

Introduction

Modeling complex ecological systems: an introduction

1. What is complexity?

The world is replete with all kinds of complex systems, be they ecological, social, economic, or political. Nevertheless, complex systems share several common characteristics. First, they are thermodynamically open, meaning that they exchange energy and/or mass with their environment. Second, they are often composed of a large number of diverse components. Third, system components interact with each other nonlinearly, and frequently have response delays and feedback loops among them. Fourth, complex systems exhibit a high degree of heterogeneity in both time and space. Consequently, complex systems are often characterized by emergent properties, multiscale interactions, unexpected behaviors, and self-organization (Jørgensen, 1995; Prigogine, 1997; Levin, 1999; Wu, 1999). Furthermore, a comprehensive concept of complexity not only needs to include the inherent system properties, but also the role of the observer (Allen and Starr, 1982; Flood, 1987; Wu, 1999).

While the term ‘complexity’ has become a buzzword across many fields in science, it has various meanings. For example, structural complexity may refer to the compositional diversity and configurational intricacy of a system; functional complexity emphasizes the heterogeneity and non-linearity in system dynamics; and self-organizing complexity hinges on the emergent properties of systems co-evolving with their environment primarily through local interactions and feedbacks at different spatiotemporal scales. Such self-organizing systems have often been referred to as ‘com-

plex adaptive systems’ (Cowan et al., 1994). According to Levin (1999), a complex adaptive system is ‘a system composed of a heterogeneous assemblage of types, in which structure and functioning emerge from the balance between the constant production of diversity, due to various forces, and the winnowing of that diversity through a selection process mediated by local interactions’. Most ecological and socioeconomic systems exhibit different degrees of self-organizing complexity, and thus may be considered as complex adaptive systems (Cowan et al., 1994; Levin, 1999).

Scientists have long been interested in unraveling the problem of complexity. The late Noble Laureate Herbert A. Simon (Simon, 1996) identified three bursts of interest in the study of complexity in the 20th century. The post-World War I period was characterized by such terms as ‘holism’, ‘Gestalts’, and ‘creative evolution’. The post-World War II period was signified primarily by general systems theory, information theory, and cybernetics, focusing primarily on the roles of feedback and homeostasis in maintaining system stability. The current period of complexity research has focused mainly on causes, mechanisms and methods, and a diversity of views can be identified with terms such as ‘chaos’, ‘catastrophe’, ‘fractal’, ‘cellular automata (CA)’, ‘genetic algorithms (GA)’, ‘neural networks’, ‘hierarchy’, ‘self-organization’, and ‘complex adaptive systems (CAS)’ (Wu, 1999). Different concepts and theories entail different approaches to modeling complex systems. In many cases, however, they are more complementary than contradictory. It is in-

interesting that the development of ecological modeling in theory and practice seems to follow this 'historical trajectory' of complexity research rather closely.

2. Some history of modeling complex ecological systems

As a science that deals with complexity of physical, biological, and socioeconomic origins in concert, ecology has experienced successes and failures in applying a variety of theories and methods developed from multidisciplinary research in complexity. Although the first period of complexity research did not seem to have stimulated much activity in ecological modeling, a much closer relationship between ecological modeling and complexity research in terms of both theory and methods is found when Simon's second and third developmental stages are considered.

As in several other earth sciences, the Newtonian mechanics approach characterized by determinism and mathematical tractability represents the classical way of modeling ecological systems. It was first adopted by population ecologists, and remains very much alive as a legacy of the 'Golden Age' of theoretical ecology from 1920s and 1940s (see Scudo and Ziegler, 1978; McIntosh, 1985 for reviews). Being able to handle systems with only a small number of components, this approach is opt for dealing with the 'organized simplicity'. The statistical mechanics approach, on the other hand, is effective for tackling the 'disorganized complexity', characterizing systems with a large number of components that each behave more or less randomly. This approach has been rather successful in modern physics, but infrequently applied in ecology partly because, for many ecological problems, the system of study does not have a large enough number of components (O'Neill et al., 1986).

Ecologists are often confronted with the so-called 'medium-number' systems that exhibit the 'organized complexity', which is the subject of systems science (O'Neill et al., 1986; Wu, 1999). No wonder that, as systems science emerged in

the 1950s and 1960s, ecologists were among the most active, applying and contributing to the three major theories in systems science: general systems theory, cybernetics, and information theory (Patten, 1959; Van Dyne, 1966; Watt, 1966; Margalef, 1968; Dale, 1970; Patten, 1971, 1972, 1974, 1976; Reichle et al., 1973; Hall and Day, 1977; Shugart and O'Neill, 1979; Odum, 1983). By the 1970s, this 'systems modeling movement' apparently had a significant influence in ecology, particularly through the IBP (International Biological Program), and some began to see the 'new ecology' as a 'big science' (McIntosh, 1985; Wu, 1991). This may be called the 'Golden Age' of systems ecology, broadly defined as the application of systems analysis to ecology (Walters, 1971), which coincided with the rapid developments in systems science. In fact, even prior to this time the holistic perspective was essential for the supraorganismic ecological theory pioneered by Clements in the context of community ecology (e.g. Clements, 1916) and later championed by R. Margalef and E.P. Odum in the context of ecosystem ecology (e.g. Margalef, 1968; Odum, 1969; McIntosh, 1985; Wu and Loucks, 1995 for reviews).

However, the enthusiasm for systems ecology faded away quietly (notably in North America) during the 1980s in the wake of the failure of several large, monolithic computer models produced by the IBP and with the increasing recognition of the importance of ubiquitous spatial heterogeneity and scale. While the systems modeling approach continued to be dominant in modeling energy flow and matter cycling of various ecosystems, spatial modeling approaches, including diffusion-reaction, patch (or gap) dynamics, cellular automata, and fractal models, seemed to take over the central place in ecological modeling during much of the 1980s and the 1990s (e.g. Shugart, 1984; Hogeweg, 1988; Sugihara and May, 1990; Levin et al., 1993; Wu and Levin, 1994; Wu and Loucks, 1995). Models based on catastrophe theory and chaos theory have also had profound influence on the way ecologists think of ecological stability and predictability (Hastings et al., 1993). This shift of emphasis in modeling approaches seems reminiscent of the

new developments in the science of complexity (the third developmental stage of complexity research as per Simon, 1996).

One of the most intriguing recent developments in both complexity research and ecological modeling is the resurgence of interest in self-organization, emergent properties, and order (be it spatial or temporal). These concepts have been familiar to systems ecologists since the Clements' supraorganismic theory of succession (e.g. Clements, 1916; Margalef, 1968; Odum, 1969; Ulanowicz, 1979; De Angelis et al., 1981). However, new theories and methods such as self-organized criticality, complex adaptive systems, fractals, and cellular automata provide new insights and opportunities for understanding ecological complexity (Cowan et al., 1994; Patten et al., 1995; Jørgensen, 1997; Jørgensen et al., 1998; Levin, 1999; Wu, 1999). All these new theories and methods seem to have an explicit emphasis on the individual (or agent) behavior and local interactions, and this common theme is evident in many recent ecological models that are often characterized as individual-based models (IBMs), patch models, and a variety of cellular models (Hogeweg, 1988; Levin et al., 1993; Judson 1994; Grimm, 1999). However, it would be mistake to perceive this bottom-up oriented approach simply as another reductionist route. Complex systems are complex primarily because they are not completely 'reducible' to their components, and thus top-down constraints and hierarchical linkages must be adequately considered. An obvious challenge in modeling complex ecological systems is, then, to integrate the rigor of reductionism with the comprehensiveness of holism.

It is perceivable that with the renewed and broad interest in the issues of complexity and needs for more holistic perspectives for understanding large-scale ecological and environmental problems (Naveh, 2000; Wu and Hobbs, 2001, in review), systems ecology is regaining its important role in ecological science and applications. While new modeling approaches provide needed insights into different aspects of ecological complexity, the systems methodology remains a powerful framework to integrate 'parts' to understand the 'whole'.

3. The special issue of modeling complex ecological systems

This special issue has evolved out of the Modeling Complex Systems Conference held in Montréal, Canada between 31 July and 4 August 2000. Most of the papers originated from the presentations at the conference. These papers by no means cover the whole spectrum of the diverse ecological models, but are reflective of several major approaches and challenges for modeling complex systems. In the following, we present a synoptic overview of these papers.

Wu and David argue that the large number of diverse components, nonlinear interactions, scale multiplicity, and spatial heterogeneity are the major sources of ecological complexity. They advocate that the hierarchical patch dynamics paradigm provides a powerful framework for breaking down complexity and integrating pattern with process and parts with the whole. They present a spatially explicit hierarchical modeling approach to study heterogeneous landscapes following a scaling ladder strategy. The hierarchical urban landscape model (HPDM-PHX) is presented as an implementation of this approach. They further discuss the development of a modeling environment, the hierarchical patch dynamics modeling platform (HPD-MP) that is designed to facilitate hierarchical patch dynamic modeling. Detecting and quantifying scale-multiplicity and hierarchical structure in space are important and represent a new dimension in modeling complex ecological systems. Hay et al. consider landscapes as complex systems which necessitate a multiscale or hierarchical approach in their analysis, monitoring, modeling and management. They propose that Scale-Space theory, combined with remote sensing imagery and blob-feature detection techniques, satisfy many of the requirements of an idealized multiscale framework for landscape analysis. Scale-Space theory is a framework developed by the computer vision community for early visual operations, and can be used to automatically analyze real-world structures at multiple scales without requiring a priori information about such structures or appropriate scale(s) of analysis. The authors hypothesize that the spa-

tially explicit features derived from the scale-space methodology correspond to ecologically meaningful entities in landscapes, which can be used as inputs in geographic information systems or spatially explicit models to better represent the spatial complexity of ecological systems. From a different perspective, Borcard and Legendre present a statistical method for detecting and quantifying spatial patterns over a wide range of scales, using eigenvalue decomposition of a truncated matrix of geographic distances among sampling sites. Through numerical simulations and a contrived data set they demonstrate that the method is effective in characterizing the multiscale patterns of ecological systems.

Thermodynamic approaches are powerful in studying macroscopic patterns and processes in ecological systems, but their potential is yet to be fully explored. Zhang and Wu develop a statistical thermodynamic model of the organizational order of vegetation (OOV) that can be used to derive broad-scale vegetation patterns. OOV is a thermodynamic measure of the degree of structural and functional self-organization of vegetation, and a macroscopic representation of the steady state reached between vegetation and its environment over large spatial and temporal scales. The model unites OOV, ecosystem entropy, actual annual evapotranspiration, and mean annual temperature in the same thermodynamic framework. They argue that statistical and non-equilibrium thermodynamics may serve as both a theoretical framework and a practical modeling approach for dealing with the complexity, diversity, and heterogeneity of ecological systems. Ménard et al. investigate the effects of local-scale disturbances on the dynamics of forest ecosystems using one of the better-known forest simulators, SORTIE, a stochastic and mechanistic spatially-explicit and individual-based forest succession model. Their results indicate that the species spatial structure and dynamics are not sensitive to initial conditions after 300 years of simulation. This may be interpreted as a result of self-organizing processes in the complex model forest system. These authors suggest that SORTIE can be a valuable complementary tool to field studies for understanding the impact of local disturbances on forest dynamics.

While SORTIE is primarily a plant succession model based on the life cycle of individual trees, Childress et al. present a systems model that mechanically simulates essential ecosystem processes and management activities. Like in most cross-scale modeling efforts today, the plot-level ecosystem is scaled up to the landscape using a grid-based, direct extrapolation approach. They also discuss several practical challenges in applying complex models in a management context. To meet the multifold needs of quantifying carbon budgets, assessing climate change effects, and projecting forest yield for management decisions, Peng et al. have developed a hybrid model of forest growth and carbon dynamics by integrating parts of existing empirical and mechanistic models. They argue that many process-based ecosystem models, some of which are well-established and tested, are not appropriate for management applications because their output is not directly useful in management planning, and that this hybrid modeling approach strikes a balance between science and application. In general, it seems wise to build the complexity upon well-established models or modules in modeling complex ecological systems.

Qi et al. examines one of the salient characteristics of all complex systems—the nonlinearity and its manifestation in several well-known ecosystem models of biogeochemical cycles. In particular, they demonstrate that, due to the nonlinear response of soil respiration to changes in temperature sensitivity, the accuracy of these models in predicting carbon fluxes at large scales is seriously questionable. Based on their earlier finding that the temperature sensitivity is often a function of temperature itself, soil moisture and possibly other factors (Xu and Qi 2001), they develop a general model of temperature sensitivity of soil respiration as affected by multiple factors. This model deals more realistically with this nonlinearity and variability in model prediction, which is particularly useful for addressing the complex feedback mechanisms between climate and terrestrial ecosystems. Wang et al. also address the problems of model accuracy and uncertainty in the context of soil loss, which has been a rather complex and long-standing issue. Apparently, a

full understanding of soil loss requires a landscape ecological perspective. The Revised Universal Soil Loss Equation explicitly considers several factors, including runoff erosivity, soil erodibility, slope measures, and land cover. Wang et al. demonstrate that the sequential Gaussian simulation algorithm can be effectively used to estimate spatial and temporal variabilities of the factors directly affecting soil loss over a region. Clearly, accuracy assessment and uncertainty analysis of complex models are essential, but much more research is needed.

Optimization methods provide another suite of tools for dealing with complex ecological systems. Turner et al. examine two optimization packages, one based on linear programming and the other based on a heuristic search algorithm, in the context of forest resource management and planning. Their results show that, while both packages can handle the problems at hand, the second package is preferable for solving multi-objective problems with spatial components as in modeling sustainable forest management. Complex ecological systems become even more complex when human actions (e.g. disturbances, and management or conservation interventions) are explicitly considered. Roberts et al. present such an example in modeling the recreational rafting behavior on the Colorado River within the Grand Canyon National Park of the United States. The Grand Canyon River Trip Simulator is a model of complex, dynamic human-environment interactions which integrates agent-based modeling, artificial intelligence, and statistical analysis. Such approaches are promising for modeling complex adaptive systems such as many ecological systems, especially, when individual behavior and decision making processes at various scales must be explicitly considered.

Again, this special issue is only a sample of the many topics and approaches for modeling complex ecological systems. Yet, they represent some of the major directions of the current research in this area. Some other important topics, not directly dealt with in this special issue, are mentioned in the first two sections of this introductory paper and referred to the literature cited. As a number of new theories and methods continue to

emerge in the science of complexity, ecological modeling is entering another exciting period. Although we may never be able to adequately predict the exact dynamics of complex systems, improving our understanding of the complex world through modeling is surely expected.

Acknowledgements

The Modeling Complex Systems Conference would not have been a success without the hard work and dedication of the Organizing Committee (J. Carter, D. Marceau, K. Porter, J. Wu) and all participants from several countries. We thank Dr Sven E. Jørgensen for providing us with the opportunity to organize this special issue. We are also grateful to all the reviewers whose valuable criticisms and suggestions have subsequently improved the quality of the special issue. J. Wu's research in ecological complexity and modeling has in part been supported by grants from US EPA (R827676-01-0) and NSF (DEB 97-14833; CAP-LTER). D. Marceau's research on forest modeling and scale-space has been funded by a NSERC grant (to Danielle Marceau) and a team grant (to A. Bouchard).

References

- Allen, T.F.H., Starr, T.B., 1982. *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago, p. 310.
- Clements, F.E., 1916. *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institution of Washington, Washington DC.
- Cowan, G.A., Pines, D., Meltzer, D. (Eds.), 1994. *Complexity: Metaphors, Models, and Reality*. Perseus Books, Reading, MA, p. 741.
- Dale, M.B., 1970. Systems analysis and ecology. *Ecology* 51, 2–16.
- De Angelis, D.L., Post, W.M., Travis, C.C., 1981. Self-organizing characteristics of ecological communities. In: Roth, G., Schwegler, H. (Eds.), *Self-organizing Systems: An Interdisciplinary Approach*. Campus Verlag, New York, pp. 84–101.
- Flood, R.L., 1987. Complexity: A definition by construction of a conceptual framework. *Syst. Res.* 4, 177–185.
- Grimm, V., 1999. Ten years of individual-based modeling in ecology: what have we learned and what could we learn in the future? *Ecol. Model.* 115, 129–148.

- Hall, C.A.S., Day, J.W. (Eds.), 1977. *Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories*. Wiley, New York, p. 684.
- Hastings, A., Hom, C.L., Ellner, S., Turchin, P., Godfray, H.C.J., 1993. Chaos in ecology: is mother nature a strange attractor? *Ann. Rev. Ecol. Syst.* 24, 1–33.
- Hogeweg, P., 1988. Cellular automata as a paradigm for ecological modeling. *Appl. Math. Comput.* 27, 81–100.
- Jørgensen, S.E., 1995. Complex ecology in the 21st century. In: Patten, B.C., Jørgensen, S.E., Auerbach, S.I. (Eds.), *Complex Ecology: The Part-Whole Relation in Ecosystems*. Prentice-Hall, Englewood Cliffs, pp. xvii–xix.
- Jørgensen, S.E., 1997. *Integration of Ecosystem Theories: A Pattern*. Kluwer, Boston, p. 388.
- Jørgensen, S.E., Mejer, H., Nielsne, S.N., 1998. Ecosystem as self-organizing critical systems. *Ecol. Model.* 111, 261–268.
- Judson, O.P., 1994. The rise of the individual-based model in ecology. *TREE* 9, 9–14.
- Levin, S.A., 1999. *Fragile Dominions: Complexity and the Commons*. Perseus Books, Reading, p. 250.
- Levin, S.A., Powell, T.M., Steele, J.H., 1993. *Patch Dynamics*. Springer, Berlin, p. 307.
- Margalef, R., 1968. *Perspectives in Ecological Theory*. University of Chicago Press, Chicago, p. 111.
- McIntosh, R.P., 1985. *The Background of Ecology: Concept and Theory*. Cambridge University Press, Cambridge, p. 383.
- Naveh, Z., 2000. What is holistic landscape ecology? A conceptual introduction. *Landsc. Urban Plann.* 50, 7–26.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B., Allen, T.F.H., 1986. *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, p. 253.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Odum, H.T., 1983. *Systems Ecology: An Introduction*. Wiley, New York, p. 644.
- Patten, B.C., 1959. An introduction to the cybernetics of the ecosystem: the trophic-dynamic aspect. *Ecology* 40, 221–231.
- Patten, B.C., 1971. *Systems Analysis and Simulation in Ecology*, vol. I. Academic Press, New York.
- Patten, B.C., 1972. *Systems Analysis and Simulation in Ecology*, vol. II. Academic Press, New York.
- Patten, B.C., 1974. *Systems Analysis and Simulation in Ecology*, vol. III. Academic Press, New York.
- Patten, B.C., 1976. *Systems Analysis and Simulation in Ecology*, vol. IV. Academic Press, New York.
- Patten, B.C., Jørgensen, S.E., Auerbach, S.I. (Eds.), 1995. *Complex Ecology: The part-whole relation in ecosystems*. Prentice-Hall, Englewood Cliffs, p. 388.
- Prigogine, I., 1997. *The End of Certainty: Time, Chaos, and the New Laws of Nature*. Free Press, New York, p. 240.
- Reichle, D.E., O'Neill, R.V., Kaye, S.V., Sollins, P., Booth, R.S., 1973. Systems analysis as applied to modeling ecological processes. *Oikos* 24, 337–343.
- Scudo, F.M., Ziegler, J.R., 1978. *The Golden Age of Theoretical Ecology: 1923–1940*. Springer, Berlin, p. 490.
- Shugart, H.H., 1984. *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. Springer, New York, p. 278.
- Shugart, H.H., O'Neill, R.V. (Eds.), 1979. *Systems Ecology*. Dowden, Hutchinson & Ross, Inc, Stroudsburg, PA, p. 368.
- Simon, H.A., 1996. *The Sciences of the Artificial*. The MIT Press, Cambridge, p. 231.
- Sugihara, G., May, R.M., 1990. Applications of fractals in ecology. *Trends Ecol. Evol.* 5, 79–86.
- Ulanowicz, R.E., 1979. Complexity, stability and self-organization in natural communities. *Oecologia* 43, 295–298.
- Van Dyne, G.M., 1966. *Ecosystems, systems ecology, and systems ecologists*. Report No. ORNL-3957, Oak Ridge National Laboratory, Oak Ridge.
- Walters, C.J., 1971. Systems ecology: the systems approach and mathematical models in ecology. In: Odum, E.P. (Ed.), *Fundamentals of Ecology*. Saunders, Philadelphia, pp. 276–292.
- Watt, K.E.F., 1966. *Systems Analysis in Ecology*. Academic Press, New York, p. 276.
- Wu, J., 1991. Dissipative structure, hierarchy theory and ecosystems. *Chin. J. Appl. Ecol.* 2, 181–186.
- Wu, J., 1999. Hierarchy and scaling: extrapolating information along a scaling ladder. *Can. J. Rem. Sens.* 25, 367–380.
- Wu, J., Levin, S.A., 1994. A spatial patch dynamic modeling approach to pattern and process in an annual grassland. *Ecol. Monogr.* 64 (4), 447–464.
- Wu, J., Loucks, O.L., 1995. From balance-of-nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q. Rev. Biol.* 70, 439–466.
- Wu, J., Hobbs, R., 2001. Key issues and research topics in landscape ecology. *Landsc. Ecol.*, in review.
- Xu, M., Qi, Y., 2001. Spatial and seasonal variations of Q_{10} determined by soil respiration measurements at a Sierra Nevada forest. *Glob. Biogeochem. Cycl.* 15, 687–696.

Jianguo Wu ^a, Danielle Marceau ^b

^a *Department of Plant Biology,
Arizona State University,
Tempe,
AZ 85287-1601,
USA*

^b *Department of Geography,
University of Montréal,
Montreal,
Quebec,
Canada H3C 3J7
E-mail: jingle@asu.edu*