*Chapter* 4

# PREDICTION, CHAOS, AND ECOLOGICAL PERSPECTIVE

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## 1. INTRODUCTION

### 1.1. The Modeling Process

A glance at the table of contents of this volume reveals that the organization of the chapters bears close resemblance to the much-discussed phases of the modeling process.

For example, the first step in a multicomponent systems analysis is usually the definition of what the compartments are and how their state may be described quantitatively. The first three chapters on the aggregation problem indicate that this task is certainly nontrivial.

The identification of the qualitative interactions between components usually follows. While one may speak in general terms about causality, in

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the ecological realm it is usually the transfer of matter, energy, or information that constitutes such interaction.

Choosing a mathematical statement to describe the time evolution of the interactions (usually in terms of the states of the compartments) constitutes what some (Dale, 1970) refer to as the modeling step in systems analysis. Despite the fact that this phase is the most explicitly mathematical, it generates relatively little theoretical interest as witnessed by the absence of contributions on the problem in this book.

This brings us to the final step of model verification (elsewhere referred to as model validation). A model is generally held to be valid insofar as it can reproduce the behavior of the system under conditions different from those used to create the model, i.e., to the degree that it has prediction ability. To be sure, there are occasions where invalid models provide useful insights, and the organization which the modeling scheme lends to one's thought processes or experimental program is not to be underestimated; but it may still be argued that the *sine qua non* of model validation remains—prediction ability.

## 1.2. Incomplete Results of Ecosystem Models

As defined, the modeling procedure is quite broad. For example, the chosen compartments may contain a single organism, a population of organisms, or an ensemble of populations. A population compartment, in turn, could be homogeneous or possess structure in size or age. Likewise, the mathematical statements may be deterministic or probabilistic in nature, linear or nonlinear, autonomous or able to possess memory. Examples of all types appear in the literature.

In practice, however, ecosystem modelers have focused upon particular types of model constructions. Most analyses seem to treat compartments which are nonsegregated (populations or trophic levels) and homogeneous. The accompanying mathematics is, for the most part, deterministic and autonomous.

Despite the enormous effort which has gone into such ecosystem modeling, there remains a paucity of models which meets the rigorous validation criteria which might be applied to a model of a mechanical system. Most ecosystem models are short on prediction ability. Even some classical examples, such as the Lotka–Volterra predator–prey scheme, have not spawned validated examples.

## 1.3. Three Views on the Adequacy of Ecosystem Modeling

There are three possible schools of thought concerning the apparent failure of ecosystems analysis to predict with confidence.

The first school points to our ignorance and the need for more data. The present approach is considered to be sound, but our inability to gather enough information on the components and interactions proscribes ascertaining the proper constitutive relations which will lead to valid models. In time, additional information will evolve models with greater predictive ability. Meanwhile, we can appreciate the new insights into particular ecosystems which the modeling exercise uncovers. This is a frequent argument given to funding agencies to support modeling projects. I have used it on occasion myself.

The second group is more iconoclastic (Mann, 1975). The current approach is futile because the models are poorly posed. To use populations as components is reductionistic and blinds one to emergent properties. To use trophic levels as compartments is nonsensical in light of the confused webs which characterize most ecosystems. Anyhow, stochastic influences upon model parameters yield confidence limits on ecosystems predictions which are too large to make them of any practical use. This group is not without its optimism, however. As our ability to look at ecosystems holistically advances, properties will appear along with their own laws, just as ethology emerges when we expand our scale of observation from the cellular level to the organism and then to the social unit.

Several published works of the past few years reveal that a third opinion on the ecosystem modeling problem is possible. This outlook allows that the modeling construct in vogue may be sound; however, it will not lead to useful results on the systems level because the deterministic behavior of large ecosystem models is indistinguishable from chaos. That is, prediction ability is short range at best. The only obvious emergent property of ecosystems is chaos. This does not exclude the possibility that macroscopic properties with their own laws exist. But the likelihood is that they are imposed by constraints from without (the abiotic universe) rather than emergent from within.

Because this outlook is relatively new and seemingly paradoxical, it is helpful to regard its development in more detail beginning with its theoretical origins in meteorology.

## 2. DETERMINISM AND CHAOS

The transition of a fluid flow field from laminar to turbulent has long intrigued theoreticians. Whether the Navier–Stokes equations (or any other form of Newton's second law) were germane to the turbulent field was a matter of much debate. To the meteorologist the issue was more than an interesting theoretical question. With the advent of computational

machinery efforts were underway to apply the discrete forms of the equations of motion to meteorological flow fields for the purpose of forecasting weather. The limits to employing deterministic tools on a turbulent field thus became a matter of applied interest.

It was against this background that Lorenz (1963) published his elegant treatise on deterministic nonperiodic flow. Lorenz reduced the equations of motion for a particular two-dimensional, rotating, heated fluid to three, first-order, quadratic differential equations:

$$\dot{x} = -10x + 10y, \qquad \dot{y} = -xz + 27x - y, \qquad \dot{z} = xy. \tag{1}$$

Here $x$, $y$, and $z$ are complicated transforms of the stream function and excess temperature. The exciting point of this analysis is that these simple equations (mathematical cousins of the Lotka–Volterra equations) behave in such a peculiar manner.

The solutions to Eq. (1) always remain bounded. After a given period of time, however, the variables $x$ and $y$ go into oscillations with no finite period. This is strange behavior for a deterministic function; however, the path is uniquely determined in that starting the solution at any point on the trajectory will always result in tracing out the same pathway. Further experimentation with the system reveals that the trajectories are not stable in the strict mathematical sense. Starting the system arbitrarily close to the given initial conditions will result in a trajectory that eventually bears no coherence to the given one.

Trying to predict the future behavior of such a system is obviously perplexing. Since one can never measure initial conditions with exactitude, model and prototype evolutions are bound to become incoherent eventually. Likewise, efforts to replicate the behavior of such a system under controlled conditions is sure to meet with difficulty. In short, there is little to distinguish this deterministic entity from one that behaves chaotically.

Lorenz traced the chaotic behavior of his continuous system to discrete transitions of the trajectory between regions with qualitatively different behavior. He characterized these transitions by the numerical sequence:

$$
\begin{aligned}
m_{n+1} &= 2m_n && \text{if} \quad m_n < \tfrac{1}{2}, \\
m_{n+1} &\text{ is unidentified} && \text{if} \quad m_n = \tfrac{1}{2}, \\
m_{n+1} &= 2 - 2m_n && \text{if} \quad m_n > \tfrac{1}{2}, \\
& 0 < m_0 < 1,
\end{aligned}
\tag{2}
$$

and showed for a nondenumerable set of irrational $m_0$ that the behavior of the sequence was qualitatively similar to that of Eq. (1). At about the same time that Lorenz was making these observations, Ulam (1963) was

reporting chaotic-like behavior in quadratic numerical transforms such as

$$
\begin{aligned}
x_{n+1} &= 2x_n y_n + 2x_n z_n + 2y_n z_n, \\
y_{n+1} &= x_n^2 + z_n^2, \\
z_{n+1} &= y_n^2.
\end{aligned}
\tag{3}
$$

Needless to say, the bizarre behavior of these numerical sequences captivated applied mathematicians such as Li and Yorke (1975), who set about elucidating the kinetics of pathological nonlinear numerical sequences. Fortunately, Yorke also appreciated the potential application of such mathematics to ecological situations. He brought his example of the discrete form of the logistic equation

$$
x_{n+1} = y x_n [1 - x_n/K]
\tag{4}
$$

to the attention of May (1974), who thereupon devoted much effort to making deterministic, chaotic behavior familiar to ecologists (May, 1975; Hassell *et al.*, 1976; May and Oster, 1976).

May's analyses center about the simple, one-dimensional discrete logistic equation:

$$
x_{n+1} = x_n \exp[r(1 - x_n/k)],
\tag{5}
$$

which is qualitatively similar to Eq. (4). It is not too difficult to show that Eqs. (4) and (5) possess three parameter ranges, each endowed with qualitatively different behavior. In particular, Eq. (4) always possesses a stable equilibrium point when $2 > r > 0$. In the range $2.570 > r > 2.00$ the solutions possess stable cycles of period $2^n$ ($n$, integer) beginning with a two-point cycle near $r = 2.0$ and changing to 4-, 8-, 16-,..., etc., point cycles as $r$ increases. Finally, cycles of arbitrary period, or aperiodic (chaotic) behavior occur for $r > 2.570$.

May's emphasis upon these one-dimensional systems has the advantage that analytical methods can readily be brought to bear on the equations. It also points out the fact that even the simplest of nonlinear ecological models can give rise to chaotic behavior.

When data from real populations are applied to the discrete logistic algorithms, however, none of the naturally occurring populations possesses parameters in the chaotic range. Indeed, few naturally occurring populations show behavior more interesting than a monotonically damped return to steady state. The single example of a real population in the chaotic regime comes from a laboratory controlled population of blowflies (Nicholson, 1954).

Hence, the behavioralist or experimental ecologist might be inclined to dismiss the whole discussion about determinism and chaos as the rantings of theoreticians more concerned with their equations than with

reality. To do so at this time, however, would be unfortunate and premature—for two reasons.

To begin with, the analytical work has emphasized single populations, whereas ecosystems, by definition, consist of collections of interacting populations. The little theoretical work that has been done on interacting populations indicates that chaotic behavior is *more likely* to occur with several species (May and Oster, 1976). Theoretical studies of host–parasite interactions (Beddington *et al.*, 1975) and competing species (Hassell and Comins, 1976) indicate that chaos will intercede sooner (at lower parameter values) than in the single-population case.

It is tempting to proceed by induction to the many-species problem, where interactions which deviate only slightly from linearity give rise to chaos. In fact the mechanical analog of this many-species problem has been well studied (Tuck and Menzel, 1972). The Fermi–Pasta–Ulam system of many mass points connected by springs with weakly nonlinear properties readily gives rise to apparent chaos. Hence, if these analogies and intuitions hold, the most obvious *emergent* property of ecosystems is chaos!

The second reason for not dismissing the possibility of chaotic-like determinism in ecosystems lies with the consequences of a negative result. One way to argue the nonexistence of chaos on an ecosystems scale would be to demonstrate the existence of an emergent, organizing property. Such a discovery would be a major breakthrough in ecological theory.

There remains one final possibility—total ecosystems do not become chaotic because they are inherently linear. The radical hypothesis that ecosystems are fundamentally linear was formalized by Patten (1975). Furthermore, there are empirical results which purport that linear models are somewhat more robust than their nonlinear counterparts (Ulanowicz *et al.*, 1978). It is yet to be resolved, however, whether linear models work a little better because the prototype systems are inherently linear or because, within the limited predictability possible in chaotic systems, linear models work just as well as (or better than) anything else.

Before leaving the subject of deterministic, chaotic-like behavior, it should be pointed out that the discussion in the ecological literature has dwelled upon discrete-time numerical sequences. The possibility that discrete-mass or discrete-space numerical models might also lead to chaotic-like behavior has not been fully assessed. Cohen (1976), for example, shows how certain discrete reproduction processes such as the breeding of pigs or the growth of algae may not converge to a single limit as numbers become large (i.e., they possess a nondegenerate limit). He points out how his examples share the lack of predictability and reproducibility exhibited by those of May.

Of course, one should always remember, too, that chaotic-like

behavior is not confined to discrete sequences and was, in fact, first studied as resulting from continuous, ordinary differential equations with constant coefficients.

## 3. ECOLOGICAL PERSPECTIVE

From a pragmatic point of view, it matters little whether the holist or the chaoticist holds the proper perspective on ecosystems behavior. (The two are not necessarily mutually exclusive.) Common to both philosophies is the belief that ecosystems modeling, as it has been known for the past few decades, has reached the point of diminishing returns, and that radical progress in the understanding of ecosystems will ensue only by expanding the scales of observation in ecosystems modeling. Conceptually, this means defining new macroscopic variables and deriving meaningful relationships among them.

The search for a macroscopic ecosystems theory is likely to be a long and costly endeavor wrought with much futile effort. Nevertheless, it is one of the most intriguing contemporary issues in basic science. It should command the attention of the best theoretical ecologists and the support of every sponsoring agency.

But how do we begin? In fact, efforts are already underway—it is just that some efforts are not advertised as endeavors in macroscopic ecology and thereby escape our recognition.

A case in point is the long controversy over the relationship (if any) between diversity and stability. These variables are properly macroscopic. Diversity is an ensemble property abstracted in an ad hoc manner from physics and information theory. Much attention has been focused on the ambiguities of defining diversity. Unfortunately, much less effort has been devoted to unambiguously defining stability.

The issue is not always perceived as macroscopic, however. The proper approach would then be phenomenological in nature, with effort aimed at defining stability as a function of diversity in much the same empirical way that engineers once sought to relate the efficiency of engines to the temperature difference driving them. Instead, the literature is replete with attempts to arrive at the relationship deductively from simple model examples, that is, from the lower level in the hierarchy (see May, 1973).

Other efforts are appropriately empirical, but are so presented by conventional modeling philosophy that their potential value to macroscopic ecology is obscured. Thus Bargmann and Halfon (1977), Mobley (1973), and Ulanowicz *et al.* (1978) approach modeling in an *a posteriori* fashion, allowing the data to define interactions. The same methodologies applied to macroscopic variables could prove to be very useful tools.

One empirical approach is intentionally divorced from the mainstream of ecological modeling. Platt and Denman (1975) have advocated spectral analysis as a useful way of presenting time series data so as to evoke new hypotheses. Their strategy is to relate the Fourier spectrum of one component to that of another. In this vein Platt (1972) and Powell *et al.* (1975) compare the spectra of chlorophyll abundance with that of turbulent water motion to define regions of frequency space where the profiles are closely related or significantly different. One can envision the result of such analysis as an empirical correlation between two variables over segments of their spectra. This is in contrast to the cause–effect relation which conventional modeling assumes valid for any continuous time scale.

Platt and Denman emphasize a tendency of nonlinear systems towards "periodic (cyclic) organization in time, in space, or in both." They further argue that characteristic periods should emerge from many-species nonlinear ensembles such as ecosystems. Their speculations on this point stand in contradiction to the intuition of May and Oster. Therefore, further work with spectral analysis of whole ecosystems may help to resolve whose notion is in closer agreement with biological reality.

Of course, the argument for a macrobiology is not new. It arises by analogy to the relationship between statistical mechanics and classical thermodynamics (e.g., Kerner, 1971). It seems, therefore, that the tools of statistical thermodynamics would be the proper instruments with which to begin the development of a macrobiological theory.

Unfortunately, there seems to be little inclination among the ecological community to pursue this line of investigation (the sole exception being diversity indices which come to ecology from statistical mechanics via the intermediate discipline of information theory). The reason for this reticence seems to be twofold.

First, there exists the usual communications barrier between the physicist and ecologist, promoted by the reluctance of most of the parties to spend a significant period of study in the other's discipline.

More easily remedied, however, is the desire of both parties to draw the analogy too closely. Kerner's (1957) work provides a good example.

Without going into detail, Kerner began with a set of generalized Lotka–Volterra predator–prey differential equations written for many species. Under the assumption of antisymmetry of the interaction terms, one may derive a constant of motion for the system, invoke the ergodic hypothesis, and thereby define macroscopic variables such as ecotemperature.

In the eyes of Kerner and his critics the validity of the concept of ecotemperature rests upon the strengths or weaknesses of the derivation.

But this is drawing the analogy with statistical mechanics too tightly. After all, the laws of mechanics and thermodynamics are quite precisely defined. In ecology the models for population dynamics are usually analogies in themselves and only the vaguest notions exist for what macrobiological laws might be. Therefore, it appears premature to argue whether the ergodic hypothesis is applicable to ecosystems, when the entire argument is to connect two realms whose underpinnings are quite uncertain. Rather, Kerner's arguments can be regarded as heuristic in nature and the variable ecotemperature can be subjected to empirical scrutiny in its own right. Such an ad hoc adaptation of a variable is, after all, what occurred with species diversity.

In qualitative terms, the ecotemperature of a species is the expectation value of the square of the deviation of a species from its mean, divided by the mean. When expressed in energetic terms, the "temperature" of lower trophic species is probably greater than that of more predatory species. The difference in ecotemperature, therefore, suggests itself as a candidate for the force conjugate to the energetic flow between compartments (Ulanowicz, 1972). Of course, temperature and energy flow immediately suggest an analog to entropy and an inverse to Odum's (personal communication) much sought after "energy quality."

"Ecopressure" as a quantity which is equal throughout an ecosystem at steady state could likely be heuristically derived. The analogs from classical and irreversible thermodynamics are manifold and exciting. However, caution should be exercised so as to not blind oneself to any new phenomena peculiar to the thermodynamics of macrobiological systems. Phenomenology, not strict analogy, is what is necessary.

## 4. SUMMARY

In the relative inability of ecological models to provide a degree of robust prediction, ecosystems analysis has encountered its counterpart to the "Ultraviolet Catastrophe" of physics. Just as the difficulties posed by the breakdown of previous theories led to the magnificent advances of quantum physics, the search for alternate strategies of ecosystems analysis holds promise for a major breakthrough in the understanding of ecosystems function. Dilemma and chaos usually force a new perspective, and a different perspective is necessary if one is to view new wonders.

## ACKNOWLEDGMENTS

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