effective decision making. This chapter, organized as a set of inter-related analytical vignettes, seeks to expose some of these hidden dangers and to recommend strategies to overcome them in the process of environmental decision making. In particular, this chapter will try to distill some of the lessons gleaned from research on modeling, prediction, and decision making in the earth and atmospheric sciences for quantitative modeling of ecosystems. One clear implication is that conventional approaches to modeling and prediction cannot simultaneously meet the needs of both science and decision making. For ecosystem science, there fortunately exists a body of experience in understanding, using, and producing predictions across the sciences on which to develop new understandings of the relationship of science and decision making to the potential benefit of both research and policy.