INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

SMR.478 - 46

THIRD AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(29 October - 16 November 1990)

"Ecology in Theory and Application"

S.A. LEVIN
Cornell University
Centre for Applied Mathematics
Section of Ecology and Systematics
Ithaca, NY 14853-7801
U.S.A.

Reprint from

Biomathematics, Vol. 18
Levin, Hallam, Gross (Eds.) · Applied Mathematical Ecology

Printed in the United States of America

Springer-Verlag
Berlin Heidelberg New York
London Paris Tokyo

Ecology in Theory and Application

Simon A. Levin

Fraser Darling (1967) wrote that "Ecology.... was a bigger idea than the initiators grasped." Darling and others, writing in the 1960's, addressed the new demands placed upon ecologists as public awareness of an environmental crisis grew. The science of ecology had, until that time, been developed to satisfy purer, more abstract, objectives—a search for understanding and explanation. It was ill prepared to do more than provide anecdotes in support of the need to guard nature's treasures and the "balance of nature." Only in the last two decades have serious efforts been directed to developing the theoretical basis we need to manage natural systems from a sound ecological basis.

The notion of the balance of nature was evident even in the writings of St. Thomas Aquinas. Such ideas pervade the nonmathematical literature; and thus, it is not surprising that they were also represented in early theoretical work. John Graunt, Thomas Malthus, and Charles Darwin all recognized that population growth must carry with it the roots of its own diminishment, and this led naturally (but not inescapably) to the notion of equilibrium. Sadler, Quetelet, and others, mesmerized by parallels from physics, introduced models of population regulation built upon vague forces underlying the system's "resistance to growth" (Hutchinson, 1978). Verhulst introduced the logistic, the simplest and most commonly used nonlinear growth model; and other such efforts were little more than variations on the logistic theme. Characteristic of all of this early work were the concepts of balance and equilibrium, of homogeneity, and of determinism. The predominant emphasis was on individuals and their adaptations, and on the populations they comprised.

The early 20th century saw a growth of theoretical ideas, with increased attention to dynamics and change. The interrelatedness of species became a central subject of investigation in plant community theory, where Gleason's individualistic and stochastic concepts lost out to Clements' notion of the plant formation as a holistic superorganism that developed over time to a climax state determined by the local climate (Whittaker, 1975; McIntosh, 1985). Again, homogeneity and determinism prevailed.

Meanwhile, Grinnell, Elton, and other animal ecologists were developing and refining the intertwined notions of niche and community, elucidating the role of the species within its community. Mathematical models assumed center stage; and the investigations of Volterra, Lotka, and Kostitzin became recognized for their power in aiding understanding, in explanation, and in developing and exploring hypotheses. Volterra, motivated by his son-in-law d'Ancona's discussion of the fluctuations of the Adriatic fisheries, demonstrated that it was at least possible that such fluctuations were simply the consequence of the interactions between predators and their prey. His related work in competition theory led to fundamental insights concerning the coexistence of species, and inspired the young Russian ecologist Gause to conduct his classic experiments on competition between species of microorganisms. It was the "Golden Age of Theoretical Ecology" (Scudo and Ziegler, 1978). Yet homogeneity and an only slightly modified emphasis on equilibrium, determinism, and asymptotic behavior remained powerful aspects of the theory.

In the middle of the 20th century, the concepts of spatial and temporal variability as essential properties of a healthy ecosystem were placed on firmer theoretical footing by community ecologists such as A.S. Watt, R.H. Whittaker, G.E. Hutchinson, and Robert MacArthur. Simultaneously, the concept of the *ecosystem*, as introduced by Tansley (1935), received attention as the context for studying nutrient and energy flows and biogeochemical cycling.

Following Watt's prescient presidential address to the British Ecological Society (Watt, 1947), appreciation grew for the importance of variability in space and time as a factor structuring communities, and as a key to coexistence and coevolution. As Watt's work and much that followed showed, natural biotic and abiotic disturbance recycles limiting resources, developing mosaics of successional change that allow species to subdivide resources temporally. Woody Allen has said, "Time is nature's way of making sure everything doesn't happen at once." The explicit incorporation of disturbance, variability, and stochasticity as part of the description of the normative community is thus an imperative. As Robert Paine and I have argued, local unpredictability is for many species globally the most predictable aspect of systems.

Theoretical and experimental investigations into the importance of gaps and mosaic phenomena have demonstrated the inseparability of the concepts of equilibrium and scale. As one moves to finer and finer scales of observation, systems become more and more variable over time and space, and the degree of variability changes as a function of the spatial and temporal scales of observation. Such a realization has long been part of the thinking of oceanographers, who observe patchiness and variability on virtually every scale of investigation. A major conclusion is that there is no single correct scale of observation: the insights one achieves from any investigation are contingent on the choice of scales. Pattern is neither a property of the system alone nor of the observer, but of an interaction between them.

The importance of scales also becomes apparent from an examination of population models, both in terms of their general dynamic properties and in terms of their applicability to real populations. Much recent mathematical work has demonstrated that even the simplest models of population dynamics can exhibit oscillatory and even chaotic behavior; as a consequence, it is impossible to predict accurately the precise dynamics of populations governed by such equations.

To some extent, such observations render moot the classical debate over whether populations are controlled by density-dependent or density-independent factors. Close to the theoretical equilibrium, the dynamics of populations may to risk assessment and management. It also will require an increased public awareness that there are limits to predictability, and that the fuzzy boundary between science and policy justifies, even necessitates, public involvement in the decision-making process. There are few scientific absolutes in environmental decision-making; rather, environmental management must be an expression of the values and needs of society, as manifest in the statutes the people's representatives enact and in societal participation in public discourse on environmental issues.

Acknowledgments. The author's research is sponsored by the U.S. Environmental Protection Agency and by the National Science Foundation. The views expressed herein are those of the author, and do not necessarily represent those of the sponsors or of Cornell University. The first part of this article is the text of a lecture originally developed as the 1985 Charles A. Alexander lecture at Cornell University. Parts of this text have appeared in various other publications.

References

Darling, F.F. (1967) A wider environment of ecology and conservation. Daedalus *96*, 1003–1019.

Hallam, T.G., Levin, S.A. (eds.) (1986) Mathematical Ecology—An Introduction. Biomathematics, vol. 17. Springer Berlin Heidelberg New York London Paris Tokyo, 457 pp.

Holling, C.S. (1986) The resilience of terrestrial ecosystems; local surprise and global change. In: W.C. Clark, R.E. Munn (eds.) Sustainable Development of the Biosphere. Cambridge University Press, Cambridge, pp. 292–317

Hutchinson, G.W. (1978) An Introduction to Population Ecology. Yale University Press. New Haven, Conn., 260 pp.

Jacob, F. (1976) The Possible and the Actual. Allen & Unwin Ltd., London, 72 + viii pp.

Jacob, F. (1977) Evolution and tinkering. Science *196*, 1161–1166

McIntosh, J.P. (1985) The Background of Ecology: Concept and Theory. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, 383 pp.

Paine, R.T. (1966) Food web complexity and species diversity. Am. Nat. *100*, 65–75

Scudo, F.M., Ziegler, J.R. (1978) The Golden Age of Theoretical Ecology: 1923–1940. Lecture Notes in Biomathematics, vol. 22. Springer, Berlin Heidelberg New York, 490 pp.

Tansley, A.G. (1935) Use and abuse of vegetation concepts and terms. Ecology *16*, 284–307

Watt, A.S. (1947) Pattern and process in the plant community. J. Ecol. *35*, 1–22

Whittaker, R.H. (1975) Communities and Ecosystems, 2nd edn. Macmillan, New York, 162 pp.

objects of scientific scrutiny for decades. The difficulties relate to our inability to identify and predict changes in the factors controlling dynamics, to the spatial and temporal variability of parameters and even mechanisms of control, and to the inherent propensity of nonlinear dynamical models to exhibit turbulent dynamics that make parameter estimation a daunting challenge. When communities and ecosystems are considered, with the consequent multiplication of pathways of interaction, the problems are similarly multiplied. Some relief can be achieved by judicious simplification that properly recognizes the shift in detail appropriate to the shifts in levels of organization, but a core of irremovable uncertainty will always remain. Scientific advisers must make clear to managers the levels of uncertainty, and must not give in to the temptation to seem to present the certainty that their clients seek. Model outputs must be presented not just in terms of averages, but with associated variances in relation to stochastic effects and uncertainties in parameter estimation. Finally, as Crawford Holling has emphasized (Holling, 1986), an inescapable conclusion from the existence of such uncertainty is that there will be surprises associated with virtually any management action, and that any management strategy must have some potential for (adaptive) modification when experience and monitoring so dictate.

As we enter the last decade of the 20th century, we face environmental challenges greater than ever before as the scale shifts from local problems to global and regional ones. We are confronted with changes in the distributions and exchanges of elements on broad scales, with the alarming loss of biotic and habitat diversity, with the consequences of species invasions, with toxification and contamination of our aquifers and other systems, with the need for alternatives for waste disposal, with the collapse of resource systems, and even with the risk of global thermonuclear war. As never before, these challenges mandate a better integration across disciplines, especially across the physical and biological sciences, and an integration set in a holistic perspective encompassing ecosystems, regions, landscapes, and the biosphere. We must recognize explicitly the multiplicity of scales within ecosystems, and develop a perspective that looks across scales and that builds upon a multiplicity of models rather than seeking the single "correct" one. We need to couple system-level testing that allows identification of emergent phenomena with mechanistic studies designed to provide understanding and the basis for extrapolation.

In dealing with the effects of chemicals in the environment and their local and global consequences, the control of agricultural pests and human disease, the management of scarce resources and other problems facing society, we must develop more sophisticated quantitative tools for prediction, for aiding understanding, and as guides to management. This volume, built upon the foundations laid in Hallam and Levin (1986), is dedicated to those objectives. The chapters explore current approaches to problems in demography and epidemiology, resource management, and ecotoxicology, and apply classical and modern mathematical developments in ecology and epidemiology to a variety of case studies.

Finally, we must acknowledge the limits of our ability to predict—the ecologist's uncertainty principle—and be prepared to manage in the face of that uncertainty. That will require the development of more sophisticated and flexible approaches and recognition of this multiplicity of scales is fundamental to describing and understanding ecosystems. It is essential to strip away what is irrelevant detail, and to determine those processes and components that are central to the integrity of the system: the keystone species of Robert T. Paine (Paine, 1966), or the factors controlling recruitment and larval survival. The emphasis on equilibrium and homogeneity obscures the search for pattern, and represents the baggage of historical tradition.

Moreover, overly detailed and reductionistic models of populations and systems obscure any pattern by introducing irrelevant detail, often on the specious premise that somehow more detail and more reduction assures greater truth. This point of view is predicated in part on the fallacious notion that there is some exact system description possible, and that any model is an approximation to that exact description. In reality, there can be no such ideal, because there can be no "correct" level of aggregation. The taxonomic species, for example, is an imperfect tool of classification, and ignores the differences among the individuals of the species with regard to demographic and phenotypic properties; thus it is just one possible grouping within a particular nested hierarchy. More importantly, the particular hierarchical decomposition that arises from a taxonomic classification system bears much less relevance for some ecological descriptions than would one that was functionally based.

What society values, and what environmental laws are designed to protect, are not the intricate details of systems, but rather the essential features that make those systems recognizable to biologists and that are somewhat predictable over time. We should not expect to make systems more predictable in our models than natural variability dictates; in fact, variability, such as that associated with seasonality, gap phase dynamics, or fire, is one of the most predictable features of many systems, and is essential to the maintenance of resiliency and to the persistence of most species. Moreover, it is well recognized that the climatic and atmospheric systems driving biotic systems are very limited in predictability. In 1985, Neil Frank, Director of the National Hurricane Center, said "All our weather planes and radars create a false impression that we can do a great job forecasting. That's a myth. What we're doing is a great job observing."

Furthermore, predictability is inextricably intertwined with variability, and with the temporal and spatial scales of interest. Thus, a central challenge in ecological theory must be an elaboration of the understanding of how scales relate, how systems behave on multiple scales, and how the measurement and dynamics of particular phenomena vary across scales. The inherent limits to predictability on long time scales emphasize the importance of monitoring, and of coupling any management action with some mechanism for modification based on analysis of the data obtained from monitoring. Such adaptive management recognizes explicitly the limits to predictability, and places emphasis on short-term prediction in which nonlinear phenomena have diminished importance.

In this regard, environmental management presents a number of problems that are generic in the consideration of the responses of systems to quite distinct stresses. The prediction of the dynamics of natural populations has never been resolved adequately, even for renewable resources such as fisheries, which have been the be indistinguishable from those of appropriately chosen stochastic density-independent models; near equilibrium, density dependence is very weak, and will be obscured by any overriding density-independent variation. On the other hand, far from equilibrium, density-dependent factors assume more importance because the nonlinearities are stronger. Thus, density dependence is the primary mechanism constraining major excursions in population density and keeping populations within bounds; but within those bounds, density independent phenomena predominate. Concepts of stability that rely on asymptotic return to an equilibrium state are seen to be irrelevant on many scales of interest, and more general concepts such as boundedness and resiliency replace them.

The major conclusions of such studies are that there are inherent limits to predictability, that predictability depends on the scale of investigation, and that there is no single correct scale of inquiry. This recognition is of central importance in the current revitalization of mathematical theory, inspired by applied imperatives arising from renewable and nonrenewable resource management, epidemiology, and environmental protection. Through these needs and studies came a clarification of what ecological theory could and could not do. Francois Jacob (1976, 1977), in his insightful discussions of evolutionary theory, made clear the distinctions between explanation and prediction, and the degree to which prediction of evolutionary events is hampered by the importance of stochasticity, historical contingency, and constraints. Such ideas apply equally to prediction of ecological responses to stress.

In the late 1960's and early 1970's, as a result of environmental activism and concern over the effects of chemicals in the environment, a suite of environmental laws were passed that, in one form or another, called for the protection of ecosystems. In general, those laws tended to be vague when it came to establishing criteria for measuring ecological effects, since they were designed to address broad objectives without being hampered in applicability by specific references to particular systems. Much legislation, and certainly the conceptual and mathematical models that they spawned, still emphasized ideas such as equilibrium, constancy, homogeneity, stability, and predictability. This in turn led to the development of simple-minded and misguided predictive approaches, built upon large-scale and highly detailed models. Finally, as the need for tools and answers grew, this necessity led to the flagrant abuse of mathematical theory. Ideas developed for explanation and pedagogical purposes were recruited for prediction, without the warnings that belonged on the label. The message of Francois Jacob, that explanation and prediction were quite different animals, was ignored; and the distinctions between what was basic and what was applied became blurred.

One of the conclusions from the early frustrating experiences in predicting the responses of ecological systems to stress was the need to develop a deeper theory of how ecosystems operate. The description of the behaviour of any system can be carried out blindly, or it can be based on some degree of understanding of the basic mechanisms underlying system dynamics. The search to understand any complex system is a search for pattern; that is, for the reduction of complexity to a few simple rules, principles that allow abstraction of the essence from the noise. This is also the key to management: pattern exists at all levels and at all scales,