# The Limits to Models in Ecology

CARLOS M. DUARTE, JEFFREY S. AMTHOR, DONALD L. DEANGELIS, LINDA A. JOYCE, ROXANE J. MARANGER, MICHAEL L. PACE, JOHN J. PASTOR, AND STEVEN W. RUNNING

### Summary

Models are convenient tools to summarize, organize and synthesize knowledge or data in forms allowing the formulation of quantitative, probabilistic, or Bayesian statements about possible or future states of the modeled entity. Modeling has a long tradition in Earth sciences, where the capacity to predict ecologically relevant phenomena is ancient (e.g. motion of planets and stars). Since then, models have been developed to examine phenomena at many levels of complexity, from physiological systems and individual organisms to whole ecosystems and the globe.

The demand for reliable predictions, and therefore, models is rapidly rising, as environmental issues become a prominent concern of society. In addition, the enormous technological capacity to generate and share data creates a considerable pressure to assimilate these data into coherent syntheses, typically provided by models. Yet, modeling still encompasses a very modest fraction of the ecological literature, and modeling skills are remarkably sparse among ecologists (Chapter 3). The growing demand for models is in contrast with their limited contribution to the ecological literature, which suggests that either there are serious constraints to the development of models or that there are limitations in the conceptualization and/or acquisition of the elements required for model construction that result in the requirements of products from models not being met at present.

Models are apparently not being as widely used as expected given the present demand. Hence, the identification of bottlenecks for the development of models in ecology, and limitations of their application are important goals. This chapter reports on the conclusions of a discussion group at the IX Cary Conference set to address these issues.

Background

# 24

Ecological models can be classified in a number of ways. One of the most useful is the distinction between single-level descriptive (or empirical) models and hierarchical or multilevel explanatory (or mechanistic) models (de Wit, 1970, 1993, Loomis et al., 1979). An example of a single-level descriptive model is a regression equation relating annual net primary production, NPP, or crop yield to annual precipitation and/or temperature. When used within the range of precipitation and temperature included in the formulation of the regression equation(s), such a model may be rather accurate for interpolative prediction. It does not, however, 'explain' the operation of the systems, and the model may fail when applied to conditions outside the environmental envelope used for parameter estimation, or when applied to a different ecosystem. Explanatory models often include at least two levels of biological/ecological organization, using knowledge at one level of organization (e.g., biological organs) to simulate behavior at the next higher level of organization (e.g., organisms), although other factors may come into play. Information at the lower levels may be empirical or descriptive information (Loomis et al., 1979) that helps explain behavior at the level of the organism. Of course, in explanatory ecological models, knowledge gaps arise and simplifications are inevitable.

Modeling terrestrial net primary production provides a robust example of the spectrum of modeling possible in ecology (Fig. 1). The highest modeling complexity is found with mechanistic carbon flux models for plot level applications that require intensive data for execution (Rastetter et al 1997), and yet more sophisticated mechanistic models are becoming now available (Amthor et al. 2001). These models compute photosynthesis minus respiration balances of leaves and model the allocation of photosynthate to plant growth. Somewhat more generalized models such as FOREST-BGC do not treat each plant explicitly, but compute the integrated carbon, water and nutrient biogeochemistry of a landscape (Running 1994). Recent attempts to distill these complex NPP models to require more simplified input data, such as PnET-II and 3-PGS, have been impressively successful for forests (Law et al 2000, Aber and Melillo 2001). Other models have explicitly considered treatment of NPP by different vegetation biomes from a common logical framework (VEMAP 1995). These multi-biome NPP models are becoming important to drive policy issues regarding terrestrial carbon sources and sink dynamics. (Schimel et al. 2000). A new generation of NPP models uses satellite data for input, and uses a simple light conversion efficiency factor to compute NPP from absorbed photosynthetically active radiation. Use of satellite data for primary input data has allowed broad mapping of NPP from regional up to global scales (Coops and Waring 2001, Running et al 2000).

This dramatic simplification from full photosynthesis-respiration balances to a simple light use efficiency model to compute a common variable, NPP, exemplifies the range of logic used in ecosystem modeling (Fig. 1). No single model can be optimally used throughout all scales (Fig. 1) that span from the individual leaf to the global biosphere (Waring and Running 1998).

#### 24. The Limits to Models in Ecology



Figure 1. The scaling of models across ecological scales requires means to integrate the model logics.

3

### Limits to the development of models

Bottlenecks impairing the development of models seem to be multiple and to encompass limitations in the scientific community (Chapter 23). Improvement will require actions at the capacity-building stage, and the removal of technological bottlenecks, and limitations in the data available to build, drive, and validate the models.

#### Capacity Building

University curricula in biology are notoriously poor in providing students with modeling skills, which probably derives from a general neglect of solid mathematical training in biology programs, at both undergraduate and graduate levels. Consequently, modeling is largely a self-taught craft. This imposes severe limitations in the recruitment of modelers to the community, which accounts for the relatively small number of ecological modelers. Poor training also limits the understanding of the data requirements for model construction by experimental ecologists, resulting in insufficient coordination between data acquisition and the requirements of the models. The ineffective communication between modelers and experimental ecologists has other important consequences, such as the present tendency of papers on ecological models to be "ghettoed" into particular journals. This tendency further enforces, by increasing isolation, the insufficient communication between modelers and experimental ecologists.

Ecological modeling will also benefit from establishing firm interdisciplinary links, which will allow capitalizing on developments in other fields. Such developments include recent advances in computing science and technology, such as optimized algorithms for parallel computing. In addition, recent developments in new modeling approaches, such as dynamic modeling of complex systems in mathematics and theoretical physics, could be conveyed faster to the community of ecological modelers if platforms to foster interdisciplinary links between these different disciplines were better established. The opportunity to interact with ecological modelers could also benefit mathematicians and theoretical physicists, who are in a continuous search for complex systems to serve as test benches for their new developments. In addition, human intervention in ecological processes is now widespread at all scales, requiring this forcing to be factored into model formulations. This will require greater collaboration between social scientists and ecologists to incorporate human influence in ecological models (National Assessment Synthesis Team 2000).

#### Technological Developments

Technological bottlenecks appear to be minor at present, because computing power has increased so rapidly that the gains made since ecological simulation began more than 30 years ago are no less than staggering. Only the larger, global models seem to be constrained by access to adequate computing facili-

4

ties. In addition, software developments have provided modeling platforms and analytical tools that now render model construction and analysis a relatively simple task. Quantitative, robust approaches to decide on the optimal size of ecological models are now becoming available (Chapter 8), guiding model development. As a result, technological bottlenecks cannot, in general, be held responsible for the insufficient development of models in ecology, although increased networking between supercomputer facilities could improve their availability to the scientific community.

#### Appropriate Observational Basis

The empirical basis for developing and testing models is generally insufficient, and may well be the ultimate bottleneck for the development of mechanistic models. Even available data are usually poorly fit to model needs, for they may lack the required spatial and temporal coverage, or they may poorly encompass the range of gradients that must be encompassed covered by the model. This limitation may be somewhat alleviated by developing modeling approaches flexible enough to incorporate and combine a variety of data, including data at various hierarchical levels (population, classes within a population, individuals), and addressing tactical questions that do not require complete data descriptions of a system (Chapter 5). Nevertheless, data limitation will remain a chronic problem, because, despite the activity of many ingenious field ecologists, collection of some types of data is by its nature difficult and expensive. The data sets available to test models are, therefore, limited, leading to growing concern that most models may be validated against a few, common data sets, which - while allowing for model comparison - involves the danger that these few data sets become the "world" the models recreate. Moreover, there are also unduly long time lags between data acquisition and the time these data are made available for model construction and validation, precluding the development of on-line models, which are becoming available in other disciplines (e.g. operational oceanography). The inadequacy of ecological data for modeling purposes largely stems from insufficient appreciation of the requirements for model construction, again calling for a greater connection between modelers and experimental ecologists in education programs and during the formulation of research programs. Results from present experimental research focuses heavily on statistical analysis of end points rather than explanation of the processes yielding those end points, whereas knowledge of processes forms the basis of explanatory (or extrapolative) models. In addition, experiments are rarely useful as a base for modeling because of the emphasis on contrasts and ANOVA-directed designs, instead of gradient designs (Chapter 12).

### Limits to the Achievements of Models

The bottlenecks identified above are substantial, but cannot alone explain the limited application of modeling approaches to ecological problems. We suggest that there must be other, external limits to what models can achieve. An appreciation of these limits requires, however, an identification of the goals of models as a pre-requisite to identifying the circumstances that may preclude the achievement of these goals.

#### The Goals of Models

Models are often used as heuristic tools to organize existing knowledge, identify gaps, formulate hypotheses, and design experiments. Models can also be used as analytical tools to increase our understanding about the relative importance and interplay of the various processes involved in the control of populations, communities or ecosystems, and to use this understanding to examine their behavior at scales that extend beyond direct observation. Societal needs impose increasing pressure for ecological models to help inform management decisions, as to the likely consequences of alternative management options and future scenarios of the status of populations, communities or ecosystems (Chapter 7). Indeed, heavy human pressures upon the Earth's resources are leading to major changes in the functions of the Earth system and loss of the biodiversity it contains. The need for ecological models by society in the 21st century will become a benchmark upon which the robustness of ecological knowledge will be assessed. This demand is largely articulated through the societal request for predictions, which must be supplied along with the logical rationalization of the models' mechanistic basis that provides reassurance on the reliability and generality of the model's principles.

The role of models as tools in formulating hypotheses is a non-controversial - although insufficiently explored - use. In contrast, conflicts between the goals of understanding vs. prediction have been the subject of recurrent debates (e.g. Peters 1986,1991, Lehman 1986, Pickett et al. 1994, Pace 2001). These debates mirror those in other branches of science, where in some cases mechanistic models have been claimed to be overemphasized to the detriment of progress (Greene 2001). We contend, however, that prediction and understanding are mutually supportive components of scientific progress and that ecological modeling would greatly benefit from an improved integration of both these goals, which should if possible progress in parallel (Fig. 1). Even the simplest statistical models are used to test hypotheses (Peters 1991), through the mechanistic reasoning that generally guides the selection of candidate predictors, thereby leading to increased understanding (Pace 2001). On the other hand, models developed to test the reliability of our understanding generally do so by comparison between model output and observations, thereby assessing the predictive power of the models. We, therefore, contend that the discussion on the priority of prediction vs. understanding in model formulation is largely futile. Whether the models are empirical, statistical models that make few assumptions on the underlying mechanisms or are mechanistic-rich, this cannot be considered, *a priori*, to offer any particular advantage when predictions are sought, for "Whether the cat is black or white does not matter, as long as it catches the mice" (Mao Tse-tung).

The key issue is, therefore, whether the model works, i.e. is conducive to the formulation of reliable, validated predictions. For instance, Chinese observers were able to accurately predict tides > 2,000 years ago, despite the fact that they understood the process to result from the breathing of the sea (Cartwright, 2001). More than two millennia later, we have been able to improve somewhat our capacity to predict tides. However, despite what we believe is an adequate understanding of the tide phenomenon, the prediction is still based on site-specific empirically fitted curves (Cartwright, 2001).

### The Complementary Goals of Prediction and Understanding

Whereas predictive capacity is an objective trait amenable to quantitative test (Chapter 8), the degree of understanding achieved through modeling is more difficult to assess in any specific way. Although understanding is not a pre-requisite to the achievement of predictive power, modeling approaches that offer absolutely no possibility to test hypotheses and, therefore, gain understanding are regarded as suspect and have not being used as reliable sources of predictions. Hence, both scientists and society are not satisfied with projections of past dynamics into the future that provide little or no understanding, but rather require predictions, which must be derived or be consistent with theory (Pace 2001). This requirement provides an indication of the importance scientists and humans in general assign to understanding, as reflected in the quote: "I believe many will discover in themselves a longing for mechanical explanation which has all the tenancy of original sin..." (Bridgman 1927).

In addition, prediction and understanding are linked through effective feedback processes, for predictions are derived from theory, and, at the same time, their success or failure serves to improve theory. Predictions can be derived from simple, statistical models, analytical models, or complicated simulation models. The growing complexity of the models may provide a greater sense of understanding, if successful predictions can be derived, but often this complexity leads to reduced predictive power and/or various interpretive constraints (Fig. 2). Such loss of predictive power is clearly illustrated in the comparison of the predictive record of statistical vs. mechanistic models of El Niño-La Niña events (Chapter 4). Probably the most studied and implemented use of statistical (regression) models in ecology involves "prediction" of crop yield based on environmental conditions (e.g., mean air temperature during the growing season, or total precipitation). However, simple statistical models are not formulated from a random trial and error approach. Rather, the candidate independent variables that achieve predictive power are deduced from theory, such as sea surface temperature anomalies and atmospheric pressure locations in the case of

statistical models used for El Niño-La Niña prediction (Chapter 4), or evapotranspiration in models of terrestrial net primary production (Leith 1975).

Mechanistic models are not necessarily bounded in their predictive capacity, for the predictive capacity of net primary production models has increased significantly since the initial formulations. However, the requirements of mechanistic models do exceed those of statistical, descriptive models by virtue of the simple fact that they contain (and therefore need as input) <u>more elaborated</u> information that is more scientifie. Indeed, the more realistic an explanatory model is sought to be, the more information is needed to parameterize the model and initialize its driving variables. "If these (data) are unavailable, then the regression model may still be our best option" (Penning de Vries 1983). A common pitfall of statistical models is, however, oversimplification ("every-thing should be made as simple as possible, but not one bit simpler," A. Einstein). Applying simple models to different locations, or even different years, often fails to yield accurate predictions unless the environment is relatively uniform (Penning de Vries 1983).

Mechanistic constraints can also be imposed upon empirical models (e.g., potential quantum use efficiency based on underlying biophysics can be used to constrain an empirical light-response curve for leaf photosynthesis), thereby using understanding to formulate them. Indeed, most models are neither purely statistical nor mechanistic models, but rather hybrids between the two, usually containing empirical relationships or parameters, linked according to theory. Freshwater eutrophication models are amongst the most widely applied in the management context (e.g. Dillon and Rigler 1975, Vollenweider 1976, Smith 1998). The model generally applied is a semi-empirical one (Vollenweider 1976), combining regression-derived relationships between chlorophyll a concentration and total phosphorus concentrations, with a simple mass-balance approach to predict the phosphorus concentration in lake waters. Mass balance approaches, which are essentially empirical models guided by simple, fundamental principles, are widely used in ecological modeling (Chapter 15). The search for the optimal compromise in the complexity and the empirical vs. mechanistic components of models must be guided by parsimonious criteria, and is a key milestone in the successful development of models (Chapter 8). Indeed complex models should be rigorously evaluated to be made as "minimalistically-complex" as possible (Fig. 2). This objective would allow for a greater focus on more specific or relevant mechanistic understanding of a given process and would provide a more useful tool to policy makers and managers with a greater change of being appropriately validated.

(Insert Figure 2 here)

9

The successful formulation of predictions from simple empirical models inspired by theory is eventually assimilated as providing "understanding," defined by Pickett et al. (1994) as "an objectively determined, empirical match between some set of confirmable, observable phenomena in the natural world and a conceptual construct." Indeed, many parameters in mechanistic models are but empirically determined quantities that are "understood" in the sense that they have been repeatedly tested and are consistent and linked with the consolidated body of principles or laws in ecology (Fig. 2).

The preceding discussion clearly indicates that the goals of prediction and understanding are self-supportive, and that, as a consequence, they advance in parallel (Fig. 2). Yet, this parallel advancement is dynamic, involving lags and delays, and may be, therefore, somewhat out of phase. Indeed, empirical predictions derived from simple models inconsistent with current theory or mechanisms may be suspect, but may also hint at flaws in the current understanding or theory. A mismatch between empirical observations and the desired understanding of underlying mechanisms has been a recurrent stumbling block in science, as illustrated by the long resistance to accept the theories of evolution by natural selection and continental drift, simply because they lacked a clear mechanism at the time they were formulated (Greene 2001). Hence, ecologists must be prepared to accept that prediction and understanding may be at times discordant, and that the process of model development for prediction is dynamic. Indeed, increased understanding results in model reevaluation and improved predictive capacity. For these reasons, the following sections assess the limits to the use of ecological models for prediction and understanding separately.

## Limits to Prediction

Uncertainty in the observational data available to develop the models leads to uncertainty about the model predictions, which imposes a limit on the precision of the predictions (Amthor et al. 2001, Chapter 8). Similarly, uncertainties about the data available to test and validate models lead directly to uncertainty about the accuracy of model predictions (Amthor et al. 2001, Chapter 8). A key related difficulty is that "biological principles which have to form the base of model-building are too fragmentary to embark on straightforward modelbuilding along the same lines as in the physical sciences" (de Wit 1970). Ecological modelers must continuously make compromises to overcome knowledge gaps, and modeling may be reduced to expressions of intuition or educated guesses in some cases. Indeed, de Wit (1970) concluded that success "is only possible when we have the common sense to recognize that we know only bits and pieces of nature around us and restrict ourselves to quantitative and dynamic analyses of the simplest ecological systems." This is not encouraging

when the goal is to understand and predict complex systems such as ecosystems.

Models often develop from a need to formulate predictions on processes that elude direct observation, such as processes that are very slow (e.g. seagrass meadow formation, Duarte 1995), operate at very small spatial scales (e.g. submillimeter plankton patchiness, Duarte and Vaqué 1992), or result from episodic or extreme phenomena (e.g. floods, extreme droughts; Turner et al. 1998, Changnon 2000), which are difficult to observe directly, as well as future events (e.g. global change, National Assessment Synthesis Team 2000). Lack of adequate observations precludes the assessment of predictive power in these circumstances, so that the models' reliability is entirely dependent on the confidence in its mechanistic basis. The extensive evaluation of model outputs is particularly useful to help assess the models and examine, in detail, their behavior. For example, the ability of a model to hindcast a historical event such as a drought or a fire improves the model's acceptance for prediction.

Models are, to a variable extent, specific, and their predictive power is restricted to a particular domain (e.g. independent variable range in regression models, particular vegetation type or species), beyond which the reliability of the predictions requires additional testing. Because model components are typically multivariate, their corresponding domains are complex, multivariate spaces that cannot be reliably probed even if multiple validation tests are conducted. The model domain also encompasses the assumptions built into the model (e.g. homogeneity of the variances, steady-state, equilibrium, etc.), which must be met by the subject if they are to be applied with any confidence. Any extension of models beyond the domain over which they were originally developed or tested involves uncertainty in the predictive power achievable. Most models predicting NPP were developed for specific biomes, although they have been since applied to other vegetation types or climatic regimes. This extension involves a re-examination of the underlying theory in the model; it's appropriateness to these new biomes, as well as the parameterization of the model parameters for these new biomes. General models do exist, such as the so-called Miami model (equations 12-1 and 12-2 in Leith 1975), a simple statistical model relating NPP to annual mean temperature and annual precipitation based on field data/estimates from multiple biomes. Such global models, however, have been found to poorly represent the dynamic changes occurring within a particular site, which seem to be due, in the case of the Miami model, to time lags in responses of vegetation structure to the changing conditions (cf. Lauenroth and Sala 1992).

Model outputs are not always deterministic, for even simple models can display complex behavior derived from both deterministic and stochastic components of the model. This results in undefined predictions, where very different outcomes are equally likely. These sources of uncertainty are, however, poorly addressed by current sensitivity analysis in ecological modeling, which, by in large fails to address the consequences of simultaneous variability in the driving parameters and variables, and tests for alternative expressions of ecological processes.

### Limits to Understanding

The history of science provides evidence that a model's capacity to accurately predict cannot be used to infer the veracity of the processes underlying a mechanistic model. This implies no more than the acknowledgement that ecological modeling does not escape the generic limitation of science's capacity to never fully prove hypotheses. Yet, the successful application of a model to a variety of different subjects, encompassing the broadest possible ranges in the key traits or variables would increase the confidence on the robustness of the model's principles. Even if the results of an explanatory ecological model correspond to observations of the system being modeled, "there is room for doubt regarding the correctness of the model" (de Wit 1993). Whenever discrepancies between model output and reality occur, the model may be adjusted ("tuned") to obtain better agreement, and since there are typically many equations and parameters, this is easy to do. It is, however, a "disastrous" way of working because the model then degenerates from an explanatory model into a descriptive model (de Wit 1970). The word "degenerates" does not mean that descriptive models are inferior, but simply that they no longer explain the system. The attribution of explanation to such descriptive models "is the reason why many models made in ecological studies...have done more harm than good" (de Wit 1993). The limitation of our fragmented ecological knowledge can and will, therefore, undermine explanatory modeling.

Mechanism-driven models cannot be formulated in cases where there is little or no understanding of the problems, or where the empirical base is thin and critical data are missing. The contribution of modeling must derive, in these cases, from the development of simple, empirical or conceptual models that promote the emergence of sufficient understanding as to render the development of mechanism-driven models possible (Chapter 25).

Increasing model complexity may increase the extent to which models are believed to reproduce nature, but at the same time, they become more open to unexpected behavior. This has both potential advantages and disadvantages. One advantage is that a model's prediction of unexpected behavior, if it can be tested against observations, can offer either strong corroboration or rejection of the model. Another advantage is that complex models are likely to produce a variety of outputs (intermediate-level output) other than merely that of the particular variables of interest. These outputs may provide predictions that can be tested against independent data, thus partially checking the model. Unexpected behavior, including erratic predictions, may derive from either deterministic or stochastic processes in the model. The uncertainties in the numerous mechanisms may add or multiply, and, if there is no way of observing intermediate variables in order to correct for this process, lead to a large and perhaps unknown amount of uncertainty in the variables of interest, and a model that is

difficult to interpret or understand (Fig. 2). This results in the paradox that the more mechanism-rich a model becomes (the more knowledge it incorporates), the more uncertain it becomes (Chapter 2). Much of the art of modeling lies in constructing models that avoid this paradox by producing a variety of outputs that can be tested against as much independent observational data as possible.

### Conclusions and Recommendations

#### Consequences for Model Use

Efforts to promote the use of existing models must be enhanced, for only widespread use of a model can help assess the model domain and predictive power under sufficiently contrasting situations. Failures and successes derived from model use open opportunities for improved model design and reformulation. Therefore, model validation should rely heavily on the widest possible use of the models by the scientific community. Consequently, modelers – and the funding agencies that fund model development – must make all possible efforts to make the models widely available as stand-alone products. The users must be, however, fully aware of the model assumptions, limitations, behavior, and domain of construction, which must be supplied as extensive metadata accompanying the model. The latter is the responsibility of the model developers (Aber 1997). Obviously, this lack of communication on behalf of model developers has lead to the misinterpretation or misuse of their models by able model-users (Chapter 13).

#### Consequences for Model Design

Limited data availability implies that site or subject-specific models may be possible only for a limited number of subjects (ecosystems, communities, or species). As a consequence, there is little hope that the large-scale problems of ecosystem alteration, habitat loss and biodiversity erosion may be addressed merely through a mosaic of subject-specific models. Addressing these questions on the large scale will require the development of ecological models aimed at achieving generality at the expense of detail. This does not reduce the usefulness of site- and subject-specific models when data are available for them. Tactical models, addressing key specific goals, such as the conservation of highprofile endangered species or of critical ecosystem functions, can be designed to be flexible enough to utilize a variety of types of available data (Chapter 5). However, for the most part, more generic models will be necessary.

We contend, therefore, that model design should proceed hierarchically, stemming from simple empirical rules to formulate a parsimonious, generic simple model, to eventually result in case-specific applications. A modular construction approach should clearly specify the reduction in the model domain and generality at each development stage, so that the transferability of the models produced is explicit at each level. Effort allocation in ecological models needs to be readjusted to provide the needed attention to the development of general models, even if these are perceived to be imprecise or provide less understanding.

Model construction must engage experimental ecologists and modelers throughout the entire process from model conception to validation, ensuring, thereby, a more adequate match between data acquisition and model requirements. The full potential of models to achieve synthesis should also be explored further than it is currently done, and large research programs will benefit from such exercises, which should be facilitated by program managers. An improved feedback between statistical and mechanistic models must be established. The development of ecosystem models will also greatly benefit from increased interdisciplinary connections (Fig. 3), which would allow the rapid implementations of new approaches to model complex systems – the stone against which many disciplines (physics, health science, etc.) are presently stumbling - and to analyze model output and behavior, as well as a better represent human intervention in ecological models.

(Insert Figure 3 here)

In summary, present demand for predictions in ecology implies that models are called to be at the forefront of ecology. The limitations to model development and achievements outlined here are, largely, derived from poor coordination within the scientific community. A commitment to the participation in model construction and validation by the entire community is, therefore, required (Chapter 27). This effort must extend beyond the boundaries of ecology to benefit from inputs and progress in other disciplines (Fig. 3). Ecologists must also be sufficiently educated as to be able to understand models and model requirements and to formulate, at least, simple models (Chapter 23) (Fig. 3). Progress in model development is also likely to benefit from a better coordination, as opposed to competition, between the development of simple statistical models and their integration into mechanistic models. These actions require a substantial effort from all ecologists. Benefits will become apparent in the form of better synthesis, through modeling, and a better service to society through the use of the models for the effective preservation of biological diversity and ecosystem function.

#### References

- Aber, J., and J. Melillo. 2001. *Terrestrial Ecosystems. 2nd Ed.* Burlington (MA): Harcourt/Academic Press. pp 556.
- Aber, J.D. 1997. Why don't we believe in models? *Bulletin of the Ecological Society of America* 78: 232-233.
- Amthor J.S., J.M. Chen, J.S. Clein, S.E. Frolking, M.L. Goulden, R.F. Grant, J.S. Kimball, A.W. King, A.D. McGuire, N.T. Nikolov, C.S. Potter, S. Wang, and S.C. Wofsy. 2002. Boreal forest CO<sub>2</sub> exchange and evapotranspiration predicted by nine ecosystem process models: intermodel comparisons and relationships to field measurements. *Journal of Geophysical Research – Atmospheres* 106 (D24): 33,623.

Bridgman, P.W. 1927. The logic of modern physics. New York: MacMillan.

- Cartwright, D.E. 2001. *Tides: A scientific History*. New York: Cambridge University Press.
- Coops, N.C., and R.H. Waring. 2001. The use of multi-scale remote sensing imagery to derive regional estimates of forest growth capacity with 3-PGS. *Remote Sensing of Environment* 75: 324-334.
- Changnon, S.A. 2000. Flood prediction: Immersed in the quagmire of national flood mitigation strategy. Pages 85-106 in D. Sarewitz, R.A. Pielke, and R. Byerly, Jr., editors. *Prediction: Science, Decision Making, and the Future of Nature*. Washington, DC: Island Press.
- de Wit, C.T. 1970. Dynamic concepts in biology. Pages 17-23 in I. Setlik, editor. *Prediction and measurement of photosynthetic productivity*. Wageningen, the Netherlands: Center for Agricultural Publishing and Documentation.
- de Wit, C.T. 1993. Philosophy and terminology. Pages 3-9 in P.A. Leffelaar, editor. *On systems analysis and simulation of ecological processes*. Dordrecht: Kluwer.
- Dillon, P.J., and F.R. Rigler. 1975. A simple method for predicting the capacity of a lake for development based on trophic state. *Canadian Journal of Fisheries and Aquatic Science*. 31: 1518-1531.
- Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87-112.
- Duarte, C.M., and D. Vaqué. 1992. Scale dependence of bacterioplankton patchiness. *Marine Ecology Progress Series* 84: 95-100.
- Greene, M. 2001. Mechanism: A tool, not a tyrant. Nature 410: 8.
- Lauenroth, W.K., and O.E. Sala. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2: 397-403.
- Law, B.E., R.H. Waring, P.M. Anthoni, and J.D. Aber. 2000. Measurements of gross and net ecosystem productivity and water vapor exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology* 6: 155-168.
- Lehman, J.T. 1986. The goal of understanding in limnology. *Limnology and Oceanography* 31: 1160-1166.

- Leith, H. 1975. Modeling the primary productivity of the world. Pages 237-263 in H. Leith and R.H. Whittaker, editors. *Primary Productivity of the Bio-sphere*. New York: Springer-Verlag.
- Loomis, R.S., R. Rabbinge, and E. Ng. 1979. Explanatory models in crop physiology. Annual Review of Plant Physiology 30: 339-367.
- National Assessment Synthesis Team. 2000. Climate Change Impacts on the United States. *The Potential Consequences of Climate Variability and Change, Overview*. US Global Change Research Program, 400 Virginia Avenue, SW, Suite 705, Washington DC, 20024.
- Pace, M.L. 2001. Prediction and the aquatic sciences. *Canadian Journal of Fisheries and Aquatic Science* 58: 63-72.
- Penning de Vries, F.W.T. 1983. Modeling of growth and production. Pages 117-150 in O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, editors. *Plant physiological ecology* IV. Berlin: Springer-Verlag
- Peters, R.H. 1986. The role of prediction in limnology. *Limnology and Ocean*ography 31: 1143-1159.
- Peters, R.H. 1991. *A Critique for Ecology*. New York: Cambridge University Press.
- Pickett S.T.A., J. Kolasa, and C.G. Jones. 1994. Ecological Understanding. San Diego: Academic Press.
- Rastetter, E.D., G.I. Agren, and G.R. Shaver. 1997. Responses of N-limited ecosystems to increased CO<sub>2</sub>: A balanced nutrition, coupled element-cycles model. *Ecological Applications* 7: 444-460.
- Running, S.W. 1994. Testing FOREST-BGC ecosystem process simulations across a climatic gradient in Oregon. *Ecological Applications* 4: 238-247.
- Running, S.W., P.E. Thornton, R.R. Nemani, and J.M. Glassy. 2000. Global terrestrial gross and net primary productivity from the earth observing system. Pages 44-57 in O. Sala, R. Jackson, and H. Mooney, editors. *Methods* in Ecosystem Science. New York: Springer-Verlag.
- Schimel, D., J. Melillo, S.W. Running, et al. 2000. Contribution of increasing CO<sub>2</sub> and climate to carbon storage by ecosystems in the United States. *Science* 287: 2004-2006.
- Smith V.H. 1998. Cultural Eutrophication of Inland, Estuarine and Coastal Waters. Pages 7-49 in M.L. Pace and P.M. Groffman, editors. Successes, Limitations and Frontiers in Ecosystem Science. New York: Springer-Verlag.
- Turner, M.G., W.L. Baker, C.J. Peterson, and R.K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Eco*systems 1: 511-523.
- VEMAP Members.1995. Vegetation/ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO<sub>2</sub> doubling. *Global Biogeochemical Cycling* 9(4): 407-437.

- Vollenweider, R.A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Memorie dell'Istituto Italiano di Idrobiologia* 33: 53-83.
- Waring, R., and S.W. Running. 1998. Forest Ecosystems: Analysis at Multiple Scales. San Diego: Academic Press.

# Figure Legends

Fig. 2. A schematic overview of systems model conceptualization and formulation, driven by understanding, with the ultimate objective of prediction (or projection). Simple analytical and statistical models formulated using logic or theory and empirically derived observations are compiled into larger complex systems models. Model parameters are rigorously tested using a variety of techniques resulting in a feedback loop increasing parameter and model understanding, identifying those parameters that are the most ecologically relevant in order to create "minimalistic-complex" system models, potentially useful for prediction. Solid arrows outline this process. The large white arrow linking prediction through model development and reevaluation via understanding emphasizes that model building is a dynamic process benefiting from both elements. The broken arrow denotes the "danger" of increasing model complexity and the limitations associated with this.

Fig. 3. Network of suggested pathways to alleviate present limitations in model development.

Para ver esta película, debe disponer de QuickTime™ y de un descompresor GIF.

#### 24. The Limits to Models in Ecology 19



